A hierarchical analysis of abiotic determinants and harvesting impacts in the rocky intertidal communities of KwaZulu-Natal

by

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DECLARATION

This thesis documents original research, carried out in the Zoology Department, University of Cape Town, between 1996 and 2000. It has not been submitted in whole, or in part for a degree at any other University. Most of the data presented here are original and any other sources are fully acknowledged. Any uncited interpretations are my own and any assistance I have received is also fully acknowledged.

signature removed

Kerry J. Sink

28 May 2001

Date

This thesis is dedicated to my family
Who have loved and supported me and together with whom
I spent many happy holidays on our coastline

To Sheldon, my brother, to whom I will always look up to and who despite my efforts has greater understanding

My mother, Sandra , who taught me the importance of being a whole person, gave me an appreciation for the detail in nature and who stood by me in my individuality

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GENERAL ABSTRACT

This thesis was undertaken to provide quantitative scientific information for decision-making and conservation planning for the previously scarcely studied rocky intertidal habitats in KwaZulu-Natal on the east coast of South Africa. Biogeographic patterns were resolved and abiotic determinants and harvesting impacts were identified at three different scales. A biotope classification system was developed as a new tool for assessing the conservation status of intertidal communities, evaluating conservation priorities and monitoring change in intertidal habitats. The implications of the findings of this thesis for management and conservation planning were examined.

The biogeographic analysis was undertaken using quantitative data from 39 intertidal rocky shores along the 560-km long KwaZulu-Natal coast. Two biogeographic regions, Maputaland and Natal, were recognised with a distinct biogeographic break evident at Cape Vidal. More than 65% difference in low and mid-shore community structure was evident between these regions. There was no biogeographic break evident for the high and top shore where communities converged. There was also no evidence of a previously suggested biogeographic break near Durban. Sand inundation and wave exposure did not differ significantly between the two regions and there were no abrupt changes in sea-water temperature that corresponded with the observed biogeographic break. The most striking abiotic difference between Maputaland and Natal was the difference in riverine input, with more than 99% of KwaZulu-Natal's mean annual simulated runoff entering the sea south of Cape Vidal. There was also a significant difference in the intensity of human exploitation between regions, which was more than eighteen times greater in Maputaland than Natal, suggesting that harvesting contributed to the observed biogeographic patterns.

Within Maputaland and Natal, two-way crossed ANOSIM tests were used to identify abiotic determinants underlying between-site differences in community structure at a scale of kilometres to tens of kilometres. Within both regions, wave exposure was identified as an important determinant and its influence was greatest in the low shore. Filter feeders and grazers were generally more abundant at exposed sites with primary producers (including zoanthids) more abundant at wave-sheltered sites. The effect of sand inundation and rock type could only be examined within Natal because these factors were too uniform in Maputaland to allow comparisons. In Natal, a close association between the intensity of sanding and community structure was apparent, particularly in the mid and high shore. Heavily sand-inundated shores had higher cover of turf-forming algae, reduced numbers of patellid limpets and barnacles and had more pulmonate limpets (*Siphonaria* spp.) than lightly inundated shores. Rock type generally had a weak influence on community structure with communities differing significantly only between dolerite and Quaternary sandstone and then only in the mid shore. In Maputaland, subsistence-harvested and unexploited sites had large significant differences in low-shore community structure. Harvesting resulted in direct effects

on target species (the brown mussel *Perna perna* and the ascidian *Pyura stolonifera*) but indirect cascade effects were also apparent. At exploited sites, cover of non-target invertebrates and upright algae increased due to competitive release, and appeared to result in decreased cover of crustose algae because of overgrowth. In Natal, no differences in community structure were evident between sites subject to different degrees of recreational harvesting although the absence of unexploited sites prevented proper assessment of harvesting impacts.

Using 1630 samples from 38 sites spanning 560 km, 69 intertidal biotopes were described and defined for rocky shores in KwaZulu-Natal. Biotopes were defined objectively using a 50% Bray Curtis similarity cut-off value to separate samples. Biotopes could be recognised in the field and independent tests revealed that the biotope classification was robust, capturing significant differences in community structure between and within zones on the shore. Several biotopes failed to differ significantly in terms of species richness, diversity, dominance and evenness, indicating that univariate indices have limited application in biodiversity assessments. Biotopes proved effective in assessing the conservation status of existing marine protected areas and their value in conservation planning was demonstrated by comparing proposed protected areas. The proposed Pondoland Marine Park could improve the conservation status of intertidal biotopes by at least 24% whereas the proposed extension of the St Lucia Marine Reserve could improve biotope protection by 31%. Patterns in biotope abundance also reflected harvesting impacts showing that biotopes can be used to monitor anthropogenic or other changes in community structure. Biotopes can be employed to assess conservation status and monitor changes in community structure more efficiently and cost-effectively than species inventories. Furthermore, destructive sampling is not necessary and biotope surveys can be conducted by people with less expertise than that required for species-based approaches.

For a subset of biotopes, the use of the term "biotope" to describe different biological communities was justified by the identification of unique abiotic habitat characteristics. Nested ANOVA showed that the local habitat of different biotopes, between and within zones on the shore, had corresponding differences in rock temperature, wave exposure and sand inundation but not topography (aspect and slope). Biotope distribution between zones was best explained by differences in rock temperature with significantly greater temperatures in all mid-shore biotopes than all low-shore biotopes. The within-zone distribution of biotopes was best explained by differences in wave forces and two biotopes were only distinguishable in terms of the relative degree of sand inundation. Small-scale differences in community structure were associated with differences in wave exposure and sand inundation in a manner that mirrored patterns at larger scales. Only two biotopes failed to differ in terms of local habitat characteristics and the distribution of these biotopes was predicted to be determined by competitive interactions that are modified by human exploitation.

The impact of harvesting on intertidal community structure was investigated at multiple scales using hierarchical cluster analysis, multi-dimensional scaling, SIMPER and two-way crossed ANOSIM analyses. Temporal changes in mussel abundance and the cover of articulated coralline algae at Black Rock (the most important subsistence mussel-harvesting site in Maputaland) suggest that sustained subsistence harvesting may have changed community structure over the last 21 years. The observed changes were consistent with changes at experimentally harvesting plots and comparisons of subsistence-exploited versus unexploited or recreationally-exploited site-pairs in Maputaland and Natal respectively. Temporal changes in community structure were insignificant or minor at recreationally-harvested sites. Experimental harvesting at intensities simulating recreational and subsistence harvesting revealed that both types of exploitation can modify community structure. Harvesting was found to exaggerate biogeographic patterns and accounted for 10% of the dissimilarity between the Maputaland and Natal biogeographic regions. At all scales, direct and indirect effects of exploitation were evident. Target species (and species that depend on their prescence) were reduced by harvesting while non-target species increased due to competitive release. The impact of subsistence intensities of harvesting was greater than that of recreational harvesting intensities. This was attributed to the greater quantities of resources removed by subsistence users and to the wide-bladed tools used for harvesting. These create large patches of bare space where competitive algae can invade, and which may cause recruitment failure for resource species.

Management recommendations and implications for biodiversity conservation were drawn from all chapters of this thesis. The Natal biogeographic region is inadequately provisioned with marine protected areas. Furthermore, fully protected closed areas are urgently required in the Maputaland Marine Reserve. In both regions marine protected areas must incorporate wave-exposed and sheltered sites and should cover a range of intensities of sand inundation. This will achieve conservation of the full spectrum of intertidal biodiversity, protect stocks of different target species (which require different abiotic conditions), and provide benchmark sites against which human impacts can de assessed.

Glossary

To clarify how I have used certain terminology in this thesis, I have provided my definition of a few important terms:

Biotope - Connor et al. (1997) use the word biotope to describe a physical habitat together with an associated community of species. In my study, the word biotope refers to a community type defined on a biological basis (Chapter 4) but distinct habitat characteristics were established for a subset of biotopes (Chapter 5).

Biodiversity - I use this term to describe the variety and relative abundance of species or biotopes although I recognise that there are several levels of organisation incorporated into the concept of biodiversity, from the genetic variability within a population or species to the diversity of ecosystems encompassed within a biogeographical province (Gray 2000).

Characteristic species - those species contributing most to the overall similarity of a group of samples. The dominant characteristic species was that which had greatest cover.

Community structure - Although several components of community structure can be identified (including species composition, relative abundance, diversity, trophic complexity and spatial structure (Menge and Farrell 1989)), in my study, I use the term in a narrower sense, to embrace species composition and abundance.

Distinguishing species - species that contributed most to the overall dissimilarity between any two groups of samples.

Locality - A stretch of rocky shore that incorporates two or more sites.

Recreational harvesting - The collection of invertebrates by individual collectors in possession of a recreational license. The harvest is not for commercial gain nor is it required to meet basic food needs.

Region - A large geographic area encompassing scales of a hundred kilometres or more is termed a region. Where biogeographic analyses show a biogeographic break between two regions then those areas are considered as biogeographic regions.

Site - A single stretch of rocky shore, less than 100 metres wide and spanning between the low and high tide marks.

Subsistence harvesting - the collection of large quantities of intertidal invertebrates by harvesters who were not in possession of a recreational permit (this sector was informal at the time of data collection – see p 193) and who depend on their catch to meet basic food requirements.

