Decadal changes in rocky shore communities in KwaZulu-Natal and survey methods for future monitoring.

by

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PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Biological Sciences, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville, South Africa. The research was financially supported by the National Research Foundation (NRF).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

[redacted]

Signed: Dr Angus HH Macdonald

Date: 6 Nov 2020

DECLARATION 1: PLAGIARISM

I, Philile Emelda Mvula, declare that:

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(ii) this thesis has not been submitted in full or in part for any degree or examination to any other university;

(iii) this thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

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ABSTRACT

Intertidal rocky shores form part of the sea during high tides and part of the land during low tides. They are therefore subjected to diverse anthropogenic pressures, including climate change, pollution, coastal erosion and harvesting. Due to their accessibility, rocky shores are among the most heavily exploited marine ecosystems. The rocky shores of the East and the South coasts of South Africa have been exploited for thousands of years. With growing coastal populations, they require management practices that ensure their ecological integrity and function. Rocky shore community structure along the KwaZulu-Natal (KZN) coast has been well studied between the years 1996 and 2000 when surveys were conducted at 39 sites. A monitoring Programme has since been established by Ezemvelo KwaZulu-Natal Wildlife in partnership with the Department of Environmental Affairs, Forestry and Fisheries (DEAFF) to inform the management of these heavily impacted ecosystems. This study aimed to contribute to the monitoring Programme in two ways: Firstly, by characterising and evaluating changes in rocky shore communities that have occurred since 2000, which was done by resurveying historical sites and comparing community structure and diversity between decades. Secondly, by comparing and evaluating different rocky shore sampling methods to identify the most suitable sampling protocol for a long-term monitoring programme of KZN rocky shores. This required statistical analyses of parallel surveys conducted using different methods. Significant changes in the community structure were observed with increased species richness and evenness. A decline in the abundance of harvested mussels was also noted, coupled with an increase in coralline algae and the arrival of two species of alien barnacles. Even though more long-term studies will be required to determine the status of the intertidal communities under anthropogenically induced change, the current study can be used to initiate better management practices in order to maintain species diversity and distribution.

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CHAPTER 1: GENERAL INTRODUCTION

This chapter provides information on the status of rocky shores along the KwaZulu-Natal coastline through profiling the changes that have occurred over the past two decades. It reviews literature that relates to the community structure and individual species abundances and uses these as means to compare the community that once existed to the one that exists currently.

Intertidal rocky shores

Rocky shores are intertidal environments found across the world that are characterised by solid rock that may take the shape of steep rocky cliffs, rock pools, boulder fields and platforms (Coutinho et al. 2016). The intertidal zone is an area between the high tide mark and the low tide mark, and is the area where the land and the sea meet. The environment in this zone is continuously changing due to tidal cycles. It may be fully submerged during high tide and exposed during low tide. As a result, rocky shore communities around the world display characteristic zonation patterns (Southward 1958, Stephenson & Stephenson 1972) that are shaped by a variety of abiotic as well as biotic drivers (Connell 1961, Paine 1974, Underwood 1978, Nordlund et al. 2014), since the distribution of organisms on the rock surface and their interaction are dependent on their ability to cope with the environmental stressors. Zonation can be modulated by the intensity of the wave action (Helmuth & Denny 2003), since wave splash and spray ameliorate desiccation while making it more difficult for organisms to hold onto the rock. Organisms that inhabit the intertidal zone have thereby adapted to a mosaic of habitats shaped by waves and tides.

The rocky shores have a high richness of ecologically and economically important species (Coutinho et al. 2016). This can be attributed to nutrients derived from land runoff which promote high biomass of primary producers like microphytobenthos and macroalgae (Binet et al. 1995). Particulate matter is turned into benthic biomass by filter-feeding organisms, which thrive in this zone (Bustamante et al. 1995c). This makes rocky shores the ideal feeding, growth, and reproduction area for a range of species. Since they support high biodiversity, they supply a wide variety of ecosystem goods and services including primary productivity, bio-filtration, erosion protection, fish nursery grounds, provision of edible invertebrates and fish, recreation, and tourism (Nordlund et al. 2014, Vinagre et al. 2016), which makes rocky shores highly valuable.

Rocky shores are easily accessible to humans, and this has resulted in a range of disturbances since prehistoric times (Thompson et al. 2002, Mead et al. 2013). Many coastal communities depend on them for their livelihood; presenting a challenge when it comes to sustainable resource management and conservation planning for the coastal zone. Balancing economic growth and biodiversity conservation is a major challenge faced by conservationists, as it requires that conflicting user groups are included in decision making, such as the scientists, managers, and the communities that depend on various resources (Nordlund et al. 2014).

The biogeography of the South African coast

The South African coastline stretches 3 113 km and is home to 12 914 different species of invertebrates (Mead et al. 2013). It is therefore considered one of the most biodiverse national coastlines in the world. This diversity is influenced by, among other factors, temperature, ranging from subtropical in the East through warm-temperate in the South to cool-temperate in the West (Brown & Jarman 1978, Emanuel et al. 1992, Bustamante et al. 1995a b c). Therefore, the diversity is not uniform along the entire coastline:, it is lowest on the West coast and increases gradually towards East, with some groups of organisms reaching their maximum diversity on the South coast and declining again approaching the East (Mead et al. 2013). The South African coastline is made up of 42% sandy and 31% mixed shores, with rocky shores making up only the remaining 27% of the coastline (Griffiths et al. 2010). Contrary to species richness, productivity and biomass decline as one moves from West of the country to the East (Bustamante et al. 1995c, Porter et al. 2013). This is due to the major Benguela upwelling region, which inject nutrients along on the West coast, while the warm Agulhas Current is associated with low productivity and biomass on the East and South coasts (Bustamante & Branch 1996).

Based on these biogeographic gradients, the South African coastline has been classified onto three biogeographic regions (Brown & Jarman 1978, SANBI 2018, Sink et al. 2018), the subtropical East coast, warm temperate South coast, and the cool temperate West coast (Branch & Branch 1981). Rocky shores on the East coast have been further divided into the Delagoa (Maputaland) ecoregion and the Natal ecoregion, the latter of which was further divided into three subregions, namely Zululand, Central KZN, and South KZN (Sink et al. 2005). Relatively high diversity was recorded in the South KZN as this subregion has been suggested to be an overlap region for the Natal ecoregion and the Agulhas ecoregion. Similar relatively high diversity is expected for Zululand as it is an overlap region between the Delagoa (Maputaland) ecoregion and the Natal ecoregion (Sink et al. 2005).

Drivers of ecosystem change in rocky shore communities

Ecosystems change over time due to a variety of natural and anthropogenic factors (Parmesan 2006, Mead et al. 2013, Nordlund et al. 2014, Blamey et al. 2015). Such changes may be expressed in populations of individual organisms or by shifts in the overall community structure (Moloney et al. 2013). This manner of progression also characterises rocky shore communities, which are shaped by a range of environmental variables, such as temperature and wave energy (Bustamante & Branch 1996). In addition, anthropogenic forcing works in conjunction and interacts with natural environmental variables (Mead et al. 2013), altering marine environments globally and locally. The main anthropogenic drivers of change include exploitation, climate change, pollution, ocean acidification, alien and invasive species, and mining (Moloney et al. 2013, Nordlund et al. 2014). These pressures can have a synergistic effect on the ecosystem because they often occur concurrently (Moloney et al. 2013, SANBI 2018). In South Africa, the main anthropogenic pressures include the exploitation of living marine resources, modification of biotic communities, urban development, the introduction of invasive species, pollution and harbour construction or coastal mining (Mead et al. 2013, Jarre et al. 2015, Pfaff et al. 2019, Kirkman et al. 2020).

The exploitation of marine resources is increasing correlated with human population growth. This results in an alteration in community structure (Moloney et al. 2013). Although South Africa does not experience major industrial exploitation of rocky shores, subsistence harvesting and small-scale commercial extraction of intertidal organisms have important effects on the community structure (Siegfried et al. 1994, Dye 1998, Lasiak 1998).

Subsistence harvesting of intertidal invertebrates on South African rocky shores has a long history that dates back to prehistoric times (Griffiths & Branch 1997, Dye 1998, Lasiak 1998, Cole et al. 2011). In the past, primarily mussels were harvested with substantial amounts of limpets also taken as bycatch. Although not as intensive as now, the persistent harvesting has resulted in reduced mean sizes of both mussels and limpets (Siegfried et al. 1994). In recent years, the subsistence harvesting has become concentrated in the East and South coasts, and this has led to substantial depletion of stocks over time and cascading effects on other components of rocky shore ecosystems. There has been clear evidence of declines in the abundance of harvested species such as mussels, limpets and 'redbait' are evident (Steyn et al. 2019). The declines in harvested species have led to shifts in species interactions, resulting in secondary effects and influencing the supply of larvae of some species. For example, when grazers such as limpets are removed, there is an increased algal growth and barnacle abundance. When mussels and redbait are removed, a wider range of species are affected, as these form habitats for other species (Moloney et al. 2013). The depletion of mussels depends on the balance between recruitment and harvesting. Recruitment failure is linked to adult abundance as juvenile mussels prefer to settle on already established beds and unfortunately, the areas where recruitment rates are lowest tend to have the highest human exploitation, such is the case with the rocky shores of the South-East Coast of South Africa (Siegfried et al. 1994, Cole et al. 2011).

Climate change results in changes in the ocean's surface temperature, increased wind stress, increased oxygen depletion zones and stratification, resulting in poor nutrient distribution (Moloney et al. 2013). A growing body of evidence suggests that global climate change is altering air and sea temperatures, upwelling frequency, wind regimes, and the intensity of wave action around the South African coastline (Bustamante & Branch 1996, Helmuth & Denny 2003, Rouault et al. 2010, Lloyd et al. 2012, Blamey et al. 2015, Jarre et al. 2015, Schotanus et al. 2019). Dramatic changes are thus expected on rocky shores resulting from the upwelling shifts (Mieszkowska et al. 2005). Climate change can also result in homogenisation within rocky shore communities from different ecoregions resulting in the reduction of transitional regions (Mead et al. 2013). Climate change also increases the risk of introduction of alien and invasive species which may out-compete the local species, leading to further loss of biomass

(Newman et al. 2011). On the South African East coast climatic shifts have been observed in the form of range expansion of tropical species into temperate areas (Lloyd et al. 2012). This has been found to result in overgrazing of temperate macroalgae in counties such as Japan and the Mediterranean (Lloyd et al. 2012, Vergés et al. 2014). Another expected change is the decrease in larval settlement due to disturbances in dispersal of these larvae (Harris et al. 1998, Harley et al. 2006).

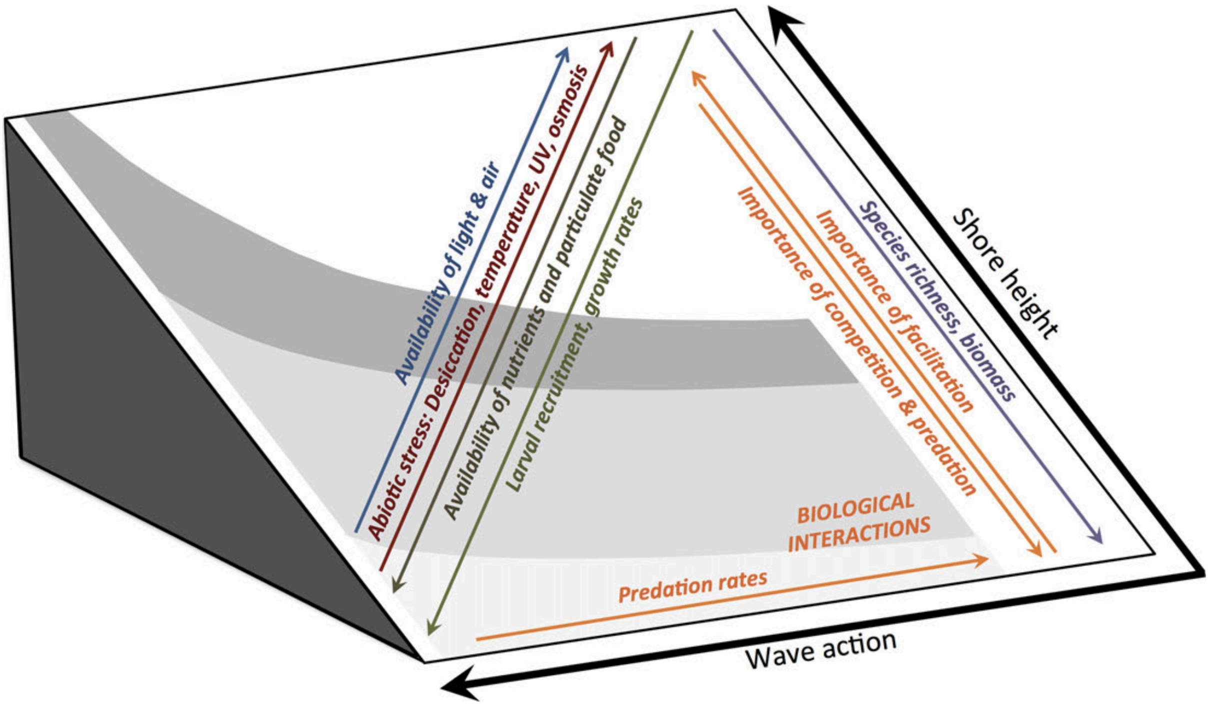

Figure 1. 1: Intertidal rocky shore zones (dark grey = high shore, medium grey = mid shore, light grey = low shore). Arrows indicate across-shore and along-shore gradients of the abiotic and biotic factors that influence intertidal rocky shore zonation patterns (Pfaff & Nel 2019).

Industrialisation and urbanisation are the primary sources of pollution in the marine environment (Ukwe & Ibe 2010). Recently the threat of microplastics on marine environments including intertidal rocky shores has been highlighted. Since microplastics are within the size range of plankton and other particulate matter, they are easily taken up by filter feeders (Botterell et al. 2019). This has been found to induce a wide range of physiological impairments in filter feeders (Green et al. 2019), *e.g.*, gut blockage (Van Cauwenberghe et al. 2015). Rocky shore organisms are also affected by oil spills, which sometimes affect invertebrates and algae to a minor extent, while causing devastating effects on mobile species that occupy the upper section of the shore (Mead et al. 2013). Nutrient runoff from farms on land has resulted in catastrophic events such as harmful algal blooms (HABs) (Pfister et al. 2014). Rapid and unsustainable algal growth during these events causes oxygen depletion and even release of toxic hydrogen sulphide in some cases (Branch et al. 2013, Gilbert & O'Connor 2013). When there is land or sea-based mining in an area, the sediment derived from these activities can end up on the rocks, resulting in scouring of rocks and smothering of grazers and allowing algae to grow uncontrollably. Sea-based diamond mining off the Northern West Coast has caused severe impacts on the rocky shores of that region (Mead et al. 2013, Pulfrich & Branch 2014).

Long term monitoring for South Africa

To identify changes in community structure due to climate change or exploitation, long-term datasets need to be collected and evaluated (Dye 1998). The longer the period of accumulation of the dataset, the more it is possible to separate interannual variability from ecosystem shifts *e.g.* those expected from climate change. The main problem with long term datasets is consistency; the researcher may not be able to collect the same type of data using the same methods for periods of ten years or more. As a result, there are either gaps in the dataset and loss of information about inter-annual variability, or there is no uniformity in the sampling protocol used by different researchers to accumulate these datasets (Hutchings et al. 2009, SANBI 2018, Kirkman et al. 2020).

The most important management strategy noted all around the world is the development of a healthy relationship between managers, communities that use the resource and scientists, to share knowledge on relationships between species and their environment, and to develop education Programmes and awareness campaigns (Nordlund et al. 2014). The South African Department of Environmental Affairs, Forestry and Fisheries (DEAFF) is applying this approach to rocky shores across the South African coastline (Harris et al. 1998). Ezemvelo KZN Wildlife (EKZNW) is an organisation that manages and conserves both the terrestrial and the marine biodiversity in the KZN region. To do their duties effectively, they have had to gather field data, through a long-term monitoring programme that involves sending scientists to representative sites to collect observational data about the conditions of that habitat as well as any changes in fauna and flora. A rocky shore monitoring Programme was established in 2008 and annual surveys at six sites have been conducted ever since (Olbers 2013, 2017). To improve the effectiveness of the monitoring Programme, there is a need for the development of a standardised protocol to be used for long-term monitoring of rocky shores in South Africa. Because the South African coastline is variable, different protocols have to be developed for each of the different ecoregions.

Rocky shore management and monitoring measures

Because rocky shores feature communities that comprise a complex network of interactions such as predation and facilitation (Rabelo et al. 2013), when an (exploited) species decreases abundance that may result in shifts in the overall community structure (Polis & Strong 1996, Griffiths & Branch 1997). It is therefore essential to identify the nature of the change of impacted communities and identify possible drivers to be able to manage their future integrity and functioning.

Visual estimation of community structure in quadrats is a method whereby the researcher makes identifications and estimates of the abundance of all species, *e.g*. as percentage cover or counts of individuals, in a given area, *e.g*. a quadrat or transect. A major advantage of this method is that it is not as time-consuming as other methods. If the observer is well trained and experienced, they can cover a larger area in little time without compromising the sensitivity of the method. Additionally, the observer can see the quadrat in a three-dimensional (3D) view, this allows the researcher to see and identify small members of the community and those that live within the fronds of others (Meese & Tomich 1992, Bustamante & Branch 1996). However, the most crucial disadvantage associated with the visual *in-situ* estimation of cover is its inherent observer bias. Discrepancies in estimating cover occur due to variability in observer experience, with more experienced observers being able to detect confounding factors such as phenotypic plasticity. There may also be variability between different surveys by the same observer when using this method (Meese & Tomich 1992). Another disadvantage that may arise from this method is that the researcher may take into account the presence-absence data and may ignore abundance, especially with mobile species, and this ends up giving an incorrect estimate of the community structure. Thus, a small periwinkle that grazes on a single algae may be misrepresented and give a poor reflection of the state of the system compared to a limpet that grazes over a large area Field & McFarlane (1968) therefore recommend that some function of size should, be included in the analyses to account for the size of the organism. Moreover, several variations exist to this method that are often not considered when reporting results, thus compromising data for comparisons with other surveys. For example, the percentage cover of seaweeds can either be scored by their attachment area, or by the area their canopy occupies, which may differ by an order of magnitude in some species.

Photographic transects are an alternative method that involves the use of a camera to capture the organisms within a quadrat in the field followed by analyses of the images on the computer using specialised software tools that have been developed for the annotation of images (Bohnsack 1979). This method is ever improving with technological advances, from improvements in the camera clarity and resolution to methods of analysing the resultant images. The major advantages of this method are that it is less time consuming in the field, since fieldwork only includes capturing images of quadrats, and the identifications are conducted *ex-situ* (Meese & Tomich 1992). It also offers a permanent record of the samples in the form of image data with dates and even GPS tags (depending on the type of camera used). These records can be useful when compiling long-term datasets and identifying changes in community structure over centuries (Bohnsack 1979, Dye 1998, Olbers et al. 2009). Furthermore, people who are unifiliar with species identification can participate in data collection, rendering this method suitable for multi-institutional long-term monitoring programmes that require great human capacity, or citizen science initiatives. However, the biggest disadvantage of this method is that it captures a 2D image of the environment which may restrict the ability of the researcher to identify small organisms that they would have been otherwise able to identify in the field (Meese & Tomich 1992). This error has been shown to increase from flat to uneven surfaces (Dye 1998), where depth-of-field of the image may render areas blurred and unidentifiable, although modern cameras help overcome this by integrating different depths of field from multiple images. The photographic method is also more costly than the visual identification, since it requires the use of cameras and species annotation software.

Meese & Tomich (1992) conducted a study to test the repeatability, robustness and sensitivity of five rocky shore surveying methods, *i.e.* (1) visual *in-situ* estimation, (2) use of random dots,

(3) evenly spaced dots or (4) stratified random dots on transparent plastic plates, and (5) electronic digitising of photographic images. They found that digitising of photographic images was the most precise, but in order to achieve the highest reliability robustness and detection of rare species digitisation of photographic images and visual estimation had to be used concurrently. In South Africa visual estimation has been used over decades to give the percentage cover of organisms on the rocky shores (*e.g.*, Bustamante 1994, Sink et al. 2005, Olbers 2013), with each researcher adapting the method to their convenience. Recently we have seen a shift towards the use of photographic transects as a method of conducting rocky shore surveys (pers. comm. MC Pfaff). It is then important to question whether this shift will give better estimations of percentage cover of species on rocky shores in South Africa or as reported by Meese and Tomich (1992) the combination of the two methods will yield better estimations.

There has been significant progress in community analyses in the terrestrial environment (Vellend et al. 2013), and the marine environment has a long way to go to catch up as it has only been developed in the recent past (Fields et al. 1993, Parmesan 2006). Globally, there has been an improvement in identification techniques. However, there are still spatial gaps. The areas with the most gaps are countries in Africa and Asia, as most of the research that does come out of these two continents can be traced to just two countries: South Africa and Japan (Parmesan 2006). In addition the management of South Africa's marine systems has been implemented in a very fragmented manner, which resulted from top-down planning (Ahmed 2008).

Thesis outline

This research aimed to provide vital information in the above context and will contribute to long-term monitoring of the rocky shores for the East coast of South Africa by, first, comparing long-term datasets and noting the limitations presented by the protocols that were used to collect the data (Chapter 2). Thereafter a study was conducted to develop the best protocol that can be used from this point onwards for evaluation of community structure in the Natal ecoregion (Chapter 3).

CHAPTER 2: MARKED TEMPORAL CHANGES IN KWAZULU-NATAL ROCKY SHORE COMMUNITY COMPOSITION WITH INCREASING SPECIES RICHNESS BETWEEN 1996 AND 2018.

Abstract

Several factors including climate change have been predicted to cause major shifts in the abundance and distribution of plants and animals globally, making climate change one of the most significant modern-day challenges for the protection of biodiversity. With the steady increase of human settlements along the coasts, there also has been growing pressure on natural resources in the coastal zone, which has likely affected the structure of biotic communities. Data from a comprehensive survey of intertidal rocky shores along the KwaZulu-Natal on the East coast of South Africa, which was conducted in the late 1990s, provided a comprehensive baseline for this study. To characterise changes that have occurred over the past 20 years, surveys were repeated at 14 of the sites previously surveyed, using identical community sampling protocols. In each of four intertidal zones in 14 sites, species richness, evenness and community structure were compared between 1996 and 2018. Total species richness increased despite a loss of some species in the high-shore and mid-shore zones. The evenness increased in most of the sites particularly in the mid- and low shore zones. Significant changes in the community structure were observed with a decline in the abundance of harvested mussels, increases in coralline algae, the new arrival of two species of invasive alien barnacles, and the range expansion of a subtropical barnacle Southward into the study area. Geographical shifts of a suite of species into a new region in response to a variety of factors including a changing climate occur faster than contractions of other species out of the same region. This may result in increased species richness, as observed in this study. This study is the first to characterise the marked changes in rocky shore biodiversity that have occurred on the South African East

coast over the past two decades. It therefore, constitutes a significant contribution to research on harvesting impacts and climate change research and provides information that is relevant to management and conservation of these heavily impacted coastal ecosystems.

