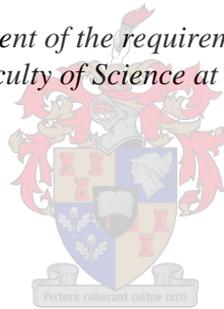


**Southern Madagascar Rocky Shores: A primary
description and comparison with northern
KwaZulu-Natal shores.**

by
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*Thesis presented in fulfilment of the requirements for the degree of
Master of Science in the Faculty of Science at Stellenbosch University*



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Dr Kerry Sink

March 2017

Declaration

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Cleo Rudman

March 2017

TABLE OF CONTENT

ACKNOWLEDGMENTS	4
ABSTRACT	5
CHAPTER 1	8
General Introduction	8
CHAPTER 2: Primary description of the rocky shore communities on the Southern shores of Madagascar	16
Introduction	16
Materials and methods	17
Results	21
Discussion	31
CHAPTER 3: A comparative study between rocky shore communities of Southern Madagascar and Northern KwaZulu-Natal	35
Introduction	35
Materials and methods	37
Results	41
Discussion	48
SYNTHESIS	57
REFERENCES	59
Appendix 3.1: Abundance (mean % cover \pm SE) of species recorded in the various shore zones on sheltered, rocky shores in southern Madagascar.	73
Appendix 3.2: Abundance (mean % cover \pm SE) of species recorded in the various shore zones on Semi-exposed, rocky shores in southern Madagascar.	74
Appendix 3.3: Abundance (mean % cover \pm SE) of species recorded in the various shore zones on Exposed rocky shores in southern Madagascar.	76

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ABSTRACT

The rocky shores of southern Madagascar are poorly studied with no publications describing intertidal biodiversity and community structure. This dissertation aimed to provide a first description of the rocky shore communities on the south-western shores of Madagascar and secondly to compare rocky shore communities of this region with northern KwaZulu-Natal. This study was part of a broader collaboration with the Suitcase Project which aimed to test the hypothesis that westward moving eddies may connect marine ecosystems in southern Madagascar and northern KwaZulu-Natal through the transport of larvae and propagules.

The intertidal shores of exposed and sheltered shores in Madagascar had an unexpected small tidal range. Despite this narrow tidal range, the distribution patterns across the shore were similar to global patterns with distinct vertical zonation patterns, high species diversity and an abundance of algae within the low-shore. Across all the wave exposure levels, a significant effect of zonation was detected between mid-and low-shore especially among communities on the low shore. Two-way ANOVA detected that (a) in sheltered conditions, fewer grazers were recorded and (b) identified differences in algal cover at each exposure level which contributed significantly to the differences seen between the shore levels (mid and low-shore). Algae species were affected by wave exposure with a trend of decreasing abundance with increasing wave exposure. The possible contributing factors for the high algae abundance include wave exposure, human impacts, combined which limited tidal ranges. Understanding community composition and the factors which influence intertidal communities are important in managing these systems sustainably. The description of undocumented shores similar to these in southern Madagascar is a vital contribution to baseline studies in a developing country. This chapter aimed to address this need and has provided an important first description for the region, one which can form the foundation for future studies.

Using the data collected in Chapter 2, Chapter 3 analysed community structure data from eight intertidal sampling sites in Madagascar and four sites in northern KwaZulu-Natal, across three exposure levels. The Madagascan shores were on average 86.47% dissimilar to shores in northern KwaZulu-Natal, with 29 taxa accounting for 90% of this dissimilarity.

The overall numbers of species recorded on the low-shores for both Madagascar and KwaZulu-Natal were 56 species of which 26 of those species were present in both countries. The articulate coralline seaweed *Jania sagittata* and brown algae *Sargassum elegans* were the predominant species, characteristic of rocky shores in both countries. The Madagascan shores supported 21 distinct species in the low shore and only nine taxa were confined to northern KwaZulu-Natal. The key species defining the assemblages present on Madagascan shores were algae (particularly *Arthrocardia* spp., *Spyridia hypnoides*), whereas distinguishing species of northern KwaZulu-Natal included the polychaete *Idanthysus pennatus* and the zoanthid *Palythoa nelliae*. In addition, the KwaZulu-Natal shores featured three ascidian species that were absent from the Madagascan shores. The brown mussel *Perna perna* was the only filter feeding species that the two countries shared and this occurred at low abundances in both countries (less than 2% mean percentage cover). The low abundances of this key food species and the field observations of high subsistence fishing effort suggests that both southern Madagascar and northern KwaZulu-Natal shores are exposed to extensive harvesting pressures. Harvesting pressures on both shores could be masking the fact that *P.perna* have higher species abundance at high wave exposure. The overlap of communities between the countries, were within exposed and semi-exposed sites, these exposures had higher *P.perna* abundance.

The results from this dissertation represent the first attempt to quantitatively examine rocky shore assemblages in contribution to a study of potential linkages between southern Madagascar and northern KwaZulu-Natal rocky shores. I quantitatively compared the rocky shore community structure between the shores of these countries and found the biocoenosis was similar but that there were significant differences between countries and within each country, shores differed with wave exposure. This aligns with intertidal ecology elsewhere as shown by previous literature.

In a global context, southern Madagascar falls within the Western Indo-Pacific and northern KwaZulu-Natal fall within the Indo-Pacific bioregion based on geographic proximity. The biogeographic province of southern Madagascar may not be part of the Western Indo-Pacific realm nor part of the tropical Western Indian Ocean Province but rather a region of overlap, in which both tropical and temperate species flourish. According to the species present on the Madagascan shores, there seems to be an overlap between Western Indo-Pacific and tropical Western Indian Ocean Province, which could be a major

contributing factor to the differences in algal species. This work has implications for the biogeographic affinities and classification of regions and the species associated within those regions.

The baseline data collected will contribute to further studies for KwaZulu-Natal and the first documented biodiversity and community structure study for the southern Madagascan region. In terms of connectivity between the countries the shores were less similar than expected with an overlap in species composition between semi-exposed and exposed shores. The low levels of similarity could be attributed to (1) the transport rate and frequency of eddies across the Mozambique Channel (2) the length of the larval and propagules phase of particular species and their ability to regenerate once on the other side and (3) both countries falling within realms of biogeographic overlap.

CHAPTER 1

General Introduction

Madagascar is the fourth-largest island in the world (Storey, 1995) and is located in the Indian Ocean off the south-eastern coast of Africa. Madagascar has been characterized as one of the largest unsolved questions of natural history in terms of its high species richness and often unresolved biotic linkages (Krause et al., 1997). Geological data indicate an ancient mid-Mesozoic separation of Madagascar from the African mainland (Rabinowitz et al., 1983; Storey, 1995). The historical biogeography of Madagascar can be better understood by considering the origins and historical division of Gondwana (Yoder and Nowak 2006). When the supercontinent Pangea divided (approximately 175 million years ago), into two landmasses namely: southern continental (Gondwana) and northern continental (Laurasia), the Madagascan island was hidden beneath the southern continent (Figure 1.1: a-b) (Rakotosolofa et al., 1999; Reeves et al., 2002). Shortly after the division of Pangea, Madagascar obtained its current position within the Indian Ocean (Figure 1: c-f).

Eastern Gondwana including Madagascar drifted southward towards Africa, descending along the Davie Ridge which is known as a strike-slip fault (Bassias, 1992; Reeves & de Wit, 2000). According to geologists this occurred between 165 and 155 Ma (Agrawal et al., 1992; Rabinowitz et al., 1983; Reeves & deWit, 2000; Scotese, 2000; Reeves et al., 2002; Briggs, 2003). Although the separation of Madagascar from Africa began as early as 165 Ma, the current understanding is that the exchange of biotic material was likely between western and eastern Gondwana within this period of approx. 20 million years, (Rabinowitz et al., 1983). Madagascar reached its current position with respect to Africa by 118-130–Ma (Harland et al., 1990; Rabinowitz et al., 1983). Presently, Madagascar is surrounded by an oceanic barrier with Africa being its closest continent with an approximate distance of 400 km to the west. Madagascar lies roughly 4000 km from India, 5000 km from Antarctica, and 6000 km from Australia (Yoder and Nowak 2006).

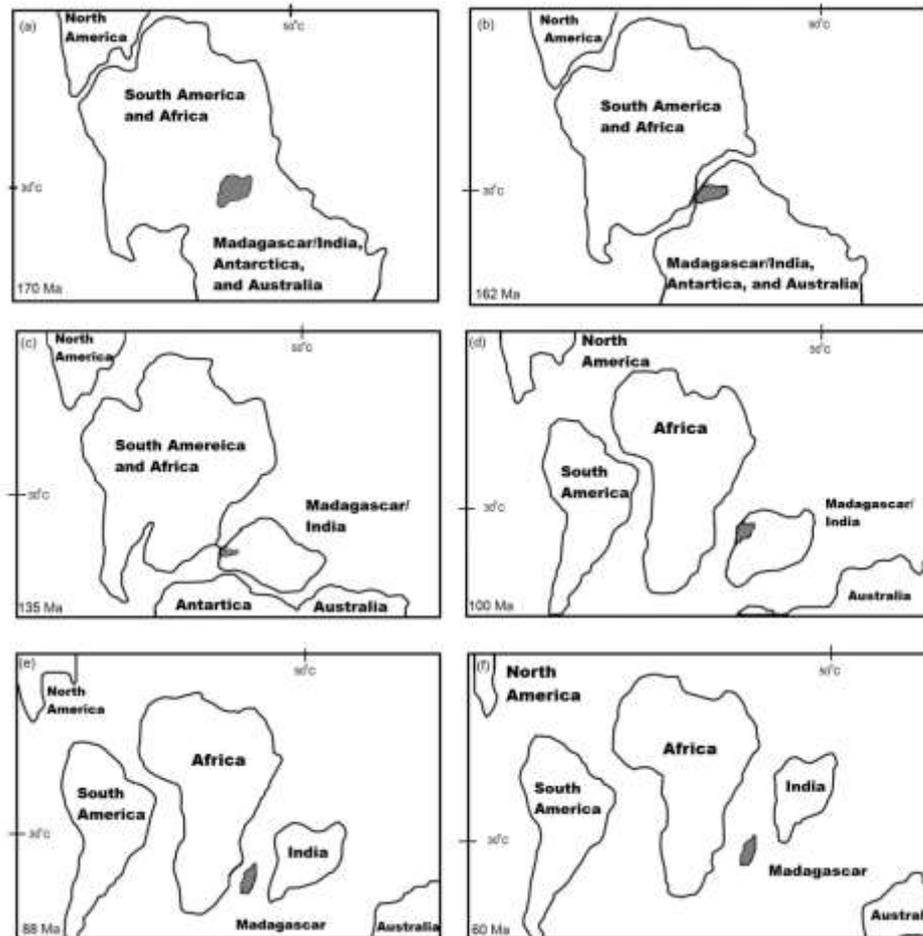


Figure 1.1(a-d): Paleo reconstructions on the breakup of Pangea, and Madagascar's subsequent geographic isolation (Redrawn from Scotese 2000).

Even though shifts in latitude and interactions with other landmasses took place over geological time, it is uncertain whether Madagascar has been stable for the last 118 million years. After the final separation of Madagascar and Africa, the sea levels have changed, which in turn affects the Mozambique Channel (3000 m, at the deepest point) which separates Madagascar and Africa (Krause et al., 1997). Based on the above information, it has been hypothesized that the separation of the main extant lineages of Africa and Madagascar may have been linked to the breakup of Gondwana (Stiassny, 1991; Farias et al., 1999). A study by Yoder and Nowak (2006) found sister group relationships between Madagascan and African taxa which suggests that some biota of Madagascar are descendants of the Cenozoic with African origins.

Madagascan species diversity and the state of ecological systems are effaced by human impacts which has resulted in conservation efforts receiving international prioritization (Goodman and Benstead, 2003). In terms of terrestrial biota, a study by Yoder and Nowak, (2006) found a distinct signature of evolution in isolation and high levels of diversity linkage between Africa and Madagascar. Although not tested, it has been assumed that the same patterns extend to marine biota, especially marine invertebrates (James, 1984). Various theories have been proposed to explain the origin of Madagascar's biota and thus far the two most plausible mechanisms are vicariance (the geographical separation of a populations) and/or dispersal. Vicariance of biota stems from large-scale geophysical events such as separation of continents and rising of mountain chains (Ronquis, 1997). Vicariance is used to explain the patterns of distribution between species that are related. Therefore, the presence of plant genera in two different countries can be due to the genus being of Gondwanan origin or as part of the separation of continents. Once a species is divided by vicariance, the population will begin to drift autonomously into several populations. Thus vicariance is a necessary precursor to geographic speciation (Ronquis, 1997).

Very little work has been undertaken on marine systems in Madagascar (Lewis, 1963; Pielo, 2013) and no published information is available about rocky shore habitats. In terms of bathymetry and oceanography, however, the region is well studied in comparison. It has been suggested that westward propagating wind anomalies associated with the Indian Ocean, affect the intensity of mesoscale activity and the frequency of eddy occurrences in the Mozambique Channel (Palastanga et al., 2006; Backeberg et al., 2006). While mesoscale eddies are found in most of the world's oceans, they are most prominent at the ends of the Western Boundary Current such as the Gulf Stream, Brazil, East Australian, and Agulhas Currents (Rhine, 2001).

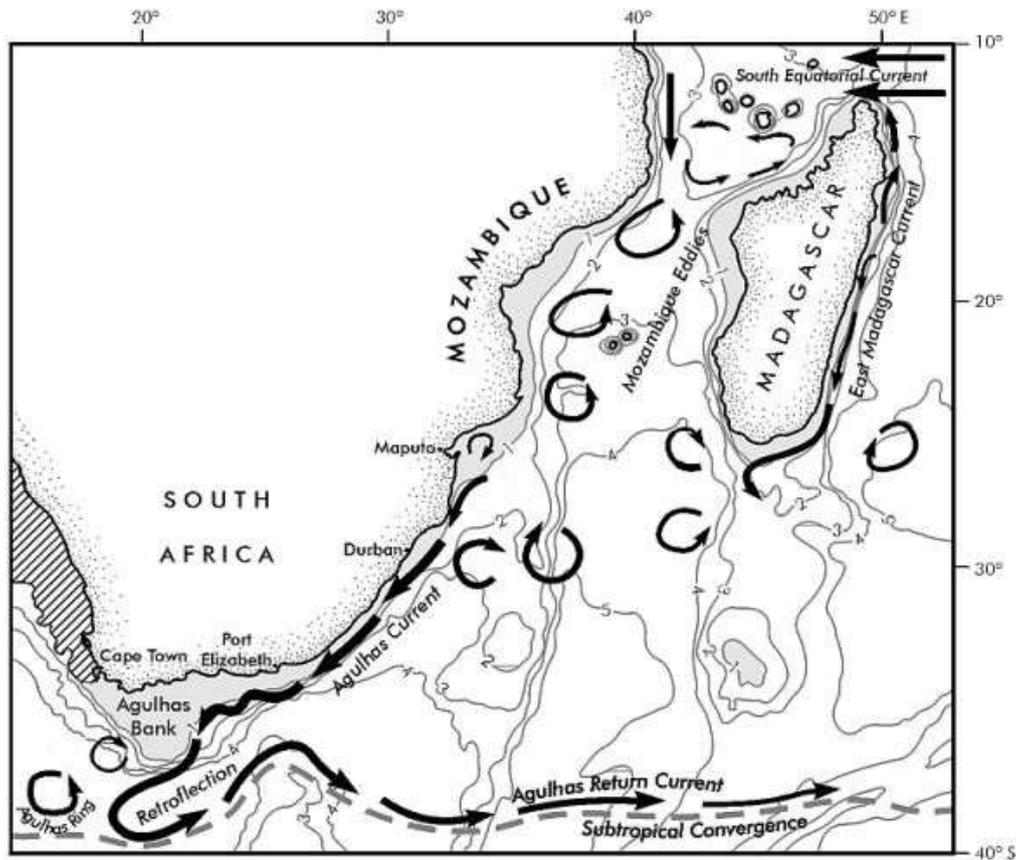


Figure 1.2: Bathymetry of the region around Madagascar and the Mozambique Channel. The main currents and flow features are schematically shown. Features shown are the South Equatorial Current (SEC), the Southeast Madagascar Currents (SEMC), the Agulhas Current (AC), and the Mozambique Current (MZC). The dotted line indicates connection between the SEMC and the AC, which is possibly formed by eddies formed near the southern tip of Madagascar (Lutjeharms and Penven, 2006).

In the region of Madagascar and Mozambique there are four predominant currents, the Agulhas Current, the east and south Mozambique Currents and the Mozambique Current (Biaostoch et al., 1999). The bathymetric configuration of the East Madagascar Current moving southwards from a very narrow shelf on the east coast of Madagascar to a much wider shelf south, is very similar to that of the Agulhas Current passing Cape St Lucia and Port Alfred on the east coast of South Africa where edge upwelling is prominent (Halo et al., 2012). The latter has also been observed off the south-eastern corner of Madagascar in both hydrographical and satellite data (Lutjeharms, 2006). The northern flow and the positive vorticity that the current obtains as it rounds the northern tip of Madagascar (Cape Amber) are suggested to be the source of meso-scale turbulence in the Mozambique Channel (Rabinowitz, 1983). Cyclonic, anti-cyclonic eddies and eddy dipoles have been shown to play an important role in the vertical pumping of nutrients into the upper mixed layer of the Mozambique Channel (Quartly et al., 2006).

These eddies are strengthened when they interact with the continental slope and induced upwelling (Roberts et al., 2014). Overall, the physical oceanographic research which has taken place in this region over the last five years has provided clear evidence that meso-scale turbulence is a major driver of production in the Mozambique Channel (Roberts et al., 2012).