Chapter 1

General Introduction

Hiscock (1995) lists five principal areas of information that are critical for the management and conservation of marine ecosystems, namely "resource data, knowledge of the physical and chemical environment, information on the structure of marine communities and on the key elements in their functioning, data on natural variability and information on the effects of human activities". To varying degrees, all five of these elements are addressed in this thesis, which focuses on rocky shores in the province of KwaZulu-Natal on the east coast of South Africa.

Detecting patterns in communities and relating these patterns to ecosystem function is one of the current challenges in marine ecology. This is necessary for rational resource use, for detection of changes in community composition and maintenance of biodiversity and for conservation planning. An understanding of how abiotic factors shape intertidal communities is relevant to management because the assessment of impacts of resource use depends on the comprehension of how natural environmental factors affect community structure. Without such an understanding, the influences of natural and anthropogenic factors are inseparable (Clarke 1993). The nature and scales of natural spatial and temporal variability need to be identified and quantified, and harvesting impacts should be evaluated concurrently. Conservation planning relies on adequate description of species composition and abundance at different scales so that prospective protected areas can be assessed in terms of representativeness. Only then can marine protected areas be rationally selected to ensure that biogeographic and habitat heterogeneity is conserved.

The starting point for understanding the functioning of rocky shore ecosystems is quantitative descriptions of natural patterns (Whittaker 1975). Intertidal communities are considerably more heterogeneous than suggested by some claims of ecological generality and broad spatial extrapolations based on studies at one or few sites may be unfounded (Foster 1990). Quantitative, comparative studies at several sites are required to develop and evaluate general models of community structure and regulation (Foster et al. 1988, Underwood 1996).

Factors that shape marine communities can be classified into three groups: namely abiotic, biotic and anthropogenic. Firstly, community structure varies with changes in the physical environment. Abiotic determinants within intertidal habitats include elevation and associated changes in rock temperature and desiccation (Colman 1933, Lewis 1964, Stephenson and Stephenson 1972), rock type (Barry 1988, Raimondi 1988, Lohse 1993), topography (Menge et al. 1985, Barry and Dayton 1991, Fuji and Nomura 1991) and wave exposure (Lewis 1964, Dayton 1971, Menge 1976, Seapy and Littler 1978, Foster et al. 1988, Menge and Farrel 1989, Bustamante and Branch 1996a). Evidence suggests that physical disturbances can strongly affect community structure (Sousa 1984, Keough and Connell 1984, McGuiness 1987a,b). Examples include sand inundation (Daly and Mathieson 1977,Taylor and Littler 1982, D'Antonio 1986) and scouring by logs or ice (Paine and Levin 1981).

The second group of factors that influence community structure are biological determinants. Recruitment (Roughgarden et al. 1985, Underwood and Fairweather 1989, Raimondi 1990, Eckman 1996, Menge 2000a), competition (Connell 1961, reviews by Branch 1984, Underwood 1986, 1992), and the activities of grazers and predators (Paine 1966, 1974, Lubchenco 1987, Underwood and Jernakoff 1984, Steneck and Dethier 1991) exert a powerful influence on intertidal assemblages.

There is great debate in the ecological literature as to the relative importance of biological versus environmental factors in regulating intertidal communities, and whether regulation is "top-down" (with predators controlling the abundance of herbivores) or "bottom-up" (with nutrients and productivity determining community structure and dynamics) (see reviews by Underwood 2000c, Menge and Branch 2001). An extensive literature shows that abiotic and biotic determinants and both top-down and bottom-up control influence intertidal communities (Menge 1976, Menge et al. 1985, Menge and Olson 1990, Menge 1991, Menge et al. 1993, Bustamante et al. 1995b, Power et al. 1996, Menge et al. 1997a,b, Menge 2000b). The challenge lies in understanding why factors influence communities differently under varying conditions. To progress in this regard, studies at a greater number of localities over larger spatial scales, involving more species, and with quantitative links between communities and determinants are required (Schoch and Dethier 1996, Underwood 2000, Menge and Branch 2001). The experimental approach is a critical component of the methodology that will prove crucial for furthering our understanding of community regulation.

Finally, the third group of factors that influence marine communities are anthropogenic. Human impact can modify intertidal community structure (Moreno et al. 1984, Duran and Castilla 1989, Siegfried 1988, Kingsford et al. 1991, Brosnan and Cumrine 1992, Brosnan 1993, Underwood 1993, Adessi 1994, Keough and Quinn 1998, Brown and Taylor 1999, Schiel and Taylor 1999). As top predators in intertidal communities, human exploitation can exert direct effects on target species as well as indirect and often subtle cascade effects on the structure and functioning of nearshore communities (Castilla 1993). A current issue in marine ecology is whether harvesting can cause trophic cascades (Steneck 1998, Babcock et al. 1999). One of the problems in resolving this question is that other human impacts and effects of natural events can mask the signals of trophic cascades (Sala et al. 1998). Castilla (1999) calls for more studies focusing on the role of humans in coastal ecosystem and advocates an experimental approach to detect trophic-cascade effects. Marine protected areas are vital as reference sites (Hockey and Branch 1994), where the often-complex effects of human exploitation can be elucidated.

Scale is also emerging as a critical aspect of ecological research and the need to evaluate determinants of community structure at multiple scales is recognised (Dayton and Tegner 1984, Foster et al. 1990, Menge and Olson 1990, Allen and Hoekstra 1991, Archambault and Borget 1996, Connell et al. 1997, Underwood 2000). Different factors are relevant at different scales and can only be detected at the appropriate sampling scale (Hewitt et al. 1998).

Comparative studies that investigate variations of community patterns over spatial scales ranging from metres to hundreds of kilometres are necessary to develop a conceptual framework that deals with community regulation (Menge and Farrel 1989, Mann and Lazier 1991). Underwood (2000) has described the shift in the focus of ecologists from broad scale patterns to those that vary at a hierarchy of spatial scales (which also vary from place to place). Hockey and Branch (1994) emphasise the importance of scale in biodiversity conservation. They advocate a hierarchical approach for selecting marine protected areas; biogeographic heterogeneity should be protected, and then, within biogeographic regions, habitat diversity should be conserved.

The United Nations Convention on Biological Diversity has been signed by more than 70 countries, including South Africa. This reflects a worldwide commitment to conserve and sustainably utilise biodiversity for the benefit of present and future generations (Rio 1992). Gray (2000) calls for a broader approach in studying marine diversity rather than simply calculating diversity indices. At the forefront of conservation planning is the question of how to prioritise conservation efforts (Myers et al. 2000). Opposing strategies (Myers 1988, Hockey and Branch 1997) are the subject of active ecological debate. New tools and approaches are needed for assessing conservation status and planning and the management of resources (Zacharias et al. 1998).

Rocky shores on the west and south coasts of South Africa have been extensively studied during the past 20 years (e.g., Field and Robb 1970, Branch GM 1971, 1974, 1975a, 1975b, 1976, 1978, 1981, McQuaid 1981, 1982, Hockey and Branch 1984, McQuaid and Branch 1984, 1985, Bolton 1986, Bosman and Hockey 1986, Hockey and Bosman 1986, Bosman et al. 1987, Griffiths and Hockey 1987, Bosman and Hockey 1988, Branch and Griffiths 1988, Dower 1989, Bolton and Stegenga 1990, Field and Griffiths 1991, Marshall and McQuaid 1993, Bolton and Stegenga 1994, Bustamante 1994, Bustamante et al. 1997). There have also been biogeographic studies at a nation-wide scale (Stephenson and Stephenson 1972, Brown and Jarman 1978, Bolton and Anderson 1990, Emanuel et al. 1992, Bustamante et al.1995, Bustamante and Branch 1996, Harris et al. 1998) recognising the principal South African biogeographic provinces and some sub-provinces. However, biogeographic breaks on the east coast including KwaZulu-Natal have not been clearly resolved. Furthermore, last year the National Research Foundation reported that the state of knowledge of intertidal resources and diversity along the KwaZulu-Natal coast was inadequate, as was the understanding of the principles of rocky shore ecosystem functioning (Griffiths et al. 2000).

In South Africa, upwelling on the west coast and its virtual absence on the east coast has resulted in a gradient of declining productivity and nutrient supply from west to east (Bustamante et al. 1995b). Consequently, mussel biomass is much lower on the east coast than the west coast but harvesting is far more intensive on the east coast (Van Erkom Schurink and Griffiths 1990, Griffiths and Branch 1997). The absence of modern quantitative analyses of intertidal communities in KwaZulu-Natal is therefore particularly problematic because of the substantial pressure on intertidal resources in this region (Fielding et al. 1991,Tomalin 1995, Kyle et al. 1997a,b, Tomalin and Kyle 1998). However, in KwaZulu-Natal, there is a strong management agency in the form of KwaZulu-Natal Wildlife. The iincreasing pressure on mussel resources is considered a serious management problem and the need to determine sustainable harvesting practices is compelling (Van Erkom Schurink and Griffiths 1990, Tomalin 1995, Anderson and Griffiths 1997). Management calls for quantitative scientific information for decision-making and conservation planning.