Introduction

Marine ecosystems have undergone substantial changes over a range of temporal and spatial scales with coastal ecosystems experiencing the most extreme environmental fluctuations as they are affected by both land-based and sea-based factors (Rust 1991). In addition to being impacted by global climate change and natural environmental fluctuations, intertidal rocky shores are specifically vulnerable to anthropogenic disturbances like coastal developments, freshwater input, sediment loading, the introduction of alien and invasive species, trampling, harvesting, and pollution (Micheli et al. 2016).

Climate change is one of the most significant modern-day threats to the maintenance of biodiversity globally (Ng et al. 2017, Phillips et al. 2018). It has been predicted to cause major shifts in the distribution and abundance of fauna and flora leading to changes in community structure and function (Walther et al. 2002, Thomas et al. 2004, Parmesan 2006, Walther 2010, Molinos et al. 2016) and an increase in the likelihood of extinctions (Fields et al. 1993, Firth et al. 2013). In coastal marine ecosystems, climate change is commonly associated with latitudinal shifts in distributions of species due to changes in their ambient environment (Fields et al. 1993, Harley 2011). Climate change effects are relatively easily and timeously detected on intertidal rocky shores as the organisms are sensitive to disturbances. This is due to their habitat which drives them to survive at, or very close, to their physiological limits (Stillman 2002, Harley 2011). Climate change often also exerts indirect effects on organisms by altering their environments, such as their prey or predator abundances, which has knock-on effects on the entire community structure and function through trophic cascades (Sagarin et al. 1999, Harley 2011). For example, declines in seaweed cover may result in declines in the invertebrates that depend on the seaweed for shelter and food (Sagarin et al. 1999). Therefore, a species response to climate change is not isolated, as it affects other species in the adjacent trophic levels (Walther 2010). Over the years, the general consensus has been that organisms found in the intertidal zone are more tolerant than other organisms found in more stable environments. Surprisingly, the less heat-tolerant low-shore species have been found to be more tolerant to climate change than the more heat-tolerant mid- to high-shore species, which live in harsher conditions and are thus more vulnerable as they live nearer to their thermal limits (Tomanek & Somero 1999, Stillman 2002).

Species from warming regions are generally expected to shift poleward from their distributional ranges (Parmesan 2006). Since South Africa is at the interface of the Atlantic and Indian Oceans, the distributional shifts are more complicated, as the species from the cold Atlantic Ocean are able to expand towards the Indian Ocean while the Warm Indian Ocean species are expanding towards the Atlantic (Fields et al. 1993, Walther 2010).

Coastal ecosystems are subject to recurrent natural disturbances; in addition, anthropogenic disturbances have exerted extra pressure on these systems, reducing their resistance and resilience (Martinez et al. 2017a b). With 40% of South Africa's population living within 100km of the coastline, the effects of human disturbances in the coastal zone are more pronounced, especially around major cities like Durban, East London, Port Elizabeth and Cape Town (Sowman 2015). Many of these coastal communities depend on natural resources as a primary food source, which has resulted in increased shellfish harvesting from these ecosystems, especially those along the South and East coasts (Siegfried et al. 1994). An increase in coastal developments also introduces other threats, such as pollution and coastal erosion, and contributes to the effects of global climate change (Moloney et al. 2013).

The East coast of South Africa has many rivers, and there are 74 estuaries on the KwaZulu-Natal (KZN) coast. The Natal ecoregion receives 99% of the mean annual simulated runoff for KZN. Riverine input affects intertidal organisms through increasing the particulate organic matter available, thus increasing productivity (Bustamante et al. 1995c, Porter et al. 2014). It also increases the turbidity and siltation while decreasing the salinity; this can affect the organisms negatively (Menge et al. 1997). These effects are elevated when the river catchment is in an agricultural area. Filter feeders are more dependent on detritus than phytoplankton; thus receive detritus through the breakdown of seaweed and trees washed into the ocean by rivers (Schleyer 1981).

The most important surface condition affecting climate is the sea-surface temperature (SST), it is the most dominant influence of climate change on in shallow tropical seas as it can give rise to effects to a rise in sea-level. The mean temperatures of the world's oceans are increasing at an accelerating rate, which, at present, is approximately 2 Celsius per century (Davis-Reddy & Vincent 2017). On the KwaZulu- Natal coastline, the increase in SST has been recorded to be between 0.25 – 0.5 degrees Celsius per decade, this was attributed to an strengthening of the Agulhas Current in response to a poleward shift of westerly winds, as well as increased trade winds in the Indian Ocean (Lutjeharms et al. 2001, Rouault et al. 2010). When the SST is higher than normal the implications can range from changes in the abundance of singular organisms to whole communities over time (Potts et al., Lloyd et al. 2012).

The effects of climate change on community composition and ecosystem processes can act synergistically with other drivers of change. For example, it is expected that the introduction of alien and invasive species, global warming and sea-level rise will interact with regional drivers of change such as nutrient supply and thus affect community structure and function in shallow-water ecosystems such as the rocky shores (Walther 2010). The combined impact of a changing climate and introduced species facilitates the establishment of mixed communities of native and alien species. With expansions in the shipping industry in recent years (Lages et al. 2011), more and more species are introduced from afar while others arrive through range shifts and expansion. The arrival and establishment of new species can modify and destabilise communities by altering ecosystem processes and make them more vulnerable to further invasions (Walther 2010, Lages et al. 2011). In other cases, the disturbance can select for more resistant organisms; making the ecosystem becomes less vulnerable to further disturbance. However, the interactive effect of multiple disturbances can be synergistic and enhance the effect of the individual disturbances (Micheli et al. 2016).

The harvesting strategy of humans, who commonly target the largest individuals of a population, is most detrimental, as the larger individuals tend to be the most reproductive. Therefore their extraction from the system can result in major collapses in population numbers, and ultimately cause changes in community structure and organisation (Martinez et al. 2017a). Shellfish harvesting has been practised in South Africa for centuries (Siegfried et al. 1994, Hockey & Branch 1997, Kyle et al. 1997), and is still practised predominantly by rural communities, particularly in Northern KwaZulu-Natal (Kyle et al. 1997) and the Eastern Cape, who use intertidal organisms for traditional healing and food. Harvesting is done by women during spring low tide (Kyle et al. 1997). Sustainable use of these resources has been achieved during times when harvesting was done according to strict bag limits, or harvester numbers were controlled, however, failing “top-down” conservation practices in South Africa have led to lack of compliance with such rules (Mieszkowska et al. 2019). As a result, intertidal resources have been overexploited in Northern KZN, where subsistence and recreational harvesting comprise the main pressures on this resource (Olbers 2017).

Local community assemblages change on historical, ecological and socio-economic timescales as a result of range shifts, invasions or extinctions with climate change forcing organisms to adapt, acclimate or move at an unprecedented pace, while coping with additional regional-scale stressors (Ahmed 2008, Queirós et al. 2015). Quantifying and managing near-future impacts of climate change on the species distributions and overall biodiversity is one of the greatest challenges. It is alarming to discover that the investment in long-term studies has declined globally, as long-term research is vital for providing us with information to understand and predict responses to global change (Clutton-Brock & Sheldon 2010). Historical datasets provide an opportunity to characterise changes that have occurred on the decadal scale. Such datasets exists for rocky shores in KZN as rocky shore community structure has been studied in the region for decades (Sink 2001, Sink et al. 2005, 2012, Olbers 2013, 2017), and a monitoring Programme was established in 2008 by Ezemvelo KwaZulu-Natal Wildlife in partnership with the Department of Environmental Affairs, Forestry and fisheries (DEAFF) to inform the management of these heavily impacted ecosystems (Olbers 2013, 2017).

This chapter contributes to this monitoring Programme by testing whether the community structure of intertidal rocky shores along the KwaZulu-Natal coastline changed over the past 20 years through addressing the following key questions: -

- has there been change in species richness over the past 20 years?
- were there changes in the evenness of species over the past 20 years?
- were there any changes in the overall community structure and function?

It was hypothesised that the rocky shore communities would have changed over the past decades due to climate change and regional warming, with an increase in warm-water and a decrease in temperate species. Also, that invasive alien species would have moved into the area, which has previously not experienced any notable invasions. With the growth of coastal populations, it is also expected that harvested species would have declined resulting in decreased species richness and increased evenness.

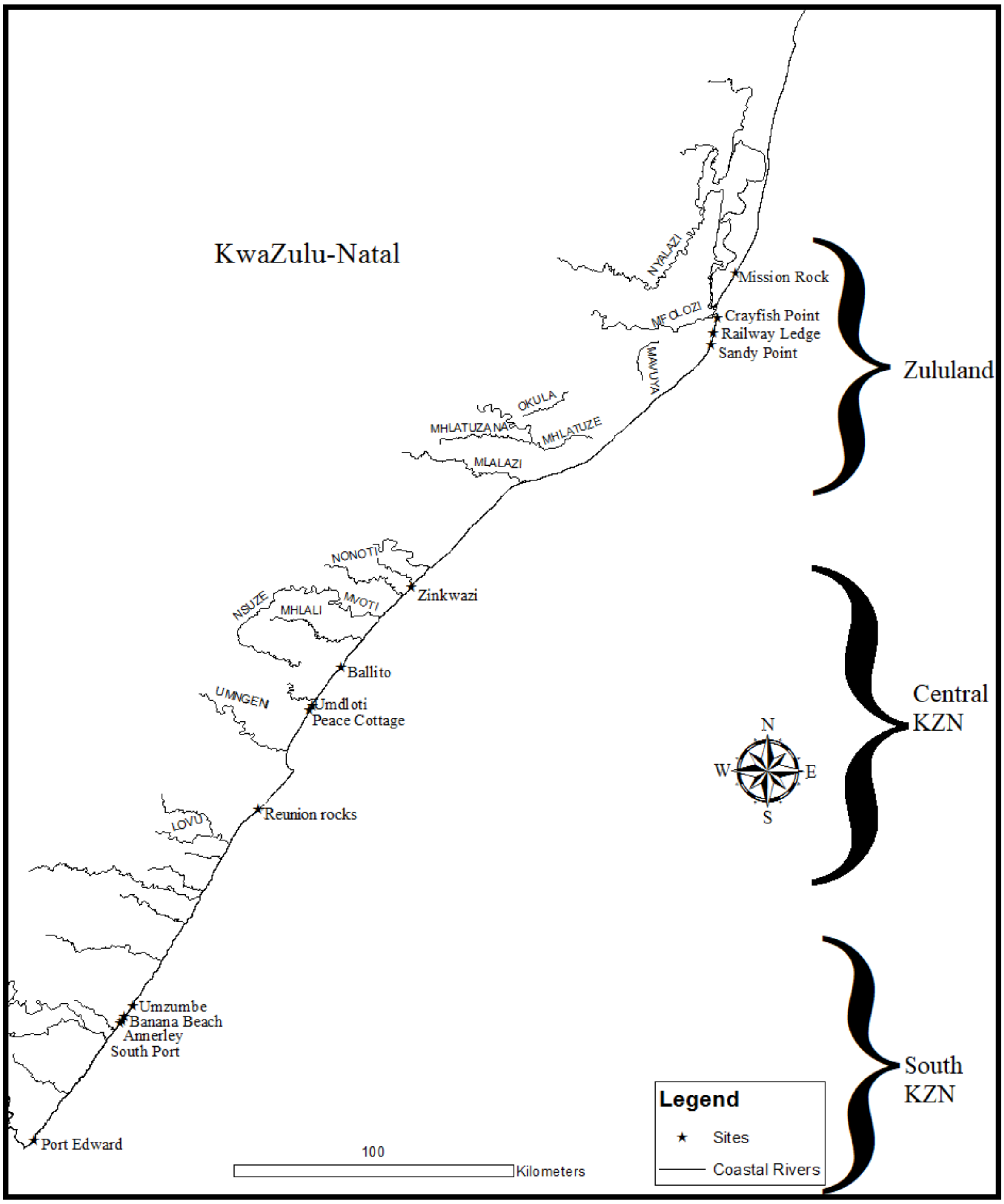

Figure 2. 1: Map of the KwaZulu-Natal coastline showing sampling sites (stars) and three sub-regions (as defined by Sink (2001)) that were surveyed in this study.

Methods

Sampling area/region

The study was conducted at 14 sites along the KwaZulu-Natal (KZN) coastline (Fig. 2.1), between February 2018 and September 2019. This was a subset of the 39 sites surveyed in 1996 to 2000 by Sink (2001). Since the original GPS coordinates were recorded at relatively low resolution, re-surveys were done of the same general location, within *circa.* 300 m of the original sites.

Sampling Design

Rocky shore surveys were conducted at each site following the same method applied by Sink (2001) to ensure that the data were comparable with the historical baseline. The method used has been widely applied in rocky shore surveys (Eg. Meese & Tomich 1992, Sink et al. 2005, Olbers 2017). Specifically, the intertidal zone was divided into four horizontal zones, comprising the top shore, high shore, mid-shore and low shore. These zones were selected based on dominant species reported by Sink (2001). Since zones were not permanently marked during the initial survey, vertical shifts of species could not be assessed, and this study therefore focuses solely on along-shore (latitudinal) changes in community structure. Twenty replicate 1.0 m x 0.5 m quadrats were randomly placed within each of the two lower zones (low and mid) and ten replicate quadrats were placed within each of the two upper zones (high and top), amounting to a total of 60 replicate quadrats per site. These sample sizes were determined by a pilot study undertaken by Sink (2001), which found that when such sample sizes were chosen, at least 95% of the total number of species were captured.

In each quadrat, estimations of percentage cover of all sessile species as well as the sizes and counts of all mobile species were recorded. The calculated mean size and counts of mobile organisms were subsequently converted to percentage cover data. For species that could not be identified in the field, images were taken and samples were collected for later identification.

Data processing and statistical analyses

The statistical analyses were performed with R version 3.5.1 (https://www.R-project.org), using the Vegan package for multivariate analyses.

Analyses were done separately for each zone to account for missing data, which in some instances existed for entire zones in the historical dataset, and for sites that did not have all the four zones represented due to the limited extent of the rock platforms or sand inundation. Where ambiguity existed in species-level identifications, species-abundance data were occasionally pooled by higher-level taxonomic groupings to align historical and present datasets.

i) Species richness and evenness

Species richness was calculated from the average number of species per quadrat and Pielou's evenness were calculated for each zone in the 1990s and 2018 datasets.

Fully crossed two-way ANOVAs were conducted for each zone to test for significant differences in species richness and evenness between years and sites (as well for as interactive effects) and post hoc tests (Tukey HSD) were applied to investigate the nature of the significant differences further.

ii) Community structure

To determine decadal changes in the spatial structure of rocky shore communities, species-abundance data were grouped into functional groups (see Table A1 in Appendix 1 for a list of species found in this study and their taxonomic and functional group allocations). This was done to ensure that the multivariate analyses could be performed (without convergence issues), which tend to be compromised by the high dimensionality of species-level data.

The percentage cover data were standardised by sample total, and double log-transformed, to compare equally scaled replicates and emphasise contributions of rare species, respectively. For each zone, fully crossed two-way PERMANOVAs (adonis using 999 permutations) were run to determine the effects of year and site and their interaction on community structure. Post hoc tests (pairwise.adonis) were performed to identify where differences occurred. SIMPER analyses were run to find out which groups contributed most to the differences between the years/sites. The sites were not nested within sub-regions because delineation of sub-regions may have shifted since the previous survey but, to better understand which species led to shifts in community structure along the coast, the changes in percentage cover of selected species were assessed in the "previously defined" sub-regions.

iii) Most notable changes in species cover

For the functional group-based community structure that experienced significant changes between years species-level information on changes in abundances was extracted and presented to identify the most notable changes in species cover for each of the three regions, providing an indication of range shifts that might have occurred over the past two decades.

Results

Decadal changes in species richness and evenness

Total species richness on rocky shores in KZN was greater in 2018 than in 1996-2000. Across all sites, 43-70% of species were observed in both surveys, with a greater number of once-off, exclusive observations of species in 2018 (Fig. 2.2). However, the apparent increase in species richness depended upon site, with often only 2-3 sites across the region driving the difference within each zone. The mid-shore appeared to have the most spatially consistent change in richness, with 6 out of 10 sites presenting significantly higher number of species in 2018. While not all sites had comparable data for all zones, 4 sites (Reunion, Umzumbe, Banana and Southport) presented significantly different richness in more than one zone (Fig. 2.3). Overall, where differences were observed, all presented consistently higher richness in 2018 than surveys conducted 20 years prior. Differences existed among sites in the magnitude of this increase, as reflected in the significant year-site interactions for all zones (ANOVAs: $p < 0.001$ for all zones; Table 2.1, Fig. 2.3).

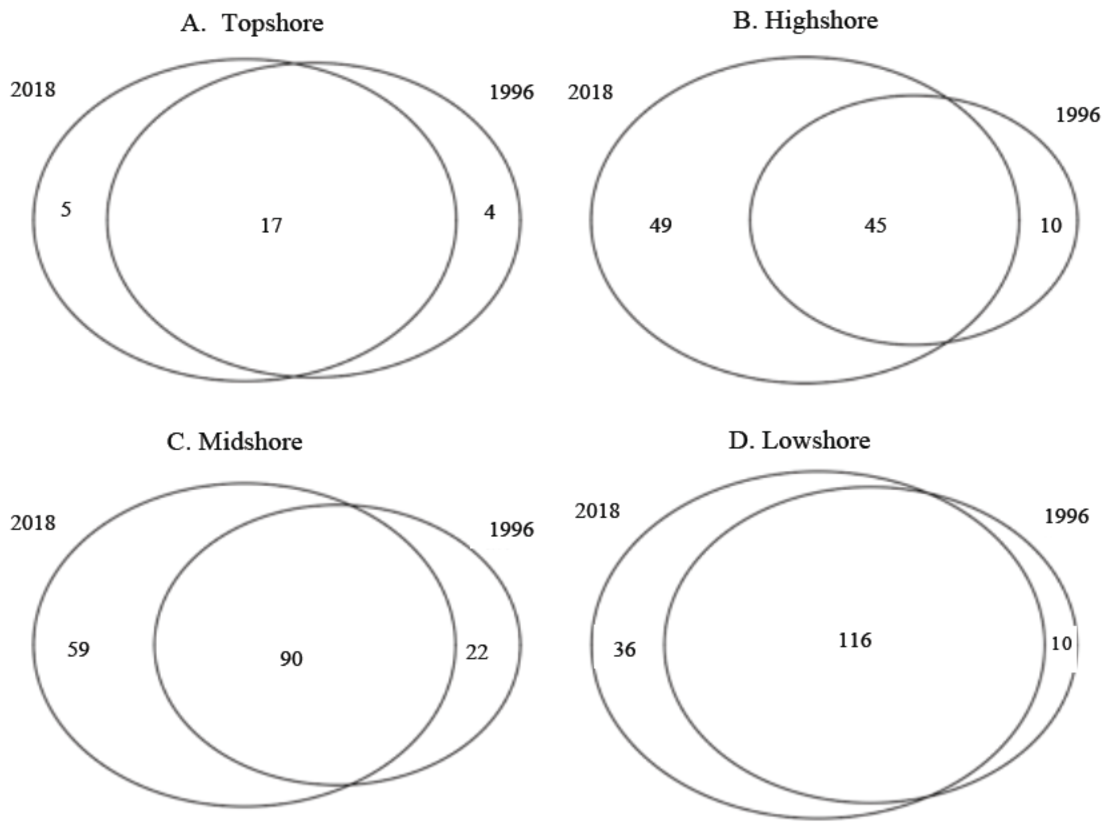

Figure 2. 2: Number of species exclusive to each of the years 1996 and 2000 and species that were shared between the two years (dark grey bars), for (A) Top shore, (B) High shore, (C) Mid shore, and (D) Low shore.

Table 2. 1: Results of two-way ANOVA showing effects of year and site on species richness in four intertidal zones. The differences in the degrees of freedom (Df) in this and the following tables reflect missing data for individual zones at certain sites, either due to sand inundation or loss of historical data

Top shore	Df	SS	MS	F	p
Year	1	23.12	23.120	28.90	0.0001 ***
Site	9	146.02	16.224	20.28	0.0001 ***
Year:Site	9	75.08	8.342	10.43	0.0001 ***
Residuals	180	144.00	0.800		

High shore	Df	SS	MS	F	p
Year	1	153.9	153.89	57.448	0.0001 ***
Site	10	260.9	26.09	9.741	0.0001 ***
Year:Site	10	322.1	32.21	12.024	0.0001 ***
Residuals	198	530.4	2.68		

Mid-shore	Df	SS	MS	F	p
Year	1	3190	3190	284.78	0.0001 ***
Site	8	1609	201	17.95	0.0001 ***
Year:Site	8	1303	163	14.54	0.0001 ***
Residuals	341	3820	11		

Low shore	Df	SS	MS	F	p
Year	1	583	583.2	66.35	0.0001 ***
Site	9	1174	130.4	14.84	0.0001 ***
Year:Site	9	846	94.0	10.69	0.0001 ***
Residuals	380	3340	8.8		

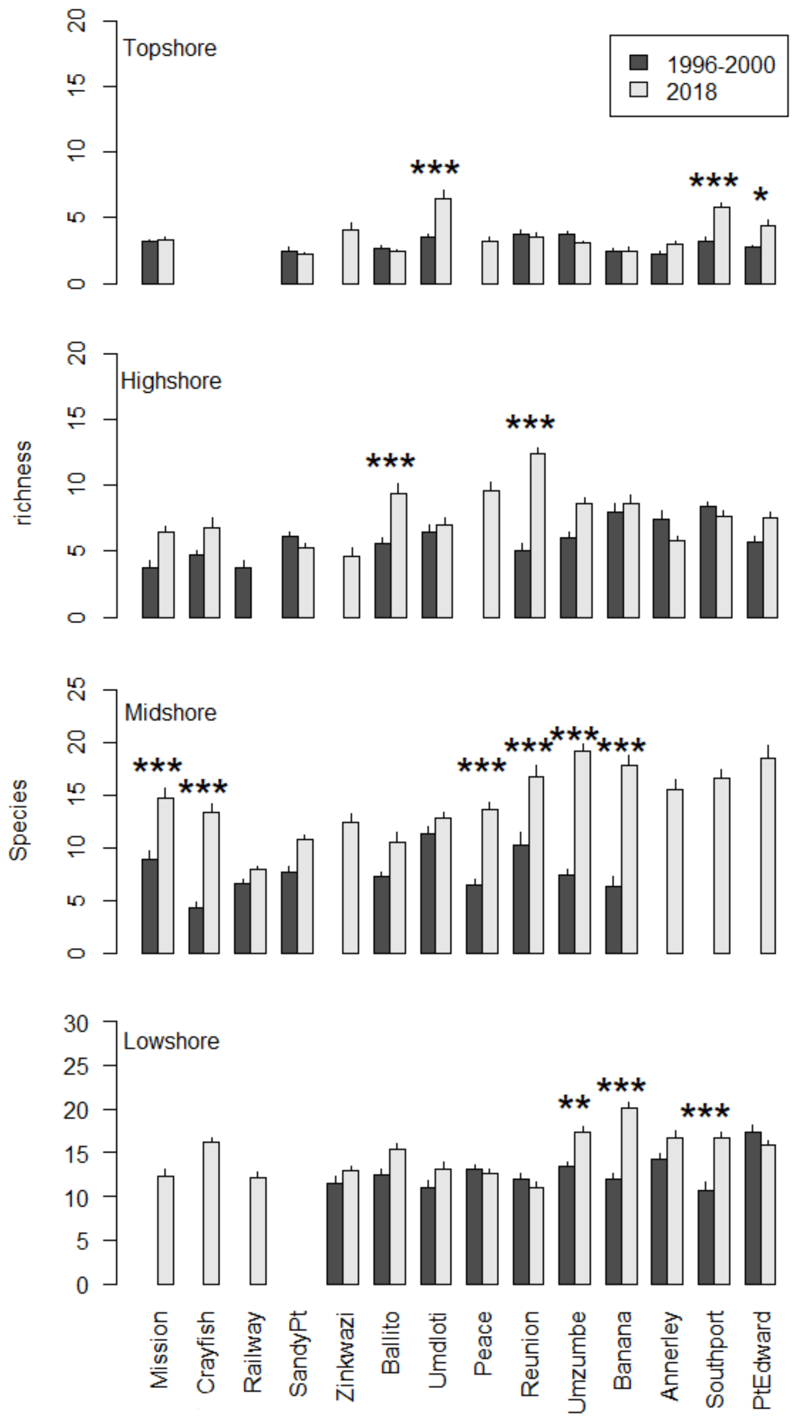

Figure 2. 3: Species richness (*i.e.* number of species) per site for the years 1996-2000 (dark grey bars) and 2018 (light grey bars), for (A) Top shore, (B) High shore, (C) Mid shore, and (D) Low shore. Gaps in the figures represent missing data due to the loss of some historical data and the natural absence of certain zones at some sites. Asterisks distinguish different levels of significance: P=0.001 (***), P<0.01 (**) and P<0.05(*).