The Western Boundary Current, the Agulhas Current and East Madagascar Current in the southwestern part of the Indian Ocean play a crucial role in affecting meridional heat transport from the warm tropical regions to the Southern Ocean (Halo et al., 2012). The flow through the Mozambique Channel contributes to the warm surface flow of the global surface ocean circulation (Zinke et al., 2004). In the Southern Mozambique Channel, waters from the East Madagascar Current provided by the South Equatorial Current round the southern tip of Madagascar (Figure 1.2). The inter-ocean exchange brought about by the warm saline Indian Ocean water entering the South Atlantic is an important part of the warm water route for the renewal of North Atlantic Deep Water (NADW) (Gordon, 1985). In addition, it stabilizes the northern overturning circulation of the Atlantic Ocean (Weijer et al., 2002). The south easterly winds which continue throughout the year are stronger during monsoon season (June-August) which causes stronger South Equator Current Mozambique Channel flow. Warm core-rings are formed when extended anti-cyclonic meanders enclose a parcel of sea water and release an anti-cyclonic vortex (Brown et al., 1986). These rings are hydrographically distinguishable regimes, 60-200 km in diameter and few thousand meters deep that maintain their identity for periods of months to less than a year (Brown et al., 1986). Satellite altimetry data shows inter-annual variability of the rate of Mozambique Channel eddy formation, probably related to the large-scale climate anomalies over the equatorial Indian Ocean (Schouten et al., 2002a). The formation of meso-scale eddies in the Mozambique Channel appears to be connected to inconsistency in the transport of the South Equatorial Current (Backeberg and Reason, 2010).

Hydrographical measurements have established the Agulhas Rings as the most energetic eddies recorded (Brown, 1984; van Ballegooyen et al., 1994). When these eddies move westward, they travel towards the northern KwaZulu-Natal coast where they can cross over the Mozambique Ridge. A large portion of such eddies propagate all the way into the Agulhas Current retroflexion region, where they are thought to trigger the shedding of Agulhas rings (Schouten et al., 2002b; Van Leeuwen et al., 2000).

Furthermore, meso-scale eddies originating in the Mozambique Channel have been implicated in producing turbulences in the Agulhas Current that ultimately affect the Indo-Atlantic inter-ocean exchange south of Africa by triggering the shedding of Agulhas rings from the retroflexion (e.g. Schouten et al., 2002b). The Agulhas shedding/leakage of rings is considered to play an important role in maintaining the Atlantic Ocean meridional overturning circulation and climate (Peeters et al., 2004). The Agulhas Current forms a critical link between the Indian and Atlantic Oceans (Beal et al., 2011; Figure 1.2). The combination of Western Boundary Current and the Agulhas Current form a region of high mesoscale activity and the importance of small-scale features like the “Natal Pulses” (Lutjeharms, 2006).

The northern Agulhas Current plays a key role in the inter ocean exchange of the sporadic meanders on the trajectory of the Natal pulses (Lutjeharms, 2006). The Natal Pulse has important implications for the shedding of Agulhas rings downstream at the Agulhas Retroflexion and thus also on the exchange of water properties between the Indian and Atlantic Ocean (van Leeuwen et al., 2000). The characteristics that makes the Agulhas Current unique are the Agulhas rings, Agulhas return currents and the fact that mesoscale eddies occur frequently in its source region (see Figure 1.2). On average between 1995 and 2000, with as many as four eddies per year were observed circulating southward through the Mozambique Channel, into the upstream Agulhas region (Schouten et al., 2002b).

Further oceanographic research has shown how temperature controls the timing of eddies and the frequency of the shedding of Agulhas rings (Schouten et al. 2002a-b). Subsequently, these rings carry warm and salty Indian Ocean waters into the South Atlantic and thus largely establish the climatically important connection between the two oceans. The process of ring shedding itself has been described based on both direct observations and modeling studies (de Ruijter et al., 2003). Recent studies have also shown that westward circulating eddies in the South West Indian Ocean (SWIO) collide with the Mozambique Ridge and then move southward along the eastern edge until they move westward into the Natal Basin (Halo et al., 2012). This occurs at one of two low points in the topography where the ridge ends (Roberts et al., 2006). According to Morris et al. (2011) some of these eddies interact with the continental slope of KwaZulu-Natal prompting significant upwelling.

Given their ability to sustain and retain biological material, it is believed eddies can act as transport vectors (Heywood, 1996). A number of studies have considered the local dynamics of the retroflection within the Agulhas Retroflection region and the shedding of Agulhas rings (Boudra and de Ruijter, 1986; Boudra and Chassignet, 1988). The configuration of the tip of South Africa combined with the inflow and outflow conditions of the Agulhas Current, makes the local dynamics unsteady, which contributes, to the retroflection and ring shedding (Ou and de Ruijter, 1986; Pichevin et al., 1999). The remote force initiates shedding of Agulhas Ring by meanders upstream (Van Leeuwen et al., 2000). It has been suggested that mesoscale eddies originating in the Mozambique Channel produce instability in the Agulhas Current that affect the Indo-Atlantic inter-ocean exchange south of Africa by triggering the shedding of Agulhas rings from the retroflection (Backeberg et al., 2010 and Schouten et al., 2002b).

The above body of research gives reason to believe that despite the lack of any distinct westward flowing ocean current, the movement of propagules and larvae from southern Madagascar to the Kwazulu-Natal coast could occur via eddies. The dispersal of marine species over such long distances is not unusual, and can be pronounced in species that have lengthy planktonic larval phases (Scheltema and Williams, 1983; Richmond, 1987; Levin, 1992; Warner and Cowen, 2002; Nathan et al., 2003; Cowen et al., 2006). This suggests that connectivity (at least for some biota) between southern Madagascar and Kwazulu-Natal is possible (e.g. Macdonald et al., 2009; Obura, 2012). In fact, Macdonald et al. (2009) and Obura (2012) both found DNA connectivity amongst coral populations and molecular markers indicated high levels of connectivity between east Africa and Maputaland. Therefore, if eddies make landfall on the Kwazulu-Natal coast then the question arises as to whether Kwazulu-Natal and Madagascar share similarities in terms of marine biota and, if these links could be maintained by eddies moving from Madagascar to South Africa?

These questions form the basis of the Suitcase Project which proposes to address the hypothesis that westward moving eddies may connect south eastern Madagascar and northern KwaZulu-Natal through the transport of larvae and propagules. This hypothesis is being tested by this collaborative and multi-disciplinary collaborative project between researchers from the Oceanographic Research Institute (ORI), the University of Cape Town (UCT), the South African National Biodiversity Institute (SANBI) and the Department of Agriculture,

Forestry and Fisheries (DAFF), the University of KwaZulu-Natal (UKZN) and Stellenbosch University (SUN), Nelson Mandela Metropolitan University (NMMU). The project African Coelacanth Ecosystem Programme (ACEP) involves multi-disciplinary work including physical and biological oceanographic research, biodiversity surveys, work on plankton, bivalves, corals, frock lobsters and fish and the examination of rocky shore assemblages. The project includes genetic components but these results are not yet available. This study focuses on rocky shore communities and originated from observed similarities in rocky shores between Madagascar and Maputaland in northern KwaZulu-Natal. During an opportunistic port stop, South African scientists noted similar geology and species assemblages for rocky shores between regions in northern KwaZulu-Natal and southern Madagascar leading to the suggestion of a quantitative study to assess similarities and differences.

As part of the Suitcase project the present study will (1) provide the first description of rocky shore communities on the southern shores of Madagascar and (2) provide a quantitative comparison of rocky shore community structure between these shores and those of northern Kwazulu-Natal.

CHAPTER 2

Primary description of the rocky shore communities on the Southern shores of Madagascar

Introduction

Throughout the world, rocky shores encompasses the most geographically diverse and dynamic communities (Hawkins and Hartnoll, 1985). The importance of intertidal ecosystems can be attributed to their high biodiversity, their provision of food and their role as indicators of change (Bianchi and Morri, 2000; Griffiths et al., 2010). The high species richness is due to the large number of ecological niches present in these systems (Davenport and Davenport, 2005). It has been suggested that rocky shore organisms are good indicators of water quality as they reflect not only the environment at the time, but also the environment to which communities have previously been exposed (Hawkins et al., 1994; Pinedo et al., 2007; Araujo et al., 2006). Collectively this body of work suggests that rocky shore species are key indicators for tracking changes in marine and coastal systems (Hawkins and Hartnoll, 1985).

The body of literature considering distribution patterns of rocky shore biota is vast. Early studies by ecologists were mainly descriptive (Stephenson, 1939; Evans, 1947a), whereas later work considered the influence of the environment on marine communities (Southward, 1958; Ballantine, 1961; Lewis, 1992, 1963; Underwood, 1981; Hawkins and Hartnoll, 1985; Griffiths and Griffiths, 1987; Branch et al., 2008, Kordas et al., 2011). Collectively this work has demonstrated how rocky shores display clear zonation patterns (Ballantine, 1961; Connell, 1961b; Little and Kitching, 1996), with biological interactions being important in structuring communities low on the shore (Branch, 1985; Williams, 1994) while high on the shore abiotic factors such as temperature and erosion become more important (Menge et al., 1978; Bustamante et al., 1997). Little published information is available on marine systems in Madagascar and even more accessible habitats like rocky shores have received little research attention (Lewis, 1963; Pielou, 2013). Earlier studies conducted in the region were mainly devoted to broad scale description of the coastal systems based on oceanographic information and coral reef studies characterized by temperature, currents, wave exposure and disturbance from cyclones (Nado et al., 2007; Obura, 2009, Obura, 2012).

The south coast of Madagascar is influenced by the Agulhas Current, with cool (15°C - 22°C) temperatures, localized upwelling, strong winds and environmental variability (Morris, 2009). In contrast, the Madagascan west coast is generally warm (23°C - 35°C), with low winds and the influence of eddies from the Mozambique Channel (Gründlingh, 1995 and Morris, 2009). The east coast of Madagascar is influenced by the East Madagascar Current and temperatures range between 11°C - 20°C (Lutjeharms and Machu, 2000).

Madagascar only has a few published works describing marine environments and secondly discussion the environmental conditions of the intertidal zones e.g. tidal height. One of these studies by Loroche et al. (1997) investigated temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar and reported the tidal range across the shore up to 3m high. Another study by McClanahan et al., 2009, which focused on the status of coral reefs, suggested parts of Madagascar are affected by large tidal ranges because of the Mozambique Channel which narrows near the coast. The lack of intertidal specific research conducted within the southern Madagascar highlights a need for studies focused on this region and offers an opportunity to conduct a base line study upon which future research can be built. As such this chapter aims to provide a first description of the rocky shore communities on the southern shores of Madagascar and secondly to consider how these communities differ between shore zones and across different levels of wave exposure.

Materials and methods

Study site

Sampling took place within the Nahampoana region of southern Madagascar in July 2013 and spanned roughly 20km of coastline (Figure 2.1). This region of coastline consists of narrow sandy beaches, interspersed with rocky outcrops and rock-pools within rocky platforms. Sampling was focused in two areas, Fort Dauphin and Locara. The area of Fort Dauphin supported only semi-exposed aeolianite platforms, while around Locara the rocky intertidal zone consisted of sloping granite shores with gullies and broken rocky ledges exposed to either sheltered or wave exposed conditions. Intermittent shelter was provided by offshore boulders, but even so, this region was exposed to heavy swash and strong south easterly winds. Sand inundation within small, narrow, sheltered bays was also a feature in this study region. Unfortunately, the presence of differing wave exposure levels at Fort Dauphin and Locara precluded a comparison of rocky shore communities among these regions.

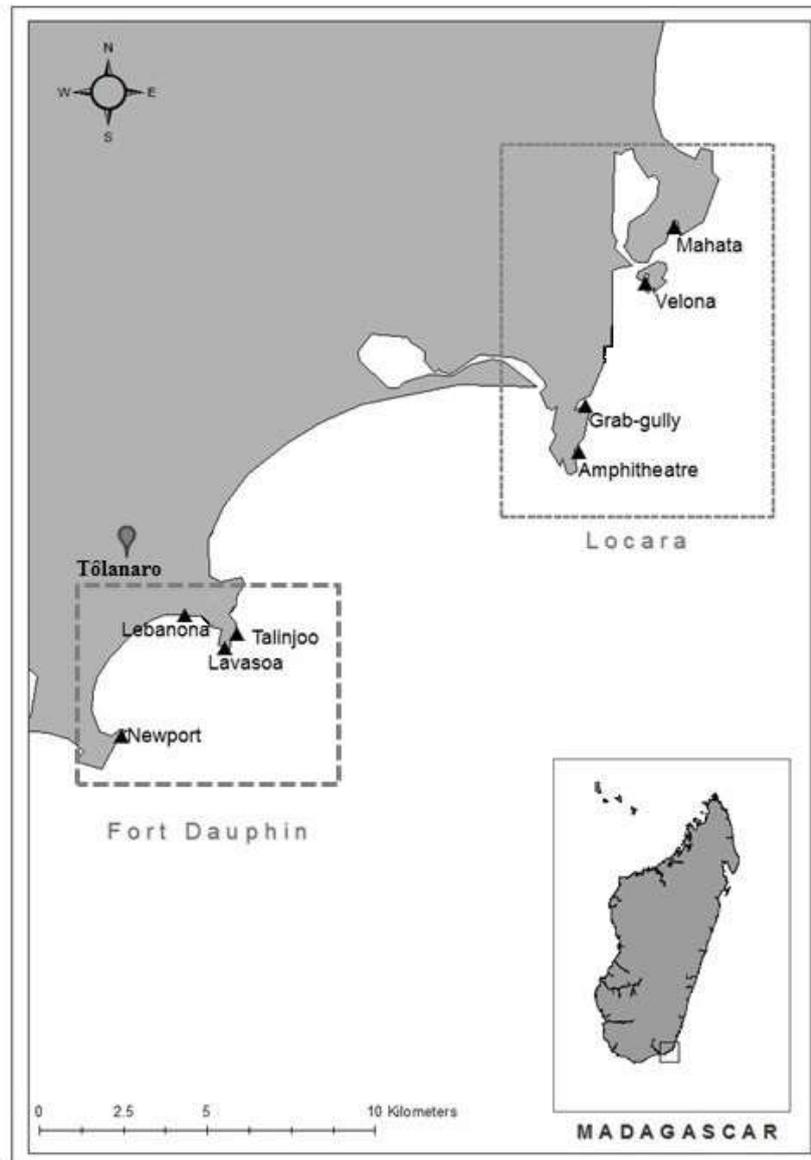


Figure 2.1: Map of the Southern Madagascan coast, indicating the sampling regions. Left: Fort Dauphin, Right: Locara.

Experimental design

As part of a collaborative field trip organised by the multi-disciplinary Suitcase research project of the African Coelacanth Ecosystem Program four study sites were quantitatively sampled in winter of 2013. Due to the prohibitive costs of traveling to Madagascar and limited space on the research vessel making the trip I was not able to be present on the trip and the data for this chapter was collected by Dr Kerry Sink. While she collected the raw data I processed it upon her return and with the aid of her input and the many photographs she took I familiarised myself with the study sites.

Due to logistical limitations, sampling locations were chosen predominantly based on accessibility and the research interests of the large team of collaborators. Within each region, four rocky shore sites were sampled (Table 2.1). While the initial aim was to sample sheltered and exposed shores in each region, only semi-exposed shores were present within the Fort Dauphin region. In addition, within this region the mid-shore zone was largely absent and could only be sampled at Newport where a vertical wall provided sufficient mid shore habitat to permit a quadrat survey. At other sites the flat shore topography and pools in the mid shore did not provided sufficient habitat to facilitate mid shore surveys. The small tidal range in the study area was unexpected and the field team were surprised to find that the wind and swell seemed to have a greater influence on sampling conditions than tide. A coral reef study by McClanahan et al., 2009, suggested parts of Madagascar are affected by large tidal ranges because of the Mozambique Channel which narrows near the coast. Within this study, a maximum tidal height of 2.6m was measured on the south coast of Madagascar and 0.5m in the southeast coast.

At each site the percentage cover of algae and sessile animals was estimated and the total number of limpets and other mobile animal species were counted in twenty randomly placed 1m x 0.5m replicate quadrats to quantify communities following the methods of Sink 2015 and 2005. Quadrats were scored in each of the mid- and low-shore at each wave exposure (excepting in the Fort Dauphin region where no mid-shore zone could be identified except at a single site (Newport)). The high shore was not included in the quantitative analyses of this study as this zone was absent at most sites and where present, was so narrow that the use of the same protocol as used by Sink 2001, would not have been feasible. Nonetheless, it was included in the qualitative description of the shores. Pools and gullies were excluded from this study following Sink et al., (2001). Identification of intertidal biota was done *in situ* whenever possible using Branch and Branch (1995) and Branch et al., (2005). In addition, photographs and samples were collected to enable consultation with relevant taxonomic experts upon return to South Africa. Back in the laboratory, species counts were converted to percentage cover using the mean sizes of mobile species that were recorded in the field (as per Sink et al., 2001).

Table 2.1: Details of the sites sampled within the two regions.

Fort Dauphin			Locara		
Site	Coordinates (ddm)	Exposure	Site	Coordinates (ddm)	Exposure
		Semi-exposed			Sheltered Exposed
S1 Talinjoo	25°02.552'S 46°59.851'E	x	S6 Mahata	24°56.442'S 47°07.433'E	x
S2 Newport	25°04.213'S 46°57.860'E	x	S7 Velona	24°56.343'S 47°07.463'E	x
S3 Lebanona	25°02.255'S 46°59.640'E	x	S8 Amphi- theatre	24°57.086'S 47°06.437'E	x
S4 Lavasoa	25°02.494'S 46°59.703'E	x	S9 Crab gully	24°56.518'S 47°07.084'E	x

Statistical analyses

In order to compare community composition among shore levels and wave exposure levels, non-parametric multivariate analyses were applied to the species abundance data using PRIMER v6 (Plymouth Routines in Multivariate Ecological Research (Clarke, 1993; Clarke and Warwick, 2001) and PERMANOVA (Anderson et al., 2008) software. The percentage cover of all species (taken as a measurer of abundance) was forth-root transformed (Field et al., 1982).

The transformed data were converted into a similarity matrix using the Bray-Curtis similarity measure. Due to limitations imposed by the fact that sheltered and exposed sites occurred only in the Locara area and semi-exposed shores only in Fort Dauphin, 'area' could not be included as a factor in the statistical analyses. In addition, as only one semi-exposed site supported a mid-shore zone, a model accounting for zonation and exposure would have been unbalanced and lacking replication of one level of each factor. As such the effect of wave exposure was explored using only data from the low-shore, enabling inclusion of data from all eight sites. Here an ANOSIM was used to detect differences in community structure. The effect of zonation on community structure was then considered separately for each exposure level, using only data from sites that had both shore zones. For sheltered and exposed shores two factor PERMANOVA analyse were applied in an unbalanced two factor analysis: (i) Shore zone (fixed effect with two levels: mid and low-shore), (ii) Site (fixed effect). As only one site was semi-exposed (Newport), here the effect of zonation was considered using an ANOSIM.