Research conducted by Berry (1978, 1982, Berry and Schleyer 1983) contributed significantly to the understanding of the ecology of two important resource species in KwaZulu-Natal, the mussel *Perna perna* and the solitary ascidian *Pyura stolonifera*. Tomalin (1995) examined growth and mortality of *Perna perna* at five sites in KwaZulu-Natal and identified significant regional variability. Quantitative data detailing mussel abundance have also been collected at a few localities in KwaZulu-Natal (Fielding et al. 1991, Tomalin 1995). Fielding et al. (1994) described macroinvertebrate communities associated with intertidal beds of *Pyura*, but only at one site.

In KwaZulu-Natal, there is therefore a need for comparative quantitative studies of entire communities at several localities. Apart from early work by Stephenson (1939, 1944), there has been only one study that focused on a range of intertidal rocky sites along the KwaZulu-Natal coastline (Jackson 1976) and a few studies concentrating on single sites (eg. Lambert 1976, Lambert and Steinke 1986a,b). The most comprehensive work on intertidal rocky shores in KwaZulu-Natal was done by Jackson (1976). She provided semi-quantitative estimates (abundance ratings) for 53 species in 10 sections of the KwaZulu-Natal coast, and more detailed quantitative information for three sites. While Jackson's study provided some information on the principal species and community structure of east coast rocky shores, she noted that there was "a general lack of knowledge and understanding of the system".

In my thesis, a hierarchical approach was used to identify patterns and potential key abiotic determinants of community structure in KwaZulu-Natal. Several components of community structure can be identified, including species composition, relative abundance, diversity, trophic complexity and spatial structure (Menge and Farrell 1989). In my study, I use the term community structure in a narrower sense, to embrace species composition and abundance. Using a standardised sampling technique, based on results from a pilot study, I examined the biological composition and some of the abiotic factors relevant to the structuring of rocky intertidal communities in KwaZulu-Natal. Three scales are covered in my study: (1) a regional scale incorporating hundreds of kilometres, (2) inter-site comparisons at a scale of tens of kilometres, and (3) intra-site comparisons at a scale of metres. My approach was comparative, designed to detect large and small-scale abiotic factors that appear to influence the structure of intertidal communities. In addition, a biotope classification system was developed to describe intertidal communities in KwaZulu-Natal and the application of this system was demonstrated by using biotopes to assess conservation efforts in KwaZulu-Natal and examine human impacts. I then concentrated more particularly on the role of human exploitation and evaluated the influence of harvesting on community structure at all three scales using a variety of approaches including experimental manipulation.

In Chapter 2, using quantitative analyses, I established large-scale biogeographic patterns of intertidal community structure on rocky shores in KwaZulu-Natal. To discern biogeographic regions, I used quantitative percentage cover data from 39 localities between Kosi Bay and Port Edward, covering approximately 560km. This resulted in the recognition of a biogeographic break at Cape Vidal, separating two provinces – Maputaland in the north and Natal in the south. I compared community structure between the thus recognised provinces and identified characteristic and distinguishing species. To elucidate potential physical factors underlying the biogeographic break, I compared the biogeographic patterns with patterns in abiotic data, specifically sea temperature, riverine input, sand inundation and wave exposure. In addition, differences in human exploitation of intertidal invertebrates between regions were investigated.

In Chapter 3, between-site comparisons within regions were conducted at a scale of 10-100 km to identify potential determinants of community structure. Pairs of sites with contrasting abiotic conditions were compared to determine whether there were corresponding differences in community structure. Specifically, comparisons were made between sites of different rock types or those subject to different intensities of sand inundation or wave exposure. For the northern biogeographic region (Maputaland), exploited and protected sites were compared to determine whether harvesting influences rocky intertidal community structure. Due to the scarcity of unexploited sites in Natal, a comparable comparison could not be conducted for that region.

In Chapter 4, intra-site variability in community structure was examined at a scale of meters but spanning the entire KwaZulu-Natal coastline. An arbitrary 50% Bray Curtis similarity was used to objectively classify 1630 samples from 38 sites resulting in the recognition of 69 biotopes. Then, at two independent sites, I quantitatively tested whether different biotopes from within and between different zones on the shore differed significantly in terms of community structure. I also compared diversity estimates for a range of diversity indices to assess whether different biotopes were significantly different in terms of diversity. In the last part of this chapter, I assessed how well the full spectrum of rocky intertidal biotopes is conserved within the marine protected area network of this province. I then use the biotope classification to compare two proposed additional protected areas to demonstrate the value of biotopes as a tool for conservation planning.

In Chapter 5, I established significant differences in the physical habitats of a subset of the biotopes recognised in Chapter 4. Using quantitative abiotic data for replicate samples of each biotope, I tested whether biotopes from within and between different zones on the shore experience differed significantly in rock temperature, wave forces, aspect or slope. As in

Chapter 4, this study was also conducted at small scales of metres to tens of metres. Nevertheless, three disjunct localities, more than 130 km apart, were examined to assess the generality of the results.

In Chapter 6, I more specifically investigated the effect of human exploitation on intertidal community structure on rocky shores in KwaZulu-Natal. I employed four approaches and examined the impact of harvesting at three scales. In the first approach, I establish local-scale temporal changes in community structure at one site. Then, in the second approach, I experimentally determined the effect of recreational and subsistence harvesting on community structure and biotope abundance. This aspect of the study examined small-scale changes in community structure within two sites at a single locality, Dingini, in northern KwaZulu-Natal. In the third approach, I compared community structure at recreationally and subsistence-exploited sites in the Natal biogeographic region. The fourth approach was conducted at a regional scale. The biogeographic analyses undertaken in Chapter 2 were repeated after including data from the subsistence harvesting treatments at Dingini and additional subsistence-harvested sites examined during approach 3. On the basis of all four approaches, the role of harvesting in determining large and small-scale patterns in community structure could be assessed.

Chapter 7 concludes the thesis with a synthesis of the results from Chapters 2-6. For each chapter of the thesis, the aim and key results are reviewed and I evaluated how my findings furthered the respective fields of study. In the final section of the synthesis, I drew from all aspects of the thesis to evaluate how the information presented can be used for management and conservation planning.

Chapter 2

Biogeographic patterns on rocky intertidal shores in KwaZulu-Natal

ABSTRACT

The principle aims of this chapter were to identify and characterise large-scale patterns in community structure of rocky intertidal shores along the whole of the KwaZulu-Natal coast and then to identify potential underlying determinants. Hierarchical cluster analyses and multidimensional scaling were used to determine biogeographic breaks. ANOSIM tests indicated that rocky shores in Maputaland, the northernmost region, were significantly different from those in three other pre-defined regions lying to the south (Zululand, Central KwaZulu-Natal and South Coast). These three regions constituted a single biogeographic region that I term Natal. A clear biogeographic break was identified at Cape Vidal Point on the north coast with more than 65% Bray Curtis dissimilarity in community structure between Maputaland and Natal, which was detectable in both the low and mid shore. In the high and top shore, communities converged and there were no regional differences in community structure for these zones. There was no evidence of a previously suggested biogeographic break near Durban. The major species distinguishing between Maputaland and Natal were identified using SIMPER analyses. These distinguishing species correspond with previously described differences between Mozambique and Natal. Species characteristic of Maputaland reflect tropical affinities and this region is proposed to form part of the tropical Indo-West Pacific Province. The Natal region is sufficiently distinctive to be recognised as a discrete subtropical biogeographic province.

Quantitative estimates of sea-water temperature, riverine input, sand inundation, wave exposure and human exploitation were compared between Maputaland and Natal. There were no abrupt changes in seawater temperature that corresponded with the observed biogeographic break although it was recognised that the offshore temperatures used for that purpose do not always accurately reflect inshore sea temperatures. Sand inundation and mean wave forces did not differ significantly between Maputaland and Natal. Regional differences in riverine input constituted the most striking abiotic difference between Maputaland and Natal with more than 99% of KwaZulu-Natal's mean annual simulated runoff entering the ocean south of Cape Vidal and therefore only influencing Natal. The intensity of human harvesting also differed significantly between the two regions. The mean mass of invertebrates harvested per site per low tide was approximately eighteen times greater in Maputaland than in Natal. A scarcity of protected areas in Natal and intensive intertidal harvesting throughout the Maputaland Marine Reserve constitute serious flaws in the marine protected areas program in KwaZulu-Natal. Fully protected benchmark areas in both biogeographic regions are urgently required.

Introduction

Biogeography is defined as the study of biological life in a spatial and temporal context and is concerned with the analysis and explanation of patterns of distribution (Cox and Moore 1998). Although this definition incorporates all scales, traditional biogeographic studies have dealt with large spatial scales and biotic variability in relation to changes in geography. Most biogeographic analyses examine the distribution of species without incorporating abundance estimates. In my study, large-scale patterns in community structure (species composition and abundance) were sought along the approximately 560 km comprising the province of KwaZulu-Natal on the east coast of South Africa (Figure 2.1). Such biogeographical analyses are critical for the establishment of sensible strategies for the conservation and management of biodiversity and have important ecological applications.