The interactive effects of year and site on Pielou's evenness were also significant for all four zones (Table 2.2). An increase in evenness was consistently observed in the low and mid-shore, while there was a decrease in the evenness in the top shore and no significant difference between the years in the high shore (Table 2.2, Fig. 2.4).

Table 2. 2: Results of two-way ANOVA showing effects of year and site on evenness in four intertidal zones

Top shore	Df	SS	MS	F	p
Year	1	3.116	3.1156	129.97	0.0001 ***
Site	9	3.391	0.3768	15.72	0.0001 ***
Year:Site	9	4.146	0.4606	19.22	0.0001 ***
Residuals	174	4.171	0.0240		
High shore	**Df**	**SS**	**MS**	**F**	**p**
Year	1	0.014	0.01436	0.692	0.406
Site	10	0.816	0.08161	3.934	0.0001 ***
Year:Site	10	1.167	0.11670	5.626	0.0001 ***
Residuals	196	4.065	0.02074		
Mid-shore	**Df**	**SS**	**MS**	**F**	**p**
Year	1	8.679	8.679	611.825	0.0001 ***
Site	8	0.764	0.095	6.728	0.0001 ***
Year:Site	8	0.347	0.043	3.058	0.0025 **
Residuals	332	4.710	0.014		
Low shore	**Df**	**SS**	**MS**	**F**	**p**
Year	1	5.438	5.438	410.078	0.0001 ***
Site	9	0.938	0.104	7.864	0.0001 ***
Year:Site	9	0.770	0.086	6.451	0.0001 ***
Residuals	380	5.039	0.013		

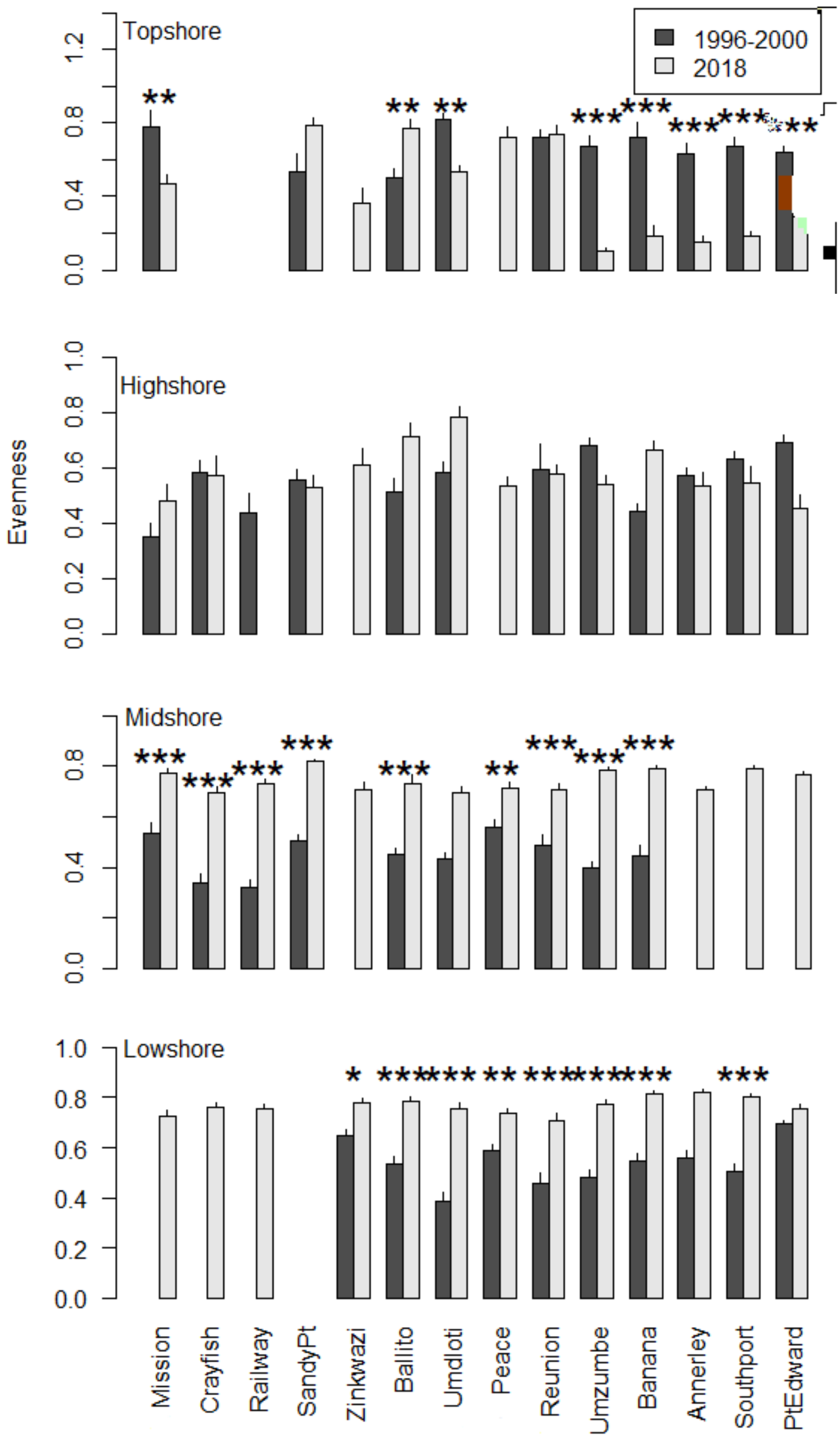

Figure 2. 4: Pielous's evenness per site for the years 1996-2000 (dark grey bars) and 2018 (light grey bars), for (A) Top shore, (B) High shore, (C) Mid shore, and (D) Low shore. Gaps in the figures represent missing data due

to the loss of some historical data and the natural absence of certain zones at some sites. Asterisk distinguishing different levels of significance: P=0.001 (***), P<0.01 (**) and P<0.05 (*).

Decadal changes in community structure

In all four intertidal zones, differences in community structure existed between decades (Fig. 2.5), but the nature and effect size of the differences varied among sites, as reflected in the significant year-site interactions (Table 2.3, Fig. 2.5). Nevertheless, significant differences were consistently found within sites between 2000 and 2018 (Table A2 A-D, Appendix, showing pairwise posthoc comparisons)

When looking at the contributions of different functional groups to differences in community composition between years (SIMPER), the following changes in abundances (*i.e.* % cover) emerged. In the top shore, the abundance of periwinkles decreased at five of the ten sites (Table 2.4). In the high shore barnacle cover consistently increased at all of the three Northern sites, whereas in the mid-shore corticated red algae increased, albeit modestly, at most of the Northern sites and zoanthids decreased at the three sites. In the low shore, mussels decreased substantially at six of ten sites (Tables 2.4, 2.5, Fig. 2.5).

Table 2. 3: Results of two-way fully crossed PERMANOVA showing effects of year and site on species abundance in four intertidal zones.

Top shore	Df	SS	MS	F	R^2	p
Year	1	1.4374	1.43744	94.954	0.14954	0.001 ***
Site	9	3.7807	0.42007	27.749	0.39330	0.001 ***
Year:Site	9	1.6696	0.18551	12.254	0.17369	0.001 ***
Residuals	180	2.7249	0.01514		0.28347	
Total	199	9.6126			1.00000	

High shore	Df	SS	MS	F	R^2	p
Year	1	3.925	3.9247	50.384	0.10355	0.001 ***
Site	10	11.412	1.1412	14.650	0.30111	0.001 ***
Year:Site	10	7.139	0.7139	9.165	0.18838	0.001 ***
Residuals	198	15.423	0.0779		0.40696	
Total	219	37.900			1.00000	

Mid-shore	Df	SS	MS	F	R^2	p
Year	1	7.297	7.2970	75.639	0.08621	0.001 ***
Site	8	28.383	3.5479	36.776	0.33532	0.001 ***
Year:Site	8	16.067	2.0084	20.818	0.18982	0.001 ***
Residuals	341	32.897	0.0965		0.38865	
Total	358	84.643			1.00000	

Low shore	Df	SS	MS	F	R^2	p
Year	1	7.323	7.3233	76.672	0.11861	0.001 ***
Site	9	11.282	1.2535	13.124	0.18272	0.001 ***
Year:Site	9	6.843	0.7603	7.960	0.11083	0.001 ***
Residuals	380	36.295	0.0955		0.58784	
Total	399	61.743			1.00000	

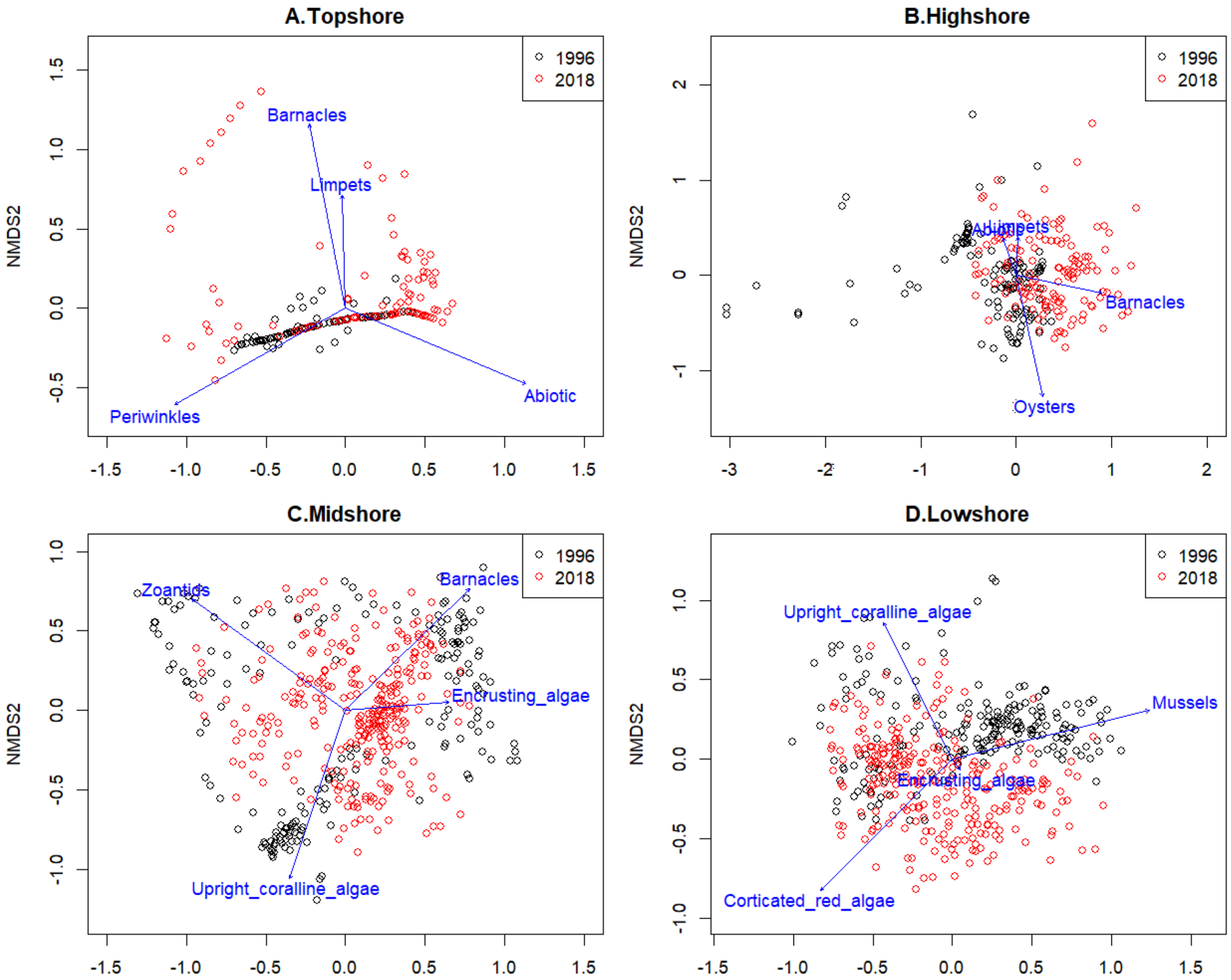

Figure 2. 5: Nonmetric Multidimensional scaling (NMDS) plots based on the functional group abundances of rocky shore organisms in 1.0 x 0.5 m quadrats. Different marker colours indicate different years: 1996-200 (black) and 2018(red). Blue vectors indicate the functional groups that contribute the highest to the observed change.

Table 2. 4: Semi-quantitative results from SIMPER analyses to identify the contributions of different functional groups to changes in community structure between years for different intertidal zones: Top shore, and High shore. The sizes of circles represent the percentage contribution of functional groups to observed differences between years for each site (large circles = 10.0-20.0%; small circle = 5.0-9.9%). Blue circles indicate an increase in mean abundance (percentage cover), whereas red circles indicate a decrease.

	Abiotic	Periwinkles	Barnacles	Limpets	Mussels	Oysters	Worms	Anemones	Zoantids	Encrusting algae	Upright Coralline algae	Corticated green algae	Corticated Brown algae	Corticated red algae	Filamentous Green algae	Filamentous Brown algae	Filamentous red algae
Top shore																	
Mission																	
SandyPt		🔴															
Ballito																	
Umdloti																	
Reunion																	
Banana		🔴															
Umzumbe		🔴															
Annerley																	
Southport		🔴		🔹													
PtEdward		🔴															
High shore																	
Mission	🔵		🔵			🔴									🔵	🔴	
Crayfish	🔴		🔵	🔸						🔵				🔹	🔴		
SandyPt			🔵	🔴							🔹				🔹		
Ballito				🔹				🔹									
Umdloti		🔵															
Reunion		🔵														🔴	
Umzumbe		🔴															
Banana														🔵			
Annerley																	
Southport				🔸													
PtEdward														🔹			

Table 2. 5: Semi-quantitative results from SIMPER analyses to identify the contributions of different functional groups to changes in community structure between years for different intertidal zones: Mid-shore, and Low shore. See caption of Table 2.5 for further details on symbol colours and sizes.

	Abiotic	Periwinkles	Barnacles	Limpets	Mussels	Oysters	Worms	Anemones	Zoantids	Encrusting algae	Upright Coralline algae	Corticated green algae	Corticated Brown algae	Corticated red algae	Filamentous Green algae	Filamentous Brown algae	Filamentous red algae
Mid-shore																	
Mission									🔴					🔹			
Crayfish											🔵		🔹				
Railway	🔵										🔴			🔹			
SandyPt					🔹					🔴		🔹	🔹	🔹			
Ballito			🔴				🔹		🔵								
Umdloti		🔹					🔹										
Peace			🔹	🔹							🔴						
Reunion		🔵			🔹				🔴								
Umzumbe		🔹	🔴												🔻		
Banana		🔵							🔴						🔹		
Low shore																	
Zinkwazi	🔹		🔹									🔻	🔻			🔻	
Ballito			🔹		🔴												
Umdloti			🔹	🔹									🔻	🔹			
Peace																	
Reunion					🔴									🔵			
Umzumbe	🔹				🔴						🔹						🔹
Banana					🔴												
Annerley					🔴									🔹			🔹
Southport		🔹			🔴												
PtEdward												🔻					

Most notable changes in species cover

Several of the observed changes were explored at the species level (Fig. 2.5), since they likely reflect larger-scale distributional shifts and/or range shifts and anthropogenic impacts. The most notable were as follows,, (1) There were significant decreases in the average percentage cover of the commonly harvested brown mussel *Perna perna* between 2000 and 2018 in Central and Southern KZN in the low shore zone (Fig. 2.5). Unfortunately, no low-shore data exist for the Northern sites (Zululand) from 1996-2000, which precludes a complete regional assessment. (2) There was a decrease in the abundances of the tiny littorinid snail *Afrolittorina africana* and another littorinid snail *Echinolittorina natalensis* in all the regions. The striped topshell *Oxystele tabularis*, found in the mid-shore zone, increased in all the regions. (3) The toothed barnacle *Chthamalus dentatus* increased in all the regions, while the eight-shell Barnacle *Octomeris angulosa* decreased in Southern KZN and the rosy volcano barnacle *Tetraclita rufoticta* increased in Zululand. The volcano barnacle *Tetraclita serrata* increased in all the regions. (4) The sandy zoanthid *Palythoa nelliae* decreased non-significantly in Zululand and significantly in Southern KZN and increased significantly in Central KZN. The Durban Zoanthid *Zoanthus durbanensis* decreased in Southern KZN, while the green Zoanthid *Zoanthus natalensis* decreased in Central KZN and the violet zoanthid *Zoanthus sansibaricus* increased in Zululand. (5) The hinged coralline algae *Arthrocardia* spp increased in Zululand and Southern KZN. The branching coralline algae *Jania* spp increased in Southern KZN, while the arrowhead alga *Jania sagittata* decreased in Southern KZN.

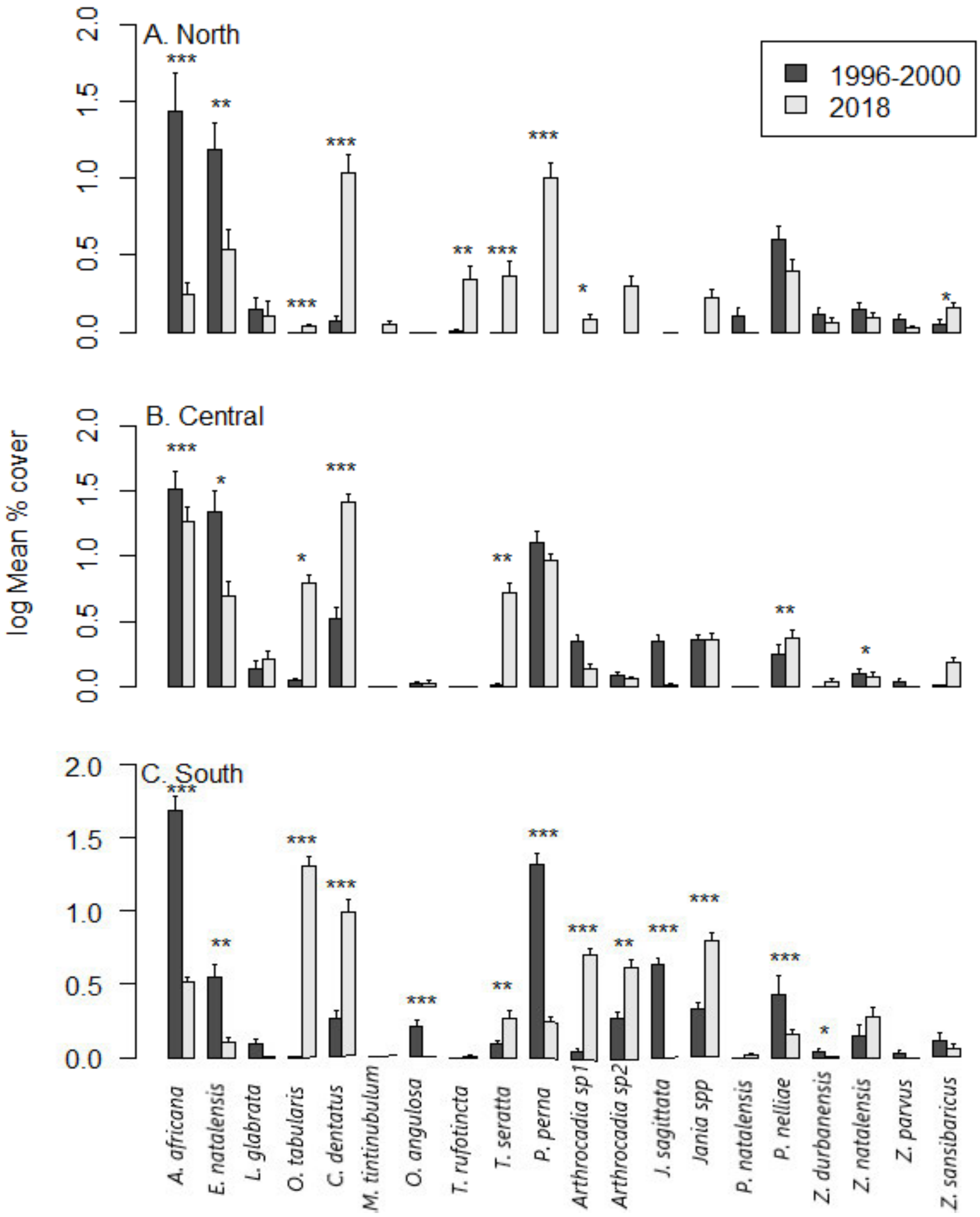

Figure 2. 6: Mean (+/-SE) percentage cover of selected species for the years 1996-2000 (dark grey bars) and 2018 (light grey bars), for (A) Zululand, (B) Central KZN, (C) South KZN. Error bars represent variability among the sites.

Gaps in the figures represent missing data due to the loss of some historical data and the natural absence of certain species in some regions. Asterisks indicate the level of significance.

The arrival of invasive alien species and range expansions

The presence of two conspicuous alien and well known invasive barnacles was detected in this study, that of the giant purple barnacle *Megabalanus tintinnabulum* (Fig. 2.7a,b) and the titan acorn barnacle *Megabalanus coccopoma* (Fig. 2.7c,d). Their presence has not been reported on South African rocky shores before, and thus constitutes a new arrival.

Figure 2. 7: The arrival of two large well-known alien species was detected in this study, that of *Megabalanus tintinnabulum* (a,b) and *Megabalanus coccopoma* (c,d).

Discussion

This study investigated changes in the biodiversity patterns on the KwaZulu-Natal coastline over the past 20 to 25 years by evaluating the changes in species richness, evenness and overall community structure through a comparison of a dataset collected between 1996 and 2000 with data from re-surveys of the same sites in 2017-2018 undertaken for my thesis. The hypothesis that the rocky shore communities would have changed over the past decades due to environmental changes including climate change and regional warming, with an increase in warm-water and a decrease in temperate species was upheld. Also, the hypothesis that stated that invasive alien species would have moved into the KZN area, which has previously not experienced any notable invasions, was also sustained. The hypothesis that stated that harvested species would have declined in abundance resulting in increased evenness was supported, but the expectation that it would result in decreased species richness particularly in the low, mid and high shore zones was found to be false. However, overall shifts in community structure were observed for all intertidal zones.