Both PERMANOVA and ANOSIM analyses made use of the Type III (partial) sums of squares which determines the minimum amount of sums of squares (SS) attributable to a given term. Type III fits all the other terms except the one that is being tested, then finally fits the term being tested and determines the SS attributed to that term. The residuals were permuted under the reduced model 9999 times. All tests considering community composition were followed by SIMPER analyses to isolate the species responsible for any differences among communities. The SIMPER analyses ranking is determined by the average contribution of each species to the overall similarity of the level in each region (i.e. S_i). %Av indicates the average percentage cover of each species from all sites. $S_i/SD(S_i)$ is the ratio between S_i and $SD(S_i)$, the standard deviation of S_i . This ratio reflects how consistently the species abundance varied within each region. $\Sigma SI\%$ is the cumulative percentage contribution of each species to the overall similarity (S). Patterns in community structure were visually explored using Multi-Dimensional Scaling (MDS) and cluster diagrams.

A two factor ANOVA was used to compare % cover of the various functional groups (4 levels: bare rock, algae, filter-feeders and grazers) among shore zones (2 factors: mid and low) for each exposure level. This analysis was chosen due to the data having a normal distribution and equal variance among groups. While bare rock is not a functional group *per se*, inclusion of this measure enables a holistic analysis of the coverage of the shore. These univariate analyses were conducted using STATISTICA for Windows (Version 6).

Results

Qualitative description

Despite the unexpected small tidal range (approximately 0.5m), vertical zonation was observed on the rocky shores of southern Madagascar. A schematic diagram of the exposure levels is presented in Fig 2.2. Three zones were apparent even though species distributions overlapped among zones. The high-shore zone was very narrow, and almost entirely absent in some instances due to shore topography with an absence of rock in the high shore. When present, littorinid snails including *Echinolittorina natalensis*, *Littoraria coccinea glabrata* and *Afrolittorina africana* were the predominant organisms present in this zone. The mid-shore zone was dominated by a variety of algae and in some cases supported molluscs (*P. perna*) and crustaceans (*Tetraclita rufotincta*) In contrast, the low-shore zone was completely dominated by encrusted coralline and different algal species.

Despite these general trends in zonation, the species present in the mid- and low- zones varied among exposed, semi-exposed and sheltered shores. On exposed shores, the mid-shore supported a diverse group of species including algae (*Jania* spp., *Chaetomorpha antennina*) brown mussels (*P. perna*), one species of limpet (*Cellana capensis*) and encrusted coralline algae (*Ralfsia* spp.). At this wave exposure, the low-shore was dominated by the algae *S. elegans*, *Jania sagittata* and *Plocamium corallorhiza*. In contrast, mid-shore zone on semi-exposed shores supported no molluscs and was dominated by algae *Laurencia* spp., *Caulerpa racemosa*, *Rhodomenia natalensis*, *P. corallorhiza* and unidentified species of encrusted coralline algae. The low-shore zone at this wave exposure level shared species in common with exposed sites (e.g. *S. elegans*, *J. sagittata*) as well as sheltered sites (e.g. *Spyridia hypnoides*). Sheltered shores were populated mostly by algal species (*Spyridia hypnoides*, *Arthrocardia* spp., *Laurencia* spp., *Caulerpa racemosa*, *Jania* spp., *P. corallorhiza*) although the limpet *Scutellastra exusta* and the urchins *Echinometra mathei*, *Diadema* spp., and *Colobocentrotus atratus* were also recorded in this zone. The semi-exposed shores at the same shore level were mostly occupied by algal species (*Jania sagittata*, *R. natalensis* and *S. elegans*). A total of 62 different species were observed (Appendix 2.1) of which algae were the most dominant across all exposure levels, accounting for 80% of the species recorded. The remaining dominant taxa consisted of Zoanthids (Cnidaria), filter feeders (Porifera, and Arthropoda) and grazers (Mollusca and Echinodermata).

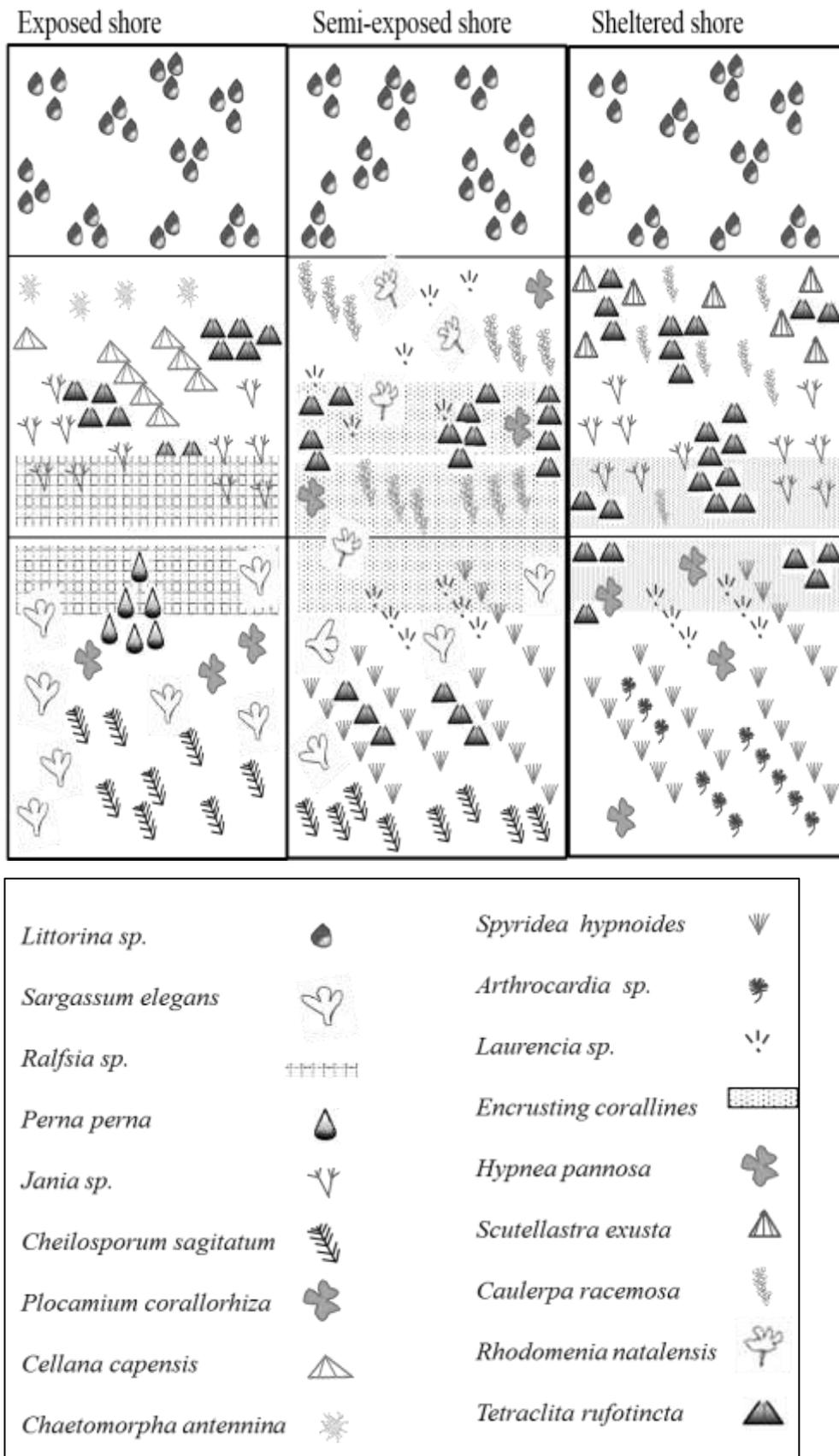


Figure 2.2: Schematic diagram of typical zonation observed on sheltered, semi-exposed and exposed shores. High shore is shown at the top and the low shore at the bottom of the figure.

Community composition

The effect of wave exposure

Multivariate comparisons revealed a significant difference in community structure among sheltered, semi-exposed and exposed shores in the low shore zone (ANOSIM, $R = 0.585$, $p < 0.01$, Figure 2.3) with differences among all wave exposure levels (Pairwise tests, $p < 0.05$ in all cases).

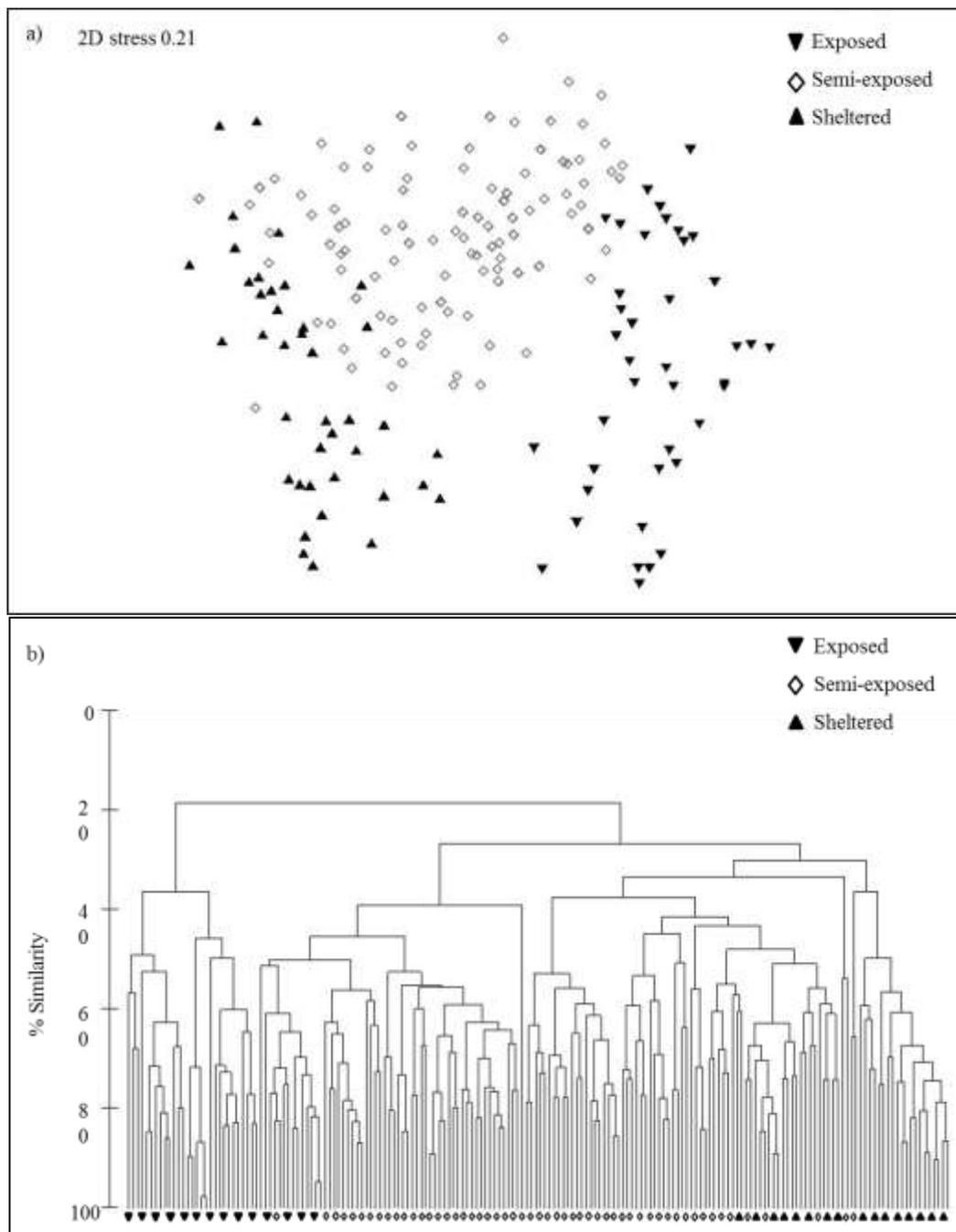


Figure 2.3: (a) Multidimensional scaling ordination and (b) Dendrogram based on group-average clustering from Bray-Curtis similarities of species abundance on the low shore of Madagascar across exposed, semi-exposed and sheltered shores.

The SIMPER analysis identified the species which typified each exposure level (Table 2.2). The exposed and semi-exposed shores were characterised by high contributions of red algae (e.g. *S. hypnoides*, *J. sagittata*), and brown algae species (e.g. *S. elegans*), whereas the sheltered shores were typified by red algae species (e.g. *Arthrocardia* spp., *Laurencia* spp., *P. corallorhiza*, *Hypnea musciformis*) and the relatively lower number of molluscs (e.g. *P. perna* and *C. capensis*). The articulated coralline algae *Arthrocardia* spp. and *Jania sagittata* species were the taxa most responsible for the observed changes between the exposure levels on the Madagascan shores.

Table 2.2: Characteristic species of each wave exposure on the low-shore of southern Madagascar, as determined by SIMPER analyses (Fourth-root transformed average percentage data).

Characteristic species	% Av	Si	Si/SD (Si)	ΣSI%
<i>Exposed (n = 2 sites; S = 42.40%)</i>				
<i>Sargassum elegans</i>	1.84	12.73	0.95	30.01
<i>Ralfsia</i> spp.	1.17	5.70	0.69	43.46
<i>Perna perna</i>	0.96	5.55	0.80	56.55
<i>Jania</i> spp.	1.14	4.78	0.49	67.82
<i>Jania sagittata</i>	0.97	3.90	0.57	77.03
<i>Plocamium corallorhiza</i>	0.87	2.65	0.40	83.27
<i>Cellana capensis</i>	0.35	1.75	0.51	87.41
<i>Chaetomorpha antennina</i>	0.46	1.40	0.39	90.70
<i>Semi-exposed (n = 4 sites; S = 42.14%)</i>				
<i>Spyridia hypnoides</i>	1.50	8.09	1.03	19.19
<i>Jania sagittata</i>	1.55	7.64	0.70	37.33
<i>Sargassum elegans</i>	1.34	7.60	1.04	55.37
<i>Encrusting corallines</i>	1.10	6.17	1.05	70.01
<i>Laurencia</i> spp.	0.81	3.39	0.64	78.04
<i>Rhodomenia natalensis</i>	0.69	2.28	0.45	83.44
<i>Caulerpa racemosa</i>	0.69	1.85	0.40	87.82
<i>Plocamium corallorhiza</i>	0.61	1.57	0.36	91.54
<i>Sheltered (n = 2 sites; S = 42.96%)</i>				
<i>Spyridia hypnoides</i>	1.65	10.01	1.30	23.29
<i>Arthrocardia</i> spp.	1.68	9.74	0.72	45.96
<i>Laurencia</i> spp.	1.09	7.01	1.16	62.27
<i>Encrusting corallines</i>	0.82	3.79	0.77	71.10
<i>Hypnea musciformis</i>	1.12	3.34	0.51	78.88
<i>Scutellastra exusta</i>	0.39	1.70	0.67	82.84
<i>Caulerpa racemosa</i>	0.59	1.53	0.42	86.41
<i>Jania</i> spp.	0.49	1.32	0.35	89.48

The effect of zonation

For all wave exposure levels, a significant effect of zonation was detected between mid- and low-shore communities (Table 2.3, 2.4; Figure 2.4, 2.5). Under exposed conditions, an interaction between shore zone and site was detected as communities in the mid-shore were more similar among sites than those in the low shore which were strongly differentiated. A similar pattern was recorded under sheltered conditions. Under semi-exposed conditions (where the effect of site could not be assessed) a significant difference was detected among mid- and low-shore community structure (Figure 2.6). The analysis showed a bigger zonation effect on sheltered sites on the mid and low-shores of Madagascar (Table 2.4).

Table 2.3: Results of a PERMANOVA and ANOSIM analysis on the effect of shore levels at different exposures (exposed, sheltered, and semi-exposed).

<i>a) Exposed</i>			
Source	MS	Pseudo-F	P (perm)
Shore level	1.075E5	117	$p < 0.001$
Sites	9798.50	10.66	$p < 0.001$
Shore level x Sites	19967	21.73	$p < 0.001$
<i>b) Sheltered</i>			
Source	MS	Pseudo-F	P (perm)
Shore level	1.2938E5	178.86	$p < 0.001$
Sites	22410	30.98	$p < 0.001$
Shore level x Sites	20479	28.31	$p < 0.001$
<i>c) Semi-exposed</i>			
Source	ANOSIM	P- value	
Shore level	R= 0.59	p= 0.1	

Table 2.4: Results of a pairwise PERMANOVA on the effects of exposure levels (exposed, sheltered). At different shore levels (mid and low-shore).