The Convention on Biological Diversity (Rio de Janeiro 1992) demands the conservation of all biogeographic regions in a network of protected areas. Major functions of marine protected areas include conservation of diversity (habitats, species and genetic diversity), maintenance of ecosystem function, contribution towards management of fisheries and the control of anthropogenic activities in sensitive habitats (Attwood et al. 1997a). Marine protected areas also serve tourism, education and science. These objectives can only be met with the establishment of a network of appropriate protected areas that should be selected by comparison of potential sites in terms of a broad set of criteria (Agardy 1997, Hockey and Branch 1997, Roberts et al. in press a and b).

Establishment of effective marine protected areas is dependent on biogeographic information (Hockey and Branch 1994, 1997, Attwood et al. 1997b). Representative marine protected areas should be established in the core of each principal biogeographic zone if a substantial proportion of any region's marine biodiversity is to be conserved (Hockey and Buxton 1989, Hockey and Branch 1997). Marine protected areas should not only represent each biogeographic region but should also cover the physical heterogeneity within a region and the variety of biological communities (Emanuel et al. 1992). Pinpointing biogeographic breaks is important in selecting sites for marine protected areas because boundaries of biogeographic regions are often areas with high species diversity, and provide important sites where range shifts in response to environmental change could be detected (Hockey and Branch 1994, Barry et al. 1995).

In South Africa, concern has been expressed that not all biogeographic zones are protected (Hockey and Buxton 1989). In particular, the southern section of the east coast (including southern KwaZulu-Natal) has no marine protected area in which representative habitats are protected (Attwood et al. 1997b). Pinpointing biogeographic breaks along the east coast is difficult, because the entire KwaZulu-Natal coastline has not previously been well represented in biogeographic studies. Stephenson (1939, 1944, 1948) did not survey north of Cape Vidal in northern KwaZulu-Natal (Figure 2.1) and the most recent biogeographic survey covering invertebrates included only two KwaZulu-Natal sites, Ballito and Cape Vidal (Bustamante and Branch 1996a). In response to these needs, the present study provides detailed information about species distribution and abundance based on equal sampling effort at several KwaZulu-Natal rocky shores spread over approximately 560 km.

An understanding of the nature and magnitude of variability in community structure and the relationship with the physical environment is important for managers with jurisdiction over coastal habitats. Differences in species composition and abundance within a stretch of coast under the custody of a management agency (in this case KwaZulu-Natal Wildlife) may demand different management and conservation strategies. Regional biological differences may necessitate different approaches in the management of exploited species. For example, mussels (*Perna perna*) are viewed as having a higher productivity in KwaZulu-Natal than in the former Transkei on the south eastern coast of South Africa (Kyle et al. 1997a, Tomalin and Kyle 1998) as they grow faster and reproduce earlier in KwaZulu-Natal (van Erkom Schurink and Griffiths 1990, Tomalin 1995). Lasiak (1991) and Dye (1992) considered *P. perna* to have low resilience to exploitation in the Transkei whereas Kyle et al. (1997) claim that *P. perna* is very resilient further north. This indicates that geographic location may impose differences in growth and productivity of harvested organisms and therefore affect resilience to exploitation.

Descriptions of large-scale patterns of community structure also provide an important database to test applicability of models of community regulation. For example, Ricciardi and Borget (1999) examined global patterns of macroinvertebrate biomass in intertidal communities to test the generality of underlying mechanisms structuring biological communities. Tropical and subtropical shores are less well studied than their temperate counterparts (Sauer Machado et al. 1996) and many of the hypotheses and supporting evidence for models of community structure on rocky shores have been based on northern or temperate southern shores (Williams 1994). The relative importance of ecological processes is predicted to vary between temperate and tropical shores (Menge and Olson 1990, Brosnan 1992). In South Africa, studies examining community regulation have mostly been conducted on the west and south coast with few examining community structure on the east coast (Field and Griffiths 1991).

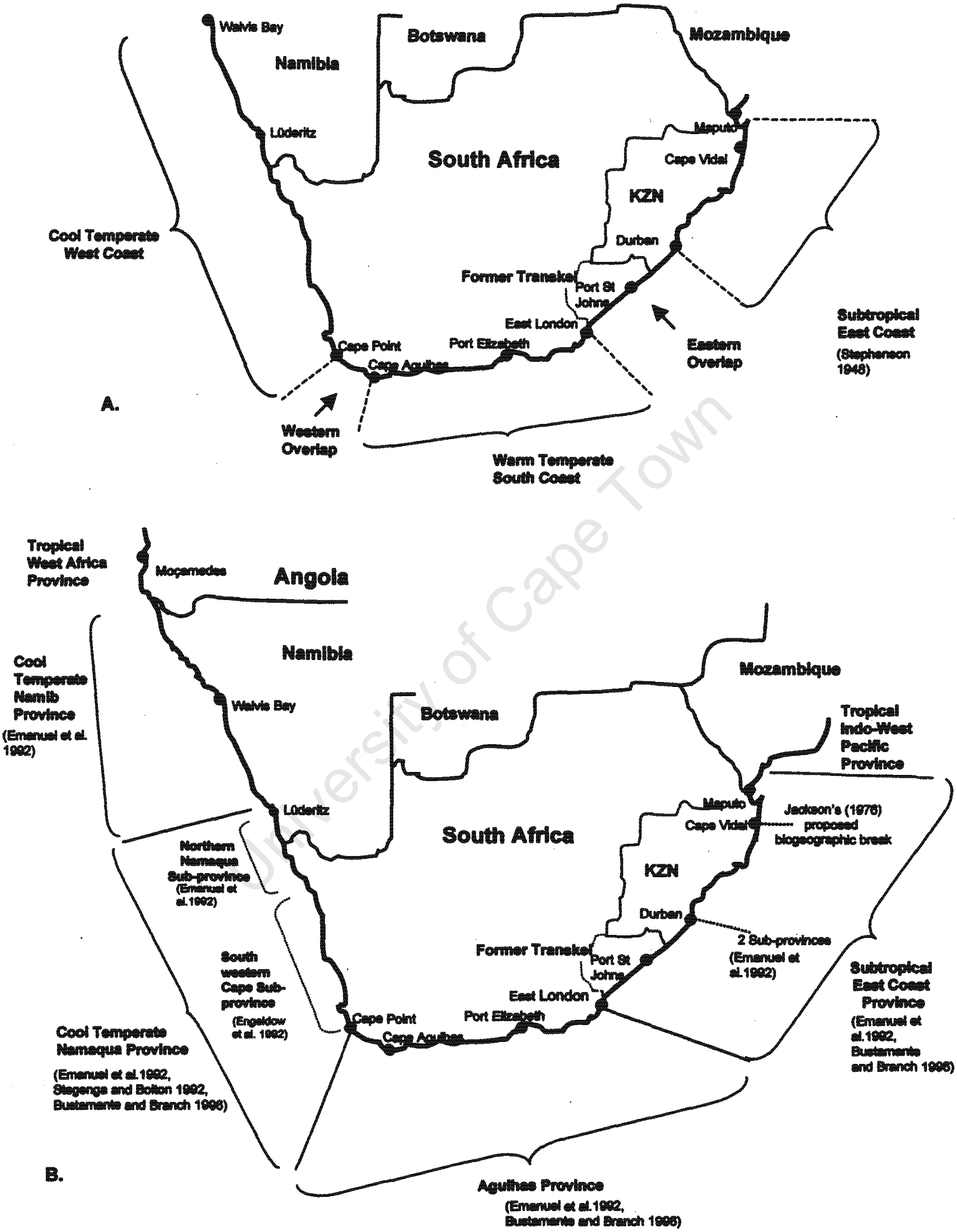


Figure 2.1. Southern Africa, showing the previously proposed marine biogeographic provinces and biogeographic breaks by (A) Stephenson (1948) and (B) by subsequent biogeographic studies based on intertidal work.