Decadal changes in species richness & evenness

Species richness consistently increased in the lower part of the shore, *i.e.* the mid- and low-shore zones. As species shift their distributional ranges, it is commonly observed that the invading species invade a region faster than local species are receding, which may result in increased species richness due to differences in the rates of invasion and evasion (Walther et al. 2002). Along with an increase in species richness, an increase in evenness was observed in the lower part of the shore, According to the intermediate disturbance hypothesis, moderate levels of disturbance can create conditions that result in increased species richness and evenness, whereas low or high levels of disturbance result in low richness and evenness (Dial

& Roughgarden 1998). The recorded increase in evenness in the lower parts of the shore could have therefore reflected moderate changes in the zones whereas the decrease in evenness on the top shore could have resulted from greater disturbance experienced in the zone possibly from the shifts in the abundance of the rosy barnacle species Tetraclita rufotincta, with an increase of this tropical organism on the top shore.

Decadal changes in functional group-based community structure/species

Most notable, and of conservation concern, was the consistent decline in the abundance of the brown mussel, *Perna perna* which is commonly harvested on the East coast of Southern Africa. Recreational fishing is common along the KZN coastline and contributes to the harvesting of mussels. Local communities report that there has been a decline in the mussel stocks on the East coast since the 1900s (Steyn et al. 2019). However, there are regional differences in human exploitation, and such differences have been reported between the Maputaland and Natal sub-regions in KZN. The rocky shores in the Natal sub-regions are exploited by recreational collectors who harvest at a significantly lower rate than the subsistence harvesters in the rocky shores of the Maputaland subregion (Sink 2001). These findings are therefore in agreement with Sink et al (2005), who concluded that subsistence harvesting plays a prominent role in determining large-scale patterns in community structure. Some of the sites reported to have experienced sharp declines in stocks gained in abundance after harvesting was reduced (Steyn and Schleyer, 2012), which further implicates harvesting as the primary factor in determining mussel abundances. Similarly, Olbers (2017) observed dramatic declines in the *Perna perna* mussels at sites in the iSimangaliso Wetland Park (in Zululand) between 2008 and 2016, which was attributed to uncontrolled harvesting and reduced mussel recruitment. A reduction in mussel-bed cover, which is a preferred substratum for mussel larvae to settle in, is likely responsible for the prolonged reduction in the mussel settlement and recruitment in the area (Harris et al. 1998). Mussels are important ecosystem engineers in the intertidal zone, and a loss of mussels may be detrimental to the entire rocky shore community (Gutiérrez & Palomo 2016). The harvesting impact can thus transform communities, especially when it is combined with other disturbances, such as the introduction of alien and invasive species (Walther 2010).

The mid-shore region also experienced similar shifts in community organisations as the low-shore (e.g. increased evenness). There was a significant decrease in the abundance of barnacles, zoanthids and coralline algae in the mid-shore. Zoanthids are cnidarians that have two modes of feeding, they capture tiny prey in the water column but mostly depend on endosymbiotic microalgae for their nutrition (Branch et al. 2016). Their dual mode of feeding allows zoanthids to be very successful their success is also driven by their ability to recolonize a cleared area within a space of a few months (Rabelo et al. 2013). Since Zoanthids tend to occupy large areas, when their abundance decreases. That coupled with decreases in the abundance of other competitive organisms such as coralline algae (Steneck et al. 1991) , it can result in increased evenness.

There was a decrease in the abundances of the African periwinkle *Afrolittorina africana* and the nodular periwinkle, *Echinolittorina natalensis* in all the regions. Periwinkles, due to their globular body shape are likely experiencing susceptible to changes in atmospheric temperature. The increase in striped the topshell *Oxystele tabularis* in the mid-shore zone in all the regions and the recorded decrease in littorinid snails is likely a reflection of range shifts due to climate change. *Afrolittorina africana* is currently expanding poleward (pers. comm. MC Pfaff), possibly due to the top shore experiencing warming. Climate warming results in poleward shifts in the geographic ranges of many marine species (Cheung et al. 2012, Mieszkowska et al. 2019).

Increased abundance of coralline algae

Upright coralline algae are known indicators of disturbance, *e.g.* by harvesting or sand inundation. Coralline algae also tend to increase in abundance when mussel beds get eliminated, because the two compete for space (Harris et al. 1998). The observed increase in the abundance of coralline algae *Arthrocardia* spp. and *Jania cultrata* in the Northern and Southern sub-regions of KZN could therefore be indicative of the thinning of the mussel bed area.

The arrival of two alien barnacles

The East coast of South Africa has been less affected by alien and invasive species than the West coast, likely due to the challenge faced by new species of becoming established in this lower-nutrient system (Branch & Branch 1981), where competition between species for resources is more pronounced. Furthermore, communities that have higher species diversity, as is the case for the South African East coast in comparison to the West coast, are thought to be more resistant to invasions than those with fewer species (Siegfried et al. 1994). Recently there has been a marked increase in the number of alien species recorded in South Africa, although most are confined to the West and South coasts. To date, no invasive alien species have been reported on intertidal rocky shores of the Natal Ecoregion (Mead et al. 2013). It is therefore a remarkable finding of this study that two large and conspicuous alien barnacles have arrived on the KZN coastline in the past 20 years. The titan acorn barnacle *Megabalanus* *coccopoma* has been previously recorded by Biccard and Griffiths (2016) to occur on buoys near Durban and Richards Bay ports. These authors remarked that "the rocky shores in KwaZulu-Natal should be monitored for this species" since the giant purple barnacle *M. tintinnabulum* is a known invasive species in other countries around the world (Yamaguchi et al. 2009, Newman et al. 2011). A follow-up survey from this study has shown that both species are now distributed along the entire KZN coast, the latter having become very common in very wave-exposed portions low down on rocky shores and in the subtidal (Pfaff et al., unpublished data).

The introduction of these aliens can have detrimental impacts on the local community structure and function as it allows the establishment of a mixed community of native and alien species. The shift driven by community reorganisation leads to shifts in the distributions of existing species, modification and destabilisation of the communities making them more vulnerable to further invasions (Walther 2010, Lages et al. 2011). The abundance of these barnacles can be reduced by harvesting, as congeneric barnacles are a common food source in other countries, such as Chile and Peru (Siegfried et al. 1994). During the follow-up surveys, it was noted that fishermen have used these large barnacles as bait (Pfaff et al., unpublished data), however, at this stage barnacles are not a common food source along the South African coast.

Species range expansions

One of the most frequently reported effects of climate change is the shift in the distribution of marine organisms (Harley et al. 2006, Jarre et al. 2015), and the shifts are continuing and becoming more prevalent with predictions indicating that the shifts will continue to be prevalent in the coming decades. The direction of the shifts is expected to be poleward, resulting in increased species invasions in temperate regions and localised extinctions in tropical regions, or increased dominance of a tropical species in the poleward portion of its distribution range (Cheung et al. 2012). The results show that in the 1990s the rosy volcano barnacle *Tetraclita rufotincta* which is a warm water species was only found on the Northern-most shores of KZN, in the Delagoa ecoregion (Sink et al. 2005), however and in the current study high abundances of it were detected in the Northern portion of the adjacent Natal ecoregion. This suggests that this barnacle has been expanding its range from the tropical Western Indian Ocean region in the North to the subtropical region of Zululand. This is an expected result in line with the predicted impacts of increased atmospheric warming. While it has been observed elsewhere that tropical species tend to move into the temperate regions (Parmesan 2006, Cheung et al. 2012), There was a decrease in the abundances of the African periwinkle *Afrolittorina africana* in all regions, the decrease was more prominent in the northern KZN region. This temperate species has been observed in other surveys and found to be undergoing a poleward expansion (pers. comm. MC Pfaff). Similar range shifts have only been recorded in fish in South African waters (Lloyd et al. 2012).

Conclusion

This study contributes substantially to the understanding of anthropogenic impacts on coastal biodiversity and is providing valuable data for the management of these vulnerable ecosystems. It did not, however, attempt to identify drivers of changes in community structure but instead focused on characterising patterns, and further investigation is required to identify the underlying mechanisms driving the observed changes. Despite this, alterations in abundance and distribution were clearly linked to both climate change and exploitation. Further research has to be conducted at the site level as well as at the region scale to clearly reflect the conditions at these finer scales.

CHAPTER 3: COMPARISON OF SURVEYING METHODS FOR MONITORING ROCKY SHORE ECOSYSTEMS

Abstract

Monitoring is an essential component of the conservation and management of ecological systems, as it ensures that the most recent status of a system is captured and changes detected; thus, impacts can be tracked and action can be taken. Therefore, it is essential to ensure that the methods are robust and can detect change easily and rapidly. In this study, a pair of rocky shore sites were sampled using two different sampling methods to determine the most effective and suitable method for monitoring rocky shores: visual in-situ surveys and photographic surveys. The visual *in-situ* estimation picked up more species than the photographic surveys. This is expected, as the 2D nature of photographs and the resolution limits the ability to pick up rare and inconspicuous species. Monitoring is often carried out by observing the overall changes in community structure rather than individual species, and for this purpose, photographic surveys save time in the field and remove the influence of rare species on the observed assemblages. When the methods were compared in terms of community structure, greater abundances were observed using visual surveys. The species and groups that contributed to the differences between the methods were explored to investigate further which species were missed by the photographic quadrats. To further explore the feasibility of each method, the statistical precision of each method was evaluated using a multivariate pseudo standard-error (MultSE) analysis, which demonstrated that the visual *in-situ* surveys had a greater statistical precision in three zones lowest on the shore while the photographic quadrats had a greater precision in the top shore zone.

Introduction

Considering the imminent threat of global climate change there is an urgent need to initiate long-term monitoring Programmes that will document the response of species, assemblages and ecosystem functioning to changes in the environment (Clutton-Brock & Sheldon 2010, Palmer et al. 2011, Phillips et al. 2018). Monitoring is necessary for the design and implementation of appropriate management plans and for the assessment of their effectiveness (Wernberg et al. 2011). Monitoring Programmes that provide data that extend over adequate periods of time are particularly valuable for determining long-term trends, which can be masked or exaggerated by shorter-term variability (Harris 2005, Jarre et al. 2015). They are consequently valuable for research in many areas of ecology and evolutionary biology. The effects of changes in climate on reproductive timing, growth, distribution and density of different organisms can be most readily observed from long-term studies (Clutton-Brock & Sheldon 2010).

Historically, changes in the distribution of fauna and flora were determined using the distribution of only the dominant and conspicuous species (Clutton-Brock & Sheldon 2010). This method is, however, considered disadvantageous when looking at whole communities, as it does not consider the effects of changes in populations of small and rare species (Field & Mcfarlane 1968) and interactions between species that may be important for understanding changes in communities (Clutton-Brock & Sheldon 2010). To address the impacts of anthropogenic and natural disturbances, it is therefore more suitable to consider the species-abundances of whole communities, before multi-species indicators can be developed (Holland & Polgar 1976, Clarke 1993, Solow 1993, Moreno 2001, Flåten et al. 2007, Kordas et al. 2011, Ferrari et al. 2016, Jaramillo et al. 2017). There are many ways to sample communities, but for the purpose of this study, visual *in-situ* estimations of species abundances and photographic surveys of species abundances were investigated.

Visual *in-situ* estimation refers to a method whereby measures of species abundance are obtained through estimating percentage cover and/or counting organisms in their natural environment by sub-sampling a habitat through scoring of replicate quadrats (Meese & Tomich 1992). Visual in-situ estimations of community attributes, such as species abundance and size distributions can generate data rapidly when a researcher is well-trained in species identification (Olbers 2017). Usually researchers work in a pairs with an observer and a scribe. In situ observers are able to identify species, estimate area by quadrat and report this directly to the scribe. Since time is usually a limiting factor and weather and swell can be challenging during intertidal surveys this method can, however, limit the number of replicates that are scored during a given period which compromises the statistical power required to detect changes.

Photographic surveys have become popular in benthic ecology since the onset of digital photography in the early 2000s. They have several advantages compared to visual *in-situ* sampling: there is less variation between observers (Meese & Tomich 1992), they require less time to capture as there is no data-recording in the field, which allows for more replicates to be sampled during a limited time in the field; and the images can be kept permanently, allowing for reanalyses by future researchers for various purposes (Bohnsack 1979). The person collecting photographic data in the field does not need species identification and taxonomic skills, which makes this method suitable in situations where expertise are limited (Dye 1998). Photographic quadrat sampling is thus often considered more practical, rapid, and reproducible than visual *in-situ* estimation and extractive sampling. For these reasons, photographic surveys probably deserve a role in most intertidal surveys (Meese & Tomich 1992). They do, however, also have specific limitations which may compromise their suitability for evaluating changes of ecosystem states. For example, the data accuracy and resolution is limited since small and obscured species cannot be detected and species identification is often challenging. To improve the accuracy, smaller sampling units (*i.e.* quadrats) are often used; this means more replicates have to be conducted to achieve the optimal sampling effort, resulting in substantial amounts of data-processing time after completion of fieldwork (Bohnsack 1979, Meese & Tomich 1992). Whilst a greater number of replicates should theoretically increase statistical power, the use of smaller quadrats will likely lead to greater variability between replicates resulting in a greater within-group variance than obtained from larger quadrats (Field & Mcfarlane 1968). Considerations of statistical power are essential when designing a long-term monitoring protocol; however, of equal importance are considerations of feasibility considering sampling effort (Hoenig & Heisey 2001).

When conducting biodiversity surveys, researchers work under the assumption that the methods used are accurate and robust enough to represent the actual state of the ecosystem *e.g.* in terms of species abundance and richness (Meese & Tomich 1992). Before conducting ecological studies, it is therefore crucial to select an appropriate method that comprises suitable sample size and number of replicates (Anderson & Santana-Garcon 2015). Another important consideration when choosing a sampling method for benthic monitoring programmes is how powerful the method is in detecting differences in community structure. Whilst univariate data lend themselves to power analysis to determine adequate sample sizes, no straightforward equivalent exists for multivariate data (Field & Mcfarlane 1968). Since statistical power is inversely related to sample variance, different methods have been developed to evaluate the variance of multivariate data derived from replicate sampling units. One of them proposes to calculate the statistical precision for multivariate data (MultSE), as an analogue to the standard error of the mean for univariate data (Anderson & Santana-Garcon 2015). MultSE gives the variance around the sample mean based on the chosen dissimilarity measure under repeated sampling for a given sample size. This method incorporates a randomised resampling technique to improve estimation of the multivariate standard error values by increasing numbers of replicate samples (Anderson & Santana-Garcon 2015). Whilst generally used to estimate optimal numbers of replicates for a study design, statistical precision can also be used to compare different sampling methods, to determine which method is more precise and therefore more powerful in detecting differences in multivariate species-abundance data (Kuno 1986).

The overarching aim of this study is to address methodological considerations of the most effective and suitable method for monitoring rocky shores within the Natal ecoregion by testing whether the visual *in-situ* estimation of percentage cover of organisms reveals comparable results in terms of community structure to those in photographic surveys. Specifically, various hypotheses were tested regarding differences between the visual *in-situ* surveys and the photographic surveys:

(i) species richness will be underestimated by photographic sampling because rare species and hidden species are missed.

(ii) broad patterns of community structure (in space and time) will be captured equally by both methods since these tend to be driven by the common species.

(iii) at lower data resolution, *i.e.* when species are pooled into functional groups, differences that exist between the two methods will be less pronounced than at species level;

(iv) the statistical precision will be greater in photographic surveys than visual *in-situ* estimations since differences between replicates that are based on rare species will not be detected in photographs.

(v) No difference in precision between the methods is expected when analyses are done at functional group-based community structure level since differences between methods are likely equalised at the lower data resolution. Based on the findings of this study, recommendations for future sampling will be made.

Methods

Sampling area/region

Sampling was conducted at two sites: (1) Reunion Rocks is a harvested and polluted aeolian (fossilised sand dune) rock ledge near in Isipingo (29°59'7.77" S 30°58'0.58" E) and (2) Ballito is a relatively pristine granite rock ledge (29°32'25.4" S 31°13'10.9" E). Once-off surveys of the intertidal rocky shore were conducted in September 2018, according to two different sampling methods.

Sampling design

At each of the two sites, the intertidal zone was divided into four horizontal zones, comprising the top shore, high shore, mid-shore and low shore. These zones were selected based on dominant species reported by Sink (2001). In each zone, five replicate 0.5m x 0.5m quadrats were surveyed using visual *in-situ* estimation, a method commonly used in rocky shore surveys (see introduction). In each quadrat, estimates of percentage cover of all sessile species as well as the sizes and counts of all mobile species were recorded. Thereafter, an image of each quadrat was also taken for a comparison between the in-situ visual estimations and photographic surveys. The calculated mean size and counts of mobile organisms were subsequently converted to percentage cover data.

Data analyses

The images captured in the field were analysed in the lab using Coral Point Count with Excel extensions (CPCe 4.1) (Kohler & Gill 2006). 100 points were laid over each image in CPCe, and the organisms under the points were identified using a species catalogue within the

Programme, based on the Two Oceans guide (Branch et al. 2016). The species found between the points were not accounted for.

To determine whether species richness is underestimated by photographic sampling, as rare species are missed, rarefaction curves were plotted for both photographic and visual methods, using Paleontological Statistics (PAST 4.03) (Hammer et al. 2001). Thereafter, a repeated measures ANOVA with the factors: method (fixed – repeated factor), site (fixed), and zone, was conducted to determine if the differences in the species richness detected by the two methods were significant (95% confidence limit). The analysis was done using R version 3.6.3 (https://www.R-project.org).

To assess whether broad patterns of community structure (space, time) were captured equally by both sampling methods, a non-metric multidimensional scaling (NMDS) plot was made to visually compare the community structure between the two methods, using the Vegan package for multivariate analyses in R. Thereafter, a two-way fully-crossed PERMANOVA with the factors: method (fixed-repeated factor) and site was conducted to determine if there were significant differences in the community structure derived by the two methods, as well as interactions between sites. The PERMANOVA was done separately for each intertidal zone, as differences between zones are known to exist but were not the focus of this study. A SIMPER analysis was conducted to highlight the species that contributed to the difference between the methods, this was also done by zone. The community analyses were first done at species level and then the data were grouped into functional group-based community structure to assess whether differences between these methods would still persist at this lower data resolution.

To compare the statistical precision according to Anderson & Santana-Garcon (2015), a pseudo multivariate dissimilarity-based standard error (MultSE) analysis was conducted in R, which estimated the standard error of the multivariate centroid for each method. The rationale for this was that the precision is obtained by taking the sampled data and drawing random subsets from sampled data, then calculating the standard error within each subset, thereafter calculating the mean of the variance from all the subsets (Anderson & Santana-Garcon 2015). This mean represents the variance of the sampled data and thus reflects its statistical precision

Results

Rarefaction and estimations of species richness

Rarefaction curves represent the accumulation of species as samples are increased. When sufficient samples are taken to account for species in the population, a rarefaction curve approaches its asymptote (Colwell et al. 2012). The confidence limits were set at 95%. At Ballito (Fig. 3.1) in all four zones the visual *in-situ* estimations showed greater species richness than the photographic quadrats and in the top shore the visual *in-situ* quadrats also were able to pick up all the species in the population, thus causing the curve to reach the asymptote. At Reunion (Fig. 3.2) in the top shore the photographic quadrats showed greater species richness than the visual *in-situ* estimations. In the high-shore, mid-shore and the low-shore the visual *in-situ* estimations showed greater species richness than the photographic quadrats (Fig. 3.1 and 3.2). The rarefaction curves did not reach a horizontal asymptote for any of the four zones, suggesting that more replicates would be needed for an adequate sampling design. However, since this study is primarily focusing on a comparison of sampling methodologies, this aspect is noted, but not investigated further here.

Differences in species richness between visual estimation and photographic methods

Differences in species richness detected by the two methods varied among sites and zones, as reflected in a significant site-zone-method interaction (Table 3.1). At Ballito, there was a significant difference in the species richness between the two methods in the mid-shore and the low-shore, with the visual *in-situ* estimations showing greater species richness than photographic quadrats in both zones (Fig. 3.3). At Reunion, in the high-shore and the mid-shore, the visual *in-situ* estimations had significantly greater species richness than photographic quadrats (Fig. 3.3).

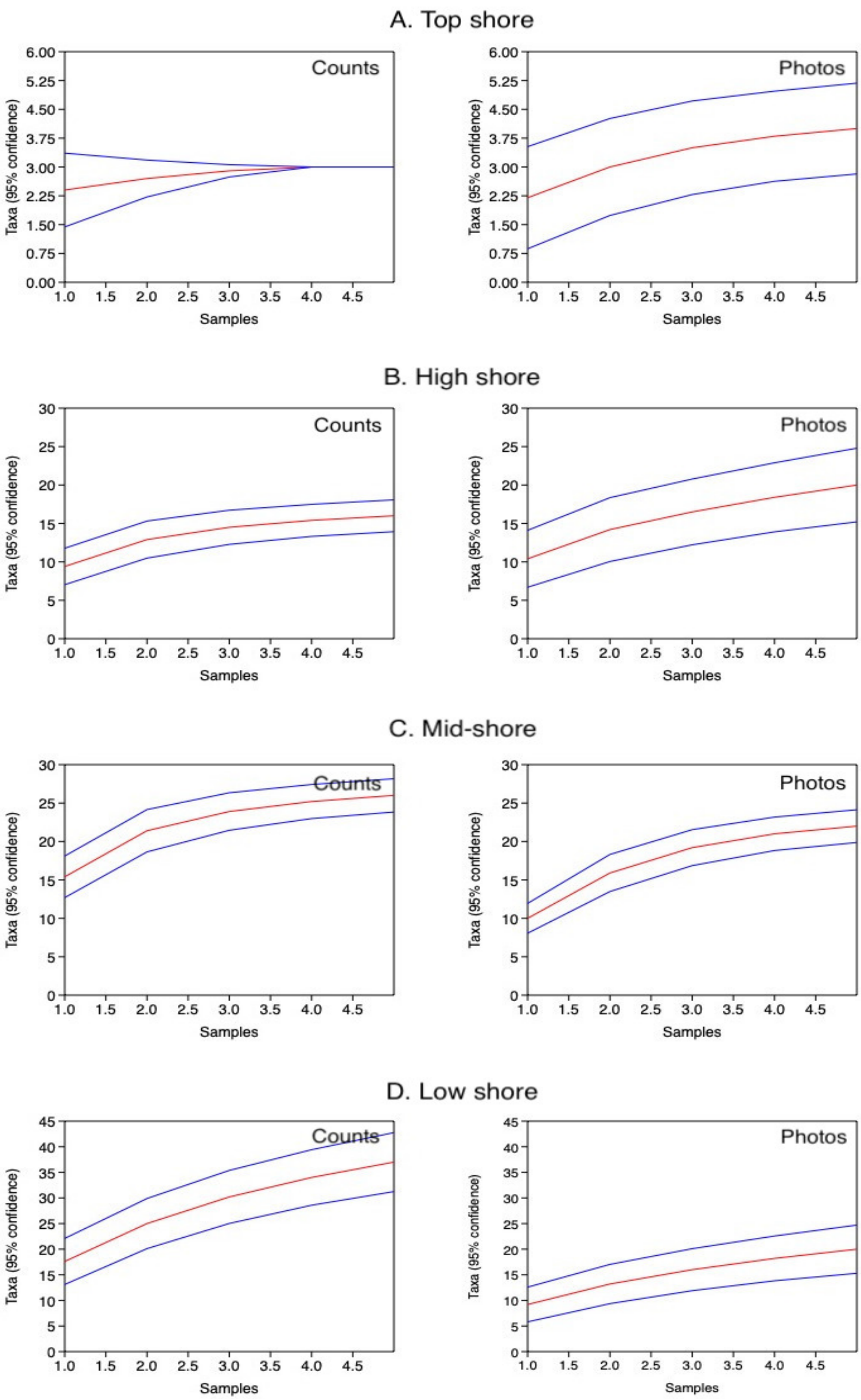

Figure 3. 1: Ballito: Rarefaction curves showing the accumulation of species (red line) and the 95% confidence limits (blue lines) for data collected using visual *in-situ* estimations (left) and photographic quadrats (right) in the (A) Top shore, (B) High shore, (C) Mid-shore and the (D) Low shore.