Source	Exposure	t-test	P (perm)
Mid-shore x Low-shore	Exposed	7.91	$p < 0.001$
Mid-shore x Low-shore	Sheltered	8.73	$p < 0.001$

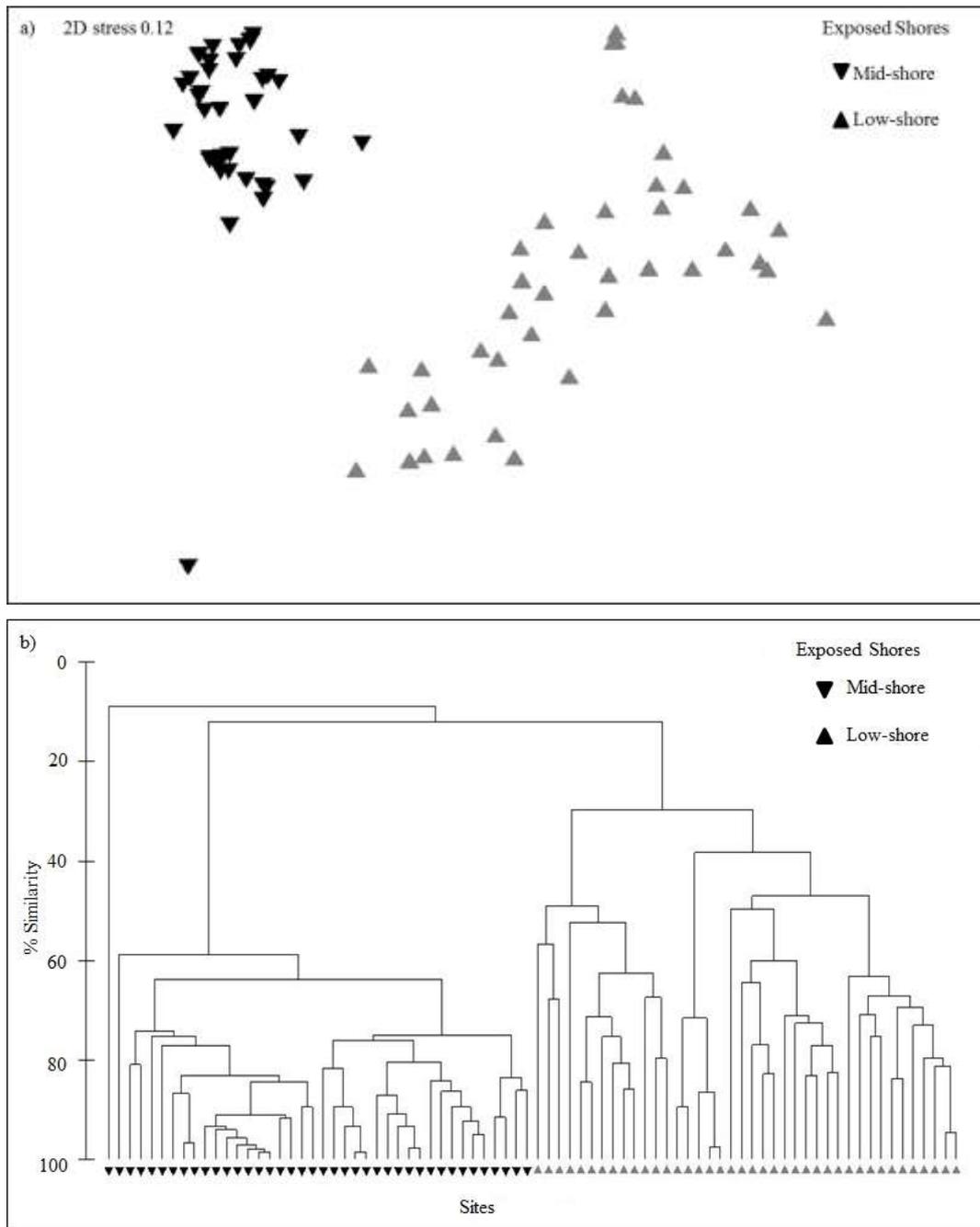


Figure 2.4 (a) Multidimensional scaling ordination and (b) Dendrogram on the hierarchical cluster analysis for the mid and low-zones on exposed shores.

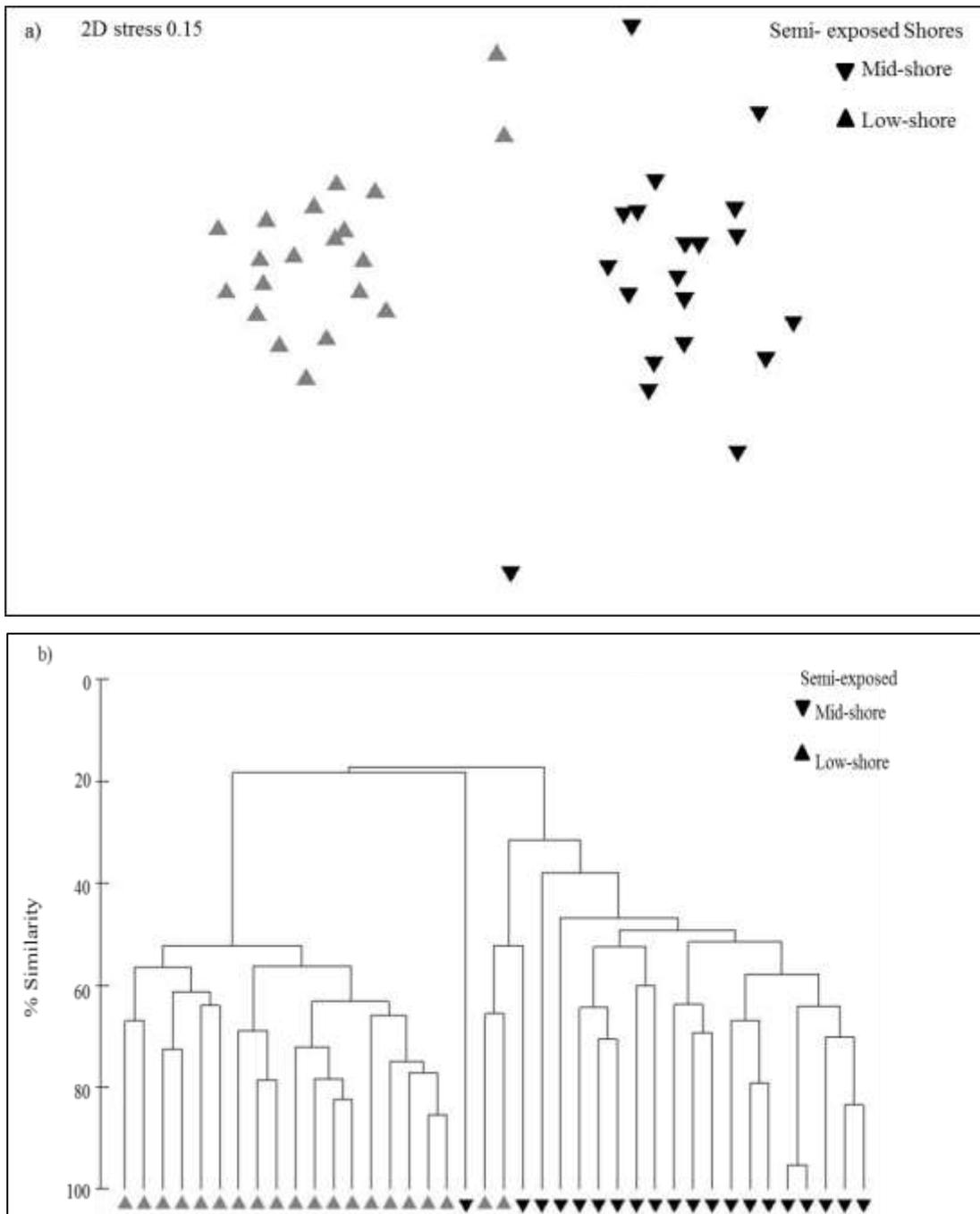


Figure 2.5: (a) Multidimensional scaling ordination and (b) Dendrogram on the hierarchical cluster analysis for the mid and low-zones on semi-exposed shores.

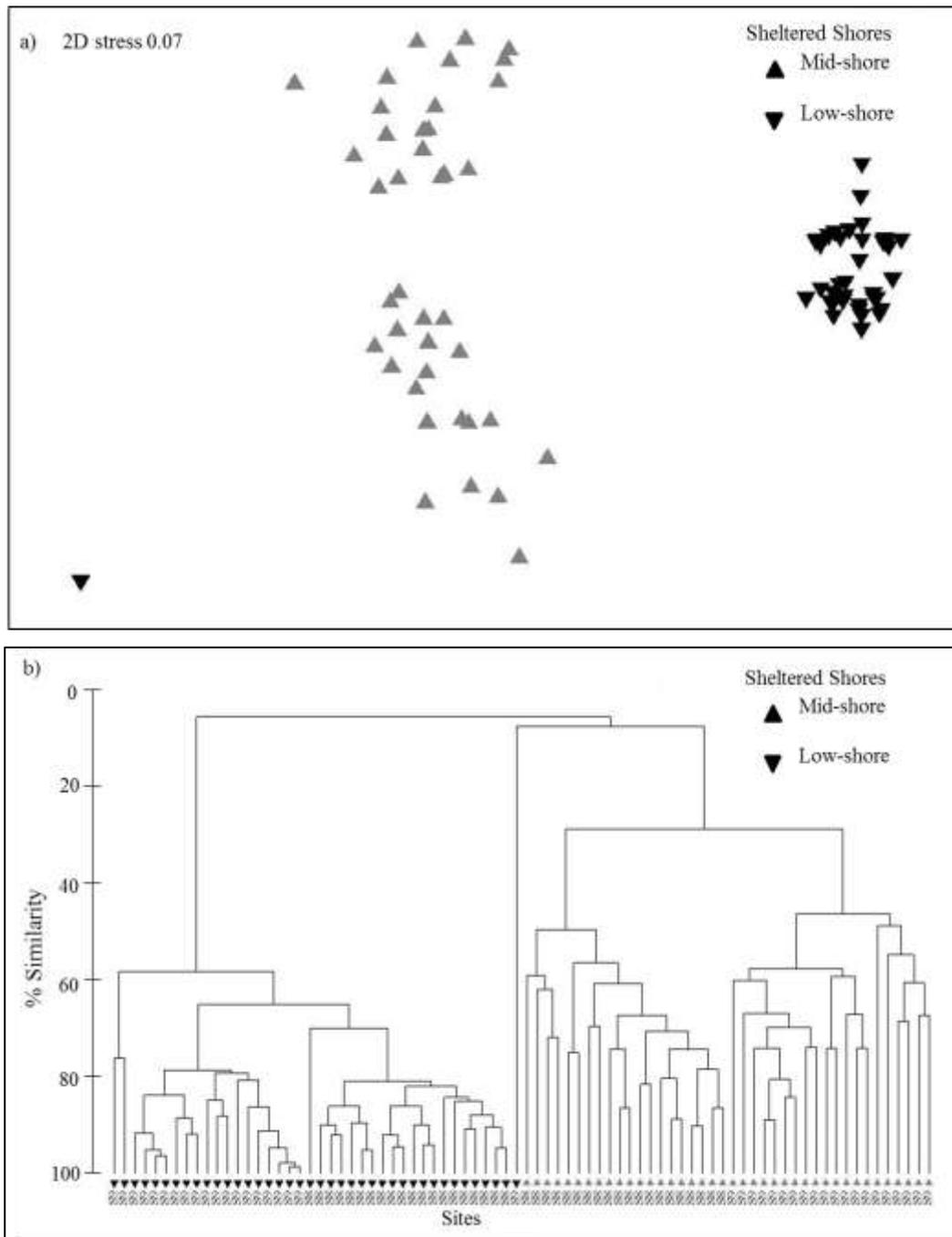


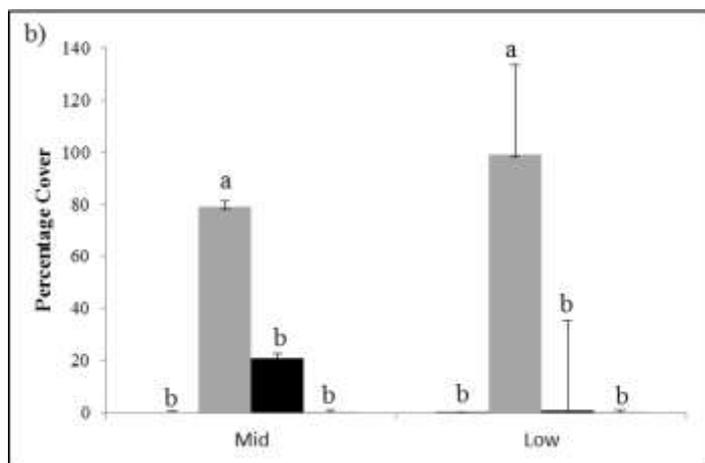
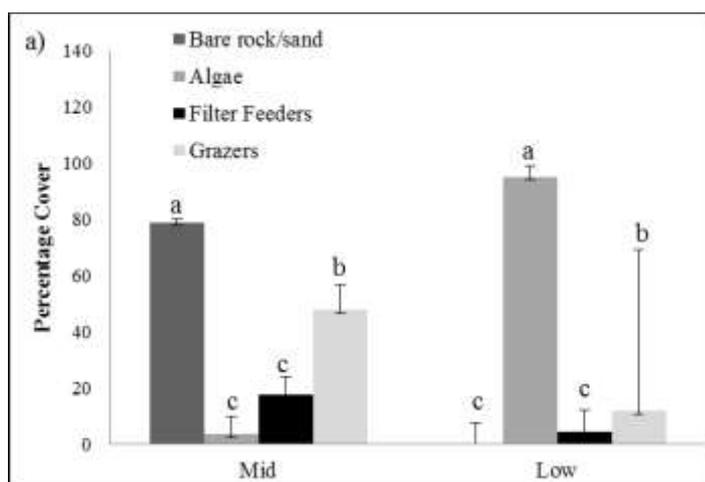
Figure 2.6: (a) Multidimensional scaling ordination and (b) Dendrogram on the hierarchical cluster analysis of the mid and low-zones on sheltered shores.

Functional Groups

At each shore level (mid and low-shore) the percentage cover of the various functional groups differed significantly and was affected by wave exposure (Table 2.4; Figure 2.7). On exposed and sheltered shores, the percentage cover differed among the various trophic groups (bare rock/ sanded, algae, filter feeders and grazers) at the different shore heights. On the semi-exposed shores, a significant difference resulted among trophic groups however not for shore-zones.

Table 2.5: Two-way ANOVA results considering the effect of exposure level and shore zone on function groups on exposed, semi-exposed and sheltered, and Madagascan shores.

Effect	SS	df	MS	Pseudo-F	p
a) Exposed					
Intercept	335923.20	1	335923.20	754.13	$p < 0.0001$
Trophic Level	64482.20	3	21494.10	48.25	$p < 0.0001$
Shore zone	6462.0	1	6462.00	14.51	$p < 0.001$
Trophic Level x Shore zone	313582.60	3	104527.50	234.66	$p < 0.0001$
Error	138978.00	312	445.40		
b) semi-exposed					
Intercept	172488.40	1	172488.40	2088.21	$p < 0.0001$
Trophic Level	380542.70	3	126847.60	1535.67	$p < 0.0001$
Shore zone	0.70	1	0.70	0.10	$p > 0.05$
Trophic Level*Shore zone	13829.50	3	4609.80	55.81	$p < 0.0001$
Error	45926.10	556	82.60		
c) Sheltered					
Intercept	394983.20	1	394983.20	2022.38	$p < 0.001$
Trophic Level	94965.00	3	31655.00	162.10	$p < 0.001$
Shore zone	17829.30	1	17.829.30	91.29	$p < 0.001$
Trophic Level*Shore zone	389326.60	3	129775.50	664.47	$p < 0.001$
Error	76364.80	391	195.30		



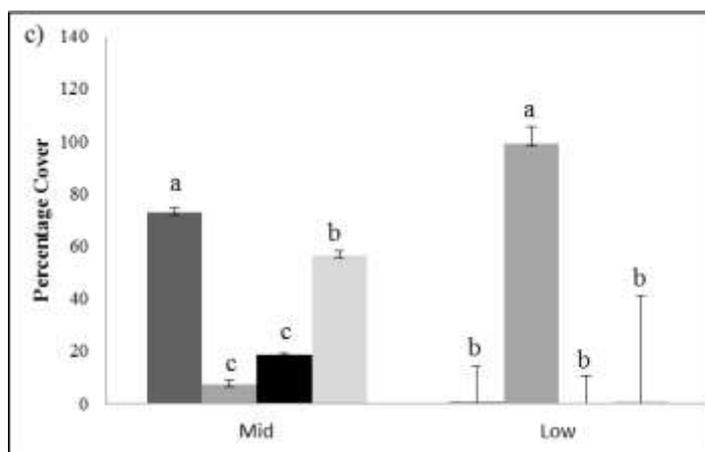


Figure.2.7: Mean (\pm SE) percentage cover of the functional groups responsible for the most community changes in the mid- and low-shore of Madagascar across three wave exposures (a) exposed, (b) semi-exposed, (c) sheltered. Shared letters indicate no statistical difference within a shore zone.

Discussion

Rocky shores are diverse and productive environments which support variable assemblages of sessile and mobile organisms and provide food for higher trophic group species (Hooper et al., 2005; Scrosati et al., 2011). These ecosystems are impacted by many different abiotic (e.g. temperature, wind, tides) and biotic factors (e.g. competition, predation, grazing) and the first step to understanding these systems are primary descriptions (Smith and Murray, 2005). This study offered a unique opportunity to provide a first description of rocky shore communities of Madagascar. Quantitative analyses revealed that communities differed among wave exposure levels and between the mid- and low-shore zones.

The distribution patterns recorded on Madagascan shores were similar to that reported in the literature (Field et al., 1982; Chappuis et al., 2014), in that the shores were divided into three main zones with the high-shore having *Littorina* spp, the mid-shore having fauna (barnacles, gastropods, mussels and limpets) and flora (encrusting algae species, macro and micro algae) present and the low-shore being more algal dominated. This dominance of algae on rocky shores has been recorded by others across the world (Dayton, 1975; Kaehler and Williams, 1996; Underwood and Chapman, 1998) and previous studies suggest that an increase in algae is associated either with sheltered conditions (i.e. low wave exposure) (Blamey and Branch, 2009) or the absence of grazers (Bertness et al., 1983). Two-way ANOVA analysis (a) verified that in sheltered conditions, fewer grazers were recorded and the combination of the above two factors contributed to the differences between the shore

levels (mid and low-shore) and (b) identified differences in algal cover as contributing most to the dissimilarity.

Wave exposure was identified as an important structuring force on its own and interacted with the shore levels to affect communities on Madagascan shores. Wave exposure has been recognised as an important factor in determining the structure of rocky shore communities by directly influencing macrobiota, causing physical damage (Dayton, 1971) and dislodgement (Trussell et al., 1993; Underwood, 1991) of biota. This may be a contributing factor to the high mean percentage cover of bare rock at both regions. In numerous studies, wave exposure has also been demonstrated to have indirect effects on changes in competitive ability (Steffani and Branch 2003a), grazing activity (Duggins et al., 2001) and predation (Menge et al., 1978; Robles and Desharnais, 2002; Lopez et al., 2010). For example on the low shore, the exposed zones had higher percentage of grazers and filter feeders present and lower percentages of algae compared to the sheltered zones. This can be due to algae species being able to occupy the space on sheltered areas which would have been taken up by its competitors like limpets and mussels at higher wave exposure conditions (Branch et al., 2010; Aguilera and Navarrete, 2012; Garner and Litvaitis, 2013).