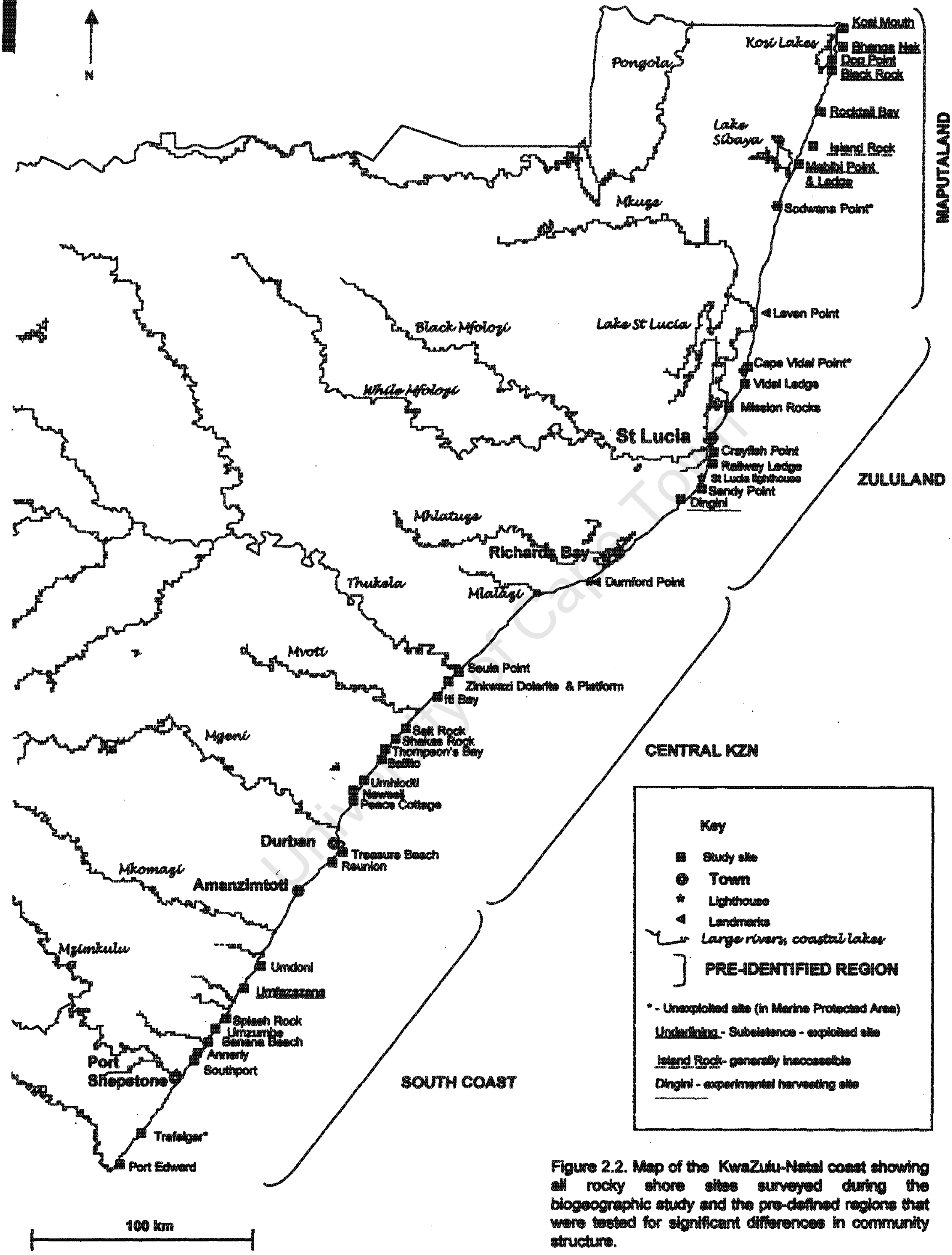


Figure 2.2. Map of the KwaZulu-Natal coast showing all rocky shore sites surveyed during the biogeographic study and the pre-defined regions that were tested for significant differences in community structure.

Previous biogeographic research relevant to the east coast

Biogeographic regions of the world are principally defined by thermal tolerances and five global biogeographic regions have been demarcated: polar, sub-polar, cold temperate, warm-temperate and tropical (Lüning 1990). The pioneering intertidal research of Stephenson (1939, 1944, 1948) indicated that the South African coast comprised three biogeographic provinces: (a) the cool-temperate west coast, (b) the warm-temperate south coast and (c) the subtropical east coast, with boundaries at Cape Point and Port St Johns (Figure 2.1A).

Subsequent intertidal work in South Africa concurred with that of Stephenson (Brown and Jarman 1978, Emanuel et al. 1992, Bustamante and Branch 1996a), confirming the presence of the three provinces (Figure 2.1B). Turpie et al. (2000) showed that coastal fishes also reflect three biogeographic provinces: the West, South and East Coast Provinces. An analysis of seaweed distributions in South Africa (Bolton 1986) suggested only two provinces, a warm temperate (with west and south coast components) and a subtropical east coast province. However, recent analyses have consistently defined the south coast as an independent province (Stegenga and Bolton 1992, Emanuel et al. 1992, Bustamante 1994). Emanuel et al. (1992) also divided the west coast of southern Africa into two separate provinces, the Namaqua and Namib Provinces, with a division near Luderitz (Figure 2.1B). Both these provinces are considered cool temperate. On the basis of seaweed flora, a third division is even recognised on the southern portion of the Cape west coast (Engledow et al. 1992, Bolton and Anderson 1997, Figure 2.1B). This sub-province is termed the Southwestern Cape sub-province and is more species-rich in terms of seaweeds than the Namib Province and the northern part of the Namaqua Province (Engledow et al. 1992, Bolton and Anderson 1997). This division is also reflected in the invertebrate fauna (Emanuel et al. 1992). Subtropical West Coast and Tropical East Coast Provinces have been identified north of southern Angola and north of central Mozambique (Penrith and Kensley 1970a, b, Kensley and Penrith 1973, Bolton and Anderson 1997).

Between the cool temperate west coast and the warm temperate south coast is an area of overlap (Stephenson and Stephenson 1972, Figure 2.1A). The Western overlap extends from Cape Point to Cape Agulhas with a rapid reduction of west coast species between Hermanus and Arniston (Stephenson 1948, Jackelman et al. 1991, Emanuel et al. 1992, Stegenga and Bolton 1992) (Figure 2.1A). The east coast is less well studied and there is no consensus regarding the position of an overlap region or the eastern limit of the Agulhas Province (Emanuel et al. 1992, Bolton and Anderson 1997). Stephenson (1948) claimed that the eastern overlap comprised the area between East London and Durban on the KwaZulu-Natal coast, with an important break near Port St Johns. The zoogeographic analysis of Emanuel et al. (1992) proposed that the division between the east coast and south coast was south of Port St Johns. Turpie et al. (2000) reported that coastal fishes do not reflect a clear biogeographic break between the East and South Coast Provinces, with gradual species turnover east of Cape Point. The Transkei region in the eastern Cape was however more similar to the south coast section than the east coast, and the east Coast Province was considered to extend northwards from the KwaZulu-Natal-Transkei border. Hommersand (1986) noted that the KwaZulu-Natal flora is poorly studied but reported that the East coast flora reflects an eastwardly decreasing number of Agulhas species, replaced largely by tropical Indo West Pacific species. Bolton and Anderson (1997) did not recognise a subtropical province as such but considered the eastern overlap to extend from around East London to Durban. The area north of Durban is considered part of the tropical Indo-West Pacific Marine Province (Bolton and Anderson 1997).

Within KwaZulu-Natal, two main biogeographic breaks have been proposed (Figure 2.1B). A marine zoogeographic analysis based on intertidal and nearshore species (Emanuel et al. 1992) described a distinct biogeographic break just north of Durban. Jackson (1976) identified differences in intertidal fauna and flora between Maputaland (Mozambique - Leven Point), southern Zululand (Leven Point - Durnford Point) and Natal (Durnford Point - Port Edward). The positions of these boundaries are shown in Figure 2.2. Jackson considered a distinct break between Cape Vidal and Mabibi and some change in the vicinity of Port Durnford. Communities in Maputaland were the most distinct, with communities in southern Zululand more similar to those in Natal than Maputaland. In Jackson's opinion the subtropical province extended from a southern boundary between Port St Johns and Quolora in the Transkei, and she proposed that the northern boundary lay between Cape Vidal and Mabibi. Stephenson (Stephenson and Stephenson 1972) considered the East Coast Province to extend all the way from Mozambique to Port St. Johns. Emanuel et al. (1992) found no further breaks north of Durban to Ponta da Barra Falsa in Mozambique. There is thus confusion about the precise position, or even existence, of the break between tropical and subtropical provinces on the KwaZulu-Natal coast.

Potential abiotic determinants of biogeographic patterns

Most studies in the marine environment examine community structure at small scales, and large-scale patterns are poorly understood (Sanvicente-anorve et al. 1996). Biogeographic analyses tend to be based on presence/absence data and do not explore patterns in community structure. Rex et al. (1993) commented that if large-scale patterns in community attributes exist, they are probably linked to natural processes that are different from those acting at small scales. Evidence derived from benthic communities that supports this idea is given by Sanvicente-anorve et al. (1996). Both physical factors and biological interactions influence community structure, although abiotic factors, especially oceanographic currents and temperature, are generally deemed more important at larger scales (Foster et al. 1988, Menge and Branch 2001). However, species interactions have been proposed to vary latitudinally (Dethier and Duggins 1988) and small differences in physical factors can be important in governing species interactions over scales covering metres to hundreds of kilometres (Bustamante and Branch 1996a, Leonard 2000).

Oceanographic influences

One reason that physical oceanographic processes exert important influences on benthic communities is that most benthic invertebrates have a planktonic larval phase (Connolly and Roughgarden 1999). The distribution and abundance of species on the largest geographic scales is generally thought to be controlled by large-scale dispersal governed by oceanographic conditions (Druehl 1981). Differences in community composition of mussel communities at different geographic locations have been related to patterns of planktonic larval dispersal by prevailing currents (Kanter 1980, McQuaid and Phillips 2000). Other oceanographic features that may influence community structure over large spatial scales include upwelling and sea-water temperature (Raffaelli and Hawkins 1996). Large-scale differences in structure and abundance of intertidal communities on the Oregon coast are associated with nearshore oceanographic conditions, including phytoplankton concentration and productivity and water temperature during upwelling (Menge et al. 1997a,b). Differences in community structure and dynamics also vary with large-scale oceanographic conditions in New Zealand (Menge et al. 1999). In rocky intertidal communities in the northeast Pacific, a latitudinal gradient in upwelling produces a gradient in intensity of species interactions (Connolly and Roughgarden 1999).