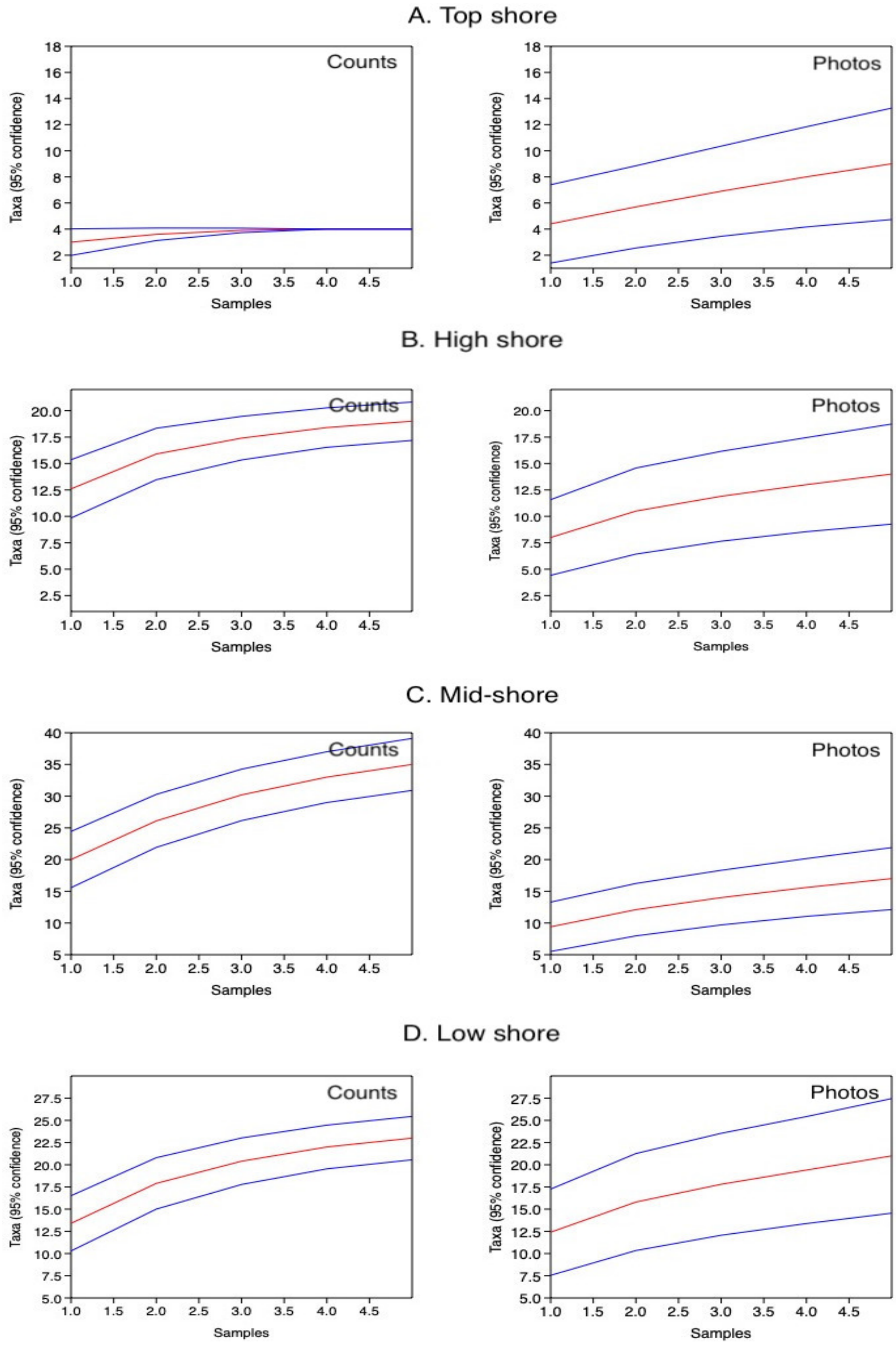

Figure 3. 2: Reunion: Rarefaction curves showing the accumulation of species (red line) and the 95%confidence limit (blue lines) for data collected using visual *in-situ* estimations (left) and photographic quadrats (right) in the (A) Top shore, (B) High shore, (C) Mid-shore and the (D) Low shore.

Table 3. 1: Results of three-way repeated measures ANOVA showing effects of method, site and zone on species richness and their interactions.

	DFn	DFd	F	p	
Site	1.00	4.00	1.993	0.231	
Zone	3.00	12.00	97.848	0.001	***
Method	1.00	4.00	304.268	0.001	***
Site:Zone	1.27	5.06	1.533	0.282	
Site:Method	1.00	4.00	0.130	0.737	
Zone:Method	1.23	4.92	23.566	0.004	**
Site:Zone:Method	3.00	12.00	9.919	0.001	***

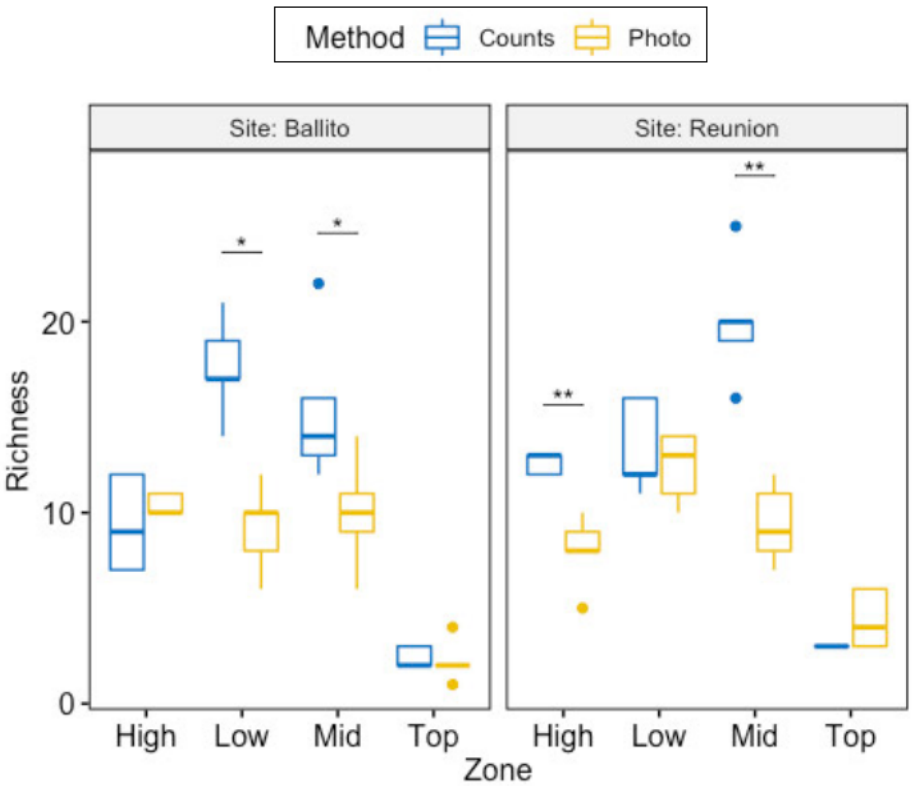

Figure 3. 3: Species richness (*i.e.* number of species) per site observed using visual *in-situ* estimations (blue boxes) and photographic quadrats (orange boxes). Asterisks distinguish different levels of significance: P=0.001 (***), P<0.01 (**) and P<0.05(*).

Differences in community structure between visual estimation and photographic methods

In all of the four intertidal zones, there was a significant interaction between method and site ($p < 0.05$) that affected the community structure, indicating that the nature of the differences between the visual *in-situ* estimations and photography surveys differed between the two sites (Figure 3.4 and Table 3.2). However, MDS plots indicate that clear differences existed in community structure recorded by different sampling methods in the low-shore and high-shore, where discrete non-overlapping clusters emerged for the two methods. In the mid-shore and top-shore, outliers obscured those differences (Fig. 3.4).

At Ballito in the top shore, the very small periwinkles *Afrolittorina africana* and *Echinolittorina natalensis* were picked up in higher abundances in the visual *in-situ* estimation method than in photographic quadrats (Fig. 3.5A), whereas at Reunion in the top shore, both these species and *Littoraria glabrata,* were picked up in higher abundances in the visual *in-situ* estimation method than in photographic quadrats (Fig. 3.6A).

In Ballito in the high shore, the affected species were limpet recruits*, Saccostrea cucullata, Siphonaria serrata* and *Tetraclita serrata*, which showed greater abundance in visual *in-situ* estimations, while *Afrolittorina. africana, Oxystele tabularis, and Siphonaria capensis* showed greater abundances in photographic quadrats (Fig. 3.5B). In the high shore at Reunion *Afrolittorina africana,* limpet recruits*, Saccostrea cucullata and Tetraclita serrata*, were recorded in greater abundances in visual *in-situ* estimations, while the *Cellana capensis, Helcion concolor* and *Octomeris angulosa* showed greater abundances in photographic quadrats (Fig. 3.6B).

At Ballito in the mid-shore, *Chthamalus dentatus, Helcion concolor,* limpet recruits*, Oxystele tabularis, Scutellastra aphanes, Scutellastra obtecta, Siphonaria capensis and Tetraclita serrata* showed greater abundance when surveyed using the visual *in-situ* estimations, whereas *Octomeris angulosa* and *Perna perna* showed higher abundances in photos (Fig. 3.5C), whereas in Reunion in the mid-shore limpet recruits*, Oxystele tabularis, Perna perna, Scutellastra aphanes, Scutellastra natalensis, Scutellastra obtecta,* and *Tetraclita serrata* showed higher abundance when surveyed using the visual *in-situ* estimations while the *Octomeris angulosa, and Saccostrea cucullate* showed greater abundances in photos (Fig. 3.6C).

In Ballito in the low shore *Cymbula sanguinans, Helcion concolor,* limpet recruits*, Oxystele tabularis, Scutellastra aphanes and Scutellastra obtecta* showed higher abundance when surveyed using visual *in-situ* estimations, whereas *Octomeris angulosa, Perna perna, Scutellastra natalensis* and *Tetraclita serrata* showed higher abundances in photographic quadrats (Fig. 3.5D), whereas in Reunion in the low shore, *Cymbula sanguinans* showed higher abundance when surveyed using visual *in-situ* estimations while *Fissurella natalensis, Helcion concolor, Octomeris angulosa, Oxystele tabularis, Perna perna, Saccostrea cucullata, Scutellastra natalensis, and Tetraclita serrata* showed higher abundances in photographic quadrats (Fig. 3.6D).

Table 3. 2: Results of two-way fully crossed PERMANOVA showing effects of method and site on species abundance in four intertidal zones.

Top shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
TMethod	1	0.20456	0.204561	6.4028	0.18815	0.002	**
TSite	1	0.24105	0.241046	7.5448	0.22171	0.001	***
TMethod:TSite	1	0.13041	0.130409	4.0818	0.11995	0.003	**
Residuals	16	0.51118	0.031949		0.47018		
Total	19	1.08720			1.00000		

High shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
HMethod	1	0.9309	0.93087	12.806	0.28145	0.001	***
HSite	1	0.4526	0.45265	6.227	0.13686	0.001	***
HMethod:HSite	1	0.7608	0.76079	10.466	0.23003	0.001	***
Residuals	16	1.1631	0.07269		0.35166		
Total	19	3.3074			1.00000		

Mid-shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
MMethod	1	0.9511	0.95112	7.6287	0.23545	0.001	***
MSite	1	0.4012	0.40123	3.2182	0.09933	0.005	**
MMethod:MSite	1	0.6924	0.69238	5.5534	0.17140	0.001	***
Residuals	16	1.9948	0.12468		0.49382		
Total	19	4.0396			1.00000		

Low shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
LMethod	1	1.2054	1.20536	12.7248	0.29775	0.001	***
LSite	1	0.7105	0.71055	7.5011	0.17552	0.001	***
LMethod:LSite	1	0.6168	0.61675	6.5110	0.15235	0.001	***
Residuals	16	1.5156	0.09473		0.37438		
Total	19	4.0483			1.00000		

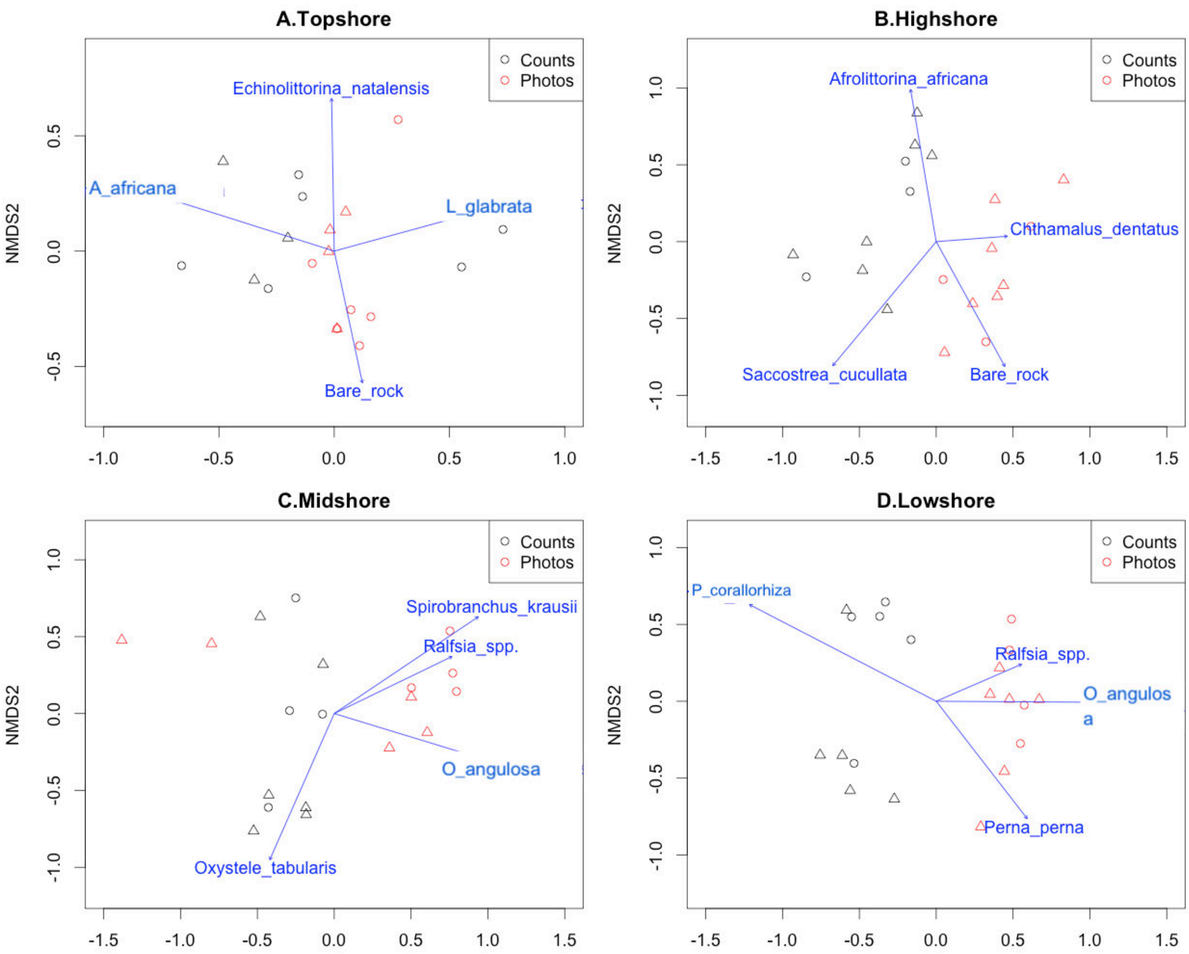

Figure 3. 4: Nonmetric Multidimensional Scaling (NMDS) plots based on the abundances of rocky shore organisms in 0.5 x 0.5 m quadrats. Different marker colours indicate different methods used to survey (visual *in-situ* estimations = black; photographic quadrats = red), and different marker symbols indicate different sites (triangles = Reunion; circles = Ballito). Blue vectors indicate the species that contribute the highest to the observed difference in abundances (*A. africana = Afrolittorina africana, L. glabrata = Littoraria glabrata, O. angulosa = Octomeris angulosa, P. corallorhiza = Plocamium corallorhiza*).

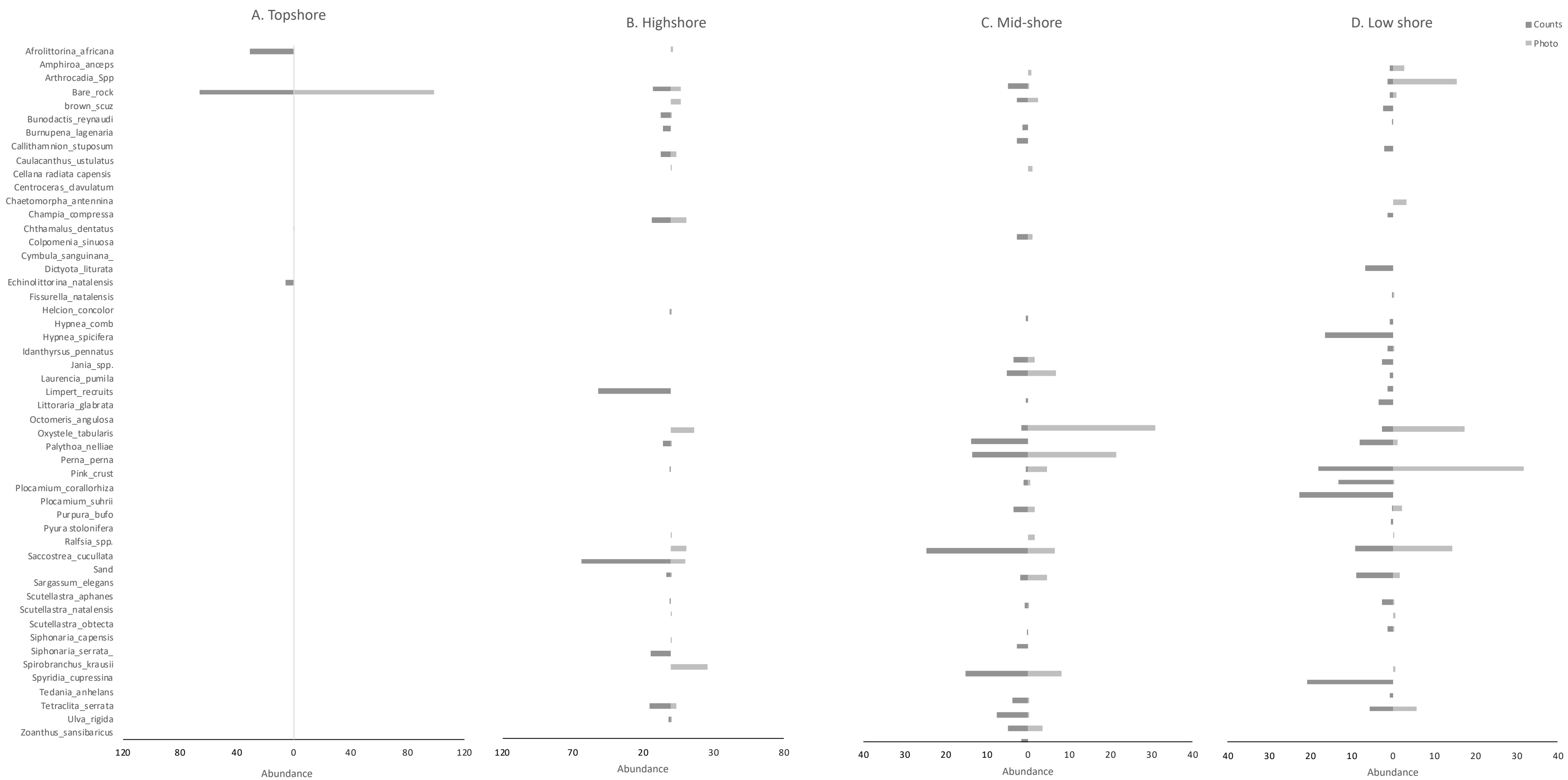

Figure 3. 5: Ballito: Semi-quantitative results from SIMPER analyses to identify the contributions of different species to observed community structure between methods for different intertidal zones in the (A) Top shore, (B) High shore, (C) Mid-shore and the (D) Low shore. (Dark grey bars = visual *in-situ* estimations and light grey bars = photographic quadrats) (showing those that contribute to 90% of the difference between methods).