Unlike natural predation, human exploitation of resources is more efficient and can therefore have a greater impact on intertidal resources (Colonese et al., 2014). Intertidal rocky shore resources are inherently open access and due to the accessibility of rocky shores, the exploitation of intertidal and shallow sub-tidal biotic resources are on the increase (Siegfried et al., 1994; Coddling et al., 2014; Oróstica et al., 2014) and this is no different for Madagascar. Human activity has been documented as a major disturbance on rocky shore assemblages often leading to drastic changes in community structure (Lasiak and Field, 2005). The increasing population densities of coastal regions places more pressure on marine living resources (Hockey et al., 1988; Griffiths and Branch, 1997). Even though harvesting was not assessed as part of this study, it is most likely that harvesting has substantial impacts on the Madagascan shores due to the close proximity to human settlements and the extreme levels of poverty experienced in this region. Higher harvesting intensity was noticed at Fort Dauphin in comparison to Locara (Sink pers comm), and is likely due to higher human populations in and around Fort Dauphin, resulting in elevated levels of subsistence activities like collecting of shells for selling and harvesting food species for survival.

Harvesting of rocky-intertidal resources may be an important structuring force on the Madagascan shores by (a) impacting directly on the population of target species (b) having consequences for intertidal biodiversity through habitat destruction due to trampling and (c) resulting in cascading ecosystem impacts (De Boer et al., 2002; Milazzo et al., 2004; Airoidi et al., 2005; Robinson et al., 2008). Harvesting of grazers has also been shown to be disruptive to biotic assemblages, leading to opening of unoccupied spaces, patchiness in the assemblages, and the development of microalgae (Airoidi et al., 2005). Harvesting could therefore be a contributing factor as to why higher percentage of open spaces (bare rock) was recorded in the exposed and sheltered mid-shores (Figure 2.7). Removal of grazing molluscs cause decrease abundance of macro-algae which they feed on (Lasiuk and Field, 1995) for example on the exposed shores *C. capensis* removed most of the encrusted pre-existing coralline and created open spaces therefore allowing for increase abundance of prey like mussels and barnacles (i.e. *P. perna*). However, when subsistence harvesting takes place and mussels and barnacles are removed, these open spaces are occupied by other functional groups like algae (Fenberg and Roy, 2008). The current study could not be used to assess the effects of harvesting on the Madagascan shore as all shores in the region were being harvested with no control areas (e.g. no-take marine protected areas).

Coastal development and the related human activities can lead to increased nutrient loading of coastal waters (Nixon, 1995). Fort Dauphin has undergone coastal development with the new port at Ehoala, as well as new ilmenite mining projects “Port d’Ehoala Madagascar” (Campbell, 2005; 2009). This increase in human population can effect eutrophication along the coastal areas (de Jonge and Elliot, 2002). It has been shown that eutrophication results in fast-growing marine seaweeds causing algal blooms by a variety of microalga e.g. *Ulva* spp., (Teichberg et al., 2009). The fact that the semi-exposed site at Fort Dauphin had more algae than the sheltered sites at Locara suggests that this could be a contributing factor to the higher abundance of algae at Fort Dauphin. With the wave exposure differences among the regions it is difficult to separate out an effect of wave exposure from an effect of regions however, some of the differences observed may be driven by regions and the varying levels of anthropogenic impacts experienced in each. Unfortunately, it is beyond this study to differentiate between these effects but this should be considered by future studies.

Substratum type can play a role in determining the distribution of rocky shore species (McQuaid and Branch, 1985). The presence of erodible sandstone substrate at Fort Dauphin could be a contributing factor to the higher algal abundances due to the unstable environment combined with harvesting efforts. The Locara region with steep granite slopes and large boulders provide a more stable and sheltered environment (McQuaid and Branch, 1984; 1985). Harvesting as well as the above factors can have effects on the rocky shore communities and these topics should be considered for future studies.

As rocky intertidal communities are faced with increasing challenges, from pollution to climate change and rising sea levels (Higgins, 2013), it is essential that we understand what communities are present and how these may be affected by global change. As such, the description of previously undocumented shores like those in southern Madagascar is an important contribution to baseline studies in a developing country. This chapter aimed to address this need and has provided an important first description for the region, one which can form the foundation for future studies.

CHAPTER 3

A comparative study between rocky shore communities of Southern Madagascar and Northern KwaZulu-Natal

Introduction

There is evidence to suggest that southern Madagascar and northern KwaZulu-Natal could still be connected via oceanographic systems and as such may share biological similarities (see Chapter 1 for details). This chapter aims to investigate potential similarities between rocky shores in Madagascar and South Africa. The Suitcase Project was developed to test the hypothesis that westward moving eddies may connect southern Madagascar and northern KwaZulu-Natal systems through the transport of larvae and other propagules (Quartly and Srokosz, 2004; Tew-Kai and Marsac, 2009; Marsac et al., 2014). One way of interrogating this hypothesis is by considering similarities and differences in rocky shore communities between the two countries. During a short initial field visit, casual observation of the rocky shores in southern Madagascar suggested high similarity in terms of physical environment and species composition to shores in northern KwaZulu-Natal. This led to the inclusion of a rocky shore component in the broader Suitcase project (see Chapter 1).

South African intertidal ecological research has focused extensively on rocky shores with a large portion of this work, dedicated to the identification of forces structuring community interactions (Branch, 1985, 1986; Branch, et al., 1987; Van Zyl and Robertson, 1991; Sink et al., 2001, 2005; McQuaid and Lindsay, 2007, Nakin and McQuaid, 2014). Research pertaining to this include, consideration of key factors that affect community structure such as nutrient supply (Bosman and Hockey, 1986; McQuaid and Lindsay, 2000), primary production (McQuaid and Branch, 1985; Branch et al., 1987), food subsidies (Bustamante et al., 1995a; Lasiak and Dye, 1989; Lastra et al., 2008), wave exposure (Hammond and Griffiths 2004; Robinson et al., 2005; Denny 2014), sand inundation (Switzer and Jones, 2008; Zardi et al., 2009) and the arrival of alien species (Robinson et al., 2007; Sadchatheeswaran et al., 2015). There is also a large body of work that has considered the implications of harvesting of intertidal resources such as mussels and other benthic invertebrates (Crowe et al., 2000; Cockcroft et al., 2002; Branch and Odendaal, 2003; Robinson et al., 2008; Griffiths et al., 2010; Mead et al 2013; Sowman et al., 2013).

South Africa has built a solid research foundation and the intertidal fauna and flora are reasonably well known, including in the province of KwaZulu-Natal (Sink et al., 2005; Griffiths et al., 2010). Preliminary work along the KwaZulu-Natal coast was compiled by Jackson (1976) and Stephenson (1939, 1944). Thereafter a few studies concentrated on describing single sites (Lambert and Steinke, 1986a.b; Crowe et al., 2000). The vast majority of studies on the rocky shores of this region have focused on subsistence and recreational harvesting of intertidal species (Kyle et al., 1997a-b; Tomalin et al., 1998; Roy et al., 2003; Sowman, 2006), biodiversity of marine resources (Lawrence, 2005; Brown et al., 2007) and large scale coastal processes (Harris et al., 2002; Reaugh-Flower et al., 2011).

One of the most comprehensive recent works on intertidal rocky shores in KwaZulu-Natal was done by Sink (2001, Sink et al. (2005)). This work identified a clear biogeographic break in rocky shore community structure at Cape Vidal with differences in intertidal assemblages between the Maputaland and Natal bioregions. The division was mainly attributed to (1) The environmental conditions of the Natal Province's being more subtropical in comparison to Maputaland, (2) Higher subsistence harvesting pressures observed in Maputaland compared to Natal and, (3) fluvial (riverine) input and the effect thereof in terms of turbidity and nutrients (also examined and established by Porter et al, 2014). Even so there is opportunity to expand on current knowledge of biological structure configuration and how abiotic factors are relevant to the structuring of rocky intertidal communities in KwaZulu-Natal. In contrast to KwaZulu-Natal, marine systems in southern Madagascar have limited published information describing communities or species composition and ecology (Lewis, 1963, Pielo, 2013) with few site specific published studies explicitly considering rocky shores. Additionally, I found no published information on the potential drivers of biodiversity pattern within Madagascan shores. Recent published information covers physical oceanography, subtidal coral communities and marine fisheries (Maina and Obura et al., 2008; Backeberg and Reason, 2010; Manach et al., 2012 add Obura, 2012).

Using the first quantitative descriptions of rocky shores from South Madagascar that was produced in Chapter 2 and data collected during an equivalent time from northern KwaZulu-Natal, this chapter aimed to compare the structure and diversity of rocky shore communities in the low shore between these two countries. If the rocky shore assemblages support the Suitcase Hypothesis, similarities between countries may reflect that propagules and larvae of intertidal taxa could be transported from Madagascar to the shores of KwaZulu-

Natal, and if this is a frequent occurrence, it is anticipated that rocky shore communities could show high similarities between the two countries.

Materials and methods

Study sites

Sampling in northern KwaZulu-Natal was conducted within the iSimangaliso Wetland park in Maputaland in spring 2013 (Figure 3.1). This coastline is dominated by wide, sandy beaches, interspersed with rocky outcrops and rock-pools created within the sandstone platforms that are sandwiched between almost continuous barriers of forested dunes (McCarthy, 1967). The initial plan for chapter 3 was to compare the data collected in northern KwaZulu-Natal with the full KwaZulu-Natal data set from Sink 2001. Unfortunately, this could not be achieved because initial analysis of sites sampled in both periods revealed a significant temporal difference (Figure 3.1). For this reason, only the 2013 data was used in this study.

The four northern KwaZulu-Natal sites were separated by a minimum of 3 km and spanned 14 km of coastline. Sampling in southern Madagascar spanned roughly 20 km of coastline and included eight sampling sites (See Chapter 2 for detailed site descriptions). In both KwaZulu-Natal and Madagascar, it was attempted, as far as possible, to select sites that represented contrasting grades of wave action i.e. sheltered bays, semi-exposed shores and exposed platforms (Table 3.1). Despite this, as explained in Chapter 2, the choice of sites in Madagascar was limited by logistical constraints and access to the shore. Sites were chosen based primarily on accessibility, and to account for the effect of wave exposure, wave action was graded at each site according to Sink (2001), who measured maximum wave force across the KwaZulu-Natal and Maputaland region.

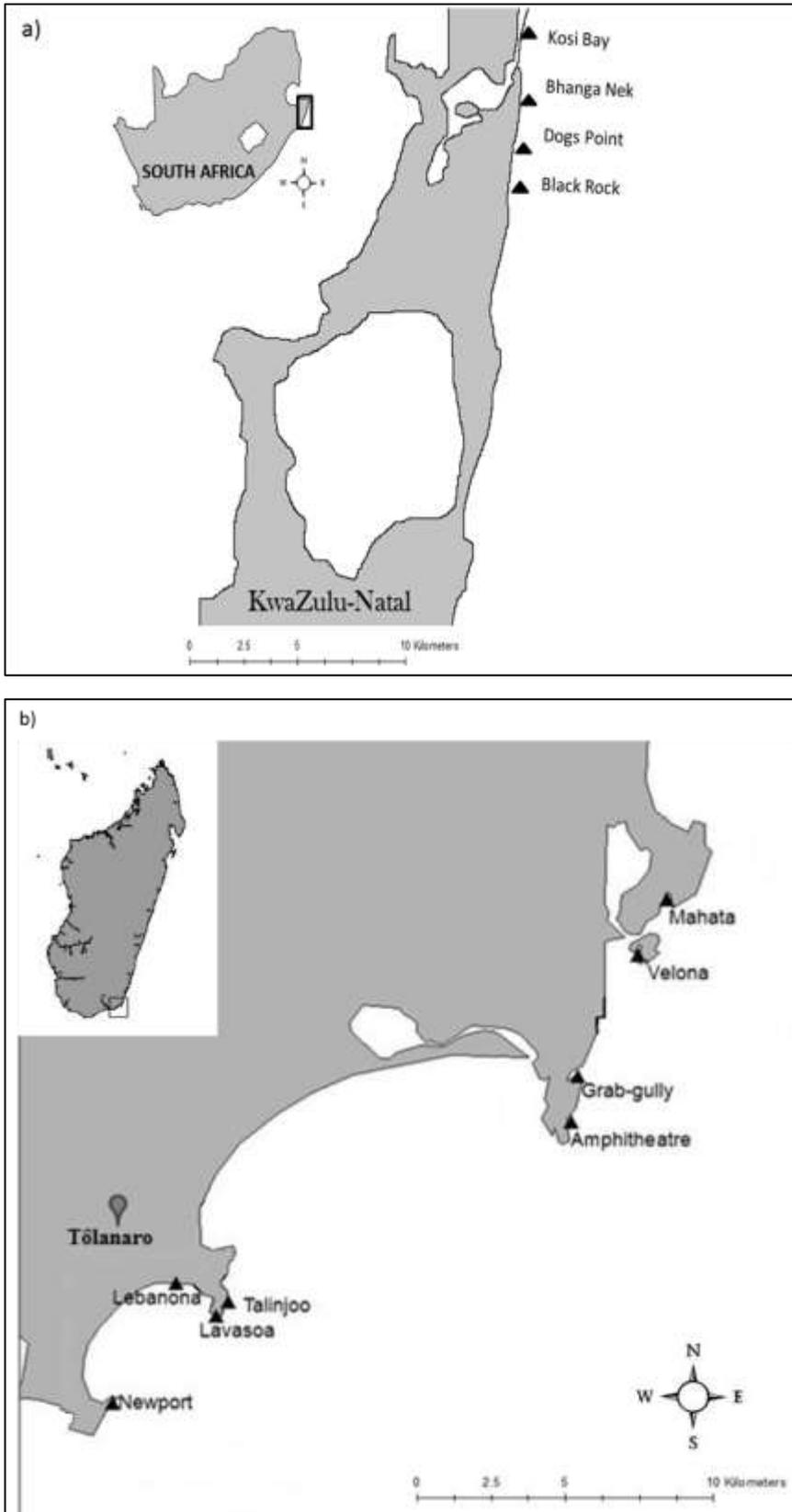


Figure 3.1: Maps illustrating the two countries sampled (a) Northern KwaZulu-Natal showing the four study sites and (b) Southern Madagascar showing the eight study sites.

Table 3.1: Geographic co-ordinates of the sites sampled within the two countries.

Southern Madagascar			Northern KwaZulu-Natal		
Site	Coordinates (ddm)	Exposure	Site	Coordinates (ddm)	Exposure
Amphitheatre	24°57.086'S 47°06.437'E	Sheltered	Bhanga Neck	27°02.624'S 32°51.424'E	Semi-exposed
Grab gully	24°56.518'S 47°07.084'E	Sheltered	Black Rock	27°04.577'S 32°50.660'E	Exposed
Lavasoa	25°02.494'S 46°59.703'E	Semi-exposed	Dogs Point	27°02.624'S 32°51.424'E	Exposed
Lebanona	25°02.255'S 46°59.640'E	Semi-exposed	Kosi Bay	27°00.905'S 32°51.956'E	Semi-exposed
Mahata	24°56.442'S 47°07.433'E	Exposed			
Newport	25°04.213'S 46°57.860'E	Semi-exposed			
Talinjoo	25°02.552'S 46°59.851'E	Semi-exposed			
Velona	24°56.343'S 47°07.463'E	Exposed			

Experimental design

The above mentioned KwaZulu-Natal region was quantitatively sampled in spring of 2013, a month after the Madagascan shore were sampled. Only four rocky shore sites were sampled due to project constraints (Table 3.1). Typical sheltered shore was absent in northern KwaZulu-Natal (Branch et al., 2010) and sampling was opportunistic and constrained by limitations of the study (e.g. time and funds). Twenty randomly placed 1m x 0.5m replicate quadrats were scored in the low-shore at each site. The average tidal height in northern KwaZulu-Natal averaged between 1.0-2.4m whereas the maximum tidal height of south-eastern Madagascar was only 0.5m (Sink, 2001; McClanahan et al., 2009) The unanticipated discrepancy in tidal amplitude between the two countries precluded the inclusion of high and mid-shore zones in this chapter as these differences (amplified by shore topography as explained in Chapter 2) result in incomparable widths of zones among the countries with much narrower high- and mid-shores in Madagascar. Pools and gullies were excluded following Sink et al., (2001).

Identification of intertidal biota was done *in situ* whenever possible using recognised identification guides (Branch and Branch, 1995; Branch et al., 2010). In addition,

photographs and samples were collected to enable consultation with relevant taxonomic experts. In each quadrat, percentage cover of all sessile species and counts of visible mobile species were recorded. Back in the laboratory, species counts were converted to percentage cover using the mean sizes of mobile species that were recorded in the field (Sink et al., 2001).

Statistical analyses

Community composition (based on percentage cover) was compared between areas using PRIMER v6 (Clarke, 1993; Clarke and Warwick, 2001) and PERMANOVA (Anderson et al., 2008) software. Analyses were conducted on non-standardized fourth-root transformed abundance values (Field et al., 1982). The transformed data were converted into a similarity matrix using the Bray-Curtis similarity measure. A PERMANOVA was used to test for significant differences between communities (Anderson et al., 2008) in an unbalanced two factor analysis: (i) Country (fixed effect with two levels: northern KwaZulu-Natal and southern Madagascar), (ii) Wave exposure (fixed effect nested within country with three levels: sheltered; semi-exposed and exposed).

The PERMANOVA analysis made use of the Type III (partial) sums of squares which determines the minimum number of sums of squares (SS) attributable to a given term. Type III fits all the other terms except the one that is being tested, then finally fits the term being tested and determines the SS attributed to that term. The residuals were permuted under the reduced model 9999 times. Multi-Dimensional Scaling (MDS) ordination was used to explore patterns in community structure by graphically representing the similarities among samples. The species diversity supported in each area was assessed by three diversity indices calculated using the following equations (Clarke and Warwick, 1994):

Shannon–Wiener diversity index (H') (a measure of diversity which incorporates components of both species richness and equitability), where p_i is the proportion of the total number of individuals arising from the i th species.

$$H' = -\sum_i p_i (\log p_i),$$

Margalef's index (d) (a measure of species richness) where S is the total number of species and N is the total number of individuals.

$$d = \frac{s - 1}{\log N},$$

Pielou's evenness index (J') (a measure of equitability) max is the maximum possible diversity, which would be achieved if all species were equally abundant.

$$J' = \frac{H'(\text{observed})}{H'_{\text{max}}}$$

These indices were calculated for each sample, thus allowing the comparison of diversity between the Madagascar and KwaZulu-Natal coasts using a Mann-Whitney test for each index. This test was chosen do to the nonparametric nature of the data. All univariate analyses were conducted using STATISTICA for Windows (Version 6).