The boundaries of the biogeographic provinces in South Africa correspond closely with oceanographic conditions (Brown and Jarman 1978, Branch and Griffiths 1988). Coastal waters in southern Africa are dominated by the contrasting Agulhas and Benguela currents. The west coast is influenced by the cold, relatively slow Benguela current that drifts northwards, and upwelling is characteristic along this coast (Brown 1978, Branch and Griffiths 1988). On the east coast, the warm Agulhas current is a well defined intense jet approximately 100 km wide and more than a kilometer deep that moves rapidly down the south east coast (Shannon 1985, Schumann 1998). Upwelling on the west coast and its virtual absence on the east coast has resulted in a productivity gradient around southern Africa (Shannon 1985, Brown and Cochrane 1991, Brown et al. 1991). Large-scale variations in biomass and community composition along the South African coast have been linked to these gradients of primary production and nutrient concentrations (Bustamante et al. 1995b).

Sea-water temperature

Temperature has long been recognised as an important governing factor in determining species distributions for littoral habitats (Isaac 1938, Stephenson 1939, 1944, Southward 1958, Lewis 1964, Stephenson and Stephenson 1972). Several authors have demonstrated correlation between seaweed distributions and temperature patterns (van den Hoek and Donze 1967, van den Hoek 1982, Searles 1984, Bolton 1986, South 1987, Bolton and Stegenga 1987, Bolton and Anderson 1990). These have been supported with results from laboratory studies linking physiological temperature limits to geographic distribution limits (Branch ML 1974, van den Hoek 1982, Bolton and Anderson 1987, Anderson and Bolton

1989, and see review by Breeman 1988). Temperature has also been demonstrated to influence growth of intertidal invertebrates including mussels in southern Africa (Van Erkom Schurink and Griffiths 1993). Latitudinal variation in temperature has also been linked to variability in survival of urchins from southern California to Alaska in the USA (Ebert et al. 1999).

In South Africa, effects of sea temperature regime on community structure have been assessed on shores on the Cape of Good Hope where the eastern shores experience warmer temperatures than the western shores, which are cooled by upwelling. McQuaid and Branch (1984, 1985) found that temperature determined species composition on rocky shores while biomass and trophic structure were attributed to other abiotic determinants, particularly wave action. In the same region, a study of seaweed communities along approximately 600 km of coastline indicated that community composition was correlated with a gradient of sea-water temperature change around the southern tip of Africa (Bolton and Anderson 1990). In KwaZulu-Natal, there has been no work examining the influence of temperature changes along the coastline on intertidal biota. Although detailed temperature investigations have not been undertaken, Jackson (1976) commented that it was unlikely that any sharp temperature breaks exist along the KwaZulu-Natal coast, except possibly at Durnford Point where the coast changes direction, the continental shelf widens and the Agulhas current moves offshore (Schumann 1998).

Riverine input

Menge et al. (1997b) wrote that the effects of rivers on nearshore communities merit investigation. Riverine input could affect intertidal biota through increased productivity due to input of particulate organic matter, reduced salinity or increased siltation and turbidity. Rivers, especially those with agriculturally developed catchment areas, could affect nutrient status of nearby inshore systems (Bosman et al. 1987). The east coast of South Africa has many rivers, and there are 74 estuaries on the KwaZulu-Natal coast (Begg 1978). Jackson (1976) claimed that the effect of the rivers on inshore salinity in KwaZulu-Natal were minimal due to the rapid mixing of fresh and salt water by the heavy and continual wave action. Intermittent floods can, however, cause mass mortality of intertidal organisms close to river mouths as seen at the Orange River on the west coast of South Africa (Branch et al. 1990). These mortalities are probably related to hypo-salinity with evidence suggesting that wave exposure compounds the effects of reduced salinity (Branch et al. 1990). Jackson (1976) reported that turbidity was unlikely to influence intertidal biota in KwaZulu-Natal, with the possible exception of the perpetually turbid water at Point Durnford. However, high loads of suspended solids are known to adversely affect certain types of benthos and high silt loads have been implicated in reducing coral growth south of St Lucia (McClurg 1988, Riegl and Branch 1995).

Sand inundation

Lewis (1968) proposed that intolerance to siltation on less wave-exposed shores may underlie patterns of spatial variation created by differences in wave exposure. No published reports implicating sand inundation in determining large-scale biogeographic patterns in intertidal community structure were found during the present study. Sand-impacted rocky shores have been investigated on the Californian and Oregon coast (Taylor and Littler 1982, Littler et al. 1983), in Namibia (Engledow and Bolton 1994) and on the south coast of South Africa (Dower 1989, McQuaid and Dower 1990). In KwaZulu-Natal, sand inundation is a common phenomenon and has been identified as a potential factor influencing variability in community structure (Berry 1978, Jackson 1976, Tomalin and Kyle 1998) although the scale of influence is not known.

Wave exposure

Latitudinal variation in wave climate has been implicated in large-scale variability in intertidal habitats (Raffaelli and Hawkins 1996). Biological responses to variation in wave exposure have been well documented (Lewis 1964, Dayton 1971, Menge 1976, Seapy and Littler 1978, Menge and Farrel 1989, Palumbi 1984, Denny et al. 1985, Leigh et al. 1987, Carrington and Denny 1994). Analysis of global patterns of macroinvertebrate biomass in intertidal communities revealed that wave exposure is a universally important factor in structuring communities on rocky shores (Ricciardi and Borget 1999).

Wave action has been identified as an important factor that governs community structure on South African shores (McLachlan et al. 1981, McQuaid and Branch 1984, Bustamante and Branch 1996, Bustamante et al. 1997). Until now, intertidal wave forces have not been measured in KwaZulu-Natal. Jackson (1976) wrote "Wave action is difficult to measure, but certainly northern Zululand is afforded some protection from Madagascar". McClurg (1988) cited increased wave energy south of St Lucia as a potential cause of reduced coral growth.

Human exploitation

Human activities have been demonstrated to modify biological community structure (Moreno et al. 1984, Castilla and Duran 1985, Oliva and Castilla 1986, Duran and Castilla 1989, Fairweather 1990, Underwood 1993, van Tamelen et al. 1997, Sharpe and Keough 1998, Keough and Quinn 1998, Lasiak 1999, Schiel and Taylor 1999). In the marine environment, most changes attributable to human activity are restricted to small spatial scales although large-scale modifications of rocky-shore communities have been attributed to human exploitation of intertidal organisms in Chile (Moreno et al. 1984, Castilla and Duran 1985, Oliva and Castilla 1986, Ortega 1987, Duran and Castilla 1989). In Mozambique, studies comparing recent and abandoned shell middens found that *Perna perna* has disappeared and this local extinction may be related to overexploitation (de Boer 2000a). This indicates that harvesting effects could influence community structure at a regional scale.

In South Africa, studies in the former Transkei on the south-east coast indicated that harvesting of intertidal invertebrates by subsistence collectors has modified community structure (Siegfried et al. 1985, Hockey and Bosman 1986, Dye et al. 1994, Lasiak and Field 1995, Lasiak 1999). In KwaZulu-Natal, subsistence collectors harvest intertidal invertebrates, principally the brown mussel *P. perna* and the ascidian *Pyura stolonifera* in the Maputaland Marine Reserve (Kyle et al. 1997a). South of Maputaland, licensed recreational harvesters gather mussels and bait organisms from all shores except one (Trafalgar). Concerns of overexploitation and unsustainable harvesting have been expressed for both subsistence and recreational fisheries in KwaZulu-Natal (Heydorn and Hughes 1969, Jackson 1976, Tomalin and Kyle 1988). The effect of harvesting on biological community structure has not been examined in KwaZulu-Natal and this factor warrants investigation at multiple scales.

Objectives

The principle aim of this study was to identify and characterise differences in intertidal community structure at large scales (hundreds of kilometres) along the KwaZulu-Natal coast and to identify potential underlying environmental factors. Patterns in biological community composition were first identified and then related to sea temperatures, riverine input, sand inundation, wave exposure and human exploitation. Rock type was not considered in this biogeographic aspect of my work because all Maputaland shores are composed of a single rock type whereas further south, several different rock types are found within regions (see Chapter 3). Implications for conservation, resource management and ecological theory are discussed.

The following specific objectives were addressed:

1. To compare biological community structure on rocky shores along the KwaZulu-Natal coast.
2. To determine whether there are significant differences in community structure between four pre-defined regions.
3. To identify biogeographic breaks along the KwaZulu-Natal coast and examine whether observed patterns conform to previously proposed biogeographic provinces or sub-provinces.
4. To identify characteristic and distinguishing species that account for similarities within and differences between regions.
5. To explore potential abiotic factors that may underlie observed differences between regions.

This chapter thus explores biogeographic patterns in a quantitative manner for the entire KwaZulu-Natal coast and relates these patterns to abiotic factors at similarly large spatial scales. This is the first set of data to provide broad-area quantification of species abundance and environmental parameters for this region. Differences in community structure and abiotic factors between sites *within* biogeographic regions are the subject of the following chapter.