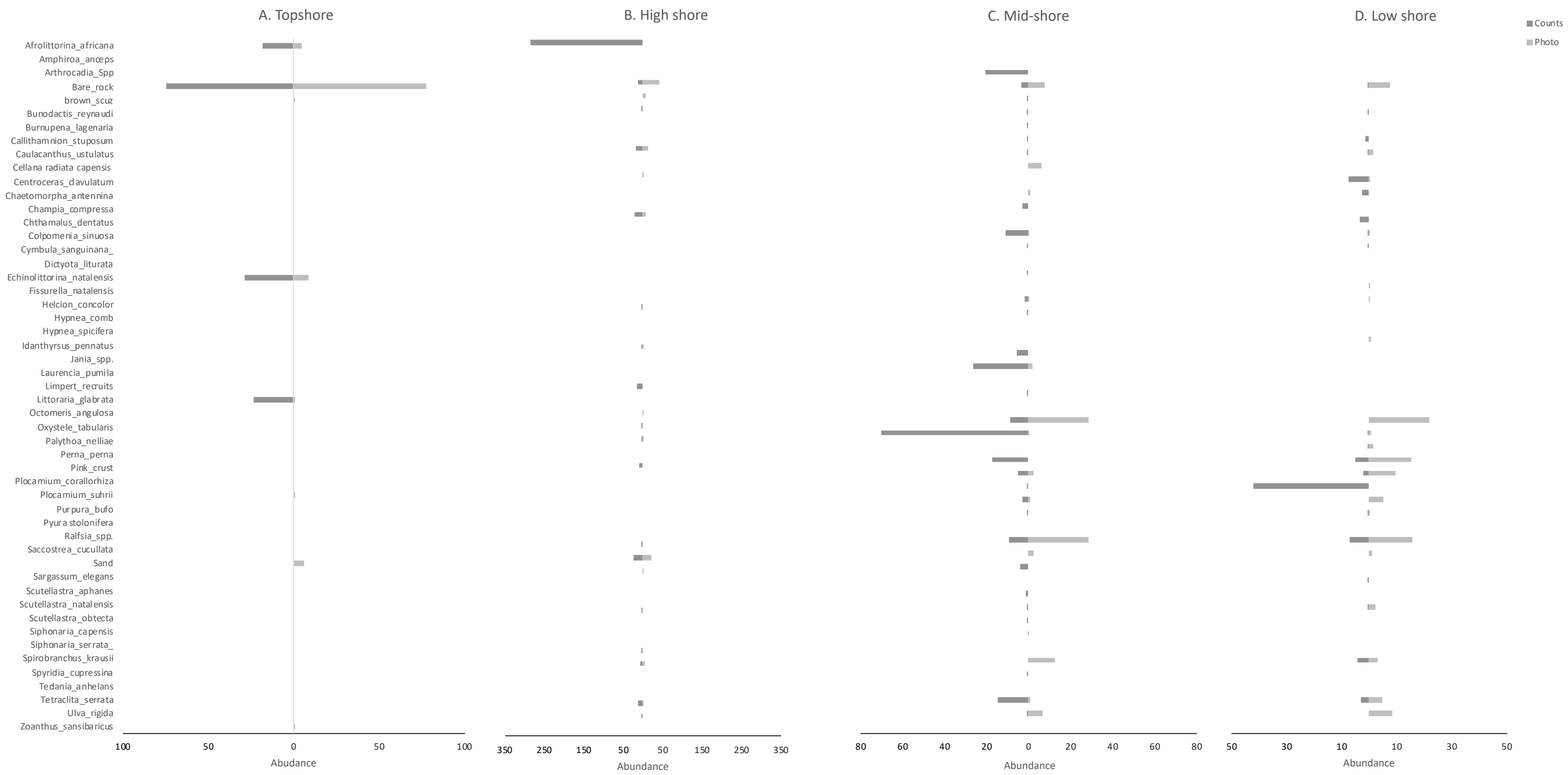

Figure 3. 6: Reunion: Semi-quantitative results from SIMPER analyses to identify the contributions of different species to observed community structure between methods for different intertidal zones in the (A) Top shore, (B) High shore, (C) Mid-shore and the (D) Low shore. (Dark grey bars = visual *in-situ* estimations and light grey bars = photographic quadrats) (showing those that contribute to 90% of the difference between methods)

Differences in the standard error in the means for each method

Figs 3.7 and 3.8 show that for both sites, the multivariate mean standard error (mean SE, *i.e.* the inverse of statistical precision) and the uncertainty of its estimation were greater for the visual *in-situ* estimations in the top shore. Conversely, in the high shore zones the mean SE was higher in the photographic quadrats than for visual *in-situ* estimations. In the mid-shore at Ballito the mean SE was higher in the photos, while no differences were evident at Reunion. In the low shore, no clear differences existed in the mean SE between methods at Ballito, while at Reunion photographic quadrats were associated with a slightly higher mean SE than visual estimates.

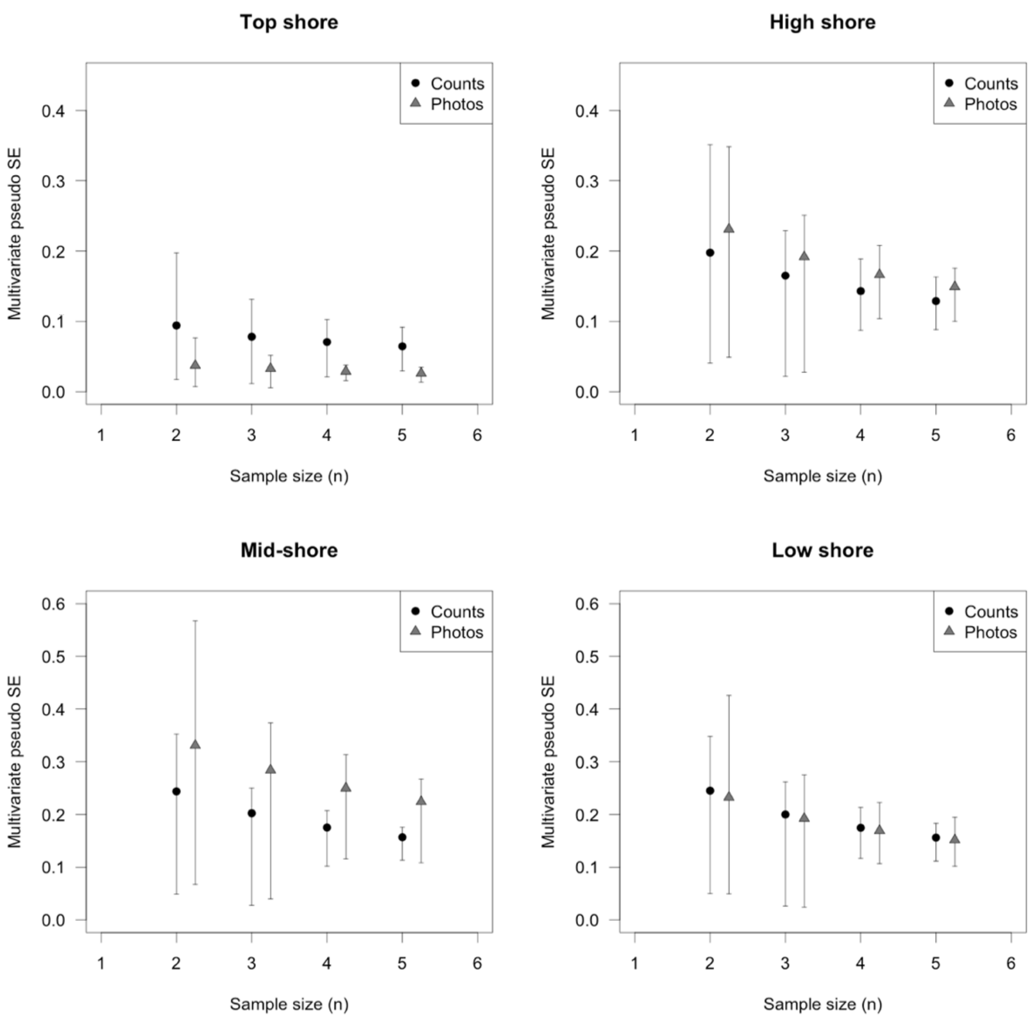

Figure 3. 7: Mean abundance and pseudo standard error for photographic quadrats and visual *in-situ* estimations in Ballito based on Bray–Curtis dissimilarities (results from 1000 resamples) (Anderson & Santana-Garcon 2015).

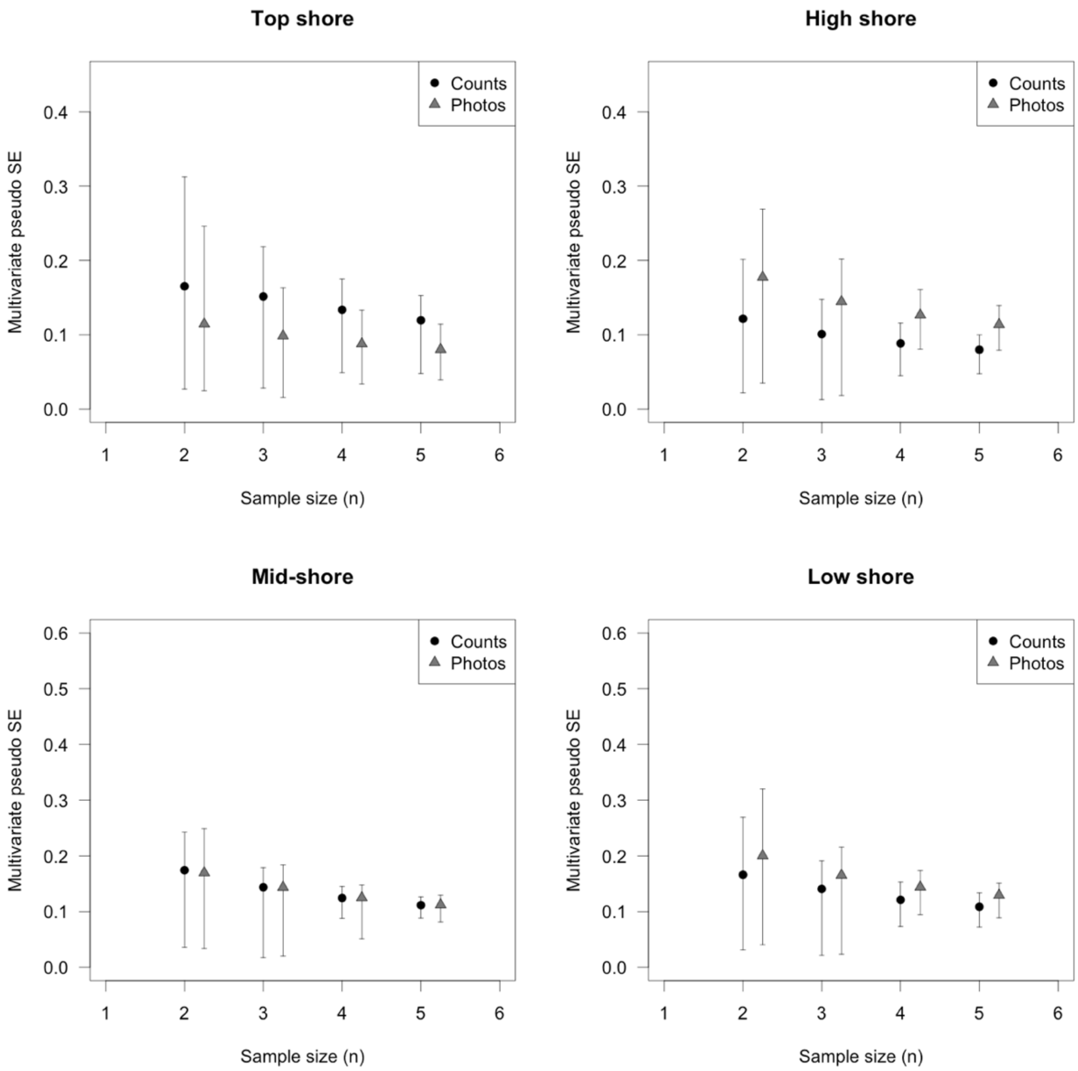

Figure 3. 8: Mean abundance and pseudo standard error for photographic quadrats and visual *in-situ* estimations in Reunion based on Bray–Curtis dissimilarities (results from 1000 resamples) (Anderson & Santana-Garcon 2015).

Differences in community structure between visual estimation and photographic methods based on functional group-based community structure.

There were significant differences in the interactions between method and site ($p< 0.05$) in the community structure for the high-shore, mid-shore and low-shore zones, suggesting that the nature of the differences between the visual *in-situ* estimations and photography surveys varied between the two sites (Fig. 3.10 and Table 3.3). However, with the exception of the Midshore, where two outliers obscured the pattern, MDS showed that for all other zones that distinct community clusters for the two methods.

In the top shore at both Ballito and Reunion, periwinkles were picked up in higher abundances in the visual *in-situ* estimation method than in photographic quadrats (Fig. 3.10A, Fig. 3.11A).

In the high shore at Ballito, the groups contributing most to the differences between methods were anemones, corticated red algae, filamentous green algae, limpets, mussels, oysters, periwinkles and whelks, which showed greater abundance in visual *in-situ* estimations, while the Barnacles, Chitons, encrusting algae, Filamentous brown algae, and worms showed greater abundances in photographic quadrats (Fig. 3.10B). At Reunion, Anemones, Barnacles, Corticated red algae, Encrusting algae, Filamentous green algae, Limpets, Mussels, Oysters, Periwinkles and Worms showed greater abundance in visual *in-situ* estimations, while the Corticated brown algae, Filamentous brown algae, Filamentous red algae, Nerites showed greater abundances in photographic quadrats (Fig. 3.11B).

In the mid-shore at Ballito, Anemones, Corticated red algae, Encrusting algae, Filamentous brown algae, Filamentous green algae, Limpets, Periwinkles, Sponges, Whelks, and Worms showed higher abundance when surveyed using the visual *in-situ* estimations whereas the

Ascidians, Barnacles, Mussels, Upright coralline algae, and Zoanthids showed higher abundances in photos (Fig. 3.10C). At Reunion, Anemones, Barnacles, Chitons, Filamentous brown algae, Limpets, Mussels, Periwinkles, and Upright coralline algae showed higher abundance when surveyed using the visual *in-situ* estimations while the Corticated red algae, Encrusting algae, Filamentous green algae, Filamentous red algae, Oysters and Zoanthids showed higher abundances in photos (Fig. 3.11C).

In low shore at Ballito, Anemones, Chitons, Corticated green algae, Corticated red algae, Encrusting algae, Filamentous brown algae, Filamentous red algae, Limpets, Periwinkles, Sponges and Worms showed higher abundance when surveyed using visual *in-situ* estimations, while Ascidians, Barnacles, Filamentous green algae, Mussels, Upright coralline algae showed higher abundances in photographic quadrats (Fig. 3.10D). At Reunion, Anemones, Corticated brown algae, Corticated red algae, Filamentous red algae and Worms showed higher abundance when surveyed using visual *in-situ* estimations, while Barnacles, Encrusting algae, Filamentous green algae, Limpets, Mussels, Oysters, Periwinkles, Whelks and Zoanthids showed higher abundances in photographic quadrats (Fig. 3.11D).

Table 3. 3: Summary of functional group abundances observed using different sampling methods

Site	**Zone**	**Method**	**Functional groups**
Ballito	Top shore	Visual *in-situ* estimations	Periwinkles (Fig. 3.9A)
		Photographic surveys	
	High shore	Visual *in-situ* estimations	anemones, corticated red algae, filamentous green algae, limpets, mussels, oysters, periwinkles and whelks (Fig. 3.9B).
		Photographic surveys	barnacles, chitons, encrusting algae, filamentous brown algae, and worms (Fig. 3.9B).
	Mid-shore	Visual *in-situ* estimations	anemones, corticated red algae, encrusting algae, filamentous brown algae, filamentous green algae, limpets, periwinkles, sponges, whelks, and worms (Fig. 3.9C).
		Photographic surveys	ascidians, barnacles, mussels, upright coralline algae, and Zoanthids (Fig. 3.9C).
	Low shore	Visual *in-situ* estimations	anemones, chitons, corticated green algae, corticated red algae, encrusting algae, filamentous brown algae, filamentous red algae, limpets, periwinkles, sponges and worms (Fig. 3.9D)
		Photographic surveys	ascidians, barnacles, filamentous green algae, mussels, upright coralline algae (Fig. 3.9D)
Reunion	Top shore	Visual *in-situ* estimations	Periwinkles (Fig. 3.10A)
		Photographic surveys	
	High shore	Visual *in-situ* estimations	anemones, barnacles, corticated red algae, encrusting algae, filamentous green algae, limpets, mussels, oysters, periwinkles and worms (Fig. 3.10B).
		Photographic surveys	corticated brown algae, filamentous brown algae, filamentous red algae, and nerites (Fig. 3.10B).
	Mid-shore	Visual *in-situ* estimations	anemones, barnacles, chitons, filamentous brown algae, limpets, mussels, periwinkles, and upright coralline algae (Fig. 3.10C).
		Photographic surveys	corticated red algae, encrusting algae, filamentous green algae, filamentous red algae, oysters and zoanthids (Fig. 3.10C).
	Low shore	Visual *in-situ* estimations	anemones, corticated brown algae, corticated red algae, filamentous red algae and worms (Fig. 3.10D).
		Photographic surveys	barnacles, encrusting algae, filamentous green algae, limpets, mussels, oysters, Periwinkles, whelks and zoanthids (Fig. 3.10D).

Table 3. 4: Results of two-way fully crossed PERMANOVA showing effects of year and site on functional group abundance in four intertidal zones.

Top shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
TMethod	1	0.128803	0.128803	32.627	0.54495	0.001	***
TSite	1	0.032557	0.032557	8.247	0.13775	0.003	**
TMethod:TSite	1	0.011832	0.011832	2.997	0.05006	0.082	
Residuals	16	0.063164	0.003948		0.26724		
Total	19	0.236356			1.00000		

High shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
HMethod	1	0.65124	0.65124	13.8984	0.28705	0.001	***
HSite	1	0.31949	0.31949	6.8182	0.14082	0.001	***
HMethod:HSite	1	0.54828	0.54828	11.7010	0.24167	0.001	***
Residuals	16	0.74972	0.04686		0.33046		
Total	19	2.26873			1.00000		

Mid-shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
MMethod	1	0.35657	0.35657	4.0124	0.13897	0.005	**
MSite	1	0.32066	0.32066	3.6084	0.12498	0.003	**
MMethod:MSite	1	0.46670	0.46670	5.2518	0.18190	0.001	***
Residuals	16	1.42185	0.08887		0.55416		
Total	19	2.56578			1.00000		

Low shore	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
LMethod	1	0.39176	0.39176	5.9828	0.19981	0.001	***
LSite	1	0.35546	0.35546	5.4284	0.18130	0.001	***
LMethod:LSite	1	0.16571	0.16571	2.5307	0.08452	0.031	*
Residuals	16	1.04769	0.06548		0.53437		
Total	19	1.96062			1.00000		

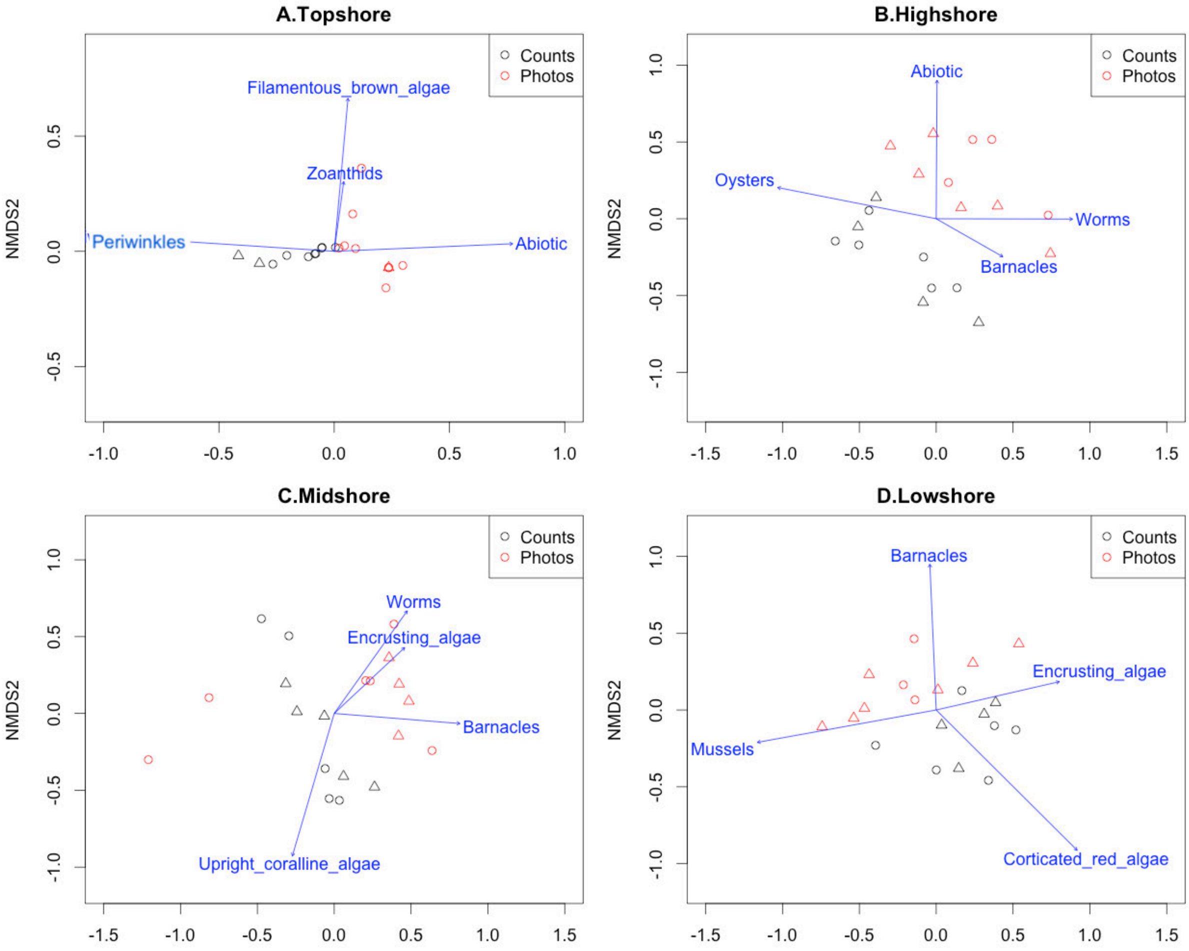

Figure 3. 9: Nonmetric Multidimensional scaling (NMDS) plots based on the abundances of groups of rocky shore organisms in 0.5 x 0.5 m quadrats. Different marker colours indicate different methods used to survey (visual in-situ estimations = black; photographic quadrats = red), and different marker symbols indicate different sites (triangles = Reunion; circles = Ballito). Blue vectors indicate the functional groups that contribute the highest to the observed change.