Results

Comparative analysis

Multivariate comparisons using PERMANOVA demonstrated significant differences of the low-shore communities between Madagascar and KwaZulu-Natal; differences among communities were detected at different wave exposures within each country (Table 3.2 and Table 3.3). Despite these significant differences, there were also some similarities. The MDS configuration that resulted from ordination of the abundance matrix, shows some overlap (Figure 3.2), where a subset of KwaZulu-Natal sites separated from the large cluster and the other half of the sites align with exposed and semi-exposed shores of Madagascar (Figure 3.2).

The sites contributing to the overlapping cluster were samples from Black rock (exposed), Newport (semi-exposed), Dog Point (exposed) and Kosi Bay (semi-exposed). *S.elegans* was identified as the species that all four of these sites shared and in high abundance, therefore, causing the closer grouping between the three Kwazulu-Natal sites and the one Madagascan site. The three KwaZulu-Natal sites were grouped together closely due to the samples having a combination of algae species, *J.sagittata*, *Sargassum aquifolium* and *S.elegans* present in all three these sites. The pairwise analysis confirmed the differences in community structure between exposure levels on the low shores of Madagascar and KwaZulu-Natal to be significantly different (Table 3.3).

Table 3.2: Results of a two-way PERMANOVA on the effects of country and exposure levels on the low shore zones.

Source	df	MS	Pseudo-F	P (perm)
Country	1	1.0965E5	54.983	$p < 0.001$
Exposure (Country)	3	50156	25.150	$p < 0.001$

Table 3.3: Results of a pairwise PERMANOVA on the effects of exposure levels on the low shore

Country	Exposure	t-test	P (perm)
Madagascar	Sheltered, Semi-exposed	5.78	$p < 0.001$
Madagascar	Sheltered, Exposed	6,95	$p < 0.001$
Madagascar	Exposed, Semi-exposed	6.00	$p < 0.001$
KwaZulu-Natal	Semi-exposed, Exposed	2.50	$p < 0.002$

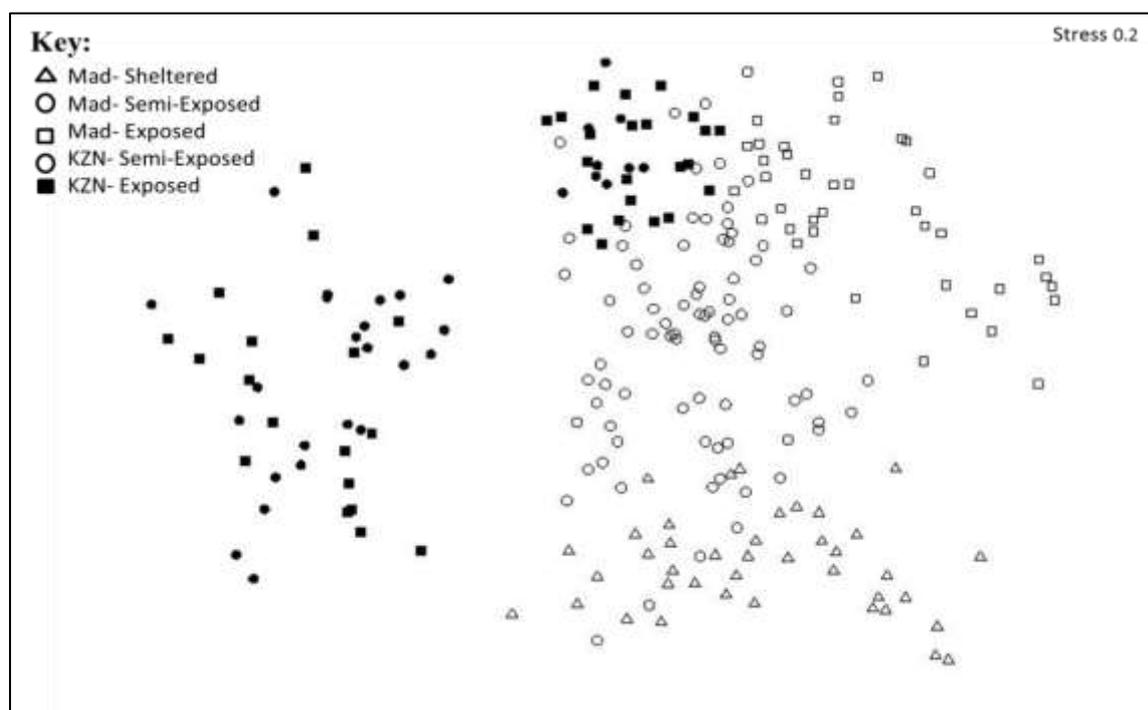


Figure 3.2: Multi-Dimensional Scaling ordination of Bray-Curtis similarity matrix comparing species abundance based on each country across the different exposure levels i.e. Exposed, Semi-exposed and Sheltered.

The SIMPER analysis identified the species contributing to the differences between countries (Figure 3.3). The Madagascan communities were on average 81.48% dissimilar to the sites sampled in KwaZulu-Natal, with 13 taxa accounting for 90% of this dissimilarity. These differences were driven primarily by the presence of the algae *P.corallorhiza* and *S.hypnoides* in southern Madagascar and their absence from the northern Kwazulu-Natal shores. On the KwaZulu-Natal shores, the polychaete *I pennatus*, an unidentified black encrusting ascidian species and two other unidentified tunicate species were present but absent on the Madagascar Shores. The other four species were present in both countries but differed in abundance.

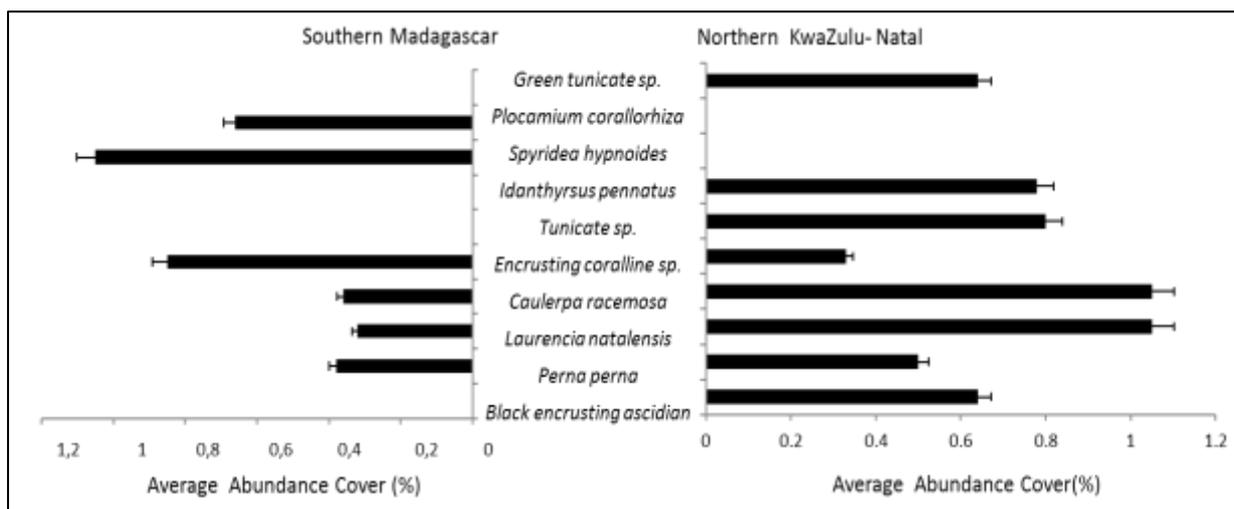


Figure 3.3: Forth-root transformed average (\pm SE) abundance cover of the top ten ranked species distinguishing Madagascar and KwaZulu-Natal low-shore communities.

On the Madagascan shores, 89% of the similarity among sites was accounted for by 11 taxa that can be considered characteristic of these shores (Table 3.4). The algal species, *S.elegans*, was the top-ranked characteristic species for both countries in which the Madagascan communities accounted for 14.69% of the average percentage cover and only 12.50% within KwaZulu-Natal. On the KwaZulu-Natal shore the most important species which characterised these shores were brown, red and green algae (Table 3.5) of which species like *Jania sagittata* contributed to an average abundance of 17.95%, *L.natalensis* 12.04% and *C.racemosa* 13.20% within the South African intertidal communities. The mussel (*P.perna*) was the only filter feeder species, which occurred on both the countries shores. Overall 48% of the total species recorded on the low-shore occurred on both countries shores. Within the KwaZulu-Natal shores the average abundance contributed to 1.69%. and in Madagascar 1.35% (Appendix 3.1). Within Madagascar, 36% of the total species observed were unique to these shores and 16% of the total species present were unique to KwaZulu-Natal shores (Appendix 3.2). Although there is a statistically significant difference in assemblages, it's very notable that almost half the species are shared.

Table 3.4: Characteristic species on the low-shore zones of Madagascar and KwaZulu-Natal, as determined by the SIMPER analyses. The ranking is determined by the average contribution of each species to the overall similarity of the level in each region (i.e. S_i). %Av indicates the average percentage cover (fourth root transformed data) of each species from all sites. $S_i/SD(S_i)$ is the ratio between S_i and $SD(S_i)$, the standard deviation of S_i . This ratio reflects how consistently the species abundance varied within each region. $\Sigma SI\%$ is the cumulative percentage contribution of each species to the overall similarity (S).

Southern Madagascar					Northern KwaZulu-Natal				
Characteristic species	%Av	S_i	$S_i/SD(S_i)$	$\Sigma SI\%$	Characteristic species	%Av	S_i	$S_i/SD(S_i)$	$\Sigma SI\%$
($n = 8$ sites; $S = 81.48\%$)					($n = 4$ sites; $S = 34.35\%$)				
<i>Sargassum elegans</i>	1.24	8.38	0.94	19.25	<i>Sargassum elegans</i>	1.09	4.07	0.62	11.85
<i>Jania sagittata</i>	1.16	7.83	0.70	17.98	<i>Laurencia natalensis</i>	1.05	4.02	0.64	11.71
<i>Spyridia hypnoides</i>	1.05	5.85	0.81	13.44	<i>Caulerpa racemosa</i>	1.05	4.02	0.63	11.71
<i>Encrusting coralline</i> spp.	0.85	4.50	0.8	10.35	<i>Jania sagittata</i>	1.00	3.62	0.46	10.53
<i>Laurencia</i> spp.	0.68	3.47	0.63	7.97	<i>Tunicate</i> spp.	0.80	3.24	0.70	9.43
<i>Arthrocardia</i> spp.	0.57	1.86	0.27	4.27	<i>Idanthyrus pennatus</i>	0.78	2.06	0.41	5.98
<i>Plocamium corallorhiza</i>	0.66	1.82	0.37	4.19	<i>Green tunicate</i> spp.	0.64	2.01	0.49	5.85
<i>Rhodymenia natalensis</i>	0.39	1.58	0.36	3.64	<i>Black encrusting ascidian</i> spp.	0.64	1.96	0.46	5.69
<i>Ralfsia</i> spp.	0.50	1.26	0.30	2.91	<i>Sargassum aquifolium</i>	0.55	1.53	0.33	4.45
<i>Perna perna</i>	0.38	1.16	0.31	2.67	<i>Perna perna</i>	0.50	1.48	0.40	4.30
<i>Jania</i> spp.	0.41	1.02	0.22	2.35	<i>Chamaedoris delphini</i>	0.52	1.34	0.39	3.90

Within the two countries, a total of 56 species were observed, 21 species were unique to Madagascar and nine species were confined to the northern KwaZulu-Natal shores. A total of 26 species were present in both countries. (Table 3.5). Articulate coralline *J.sagittata* and brown algae *S.elegans* were the dominant species present in both countries with both taxa more abundant in Madagascar. The increased of *S.elegans* can be an indirect response to high human harvesting pressures on both countries shores (Sink, 2001; De Boer et al., 2002). The remaining 26 species occurred in each country; 21 species were unique to the Madagascan shores and KwaZulu-Natal had 9 unique species. The key species defining the assemblages present on Madagascan shores were algae (*Arthrocardia* spp., *Spyridia hypnoides*), whereas the KwaZulu-Natal distinguishing species were *I.pennatus* and the zoanthid (*P.nelliae*) (Table 3.6). Table 3.6 illustrates the indicative species which occurred on both shores. The limpet *S.aphanes* and barnacle *T.rufotincta* occurred in both Madagascar and KwaZulu-Natal but did not emerge as key distinguishing species in the SIMPER analysis. These two species

however have the longest larval span compared to the other species occurring in both countries (Halo et al., 2013).

Table 3.5: Mean (\pm SE) untransformed abundance of shared species that occurred on the low-shore of both Madagascar (MAD) and KwaZulu-Natal (KZN). Species listed in descending order of abundance.

Species	MAD (\bar{Y})	\pm SE	KZN (\bar{Y})	\pm SE
<i>Jania sagittata</i>	(22.38)	31.71	(17.59)	25.56
<i>Sargassum elegans</i>	(14.69)	24.60	(12.50)	19.16
<i>Jania</i> spp.	(5.77)	19.03	(0.58)	2.07
<i>Encrusting coralline</i> spp.	(4.32)	10.39	(0.76)	1.57
<i>Ralfsia</i> spp.	(3.54)	10.39	(0.20)	0.70
<i>Laurencia</i> spp.	(2.45)	3.83	(0.36)	1.00
<i>Caulerpa racemosa</i>	(1.97)	6.74	(12.04)	19.48
<i>Laurencia natalensis</i>	(1.63)	4.21	(13.20)	23.09
<i>Perna perna</i>	(1.35)	3.65	(1.69)	3.03
<i>Ulva</i> spp.	(0.51)	1.63	(1.23)	3.31
<i>Sargassum crassifolium</i>	(0.19)	0.92	(5.81)	14.61
<i>Chamaedoris delphinii</i>	(0.10)	0.48	(1.60)	2.73
<i>Dictyota</i> spp.	(0.09)	0.47	(0.00)	0.00
<i>Dictyosphaeria versluisii</i>	(0.05)	0.29	(0.29)	0.83
<i>Tetraclita rufotincta</i>	(0.05)	0.27	(0.33)	0.27
<i>Scutellastra aphanes</i>	(0.05)	0.16	(0.43)	1.54
<i>Codium capitatum</i>	(0.04)	0.27	(0.05)	0.31
<i>Zoanthus durbanensis</i>	(0.04)	0.32	(0.08)	2.62
<i>Scutellastra exusta</i>	(0.04)	0.10	(0.03)	0.13
<i>Laurencia pumila</i>	(0.03)	0.33	(0.08)	0.67
<i>Fissurella natalensis</i>	(0.02)	0.09	(0.01)	0.01
<i>Codium prostratum</i>	(0.01)	0.16	(0.60)	1.01
<i>Dictyopteris delicatula</i>	(0.01)	0.16	(0.15)	0.53
<i>Pyura stolonifera</i>	(0.01)	0.16	(0.41)	1.38
<i>Tunicate</i> spp.	(0.01)	0.16	(2.41)	3.81
<i>Scutellastra granularis</i>	(0.01)	0.02	(0.00)	0.00

Table 3.6: Mean (\pm SE) untransformed percentage cover of low –shore species unique to sites surveyed in this study in southern MAD and northern KZN respectively. Species listed in descending order of abundance. These species were absent from sites surveyed during this study in southern MAD and northern KZN respectively.

Madagascar			KwaZulu-Natal		
Species	(\bar{Y})	\pm SE	Species	(\bar{Y})	\pm SE
<i>Arthrocardia</i> spp.	(11.02)	26.41	<i>Idanthysrus pennatus</i>	(10.44)	20.51
<i>Spyridia hypnoides</i>	(10.98)	20.23	<i>Palythoa nelliae</i>	(4.74)	16.08
<i>Plocamium corallorhiza</i>	(6.88)	17.15	<i>Tunicate</i> spp.	(3.15)	6.58
<i>Hypnea musciformis</i>	(6.16)	18.24	<i>Black encrusting ascidian</i> spp.	(2.55)	3.99
<i>Rhodomenia natalensis</i>	(2.61)	9.41	<i>Callithamnion stuposum</i>	(0.16)	0.63
<i>Caulerpa racemosa</i>	(0.45)	1.04	<i>Zoanthus natalensis</i>	(0.13)	0.72
<i>Turbinaria serrata</i>	(0.36)	1.74	<i>Codium pelliculare</i>	(0.06)	0.33
<i>Chaetomorpha linum</i>	(0.21)	0.96	<i>Halimeda cuneata</i>	(0.06)	0.33
<i>Lithothamnion</i> spp.	(0.15)	0.66	<i>Pseudocodium devriesii</i>	(0.01)	0.11
<i>Eucheuma denticulatum</i>	(0.10)	0.63			
<i>Zoanthus durbanensis</i>	(0.09)	1.11			
<i>Gelidium</i> spp.	(0.06)	0.47			
<i>Jania cultrata</i>	(0.05)	0.47			
<i>Amphiroa ephedraea</i>	(0.04)	0.35			
<i>Cellana radiata capensis</i>	(0.04)	0.14			
<i>Plocamium beckeri</i>	(0.03)	0.32			
<i>Zoanthus sansibaricus</i>	(0.03)	0.32			
<i>Neurymenia fraxinifolia</i>	(0.03)	0.22			
<i>Amphibalanus amphitrite</i>	(0.01)	0.16			
<i>Oxystele tabularis</i>	(0.01)	0.16			
<i>Ischnochiton bergoti</i>	(0.00)	0.01			

Overall little difference in diversity indices were observed in rocky shore communities from the two countries (Figure 3.4). For the sheltered shores, no analysis could be compared between the two countries as KwaZulu-Natal lacks truly sheltered shores, however, the evenness index was higher in KwaZulu-Natal compared to Madagascar (Table 3.7). The exposed sites in KwaZulu-Natal were significantly higher in species diversity and had higher values for the Pielou's evenness index than that of Madagascan sites (Figure 3.4).

Table 3.7: Statistical analysis summary performed using Margalef (d'), Shannon-Wiener diversity (H') and Pielou's evenness (J') indices, for diversity between sheltered and exposed shores of Madagascar and KwaZulu-Natal.