Methods

1. Pilot study

A pilot study was undertaken to determine appropriate sample numbers (i.e., replication) for four spatially defined zones on the shore: the low, mid, high and top shore. Eight different community types were defined and named after their dominant organisms (>50% cover): foliose algae, mussel, corraline turf, barnacle, zoanthid, oyster, littorina and *Enteromorpha*. In the low shore, "foliose algae" refers to mixed algal assemblages including *Hypnea spicifera*, and the mussel community was that dominated by the brown mussel, *Perna perna*. In the mid shore, coralline turf was dominated by *Jania verrucosa*, the barnacle community was characterised by barnacles of the genera *Tetraclita* or *Octomeris* and zoanthid communities were dominated by *Palythoa* and *Zoanthus* species. In the high shore, the oyster community comprised mainly *Saccostrea cucullata*, and moss-like expanses of unidentified green ephemeral algae were referred to as the *Enteromorpha* community. In the top shore, the highest zone examined, littorina community consisted of several species of littorinid snails, notably *Nodilittorina africana* and *N. natalensis*.

Percentage cover of all sessile species and counts of all mobile species were recorded within 30 replicate 1m x 0.5m quadrats for each community at one site each. Surveys were conducted at four sites in Zululand, Cape Vidal Point, Cape Vidal Ledge, Crayfish Point and Railway Ledge with different community types examined at different sites. The relationship between sampling intensity and species richness (sessile and mobile species) and Shannon diversity ($H' = -\Sigma_i p_i (\log_2 p_i)$) (sessile species only) was examined using cumulative diversity curves based on randomised samples. Mobile species were excluded from estimates of Shannon diversity (H') because of the difference in enumeration methods.

Quantification of species richness was dependent on sampling effort and the most species-rich communities had the highest rate of species accumulation (Figure 2.3A). Communities in the low and mid shore had higher species richness than those in the high and top shore. The algal community in the lowest part of the shore had the most species (S=35) and the high shore *Enteromorpha* community had the least (S=2). In the low and mid shore, most species were recorded after 20 samples whereas all high- and top-shore communities had no further increases in species richness after 4 samples.

Cumulative diversity curves indicated that increased sampling effort did not necessarily increase the estimate of diversity (Figure 2.3B). The Shannon index increased with increasing effort only within the foliose algae community. In the other communities, which had high dominance (indices of dominance were calculated although not shown here), Shannon diversity oscillated with increasing effort. The relationship between the abundance of the dominant species and Shannon diversity was investigated for two community types. In mussel, Shannon diversity was negatively correlated with the cover of *Perna perna* (R=-0.954, P<0.0001, n=180) and similarly in coralline turf, higher cover of *Jania verrucosa* reduced Shannon diversity (R=-0.914, p<0.0001, n=50).

The pilot study was undertaken to determine appropriate replication within sites. Because of the fluctuating diversity estimates due to changes in dominance, only species richness curves were used to determine sampling sizes. Sample sizes were chosen to include at least 95% of the species recorded. On these grounds, twenty quadrats were selected as an appropriate sample size for the low and mid shore, and ten quadrats for the high and top shore.

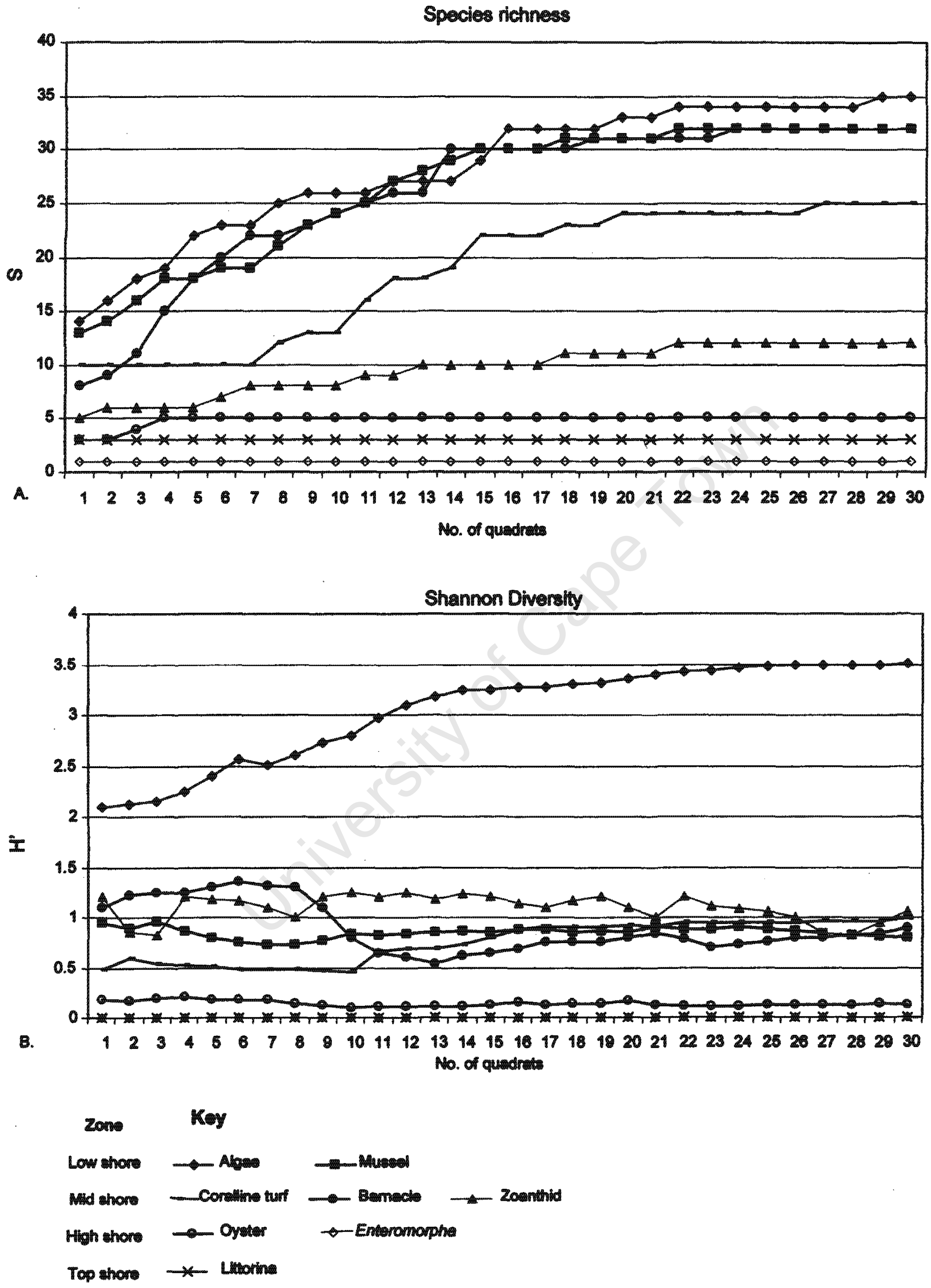


Figure 2.3 Pilot study : (A) Cumulative species richness (sessile and mobile species) and (B) Shannon diversity (sessile species only) for each community type based for each community type based on (A) 30 samples from one site.

2. Biological sampling design

The KwaZulu-Natal coast is approximately 560km long. The coast was divided into four pre-defined geographic regions, each approximately 140km long, and several sites per region were sampled to make up 39 sites in all (see Figure 2.2 for location of sites).

Maputaland	: Mozambique border to Leven Point
Zululand	: Leven Point to Durnford Point
Central KwaZulu-Natal	: Durnford Point to Amanzimtoti
South coast	: Amanzimtoti to Port Edward

The boundaries of these regions were selected to test for significant differences in community structure between previously described biogeographic regions or sub-regions, as proposed by Jackson (1976) and Emanuel et al. (1992).

Large-scale patterns in community structure were investigated in four zones (Figure 2.4). Analyses for these zones were kept separate. The low shore was surveyed at 39 sites, the mid shore at 27 sites and 22 and 13 surveys were conducted in the high and top shore respectively. Effort was greater lower on the shore, where diversity is greatest (Figure 2.3) and where human harvesting is concentrated (Lasiak 1999). Only 13 sites were surveyed in the top shore due to the continual presence of deep sand (>20cm) in this zone at many sites. Sites were surveyed during the summer of 1996/1997 (low and mid shore) and autumn 1997 (high and top shores) only during spring low tides (South African Navy 1996,1997).

At each site, 20 random replicate quadrats per site were scored in each of the low and mid shore, and 10 per site in each of the high and top shore, as prescribed by the pilot study (Figure 2.3). Percent cover of all sessile species and counts of visible mobile species and mean size per mobile species was recorded in the field. For the low, mid and high shore, counts of mobile organisms were converted to percentage cover estimates using mean size. In the top shore, counts of mobile organisms were not converted, partly to allow mobile species to dominate observed patterns but also because few sessile species were recorded in this zone.