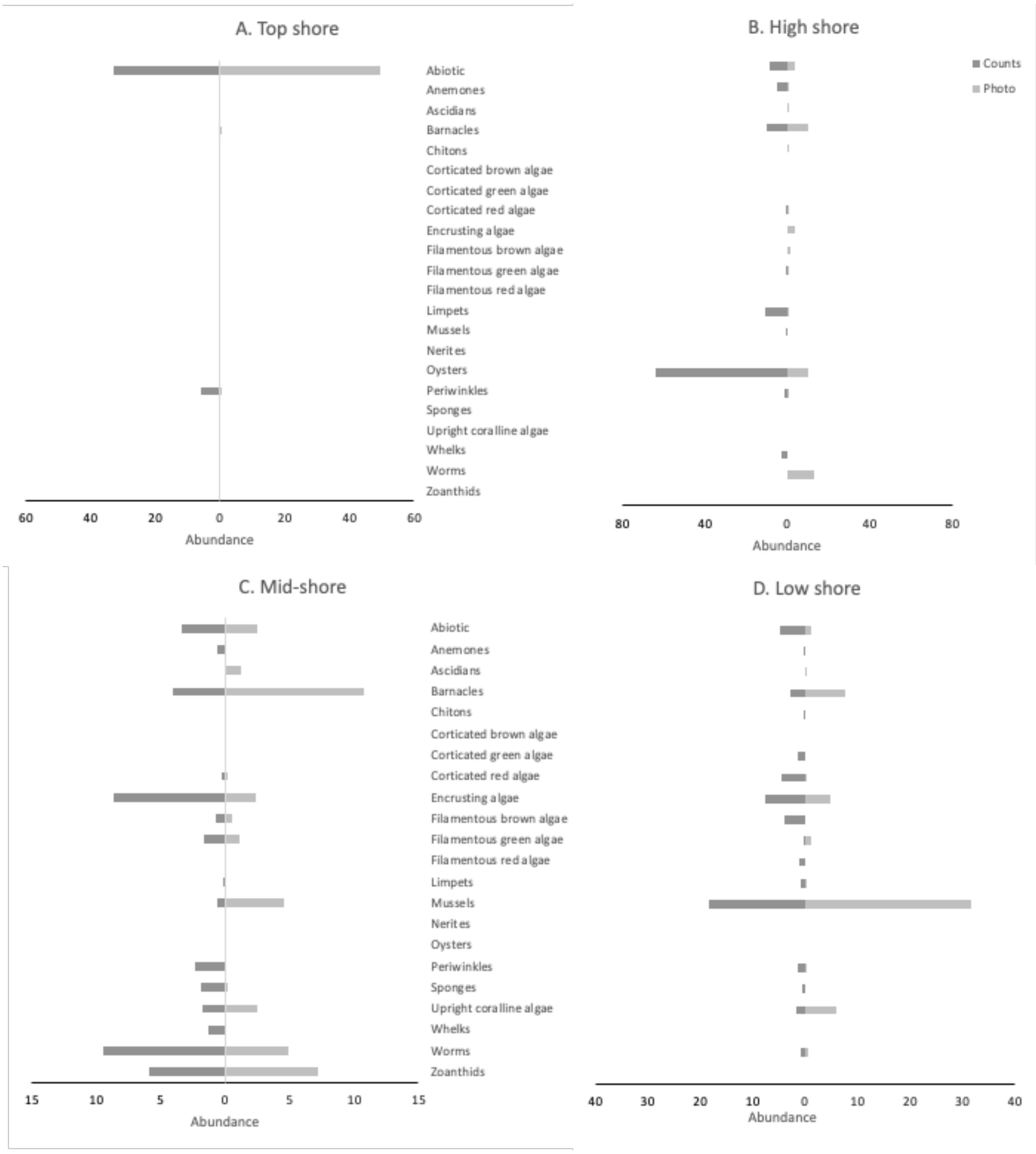

Figure 3. 10: Ballito: Semi-quantitative results from SIMPER analyses to identify the contributions of different functional groups to observed community structure between methods for different intertidal zones, (A) Top shore, (B) High shore, (C) Mid-shore and the (D) Low shore (dark grey bars = visual *in-situ* estimations and light grey bars = photographic quadrats).

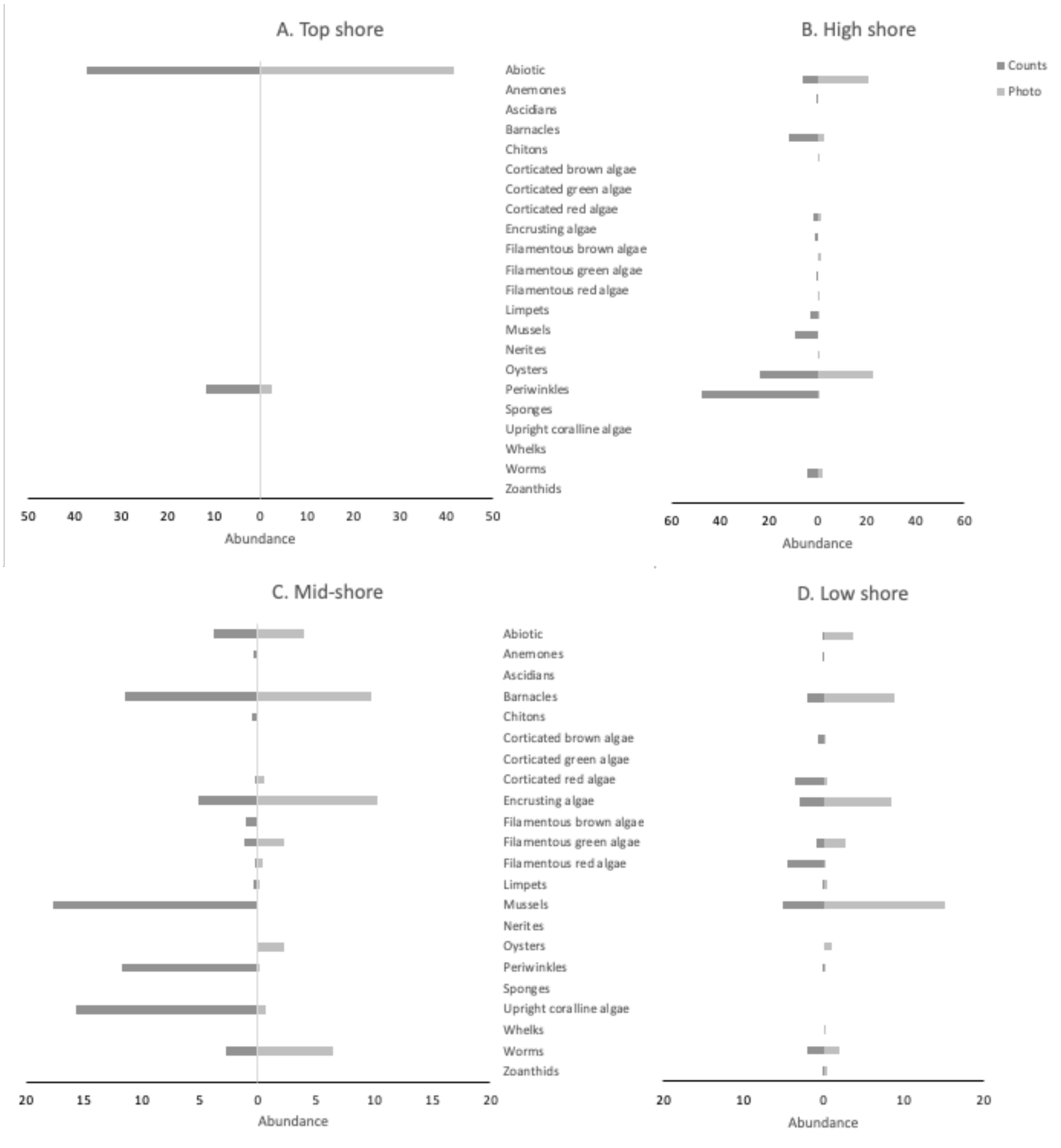

Figure 3. 11: Reunion: Semi-quantitative results from SIMPER analyses to identify the contributions of different functional groups to observed community structure between methods for different intertidal zones, (A) Top shore, (B) High shore, (C) Mid-shore and the (D) Low shore (dark grey bars = visual *in-situ* estimations and light grey bars = photographic quadrats).

Discussion

Ecosystem-based management is a holistic approach to resource management that considers the importance of the interactions among multiple species under changing environmental conditions (James & McCulloch 1990, Larkin 1996). A principal issue in ecosystem management is that many of the most important ecological changes commonly occur over multiple years or decades rather than across hours, weeks or months. Long-term studies are therefore fundamental to manage these changes (Clutton-Brock & Sheldon 2010). The most important aspect of long-term studies is to ensure that they are done with the most accurate method that is also sustainable in terms of effort (Solow 1993). This chapter compared visual *in-situ* estimations and photographic surveys for their ability to detect change in intertidal rocky shore communities by evaluating differences in species richness and community structure, as well as statistical precision. The first hypothesis tested was that there would be differences in the species richness with the photographic quadrats detecting a lower richness due to the likeliness that it will miss rare and obscured species. This hypothesis was only partially supported by the data, for some intertidal zones and with different results for the two sites. The second hypothesis that community structure would be the same for both methods was not supported by the data, as it was found that the inferred community structure differed significantly between the two methods for most intertidal zones. The third hypothesis stated that at lower data resolution, *i.e.* when species are pooled into functional groups, differences that exist between the two methods would be less pronounced than at species level, and this hypothesis was not supported. The fourth hypothesis stated that the photographic method would have a greater statistical precision, however, this was not consistently demonstrated across zones.

Species richness

At Ballito in all four zones the visual *in-situ* estimates yielded in showed greater species richness than the photographic quadrats, and this is expected as the 2D nature of photographs and their resolution limit the ability to pick up rare and inconspicuous species (Bohnsack 1979, Olbers et al. 2009). The observed differences were statistically significant in the mid-shore and the low-shore. The top-shore and the high-shore zones did not differ significantly likely because there are relatively few species in these zones, and there are few canopy-forming algae high on the shore to obscure species in photographs. At Reunion in the top-shore the opposite trend was found as the photographic quadrats showed greater species richness than the visual *in-situ* estimations. This is an unexpected result, and likely the result of identification errors that have occurred when analysing photographs, based on poor resolution at the 50x50-cm scale. It is therefore advisable to use smaller quadrat sizes for photographs, to be able to reduce ambiguous species identifications. In the high-shore, mid-shore and the low-shore the visual *in-situ* estimations resulted in greater species richness than the photographic quadrats. The differences between the methods were statistically significant in the high-shore and the mid-shore.

Community structure and functional group-based community structure vs individual species

Other studies have found that photographic sampling is more useful when observing biotic cover rather than numbers of individual species (Bohnsack 1979). When species cover was compared in this study, higher abundances were observed using visual surveys. The species and groups that contributed to the difference between the methods were explored to investigate further if it was rare species that were being missed by the photographic analyses, and this was indeed found to be the case.

Monitoring is often conducted by recording abundances of functional groups instead of individual species, as this saves time in the field and removes the influence of rare species on the observed assemblages (Olbers et al. 2009). In this study, the data were scored at species-level and then grouped into functional groups to assess whether differences between methods would persist at this lower data resolution. This was to see if the photographic method could be used for long-term monitoring despite its disadvantage of potentially missing rare and hidden species. However, there were still significant differences in the functional group composition between the visual *in-situ* estimations and photography surveys for the high shore, mid-shore and low shore zones, but there was no significant difference observed between methods for the top shore.

Statistical precision

The mean variance was lower for the photographic method in the top shore zone as this zone has low diversity (Southward 1958, Stephenson & Stephenson 1972, Bustamante 1994), and therefore the difference between sampling units was low. However in the lower zones where there is higher diversity, the sampling units tend to differ substantially from one another (Stephenson & Stephenson 1972, Dye 1998), resulting in a higher mean variance. An increase in mean variance means a decrease in statistical precision, therefore, the photographic method was more precise in estimating the abundance of fauna/flora in the upper zones than in the lower zones.

Conclusion

In a study conducted by Bohnsack (1979), the photographic sampling method was found to be more practical, rapid, inexpensive, and provided more information than visual estimations and extractive sampling. In the current study it was found that the photographic method was indeed more rapid and practical under the limitations of time, but that it was found that the method was more expensive as it required specialised cameras, and it also provided less information as the images were in two dimensions (2D) and at a resolution that was not appropriate for reliable species identification. In similar studies on the Eastern cape conducted by Dye (1998) it was found that photographic quadrats can assess the abundances of larger more dominant species easily. There were, however, challenges met when the aim was to assess entire communities especially when certain algal species overlay other species. The algae often overgrew limpets which are useful indicators of change in rocky shore communities.

CHAPTER 4: CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

Introduction

This study shows that the marine communities examined changed over time, in the face of natural and anthropogenic pressures. These changes in species richness and community structure may have substantial ecological implications. The abundance of species in each area determines the food web and biodiversity (Harley et al. 2006, Cheung et al. 2012). Populations with lower abundance are more vulnerable to impacts from environmental change (Griffiths et al. 2010).

Revisiting the aims and objectives

The main aim of the research was to determine whether the community structure of intertidal rocky shores along the KwaZulu-Natal coastline changed over the past 20 years by observing changes in species richness, evenness and overall community structure and function. Thereafter, a second aim was to determine the most effective and suitable method for monitoring rocky shores within the Natal ecoregion, by comparing two methods. Visual *in-situ* estimation of percentage cover of organisms and photographic surveys were tested for robustness in detecting changes in species richness and community structure, the statistical precision of each method was also explored

Contributions of the study

The study found that the rocky shore communities have changed over the past two decades due to environmental changes. Invasive alien species have moved into the KwaZulu-Natal coastline, which has previously not experienced any notable invasions. Harvested species have declined in abundance, this resulted in the expected increase evenness but did not result in decreased species richness particularly in the low, mid and high shore zones.

When the visual in-situ estimations and photographic surveys were compared for their ability to detect change in intertidal rocky shore communities, it was found that the photographic surveys had lower species richness, attributed to the likeliness of missing rare species. The overall community structure differed significantly between the two methods. In the top-shore zone the photographic surveys had a lower mean variance indicating higher precision, however the precision decreased toward lower shore zones.

The results from this study will be useful in developing future monitoring Programs for collecting data that could be used to detect changes in intertidal rocky shore communities over time and provide basis for better management of these systems against climate change impacts.

Challenges

In the historical comparison, limitations were encountered in the method that was previously used to monitor the intertidal zone. The limitations included the inability to detect shifts in overall community structure, and observer bias. Since community structure was detected using biotopes and the different sampling zones were not fixed, it was most likely that if the zones were to shift, the observer would move to a given zone without acknowledging they have shifted. Among observers, many changes in species composition may be lost due to the variability in experience with that particular system.

When exploring the two methods the limitations encountered with the visual *in-situ* estimation method were the inability to detect shifts in overall community structure, and observer bias as stated above. In the photographic surveys the limitations were the use of sampling units of equal size to those of the visual *in-situ* estimations, which resulted in lower resolution for the photographic surveys.

Future possibilities

Intertidal rocky shore communities have indeed changed in the past 20 years and the visual *in-situ* estimations of community structure are a viable method in observing intertidal rocky shore communities over time. For the purpose of this study the photographic surveys were conducted on the horizontal transects that the visual *in-situ* estimations were restricted to, but the optimal method for photographic surveys employs fixed vertical transects. Therefore, it would be worthwhile to retest the suitability of each surveying method by testing both fixed vertical transect surveys and random horizontal quadrats and subsequently performing power analyses to determine which method is more reliable.

To improve the precision of the photographic surveys it would be beneficial to determine the ideal number of points required to achieve the optimal sampling effort when analysing photographic samples in CPCe by comparing a range of points used to score photos and also by estimating the ideal sampling effort when analysing photographic samples by comparing results from scoring different numbers of points overlaid on the same photo quadrats.

To identify the most effective number and size of quadrats in terms of maximising statistical precision and minimising effort comparisons could be made among different combinations of quadrat sizes and quantities that add up to the same total area sampled.

To provide an (almost) absolute source of information about the ‘true’ composition and abundances, against which both of the other methods could have been compared by conducting destructive sampling by removing organisms from the quadrats, returning the samples to the lab, and sorting them to identify species and their abundances.

Final comments and summary conclusions

Considering the accelerating global climate warming, there is a need for ecosystem-based management that will focus on reducing the potential loss of high numbers of species and the risk of major shifts in ecosystems (Harley et al. 2006). In order for the management protocol to be established, there was a need to look at the changes the system had gone through since it was last comprehensively sampled. The findings from the comprehensive survey suggest that the system is heavily impacted. There was therefore a need to establish a protocol that would ensure that the system stays under constant monitoring. The findings in that regard indicated a need for further research to be done with improved protocols to ensure that a suitable monitoring protocol is developed.

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APPENDIX

Table A 1: Species found on intertidal rocky shores along the KZN coast and their taxonomic grouping and functional groups assignments. Species in BOLD were found in the 2018 study only. Descriptive names as recorded in the field are provided where species could not be identified.

Scientific name (checked (*))	Descriptive name	Taxonomic group	Functional group
Byssus		Abiotic	Abiotic
Sand		Abiotic	Abiotic
Bare rock		Abiotic	Abiotic
Dead oyster		Abiotic	Abiotic
Anthothoe stimpsonii (*)		Cnidarian	Anemones
Actinia ebhayiensis (*)		Cnidarian	Anemones
Pseudactinia infecunda (*)		Cnidarian	Anemones
Bunodactis reynaudi (*)		Cnidarian	Anemones
Bunodactis sp.		Cnidarian	Anemones
Anemonia natalensis (*)		Cnidarian	Anemones
Gyractis sesere (*)		Cnidarian	Anemones
Pyura stolonifera (*)		Chordata	Ascidians
Eudistoma caeruleum (*)		Chordata	Ascidians
Green tunicate		Chordata	Ascidians
Sandy tunicate		Chordata	Ascidians
Black encrusting ascidian		Chordata	Ascidians
Pink tunicate		Chordata	Ascidians
Trididemnum cyclops (*)		**Chordata**	**Ascidians**
Tetraclita serrata (*)		Crustacean	Barnacles
Tetraclita rufotincta (*)		Crustacean	Barnacles
Octomeris angulosa (*)		Crustacean	Barnacles
Chthamalus dentatus (*)		Crustacean	Barnacles
Amphibalanus amphitrite (*)		Crustacean	Barnacles
Megabalanus tintinnabulum (*)		**Crustacean**	**Barnacles**
Bugula dentata africana (*)		Bryozoan	Bryozoans
	Bryozoa	**Bryozoan**	**Bryozoans**
Ischnochiton oniscus (*)		Mollusc	Chitons
Onithochiton literatus (*)		Mollusc	Chitons
Acanthochitona garnoti (*)		Mollusc	Chitons
Dinoplax validifossus (*)		Mollusc	Chitons
Dictyopteris delicatula (*)		Brown algae	Corticated brown algae
Dictyopteris ligulata (*)		Brown algae	Corticated brown algae
Dictyopteris macrocarpa (*)		Brown algae	Corticated brown algae
Dictyopteris serrata (*)		Brown algae	Corticated brown algae
Padina boryana (*)		Brown algae	Corticated brown algae

Zonaria subarticulata (*)		Brown algae	Corticated brown algae
Zonaria tournefortii (*)		Brown algae	Corticated brown algae
Sargassum elegans (*)		Brown algae	Corticated brown algae
Sargassum incisifolium (*)		Brown algae	Corticated brown algae
Sargassum aquifolium (*)		Brown algae	Corticated brown algae
Turbinaria ornata (*)		Brown algae	Corticated brown algae
Colpomenia sinuosa (*)		Brown algae	Corticated brown algae
Leathesia marina (*)		Brown algae	Corticated brown algae
Spatoglossum asperum (*)		**Brown algae**	**Corticated brown algae**
Rugulopteryx suhrii (*)		**Brown algae**	**Corticated brown algae**
Stoechospermum polypodioides (*)		**Brown algae**	**Corticated brown algae**
Caulerpa filiformis (*)		Green Algae	Corticated green algae
Caulerpa racemosa (*)		Green Algae	Corticated green algae
Caulerpa denticulata (*)		Green Algae	Corticated green algae
Codium capitatum (*)		Green Algae	Corticated green algae
Codium duthieae (*)		Green Algae	Corticated green algae
Codium extricatum (*)		Green Algae	Corticated green algae
Codium lucasii (*)		Green Algae	Corticated green algae
Codium pocockiae (*)		Green Algae	Corticated green algae
Codium prostratum (*)		Green Algae	Corticated green algae
Codium spongiosum (*)		Green Algae	Corticated green algae
Codium megalophysum (*)		Green Algae	Corticated green algae
Bryopsis spp.		Green Algae	Corticated green algae
Halimeda cuneata (*)		Green Algae	Corticated green algae
Pseudocodium devriesii (*)		Green Algae	Corticated green algae
Udotea orientalis (*)		Green Algae	Corticated green algae
Chamaedoris delphinii (*)		Green Algae	Corticated green algae
Valonia aegagropila (*)		Green Algae	Corticated green algae
Valonia macrophysa (*)		Green Algae	Corticated green algae
	Green tubes – horiz & vert	Green Algae	Corticated green algae
Codium platylobium (*)		**Green Algae**	**Corticated green algae**
Caulerpa webbiana (*)		**Green Algae**	**Corticated green algae**
Spyridia cupressina (*)		Red algae	Corticated red algae
Spyridia hypnoides (*)		Red algae	Corticated red algae
Kentrophora natalensis (*)		Red algae	Corticated red algae
Laurencia flexuosa (*)		Red algae	Corticated red algae
Laurencia natalensis (*)		Red algae	Corticated red algae
Laurencia complanata (*)		Red algae	Corticated red algae
Laurencia pumila (*)		Red algae	Corticated red algae
	Spiky pink	Red algae	Corticated red algae
Gelidium abbottiorum (*)		Red algae	Corticated red algae
Gelidiella acerosa (*)		Red algae	Corticated red algae
Caulacanthus ustulatus (*)		Red algae	Corticated red algae

Gigartina minima (*)		Red algae	Corticated red algae
Hypnea rosea (*)		Red algae	Corticated red algae
Hypnea spicifera (*)		Red algae	Corticated red algae
Hypnea viridis (*)		Red algae	Corticated red algae
Hypnea specifera Small (*)		Red algae	Corticated red algae
Plocamium beckeri (*)		Red algae	Corticated red algae
Plocamium corallorhiza (*)		Red algae	Corticated red algae
Plocamium suhrii (*)		Red algae	Corticated red algae
Dichotomaria diesingiana (*)		Red algae	Corticated red algae
Galaxaura spp. (*)		Red algae	Corticated red algae
Champia compressa (*)		Red algae	Corticated red algae
	lum	Red algae	Corticated red algae
Botryocladia spp. (*)		Red algae	Corticated red algae
Hypnea rosea (juvenile) (*)		Red algae	Corticated red algae
Gracilaria vieillardii (*)		**Red algae**	**Corticated red algae**
Prionitis nodifera (*)		**Red algae**	**Corticated red algae**
Prionitis filifomis (*)		**Red algae**	**Corticated red algae**
Hypnea sp.	**Hypnea comb**	**Red algae**	**Corticated red algae**
Chondria armata (*)		**Red algae**	**Corticated red algae**
Gracilaria corticata (*)		**Red algae**	**Corticated red algae**
Laurencia prostrutum		**Red algae**	**Corticated red algae**
Hypnea tenuis (*)		**Red algae**	**Corticated red algae**
Champia sp. (*)		**Red algae**	**Corticated red algae**
Gigartina pistillata (*)		**Red algae**	**Corticated red algae**
Ralfsia spp. (*)		Brown algae	Encrusting algae
	EP = encrusting pink	Red algae	Encrusting algae
	Ered = encrusting red	Red algae	Encrusting algae
	rep	Red algae	Encrusting algae
	rep epi	Red algae	Encrusting algae
	Red crust	**Red algae**	**Encrusting algae**
	Pink crust	**Red algae**	**Encrusting algae**
Dictyota liturata (*)		Brown algae	Filamentous brown algae
Dictyota naevosa (*)		Brown algae	Filamentous brown algae
Dictyota humifusa (*)		Brown algae	Filamentous brown algae
Ectocarpus spp. (*)		Brown algae	Filamentous brown algae
Chordariaceae (*)		Brown algae	Filamentous brown algae
Canistrocarpus cervicornis		Brown algae	Filamentous brown algae
	brown scuz	Brown algae	Filamentous brown algae
	brown blades	Brown algae	Filamentous brown algae
Petalonia binghamiae (*)		**Brown algae**	**Filamentous brown algae**
Chaetomorpha antennina (*)		Green Algae	Filamentous green algae
Chaetomorpha aerea (*)		Green Algae	Filamentous green algae
Cladophora rugulosa (*)		Green Algae	Filamentous green algae
Ulva spp1		Green Algae	Filamentous green algae