(a) Semi-exposed		
Diversity measure	U	p
d	835.0	$p= 0.0000$
J'	1236.5	$p< 0.0433$
H'	833.0	$p= 0.0000$
(b) Exposed		
Diversity measure	U	p
d	530.0	$p= 0.0095$
J'	198.5	$p< 0.0000$
H'	379.0	$p< 0.0001$

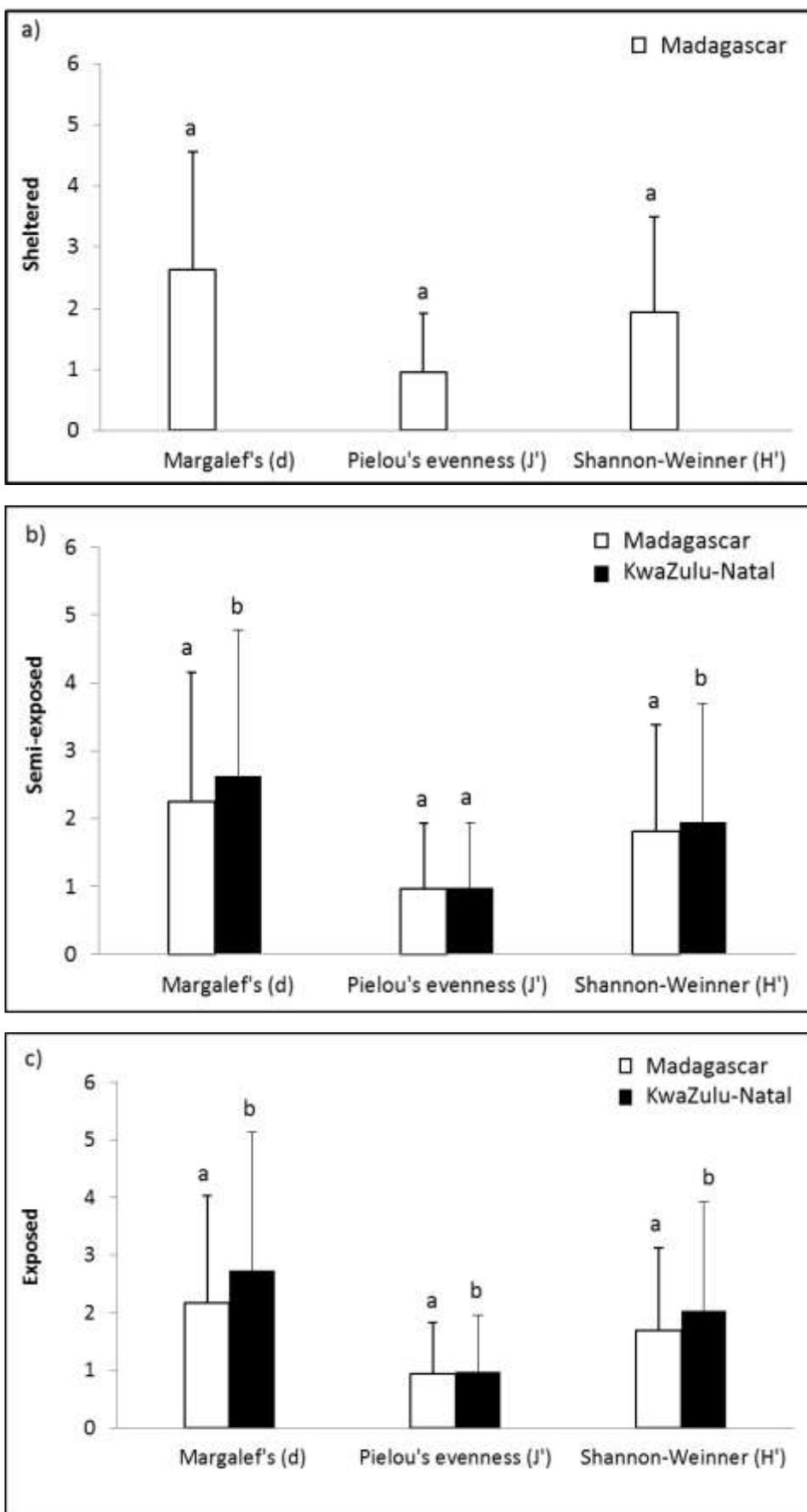


Figure 3.4: Median (25th and 27th percentiles) Margalef's, Pielou's and Shannon-Wieners, diversity indices for exposure levels for Madagascan and KwaZulu-Natal shores.

Discussion

This study was conducted as part of the Suitcase Project and aimed to explore whether rocky shore communities lend any support to the hypothesis that eddies may transport larvae and propagules from Madagascar to the shores of KwaZulu-Natal, thus maintaining a connection between these regions. This dissertation investigated whether quantitative analysis of rocky shore communities of Madagascar would lend support to the observation of potential similarity to shores in KwaZulu-Natal. To investigate similarity and differences between countries, the community structure and species diversity of rocky shore communities were compared between countries. PERMANOVA results revealed significant differences in rocky shore community structure between southern Madagascan and northern KwaZulu-Natal. Despite these differences, there was also an observed overlap in species composition.

Within the two countries, a total of 56 species were observed on the sampled shores, 21 species were unique to Madagascar and nine species were confined to the northern KwaZulu-Natal shores. A total of 26 species were present in both countries. Four of the species that occurred in Madagascar and not in northern KwaZulu-Natal namely *Arthrocardia* spp., *S.hypnoides*, *P.corallorhiza* and *H.musciformis* were however, recorded in southern and central KwaZulu-Natal in a previous study by Sink 2001. These species were recorded within the Natal bioregion but were absent from Maputaland. This suggests that the Madagascan shores may be more similar to the shores of the Natal bioregion than to Maputaland. Algae dominated the Madagascan shore with a diversity of species present. The northern KwaZulu-Natal shores had varied algae species but also a greater variety and abundance. The main factors contributing to the observed differences in rocky shore community structure include (1) the predominant algae in each country were different and (2) KwaZulu-Natal shores had higher species diversity and species were present in higher abundances compared to that of the Madagascan shores. Other differences could be driven by how those species assemble in communities (i.e. relative abundance) rather than their presence/absence within the counties (Mouritsen and Poulin, 2002; Lemieux and Cusson, 2014)

Tidal height plays an important role in structuring assemblages and abundance of species (Menge, 1976; Blamey and Branch, 2009; Cacabelos et al., 2010). It has been shown that tidal height has a significant effect on macro and microalgae assemblages, which in turn affects the distribution of grazers across the shore zones (McQuaid et al., 2000; Boaventura et al., 2002; Cacabelos et al., 2010). Unfortunately the effect of tidal height could not be assessed in this chapter for KwaZulu-Natal, we do however suspect the grazers and algae to be regulated by the tidal height as per previous studies in the area (Sink, 2001; Bolton et al., 2004). Madagascar only has a few published works describing marine environments and secondly discussing the environmental conditions of the intertidal zones.

Wave exposure is an established determinant of species in both diversity and composition within intertidal communities (Bustamante and Branch 2004; Harley, 2008; Blamley and Branch, 2009; Taylor and Schiel, 2010). Wave exposure also contributes greatly to the distribution of species across the shores, which was the case for Madagascar shown by the division between sheltered and exposed shores. Northern KwaZulu-Natal did not have any true sheltered shores (Sink, 2001) and the unexpected small tidal height in Madagascar could be a major contributing factor as to why the shores between the countries are significantly different.

Temporal variation affects communities by having an effect on population density, seasonal settlement and secondary effects on competition for space (Lively et al., 1993). Another intertidal study on distribution patterns and community structure of invertebrates in India, reported that temporal variations mostly affected phylum groups Porifera and Arthropoda with regards to species richness (Bhadja et al., 2014). The sampling for this dissertation took place in Madagascar in winter and a month later in early spring for KwaZulu-Natal. Seasonal variation cannot be ruled out as a potential contributing factor to the observed differences between the countries. However it is unlikely that the observed differences are solely attributable to only one factor, but combined with harvesting pressures, this could explain the increase in algae *S. elegans* (Bertocci et al., 2014; Stagnol et al., 2016).

In terms of similarities between countries, 21 species of the total 56 species recorded in this study were found in both countries. Of these 21 shared taxa, 19 were algal species. We found the community compositions to be similar and both countries are under the same environmental pressures, it is only the degree of pressure that differs. Environmental and

oceanographic variations, such as sea-surface temperature (SST), upwelling and wave exposure are the key variables that best explain and influence marine and coastal biogeographic structures, it has shown to contribute to the dynamics of rocky intertidal communities (Fenberg et al., 2015). In the current study, it is questionable whether SST could be responsible for the observed differences between the two countries as the temperatures were reasonably comparable. The oceanographic conditions north of KwaZulu-Natal vary between 24°C to 28°C (Griffiths et al., 2010; Smit et al., 2013; Cossa et al., 2016) and around southern Madagascar it ranges between 15°C to 22°C (Quartly and Srokosz 2001; Morris, 2009; Zinke et al., 2014; Steen et al., 2015) depending on the season. It has been suggested, that a combination of SST and upwelling are closely linked to nutrient concentrations within intertidal communities. For example in areas with cooler water temperatures (e.g. Madagascar) and more intense upwelling they have a higher nutrient concentration (Nielsen and Navarrete, 2004). The residual variability of SST is less than 2.0°C to 4.0°C and the similar temperatures could possibly account for the similar intertidal species composition, which are then modified by other abiotic, biotic variables and human impacts. The species found in Madagascar are more aligned with subtropical species whereas the species found in northern KwaZulu-Natal are not, therefore the biogeography with areas south of Maputaland, would possibly be more similar to southern Madagascar (Obura, 2012; Steen et al., 2015).

From a biogeographic perspective southern Madagascar falls within the Western Indo-Pacific and northern KwaZulu-Natal fall within the Indo-Pacific bioregion based on geographic proximity (Sink et al, 2005; Yoder and Nowak, 2006; Obura, 2012). These are close in proximity and therefore it was expected that South Africa and Madagascar share similarities in terms of species diversity and composition of marine and intertidal species. Instead, this dissertation only found 26 species which occurred in both countries, out of a collective 56 species that were present on the low-shore. When comparing the assemblage of algae species present in both countries, the species present on the KwaZulu-Natal's shores replicates sub-tropical similarities (Sink et al., 2005) whereas the species compositions in Madagascar are more tropical and therefore further studies should compare biogeography with areas south of Maputaland, where sea surface temperatures are more similar (Obura, 2012; Steen et al., 2015). On these grounds, the biogeographic province of southern Madagascar may not be part of the Western Indo-Pacific realm nor part of the tropical Western Indian Ocean Province (Steen et al., 2015) but rather a region of overlap, in which

both tropical and temperate species flourish. Other studies also found overlap of species from different biogeographically regions (Turpie et al., 2000; Spalding et al., 2007; Coll et al., 2012). This work has implications for the biographic affinities and classification of regions and the species associated within those regions. Further studies focused on bio-geographical studies are required to establish the definite realms.

The low similarity in intertidal community structure between assemblages could be due to a variety of contributing factors. Contributing factors are whether eddies are a feasible and frequent enough transport mechanism for biological material between the countries and whether the larvae and algal zygote lifespan of the shared species between the countries will survive the trip across. Other oceanographic and genetic connectivity studies between Madagascar and KwaZulu-Natal, have also found no definite linkages between the countries (Quartly and Srokosz, 2001; Backeberg and Reason, 2010). Braby et al., (2014) as part of a modelling study investigated whether eddies propagated south of Madagascar are able to cross the southern Mozambique Channel and interact with the African coast. The model suggests the eddie mechanism to likely reach the African east coast from Madagascar but not as frequently as initially anticipated (more than one per year) and that the transport mechanism is likely to be able to entrain nutrient rich waters. Eddies that originate from the South East Madagascar Current, propagate into the Agulhas retroflexion system and these eddies split off into separated independent eddies (Ridderinkhof et al., 2013). The eddies that split off and transport biological material along the Agulhas coast, could contribute to the explanation of why some southern Madagascan species are also found further south.

In support of research to understand potential biological connectivity between Madagascar and KwaZulu-Natal, a study conducted on gene flow of the spiny-lobster (*Panulirus homarus rubellus*) via mesoscale eddies between Madagascar and Africa was conducted by Reddy et al., (2014). These authors examined the DNA of 20 species and found that the lobster species *P. rubellus* to be ancestrally linked to Africa. These authors suspect the current species diversity in Madagascar to be due to genetic isolation during glacial periods, followed by successive range extensions and secondary contact. Their study recovered a total of 112 haplotypes (a set of genetic determinants located on a single chromosome), of which 78% were unique. Of the total samples collected, Africa and Madagascar did not share any haplotypes and differed by 78 mutations and 3% DNA divergence.

The results from my study are consistent with a low and infrequent oceanographic connection between the two countries. My results suggest, only species with long larval lifespans could survive the journey across the southern Mozambique Channel. Once the eddies have dissipated the biological material will need to have either, parthenogenesis, regenerative, vegetative reproductive abilities to be able to successfully survive. In accordance to the literature, most algal species are not able to successfully disperse and reproduce over long-distances, however a small group of species would be able to, by free-floating and release of spores once they have favorable conditions (Doust and Doust, 1988; Yatsuya, 2008; Mattio et al., 2013; Verbruggen en Costa, 2015; Steen et al., 2015). The key species included in this study (Table 3.8), that could possibly survive the eddie transport mechanism across the Mozambique Channel are shown in Table 3.8. These include algae that were characteristic of both countries shores, such as *C.racemosa*, *Sargassum* spp., barnacles (*T.rufotincta*) and limpet (*S. aphanes*). The larvae of species *P.perna* has the ability to survive the transport mechanism across from Madagascar to South Africa and successfully and reestablish itself on the other side. The difficulty in detecting this however is due to the high harvesting intensity in both countries this may influence the availability of larvae. Associated with the ACEP Project, an MSc student (van Rooyen) is currently investigating the feasibility of *P.perna* larvae between South Africa and Madagascar (results not yet available). Short larval lifespans species were not found/shared between the two countries for example unidentified ascidians species and *Z.sansibaricus* species, therefore only species with long larval lifespan should be considered for further studies. Species which could potentially be subjects for further connectivity are the two *Tetraclita* spp. and *S.aphanes*.

Table 3.8: The reproduction and larval lifespan of key species present on the low-shores of Madagascar and KwaZulu-Natal. References for information on reproduction were also used to provide information on estimated larval lifespan.

Taxon	Species	Reproduction	Larval lifespan
Arthropoda	<i>Tetraclita rufotincta</i>	Synchronized spawning in accordance to sea water temperature cues (Barnes and Achituv, 1981)	3 months
Ascidiacea	<i>Pyura stolonifera</i>	A-sexual and synchronized spawning by tidal cycles and when exposed to air (Griffiths, 1976; Marshall et al., 2000)	1 day
Bivalvia	<i>Perna perna</i>	During spawning- Two sexes release eggs and sperm to produce veliger larvae (Porri and McQuaid, 2006)	10-12 day
Chlorophyta	<i>Caulerpa racemosa</i>	Regenerate vegetatively-free floating species through sections of rhizome that break off the parent plant (Winston, 2012)	-
	<i>Codium prostratum</i>	Reproduction by gametophyte generation and most species are dioecious (Verbruggen and Costa, 2015)	-
Gastropoda	<i>Scutellastra aphanes</i>	During spawning- Two sexes release eggs, development leads to free-swimming, non-feeding veliger larva (Sebastian et al., 2002; Lindberg, 2007)	9-10 months
	<i>Fissurella natalensis</i>	Spawn twice a year, in accordance to sea water temperature cues (Bretos et al., 1983)	2-3 days
Phaeophyta	<i>Sargassum</i> spp.	Reproduction can be sexual -fusion of motile sperm or male gamete, and vegetative-free floating species which can release propagates (Yatsuya, 2008; Mattio et al., 2013; 2015)	14 days
Polychaeta	<i>Idanthyrsus pennatus</i>	Synchronized spawning of eggs and sperm fertilise externally (Bhaud and Fernandez-Alamo, 2001; Barrios et al., 2009)	2 months
Rhodophyta	<i>Laurencia</i> spp.	Reproduction can be sexual and vegetative (free-living (Hadfield and Paul, 2001; Bleckwenn et al., 2003)	-
	<i>Jania sagittata</i>	Three reproductive phases, two are free living and one is to attach to a female plant (Veld and Flora 1992)	-

Intertidal rocky shore community structure is regulated by a variety of factors including biotic interactions such as predation (Menge and Branch, 2001; O'Connor et al., 2013; Amundrud et al., 2015), and competition (Menge et al., 1999; Bruno et al., 2003; Aguilera, 2012; He and Bertness, 2014) and abiotic factors such as wave exposure (Menge and Branch, 2001; Denny, 2014; Tam and Scrosati, 2014), temperature (Pincebourde and Sanford, 2008; Brodie et al., 2014; Duarte et al., 2014) and temporal variation (Lively et al., 2007; Bhadja et al., 2014). Human influences like pollution (Menge and Branch, 2001; Thompson et al., 2004; Baztan et al., 2014; Cabral-Oliveira et al., 2014b) and harvesting (Thompson et al., 2004; Airoidi et al., 2005; Bertocci et al., 2014; Stagnol et al., 2016) also play a key role in species composition and abundance. While these variable influences can

act independently, they can also act together (Connell, 1972; Paine, 1974; Leonard et al., 1998; Thompson et al., 2004). In the context of this study and the absence of baseline ecological information for Madagascan shores, it is not possible to critically assess the role of biotic interactions in structuring these shores. Nonetheless, in terms of abiotic drivers of community structure, this study explicitly accounted for variations in wave exposure, with communities from all grades of wave action being assessed (KwaZulu-Natal does not have true sheltered shores (Sink 2001) and therefore we were not able to sample accordingly). This factor identified by Sink, 2001, was important in structuring shores in KwaZulu-Natal. Consequently, within each country the communities were found to differ among wave exposure levels, as previously recorded by other studies across South Africa (Bustamante and Branch, 1996; Hunt and Scheibling, 1996; Davenport and Davenport, 2005; Blamey and Branch, 2009). This could not be the leading driver of differences in community structure between these two countries but could play a role in overall differences.

Humans influence natural systems in various ways. Within the context of intertidal habitats, these influences most commonly take the form of direct disturbances such as trampling (Schiel and Taylor, 1999; Smith and Murrey, 2005) and or harvesting (Bosman and Hockey, 1986; Maneveldt et al., 2009; Stagnol et al., 2016) but also indirect disturbances such as pollution (Lasiak and Field, 1995; Bishop et al., 2002; Cabral-Oliveira et al., 2013). Subsistence harvesting of intertidal resources reduces the population density, average individual size and spawning biomass of resources (Thompson et al., 2002; Mead et al., 2013). The removal of particular species can also lead to changes in assemblage composition and structure, consequently having cascading effects beyond the targeted species and therefore creating opportunity for alien species to invade communities (e.g. Farrell, 1988; Benedetti-Cecchi and Cinelli, 1992; Burfeind et al., 2013). Although the current study did not quantify harvesting pressure, observations made during fieldwork suggest that harvesting pressure is extensive on both southern Madagascar and northern KwaZulu-Natal shores. This is supported by the finding of very low abundances of organisms typically harvested for food (e.g. the mussel *Perna perna*). It is, therefore, likely that harvesting is an important factor differentiating rocky shore communities between southern Madagascar and northern KwaZulu-Natal even though both countries shores are low on resources. Although this potentially important factor could not be considered in the present study, future work should seek to establish harvesting intensities in both regions and consider the role this may play in

structuring communities. In saying this, without Marine Protected areas and “no-take zones” assessing harvesting impacts on community structure will not be possible.

Coastal pollution whether industrial or urban (e.g. oil spills or eutrophication) are known to cause a variety of impacts to coastal assemblages, including changes to the spatial and temporal patterns of distribution of organisms (Gray and Mirza, 1979; Halpern et al., 2008; Terlizzi et al., 2002; Guidetti et al., 2002), reduction in species diversity (Borowitzka, 1972) and large-scale changes in the physical and biological structure of natural habitats (Clark, 1996; Schmitt and Osenberg, 1996). Madagascar is a developing country with a growing tourism industry, however the infrastructure has not been developed enough to maintain the influx of people and therefore some areas are affected by pollutants such as coastal eutrophication (rural farming activities), construction activities (e.g. New Forth Dauphin Harbour and ilmenite mining) and sewerage run off (i.e. Fort Dauphin has no sewerage treatment plant). These activities combined and on their own may contribute to the increase of algal species on the Madagascan shores. The sampling site Newport is located at the Fort Dauphin harbour and the Locara sites are approximately 25km away. In contrast the KwaZulu-Natal sites are within the iSimangaliso Wetland Park, a Marine Protected Area and World Heritage Site and sites are more than 200km from the nearest harbour and 99km from nearest town (Ingwavuma). The distances between sampling areas and pollution activity are greater in Madagascar than in KwaZulu-Natal, hence pollutants and other impacts associated with coastal development could be contributing to the differences observed between the countries.

The rocky shore communities of northern KwaZulu-Natal were less similar to that of southern Madagascar than expected. The analysis indicated a significant difference in community structure between countries; some overlaps in species and some species that were unique to each country. The hypothesis that the intertidal communities are similar between the countries did not hold. This may be due to the traveling distance between countries exceeding the life spans of larvae/ propagule and post larvae/ propagule phase of most rocky shore invertebrate species and algal species. Most likely the main contributing factor to the countries being different is because the sampling areas falling within biogeographic regions overlap (Obura, 2012; Steen et al., 2015). The results from this chapter represent the first attempt to examine potential linkages between southern Madagascar and northern KwaZulu-Natal's rocky shores through migrating eddies. Even though there are no undisputable

linkages found between the countries, we did however find the community compositions to be similar and both countries are under the same environmental pressures, it is only the degree of pressure that differs. The baseline data collected for this chapter will contribute to future studies for KwaZulu-Natal and Madagascan regions.

SYNTHESIS

Madagascar is the fourth-largest island in the world (Storey, 1995) and has been characterized as one of the largest unsolved questions of natural history in terms of its high species richness and often uncertain biotic linkages (Krause et al., 1997). Despite this, the rocky shores of southern Madagascar are poorly studied with no publications describing their biodiversity and community structure. To provide insight into community structure, species diversity and differences among exposure levels on the southern coast of Madagascar, my thesis had three overarching aims: (1) to conduct a base line study to assess the rocky shore communities on the Southern shores of Madagascar and (2) to consider how these communities differ between shore zones and across different levels of wave exposure and (3) evaluate potential similarities between Kwazulu-Natal rocky shores and southern Madagascar as oceanographic data shows that eddies may provide a transport mechanism for propagules and of larvae between countries.

Chapter 2: Primary description of the rocky shore communities

Rocky shores are home to biologically diverse and productive communities and have proven to be key indicators for the tracking changes in marine coastal systems (Davenport and Davenport, 2005; Pinedo et al., 2007; Hawkins et al., 2008). The main aim of this chapter was to provide a first description of the rocky shore communities on the Southern shores of Madagascar and secondly to consider how these communities differ between shore zones and across different levels of wave exposure. The distribution patterns recorded on Madagascan shores were similar to that reported in the literature, with demonstrated vertical zonation patterns. The most noticeable, were the abundance and diversity of algae that were present in the low shore. Previous rocky shore studies have also recorded dominance of algae and it was suggested that an increase in algae is associated either with sheltered conditions (i.e. low wave exposure) (Blamey and Branch, 2008) or the absence of grazers (Coleman et al., 2006). In this study, the combination of the above mentioned factors were hypothesised to be the key factors contributing to the observed abundance of algae. Wave exposure contributed greatly to the distribution of species across the shores, which resulted in a significant difference between sheltered and exposed shores. This chapter has provided an important first description for the region, one which can form the foundation for future studies.

Chapter 3: Comparative study between rocky shore communities of Madagascar and KwaZulu-Natal

The study of community dynamics in intertidal habitats is a fruitful area for research to discern bio-geographical connectivity (Connell, 1972; Mackey et al., 2008). This dissertation aimed to study the similarity between rocky shores in northern KwaZulu-Natal and southern Madagascar, as part of the broader Suitcase Project. The Suitcase Project had set out to test the hypothesis that westward moving eddies connect southern Madagascar and northern KwaZulu-Natal systems. One way of interrogating this hypothesis is through considering similarities of community composition and exposures between the two systems. Using the first description of rocky shores from southern Madagascar that was produced in chapter 2 and data collected from northern KwaZulu-Natal, this chapter aimed to compare the community structure and species diversity of rocky shore ecosystems of these two countries. The analysis uncovered some overlap in species composition, within the two countries, a total of 56 species were observed on the sampled low shores, 21 species were unique to Madagascar and nine species were confined to the northern KwaZulu-Natal shores, which contributed to the significant difference in community structure. It is likely that the main contributing factor to why these countries are significantly different is due to how long it takes the eddies to travel between the two countries and the short larval and propagules lifespan of most species.

In conclusion, despite the significant differences in community structure between northern KwaZulu-Natal and southern Madagascan, the rocky shores were similar in community composition. These shores are affected by similar environmental conditions to that of northern KwaZulu-Natal according to this dissertation and previous literature. Bio-geographically northern KwaZulu-Natal forms part of the West Indo-Pacific realm (Sink et al, 2005; Yoder and Nowak, 2006). According to the species present on the Madagascan shores, there seems to be an overlap between Western Indo-Pacific and tropical Western Indian Ocean Province, which could be a major contributing factor to the differences in algal species. In terms of connectivity between the countries, the observed low similarity in community structure could be a reflection of (1) the observed differences in overall algae present on countries shores (2) KwaZulu-Natal shores had higher species diversity and a greater abundance of species than the Madagascan shores. Other differences could be driven by how those species assemble in communities (i.e. relative abundance) rather than their presence/absence within the counties.

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Appendix 3.1: Abundance (mean % cover \pm SE) of species recorded in the various shore zones on sheltered, rocky shores in southern Madagascar.

Shore zone	Taxon	Species	\bar{Y} (SE)
High-shore	Gastropoda	<i>Littorina</i> spp.	0.0 (0.1)
Mid-shore	Arthropoda	<i>Tetraclita rufotincta</i>	16.3 (7.4)
	Bivalvia	<i>Saccostrea cucullata</i>	0.2 (0.4)
	Chlorophyta	<i>Cladophora</i> spp.	0.1 (0.6)
		<i>Ulva</i> spp.	0.2 (0.4)
	Chitonidae	<i>Ischnochiton bergoti</i>	0.1 (0.0)
		<i>Onithochiton literatus</i>	0.1 (0.0)
	Cnidarian	<i>Zoanthus natalensis</i>	1.9 (9.3)
	Gastropoda	<i>Cellana radiata capensis</i>	0.8 (0.7)
		<i>Fissurella natalensis</i>	0.1 (0.0)
		<i>Littorina</i> spp.	0.4 (0.7)
		<i>Siphonaria capensis</i>	0.1 (0.1)
	Phaeophyta	<i>Ralfsia</i> spp.	4.1 (4.8)
	Rhodophyta	Encrusting coralline spp.	1.3 (4.8)
		<i>Jania</i> spp.	1.6 (2.2)
Low-shore	Arthropoda	<i>Tetraclita rufotincta</i>	0.1 (0.3)
	Bivalvia	<i>Perna perna</i>	0.2 (0.5)
	Chlorophyta	<i>Caulerpa racemosa</i>	3.2 (10.0)
		<i>Chaetomorpha linum</i>	0.8 (1.8)
		<i>Codium capitatum</i>	0.2 (0.5)
		<i>Ulva</i> spp.	0.5 (1.0)
	Chitonidae	<i>Onithochiton literatus</i>	0.1 (0.0)
	Cnidarian	<i>Zoanthus natalensis</i>	0.2 (0.5)
	Gastropoda	<i>Fissurella natalensis</i>	0.1 (0.0)
		<i>Scutellastra exusta</i>	0.1 (0.2)
	Phaeophyta	<i>Dictyosphaeria versluysii</i>	0.2 (0.5)
		<i>Dictyota</i> spp.	0.3 (0.9)
		<i>Ralfsia</i> spp.	0.8 (1.5)
		<i>Sargassum aquifolium</i>	0.5 (1.2)
		<i>Sargassum elegans</i>	0.5 (1.1)
		<i>Turbinaria ornata</i>	0.8 (2.5)
		Rhodophyta	<i>Arthrocardia</i> spp.
		<i>Amphiroa epedraea</i>	0.1 (0.3)
		Encrusting coralline spp.	2.0 (2.0)
		<i>Eucheuma</i> spp.	0.4 (12)
		<i>Gelidium acerosa</i>	0.3 (0.9)
		<i>Haliptilon</i> spp.	0.1 (0.3)
		<i>Hypnea musciformis</i>	19.9 (29.7)
	<i>Jania</i> spp.	1.5 (2.5)	
	<i>Laurencia flexuosa</i>	0.1 (0.0)	
	<i>Laurencia natalensis</i>	0.2 (0.8)	
	<i>Laurencia</i> spp.	3.3 (2.5)	
	<i>Plocamium corallorhiza</i>	1.1 (1.7)	
	<i>Rhodomencia natalensis</i>	0.4 (1.2)	
	<i>Spyridia hypnoides</i>	21.3 (27.9)	

Appendix 3.2: Abundance (mean % cover \pm SE) of species recorded in the various shore zones on Semi-exposed, rocky shores in southern Madagascar.

Shore zone	Taxon	Species	\bar{Y} (SE)
High-shore	Gastropoda	<i>Littorina</i> spp.	0.0 (0.1)
Mid-shore	Arthropoda	<i>Tetraclita rufotincta</i>	1.7 (7.1)
	Chlorophyta	<i>Caulerpa racemosa</i>	33.7 (30.2)
		<i>Chaetomorpha antennina</i>	1.1 (2.5)
		<i>Cladophora rugulosa</i>	0.3 (1.0)
		<i>Ulva</i> spp.	0.5 (1.4)
		Chitonidae	<i>Ischnochiton bergoti</i>
	Cnidarian	<i>Zoanthus parvus</i> spp.	0.3 (1.3)
		<i>Zoanthus sansibaricus</i>	14.9 (31.3)
	Gastropoda	<i>Cellana radiata capensis</i>	0.1 (0.2)
		<i>Fissurella natalensis</i>	0.1 (0.0)
		<i>Littorina</i> spp.	0.1 (0.2)
		<i>Tenguella marginalba</i>	0.1 (0.0)
		<i>Siphonaria capensis</i>	0.1 (0.0)
	Phaeophyta	<i>Dictyota</i> spp.	0.6 (0.9)
		<i>Ralfsia</i> spp.	0.1 (0.4)
		<i>Sargassum elegans</i>	1.5 (1.7)
	Rhodophyta	<i>Encrusting coralline</i> spp.	8.4 (7.9)
		<i>Hypnea musciformis</i>	15.8 (16.5)
		<i>Jania</i> spp.	15.3 (21.7)
		<i>Laurencia natalensis</i>	3.4 (4.8)
		<i>Spyridia hypnoides</i>	2.3 (4.3)
Low-shore	Arthropoda	<i>Amphibalanus amphitrite</i>	0.1 (0.2)
		<i>Tetraclita rufotincta</i>	0.1 (0.3)
	Bivalvia	<i>Perna perna</i>	0.9 (1.4)
	Chlorophyta	<i>Caulerpa racemosa</i>	11.3 (12.0)
		<i>Chaetomorpha antennina</i>	0.7 (1.0)
		<i>Chamaedoris delphinii</i>	0.3 (0.6)
		<i>Codium prostratum</i>	0.1 (0.2)
		<i>Ulva</i> spp.	1.6 (2.0)
	Chitonidae	<i>Ischnochiton bergoti</i>	0.6 (0.9)
		<i>Onithochiton literatus</i>	0.1 (0.0)
	Cnidarian	<i>Zoanthus durbanesis</i>	0.0 (0.2)
		<i>Zoanthus parvus</i> spp.	0.3 (1.4)
		<i>Zoanthus sansibaricus</i>	0.1 (0.4)
	Gastropoda	<i>Fissurella natalensis</i>	0.0 (0.1)
		<i>Scutellastra aphanes</i>	0.1 (0.0)
		<i>Scutellastra exusta</i>	0.1 (0.0)
	Phaeophyta	<i>Brown ephemeral algae</i> spp.	0.1 (0.4)
		<i>Dictyopteris delicatula</i>	0.0 (0.2)
		<i>Dictyosphaeria versluisii</i>	0.0 (0.1)
		<i>Dictyota</i> spp.	0.0 (0.2)
		<i>Ralfsia</i> spp.	0.9 (1.2)
		<i>Sargassum aquifolium</i>	0.5 (1.5)
		<i>Sargassum elegans</i>	21.3 (14.2)
	<i>Turbinaria ornata</i>	0.9 (2.0)	
	Rhodophyta	<i>Amphiroa ephedraea</i>	0.1 (0.4)
		<i>Arthrocardia</i> spp.	4.2 (7.4)
		<i>Centroceras clavulatum</i>	0.0 (0.2)
<i>Encrusting coralline</i> spp.		12.3 (12.6)	
<i>Hypnea musciformis</i>		6.6 (11.5)	

<i>Jania cultratum</i>	0.1 (0.6)
<i>Jania sagittata</i>	64.4 (34.9)
<i>Jania</i> spp.	0.1 (0.3)
<i>Laurencia flexuosa</i>	0.1 (0.4)
<i>Laurencia natalensis</i>	5.2 (5.1)
<i>Laurencia</i> spp.	6.5 (4.6)
<i>lithothamnion</i> spp.	0.6 (0.9)
<i>Plocamium beckeri</i>	0.1 (0.4)
<i>Plocamium corallorhiza</i>	11.7 (15.9)
<i>Portieria hornemanii</i>	0.2 (0.5)
<i>Spyridia cupressina</i>	0.4 (2.2)
<i>Spyridia hypnoides</i>	36.2 (24.5)
<i>Rhodomenia natalensis</i>	9.5 (11.8)

Appendix 3.3: Abundance (mean % cover \pm SE) of species recorded in the various shore zones on Exposed rocky shores in southern Madagascar.

Shore zone	Taxon	Species	\bar{Y} (SE)
High-shore	Gastropoda	<i>Littorina spp.</i>	0.0 (0.1)
Mid-shore	Arthropoda	<i>Tetraclita rufotincta</i>	14.9 (6.6)
	Bivalvia	<i>Saccostrea cucullata</i>	2.7 (5.1)
	Chlorophyta	<i>Chamaedoris delphinii</i>	0.0 (0.2)
	Chitonidae	<i>Dinoplax validifossus</i>	0.1 (0.0)
		<i>Ischnochiton bergoti</i>	0.1 (0.0)
		<i>Onithochiton literatus</i>	0.0 (0.1)
	Gastropoda	<i>Cellana radiata capensis</i>	0.4 (0.6)
		<i>Fissurella natalensis</i>	0.1 (0.0)
		<i>Littorina spp.</i>	0.5 (0.7)
		<i>Scutellastra aphanes</i>	0.0 (0.1)
		<i>Siphonaria capensis</i>	0.1 (0.0)
	Phaeophyta	<i>Ralfsia spp.</i>	1.6 (2.0)
		<i>Sargassum elegance</i>	0.2 (1.0)
	Rhodophyta	<i>Encrusting coralline spp.</i>	0.4 (0.9)
		<i>Jania spp.</i>	1.3 (2.4)
Low-shore	Bivalvia	<i>Perna perna</i>	4.2 (6.2)
	Chlorophyta	<i>Chaetomorpha antennina</i>	0.9 (1.3)
	Chitonidae	<i>Ischnochiton bergoti</i>	0.1 (0.0)
		<i>Onithochiton literatus</i>	0.1 (0.0)
	Gastropoda	<i>Cellana radiata capensis</i>	0.2 (0.2)
		<i>Fissurella natalensis</i>	0.0 (0.1)
		<i>Oxystele tabularis</i>	0.1 (0.3)
		<i>Scutellastra aphanes</i>	0.2 (0.3)
		<i>Patella granularis</i>	0.1 (0.0)
		<i>Scutellastra exusta</i>	0.1 (0.0)
	Phaeophyta	<i>Ralfsia spp.</i>	12.3 (18.1)
		<i>Sargassum elegans</i>	36.4 (37.0)
	Rhodophyta	<i>Jania sagittata</i>	9.8 (17.8)
		<i>Encrusting coralline spp.</i>	1.6 (3.2)
		<i>Jania spp.</i>	21.5 (33.6)
		<i>Laurencia natalensis</i>	0.1 (0.4)
		<i>lithothamnion spp.</i>	0.1 (0.3)
<i>Plocamium corallorhiza</i>		12.3 (22.6)	
<i>Spyridia hypnoides</i>		0.1 (0.6)	
Tunicata	<i>Pyura stolonifera</i>	0.1 (0.3)	
	<i>Green tunicate spp.</i>	0.1 (0.3)	