Ulva rigida (*)		Green Algae	Filamentous green algae
	Green moss?	Green Algae	Filamentous green algae
	Unknown algae2-green worms	Green Algae	Filamentous green algae
	Unknown algae6-mossy mat green	Green Algae	Filamentous green algae
	grn tubes epi	Green Algae	Filamentous green algae
Willeella ordinata		**Green Algae**	**Filamentous green algae**
Cladophora prolifera (*)		**Green Algae**	**Filamentous green algae**
Chaetomorpha crassa (*)		**Green Algae**	**Filamentous green algae**
Chaetomorpha linum (*)		**Green Algae**	**Filamentous green algae**
	Green grassy algae	**Green Algae**	**Filamentous green algae**
Callithamnion stuposum (*)		Red algae	Filamentous red algae
Centroceras clavulatum (*)		Red algae	Filamentous red algae
	SOS	Red algae	Filamentous red algae
Melanothamnus incompta		Red algae	Filamentous red algae
Polyzonia elegans (*)		Red algae	Filamentous red algae
Portieria hornemannii (*)		Red algae	Filamentous red algae
Rhodymenia natalensis (*)		Red algae	Filamentous red algae
Martensia elegans (*)		Red algae	Filamentous red algae
Rhodophyllis reptans (*)		Red algae	Filamentous red algae
Turf algae (red)	Red turf	Red algae	Filamentous red algae
Centroceras spp. (*)	curl claw	Red algae	Filamentous red algae
	Forked segmented red	Red algae	Filamentous red algae
	Fred	Red algae	Filamentous red algae
	South coast red	Red algae	Filamentous red algae
	Spiky brown	Red algae	Filamentous red algae
	TLD	Red algae	Filamentous red algae
	Unknown algae1-vfred	Red algae	Filamentous red algae
	Unknown algae3-pica red	Red algae	Filamentous red algae
	Unknown algae5-red 3d	Red algae	Filamentous red algae
	Unknown algae7-brown bulbous	Brown algae	Filamentous red algae
Drouetia coalescens		**Red algae**	**Filamentous red algae**
Osmundaria serrata (*)		**Red algae**	**Filamentous red algae**
	Red bushy turf	**Red algae**	**Filamentous red algae**
Portieria tripinnata (*)		**Red algae**	**Filamentous red algae**
Acrosorium acrospermum (*)		**Red algae**	**Filamentous red algae**
Ceramium spp. (*)		**Red algae**	**Filamentous red algae**
Pocillopora verrucosa (*)		**Cnidarian**	**Hard coral**
Scutellastra aphanes (*)		Mollusc	Limpets
Scutellastra barbara (*)		Mollusc	Limpets

Scutellastra exusta (*)		Mollusc	Limpets
Scutellastra cochlear (*)		Mollusc	Limpets
Scutellastra longicosta (*)		Mollusc	Limpets
Scutellastra obtecta (*)		Mollusc	Limpets
Cymbula sanguinans (*)		Mollusc	Limpets
Scutellastra granularis (*)		Mollusc	Limpets
Helcion concolor (*)		Mollusc	Limpets
Scutellastra natalensis (*)		**Mollusc**	**Limpets**
Cellana capensis (*)		Mollusc	Limpets
Helcion dunkeri (*)		Mollusc	Limpets
Eoacmaea albonotata (*)		Mollusc	Limpets
Siphonaria capensis (*)		Mollusc	Limpets
Siphonaria serrata (*)		Mollusc	Limpets
Siphonaria concinna (*)		Mollusc	Limpets
Siphonaria oculus (*)		Mollusc	Limpets
Siphonaria “carbo” (*)		Mollusc	Limpets
Siphonaria capensis (*)		Mollusc	Limpets
Fissurella natalensis (*)		Mollusc	Limpets
Siphonaria oculus (*)		**Mollusc**	**Limpets**
Limpert recruits		**Mollusc**	**Limpets**
Helcion pruinosus (*)		**Mollusc**	**Limpets**
Perna perna (*)		Mollusc	Mussels
Brachidontes variabilis (*)		**Mollusc**	**Mussels**
Nerita albicilla (*)		Mollusc	Nerites
Nerita textilis (*)		Mollusc	Nerites
Nerita plicata (*)	white spiral	Mollusc	Nerites
Saccostrea cuccullata (*)		Mollusc	Oysters
Striostrea margaritacea (*)		**Mollusc**	**Oysters**
Striostrea margaritacea dead		**Abiotic**	**Oysters**
Trochus nigropunctatus (*)		Mollusc	Periwinkles
Oxystele tabularis (*)		Mollusc	Periwinkles
Lunella coronata (*)		Mollusc	Periwinkles
Echinolittorina natalensis (*)		Mollusc	Periwinkles
Afrolittorina africana (*)		Mollusc	Periwinkles
Littoraria coccinea glabrata (*)		Mollusc	Periwinkles
New black rock littorinid		Mollusc	Periwinkles
Tricolia capensis (*)		Mollusc	Periwinkles
Monodonta australis (*)		Mollusc	Periwinkles
Afrolittorina knysnaensis (*)		**Mollusc**	**Periwinkles**
Planaxis sulcatus (*)		**Mollusc**	**Periwinkles**
Roweia frauenfeldi (*)		**Echinoderm**	**Sea cucumbers**
Aplysia oculifera (*)	sea hare	Mollusc	Sea hares
Aplysia parvula (*)		**Mollusc**	**Sea hares**
Echinometra mathaei (*)	Oval urchin	Echinoderm	Sea urchins

Stomopneustes variolaris (*)		Echinoderm	Sea urchins
	yellow icing	Porifera	Sponges
	Unknown sponge2	Porifera	Sponges
	Unknown sponge3	Porifera	Sponges
	orange-yellow sponge	Porifera	Sponges
Hymeniacidon sp.		Porifera	Sponges
Haliclona oculata (*)		**Porifera**	**Sponges**
Tedania anhelans (*)		**Porifera**	**Sponges**
Parvulastra exigua (*)		Echinoderm	Starfish
Amphiroa anceps (*)		Red algae	Upright coralline algae
Amphiroa bowerbankii (*)		Red algae	Upright coralline algae
Amphiroa ephedraea (*)		Red algae	Upright coralline algae
Amphiroa rigida (*)		Red algae	Upright coralline algae
Arthrocardia Sp.2	Fan	Red algae	Upright coralline algae
Arthrocardia Sp.1	Compressed	Red algae	Upright coralline algae
Jania cultrata (*)		Red algae	Upright coralline algae
Jania sagittata (*)		Red algae	Upright coralline algae
Corallina officinalis (*)		Red algae	Upright coralline algae
Jania spp.		Red algae	Upright coralline algae
	Tj = tiny Jania	Red algae	Upright coralline algae
Tripneustes gratilla (*)		**Echinoderm**	**Urchins**
Tenguella granulata (*)		Mollusc	Whelks
Purpura panama (*)		Mollusc	Whelks
Purpura bufo (*)		Mollusc	Whelks
Tylothais savignyi (*)		Mollusc	Whelks
Burnupena lagenaria (*)		Mollusc	Whelks
Mancinella alouina (*)		Mollusc	Whelks
	cone shell	Mollusc	Whelks
Nucella dubia (*)		**Mollusc**	**Whelks**
Gunnarea gaimardi (*)		Worm	Worms
Idanthyrsus pennatus (*)		Worm	Worms
Spirobranchus kraussii (*)		Worm	Worms
	Unidentified reef worm	Worm	Worms
Mesochaetopterus minutus (*)		**Worm**	**Worms**
Isaurus tuberculatus (*)		Cnidarian	Zoanthids
Palythoa nelliae (*)		Cnidarian	Zoanthids
Palythoa natalensis (*)		Cnidarian	Zoanthids
Zoanthus sansibaricus (*)	Purple zoanthid	Cnidarian	Zoanthids
Zoanthus parvus	Pink zoanthid	Cnidarian	Zoanthids
Zoanthus durbanensis (*)	Grey zoanthid	Cnidarian	Zoanthids
Zoanthus natalensis (*)	Green zoanthid	Cnidarian	Zoanthids

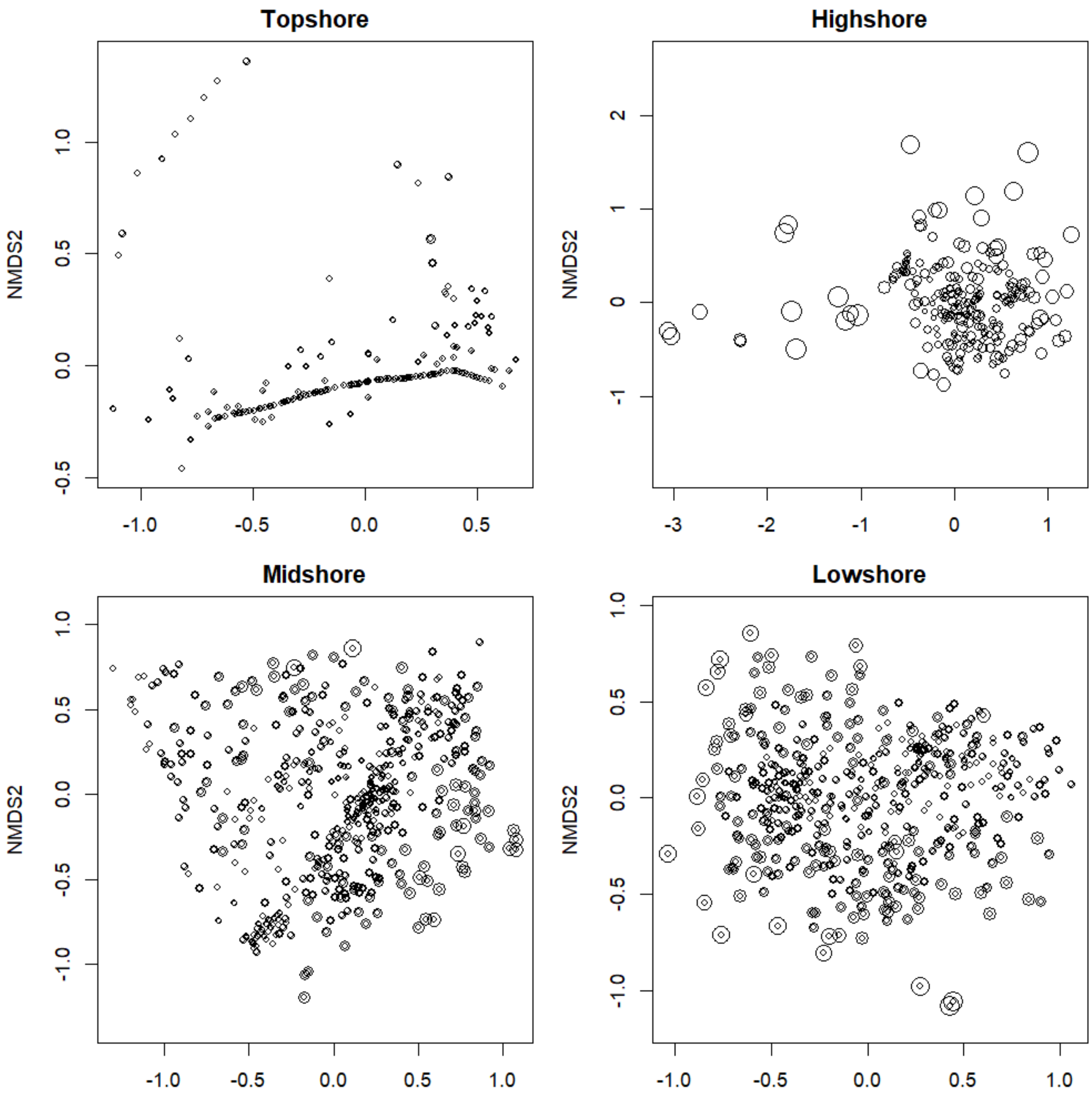

Figure A 1: Goodness of fit plot indicating the fit of the data to the model. The size of the circles shows the magnitude of the fit; smaller circles indicate the sample data fits more closely to an expected distribution; larger circle fit less.

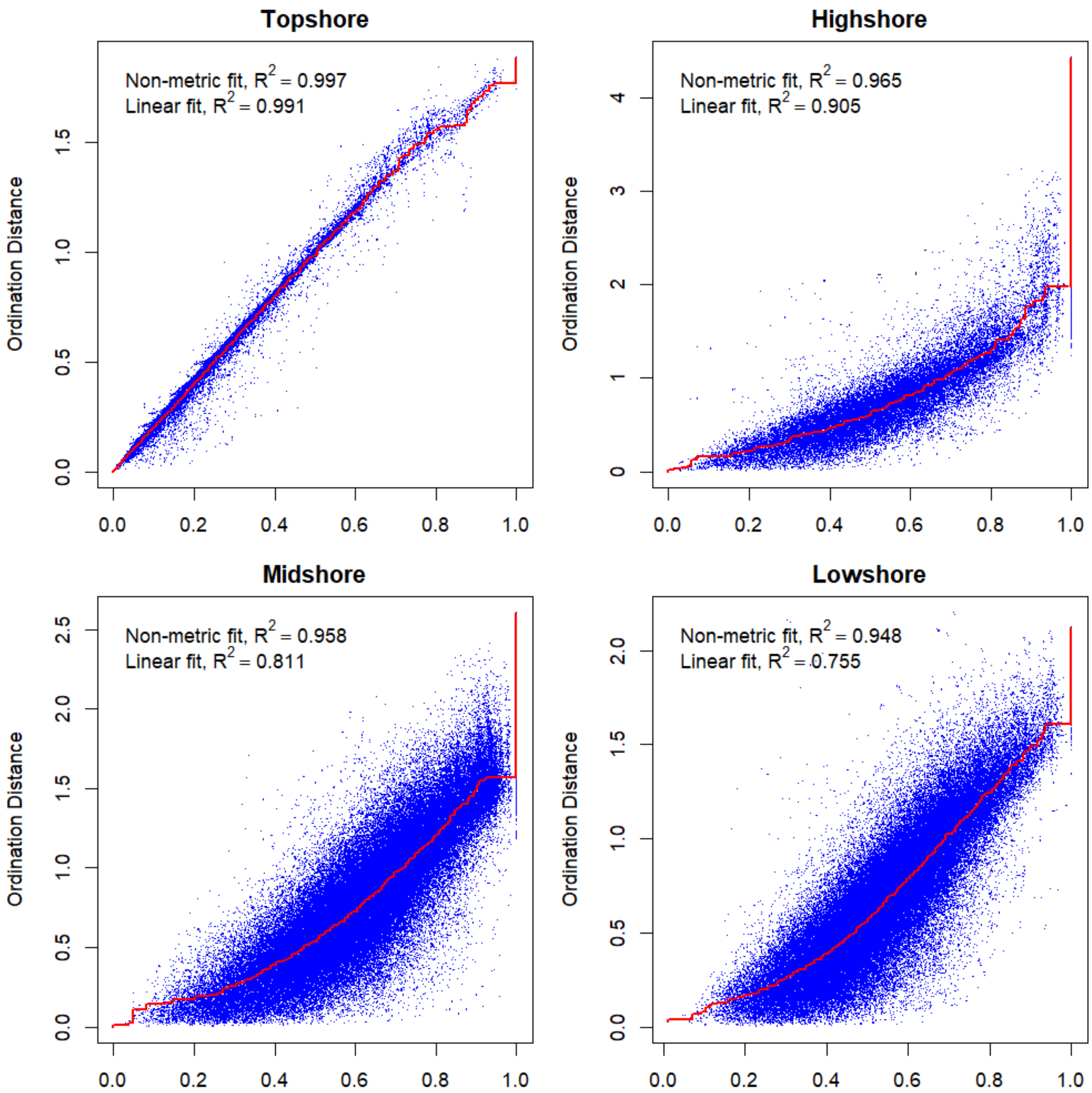

Figure A 2: stress plot indicating the magnitude of similarity between the Non-metric Multi-dimensional scaling (NMDS) plot and the original dissimilarity matrix. A linear line suggests that the MDS plot best represents the original dissimilarity matrix.

Table A 2: Significance differences in community structure at each site between 1996 and 2018, based on pairwise of a PERMANOVA posthoc tests. The yellow highlights show temporal comparisons for each of the sites. Asterisks indicate significant results, where P=0.001 (***), P<0.01 (**), and P<0.05 (*)

(A) Top-shore

	1996. Mission	1996. Sandy Pt	1996. Ballito	1996. Umdloti	1996. Reunion	1996. Umzumbe	1996. Banana	1996. Annerley	1996. Southport	1996. PtEdward	2018. Mission	2018. Sandy Pt	2018. Zinkwazi	2018. Ballito	2018. Umdloti	2018. Peace	2018. Reunion	2018. Umzumbe	2018. Banana	2018. Annerley	2018. Southport	2018. PtEdward
1996.Mission	1																					
1996.SandyPt		1																				
1996.Ballito	**		1																			
1996.Umdloti		*	***	1																		
1996.Reunion			**	**	1																	
1996.Umzumbe			**	**		1																
1996.Banana				***			1															
1996.Annerley	***			***	***	**		1														
1996.Southport			***	*				***	1													
1996.PtEdward		*	**		*		*	***		1												
2018.Mission	**			***	*	*			**	***	1											
2018.SandyPt	***	**	***	***	***	***	***	***	***	***	***	1										
2018.Zinkwazi	***	**	***	***	***	***	***	***	***	***	***	***	1									
2018.Ballito			*	***				**	*	**		***	***	1								
2018.Umdloti	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1							
2018.Peace	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1						
2018.Reunion			**	**				***		*	*	***	***		***	***	1					
2018.Umzumbe	**	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1				
2018.Banana	***		***	***	***	**	**	**	***	***	**	***	**	***	***	***	***		1			
2018.Annerley	***		***	***	***	***	***	***	**	***	***	***	***	***	***	***	***			1		
2018.Southport	***	*	***	***	***	***	***	***	***	***	***	***	*	***	***	***	***	***	***	***	1	
2018.PtEdward	***		**	***	***	***	**	**	***	***	***	***	**	***	***	***	***	***	**	**	***	1

(B) High-shore

	1996. Mission	1996. Crayfish	1996. Railway	1996. Sandy Pt	1996. Ballito	1996. Umdloti	1996. Reunion	1996. Umzumbe	1996. Banana	1996. Annerley	1996. Southport	1996. PtEdward	2018. Mission	2018. Crayfish	2018. Sandy Pt	2018. Zinkwazi	2018. Ballito	2018. Umdloti	2018. Peace	2018. Reunion	2018. Umzumbe	2018. Banana	2018. Annerley	2018. Southport	2018. PtEdward
1996.Mission	1																								
1996.Crayfish	***	1																							
1996.Railway	*	***	1																						
1996.SandyPt	***		***	1																					
1996.Ballito	***	***	***	***	1																				
1996.Umdloti	***	**	***	**		1																			
1996.Reunion		***	*	***	**		1																		
1996.Umzumbe	***	***	***	***	**	*	***	1																	
1996.Banana	***	***	***	***	**	**	***	***	1																
1996.Annerley	***	***	***	***			*	***	***	1															
1996.Southport	***	***	***	***	***		***	***	***	***	1														
1996.PtEdward	***	***	***	***			*	**	***		*	1													
2018.Mission	***	***	***	***	***	***	***	***	***	***	***	***	1												
2018.Crayfish	***	***	***	***	***	***	***	***	***	***	***	***	**	1											
2018.SandyPt	***	**	***	***	***	***	***	***	***	***	***	***		***	1										
2018.Zinkwazi	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1									
2018.Ballito	***	***	***	***	***	**	***	***	**	***	***	***	***	***	***	***	1								
2018.Umdloti	***	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	1							
2018.Peace	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1						
2018.Reunion	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	1					
2018.Umzumbe	***	***	***	***	**	**	***	***	***	***	***	***	***	***	***	***	***	**	***	***	1				
2018.Banana	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	***	1			
2018.Annerley	***	***	***	***	*	**	***	***	***	**	***	***	***	***	***	***	***	***	***	***	*	***	1		
2018.Southport	***	***	***	***	*	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	*	*		1	
2018.PtEdward	***	***	***	***	**	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1

(C) Mid-shore

	1996. Mission	1996. Crayfish	1996. Railway	1996. Sandy Pt	1996. Ballito	1996. Umdloti	1996. Peace	1996. Reunion	1996. Umzumbe	1996. Banana	2018. Mission	2018. Crayfish	2018. Railway	2018. Sandy Pt	2018. Zinkwazi	2018. Ballito	2018. Umdloti	2018. Peace	2018. Reunion	2018. Umzumbe	2018. Banana	2018. Annerley	2018. Southport	2018. PtEdward
1996.Mission	1																							
1996.Crayfish	***	1																						
1996.Railway	***	***	1																					
1996.SandyPt	***	***	***	1																				
1996.Ballito	***	***	***	***	1																			
1996.Umdloti	***	***	***	***	***	1																		
1996.Peace	***	***	***	***	***	***	1																	
1996.Reunion	***	***	***	***	***	***	***	1																
1996.Umzumbe	***	***	***	***	**	***	***	***	1															
1996.Banana		**	***	***	***	***	***	*	***	1														
2018.Mission	***	***	***	***	***	***	***	***	***	***	1													
2018.Crayfish	***	***	***	***	***	***	***	***	***	***	***	1												
2018.Railway	***	***	***	***	***	***	***	***	***	***	***	***	1											
2018.SandyPt	***	***	***	***	***	***	***	***	***	***	***	***	***	1										
2018.Zinkwazi	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1									
2018.Ballito	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1								
2018.Umdloti	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	1							
2018.Peace	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	1						
2018.Reunion	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	1					
2018.Umzumbe	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	**	1				
2018.Banana	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	***	**	**	1			
2018.Annerley	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	1		
2018.Southport	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	***	*	***	***	1	
2018.PtEdward	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	***	**	***	***	*	*	***		1

(D) Low-shore

	1996.Zinkwazi	1996.Ballito	1996.Umdloti	1996.Peace	1996.Reunion	1996.Umzumbe	1996.Banana	1996.Annerley	1996.Southport	1996.PtEdward	2018.Mission	2018.Crayfish	2018.Railway	2018.Zinkwazi	2018.Ballito	2018.Umdloti	2018.Peace	2018.Reunion	2018.Umzumbe	2018.Banana	2018.Annerley	2018.Southport	2018.PtEdward
1996.Zinkwazi	1																						
1996.Ballito	***	1																					
1996.Umdloti	***	**	1																				
1996.Peace	***	***	***	1																			
1996.Reunion	***		**	**	1																		
1996.Umzumbe	***		**	**		1																	
1996.Banana	***	*	***	**		*	1																
1996.Annerley	***		**	**	*	*	*	1															
1996.Southport	***	***	*	***	*	**	***	***	1														
1996.PtEdward	***	***	***	***	**	**	**	**	***	1													
2018.Mission	***	***	***	***	***	***	***	***	***	***	1												
2018.Crayfish	***	***	***	***	***	***	***	***	***	***	***	1											
2018.Railway	***	***	***	***	***	***	***	***	***	***	***	***	1										
2018.Zinkwazi	***	***	***	***	**	***	***	***	***	***	***	***	***	1									
2018.Ballito	***	***	***	***	**	***	***	***	***	***	***	***	***	***	1								
2018.Umdloti	***	***	***	***	*	***	***	***	***	***	***	***	***	***	***	1							
2018.Peace	***	***	***	***	*	***	***	***	***	***	***	***	***	**	**	***	1						
2018.Reunion	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1					
2018.Umzumbe	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1				
2018.Banana	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	1			
2018.Annerley	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	1		
2018.Southport	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***		**	1	
2018.PtEdward	***	***	***	***	***	***	***	***	***	**	***	***	***	***	***	***	***	***	**	***	***	***	1