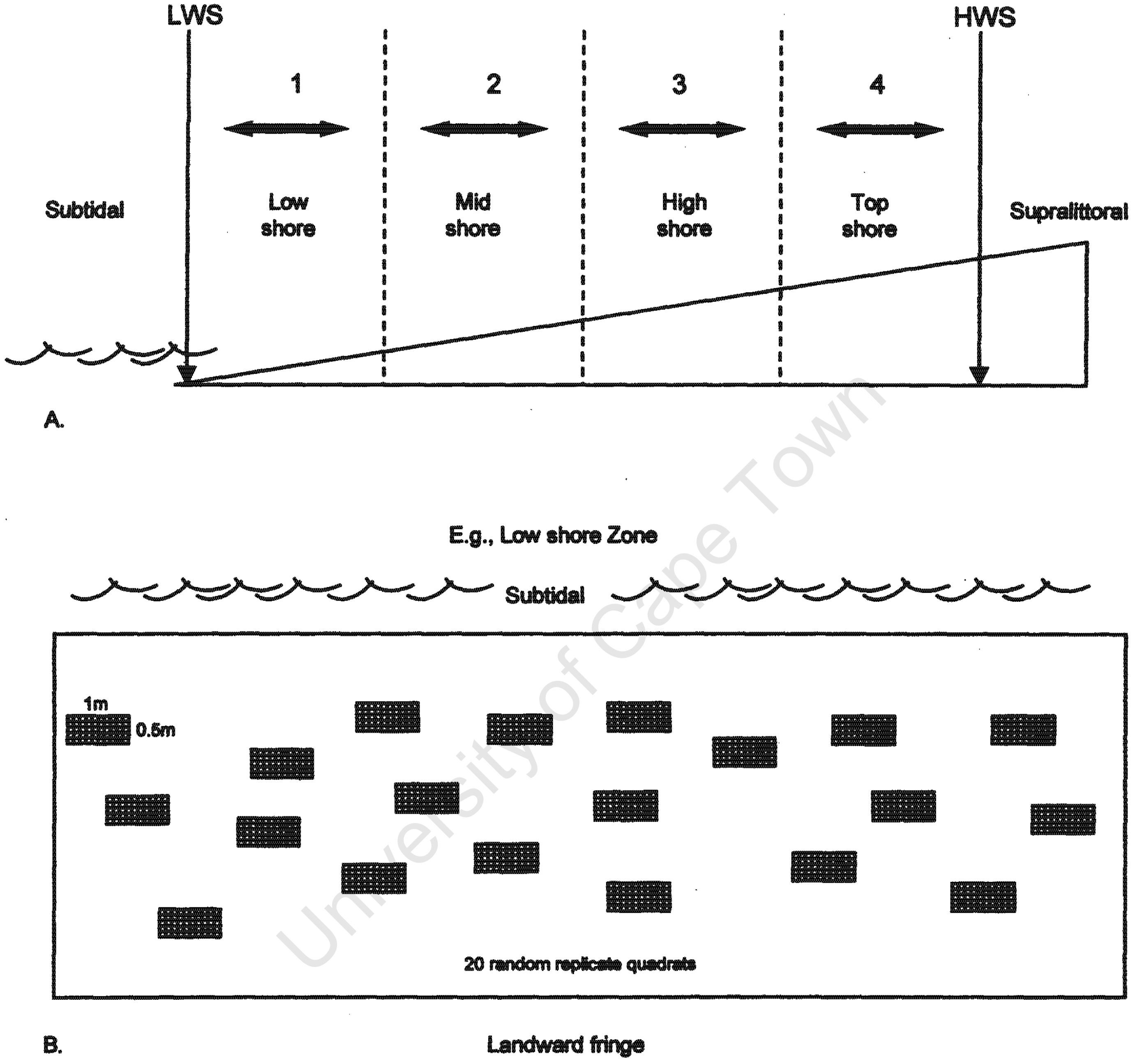


Figure 2.4. Schematic diagram illustrating (A) cross-section of a rocky intertidal shore, divided into four spatially defined zones. LWS=Low Water Slack and HWS=High Water Slack and (B) the sampling strategy within a zone. Twenty (low and mid shore) or ten (high and top shore) random replicate quadrats were sampled within the middle region of each zone. Percentage cover of all visible sessile species and counts and mean size of all mobile species was estimated within each quadrat.

3. Potential abiotic determinants of biogeographic patterns

3a. Sea-water temperature

Existing sea temperature data were collated (Center for Scientific and Industrial Research (CSIR), South African Weather Bureau, pers. comm.). There are only three inshore sites in KwaZulu-Natal at which surf temperatures are recorded, i.e., Zinkwazi and Durban in central KwaZulu-Natal and Southbroom on the South coast (L. Apps, South African Weather Bureau, pers. comm.). Mean summer and winter temperatures between 1974 and 1992 were calculated for these three sites. More extensive measurements of seawater temperature are collected by voluntary observing ships (V.O.S.) and mean summer and winter temperatures for half degrees of latitude and longitude were used to examine temperature changes along the KwaZulu-Natal coast (data from M. Grundlingh, CSIR, pers. comm.). These data are biased towards warmer offshore temperatures as most of the V.O.S. travel within the warm Agulhas current. In reality, inshore water is approximately 1.4 °C cooler that at the shelf break (Pearce 1978). However, in the absence of comparative inshore data along the entire coast, the assumption was made that the discrepancy between inshore and offshore temperatures is relatively constant along the coast. To test this assumption, the average summer and winter V.O.S. temperatures for appropriate half degrees of latitude were compared to the inshore temperature at Zinkwazi, Durban and Southbroom.

3b. Riverine input

The simulated mean annual runoff was calculated for each catchment along the KwaZulu-Natal coast from rainfall records and catchment size (Midgely et al. 1994) excluding abstraction of freshwater. These values may not accurately reflect absolute runoff but do indicate relative freshwater inputs from different catchment areas in KwaZulu-Natal. To compare riverine input in each predefined region, the total runoff within the boundaries of each region was summed. In Maputaland, riverine runoff was calculated based on an estimated 5% of total runoff (precipitation x catchment area) as no more than 5% of the precipitation enters the streams and rivers (Begg 1978, Pitman et al. 1981).

3c. Sand inundation

Fixed 20-m long transects were simultaneously monitored at 27 sites to estimate relative sand inundation in the low, mid and high shore. The top shores were not monitored because there was little variability in community structure in this zone. On each transect, the cover and depth of sand within ten 1 m x 0.5 m quadrats was scored for each zone on the shore. The data were converted to volumes of sand per m^2. This monitoring was undertaken by staff of KwaZulu-Natal Wildlife and volunteers from coastal conservancies under my supervision and was initiated in June 1997.

The data were collected simultaneously once a month for all sites from September 1997 until April 1999.There were occasions when sites were not monitored due to poor conditions or lack of manpower. Because of missing data, measurements were grouped into two-month intervals as opposed to monthly measurements. Due to staff changes at Mapelane, monitoring ceased in February 1998 and data for Crayfish point, Railway Ledge and Sandy Point were obtained from other researchers working in the area (JM Harris, KwaZulu-Natal Wildlife, pers. comm.).

3d. Wave exposure

To measure wave exposure, simultaneous maximum wave forces were recorded with 10-15 wave drogues (Palumbi 1984) at each of 30 sites on five occasions. This was conducted with assistance from staff of KwaZulu-Natal Wildlife and volunteers from coastal conservancies. These drogues have been criticised as subject to non-negligible internal friction and may record a variety of non-hydrodynamic forces (Bell and Denny 1994). They have, however, effectively been used to quantify relative wave forces on the south and west coast of southern Africa (Bustamante et al. 1997, N. Steffani, University of Cape Town, pers comm.). Only data from days with similar weather and sea conditions along the entire coast were used to compare wave exposure between regions (4 and 5 November 1988, 5 December 1998, and 18 March 1999). Data from another occasion (June 1999) were discarded as a cold front in the south resulted in disproportionately large swells in southern KwaZulu-Natal. Only one set of readings was made at Island Rock and three sets at Seula Point and Reunion.

3e. Human exploitation

Differences in human exploitation were monitored at 34 study sites simultaneously on the same days, and when weather and sea conditions were the same along the coast. Ten simultaneous counts were conducted between March 1997 and July 1998 including a range of high and low-use periods (weekdays, weekends, school holidays, public holidays) and a range of weather conditions. Patrolling KwaZulu-Natal Wildlife staff conducted these counts under my co-ordination. As replicate counts were not conducted over different days of the week and weather conditions, the effect of these factors on human activities could not be investigated. That was not, however, the purpose of the monitoring, which served only to quantify the relative intensity of use at different sites so that its relationship with differences in community structure could be determined.

Subsistence and recreational collectors were tallied separately because they gather different amounts of intertidal invertebrates. Subsistence harvesters each collect approximately 11.2 kg (total wet mass) of *Perna perna* per outing at Black Rock and Dog Point and 10.9 kg of *Pyura stolonifera* at Kosi Mouth (Kyle et al. 1997a). Licensed recreational harvesters each collect approximately 2.4 kg of *P. perna* per outing (Tomalin and Kyle 1998). To render the effect of both groups comparable, mean mass of invertebrates harvested per collector were used in conjunction with the counts of harvesters to estimate mean total mass of organisms harvested at each site.

Data analysis

Biological data

Each zone on the shore was analysed separately. PRIMER (Plymouth Routines in Multivariate Ecological Research, version 4.0 1994) was used for analysis of species composition and abundance (Clarke and Warrick 1994). Biological data were root transformed to weight the contribution of less abundant species. Hierarchical clustering analysis using Bray-Curtis co-efficients and multidimensional scaling (MDS) (Kruskal and Wish 1978) were used to compare community structure between sites and regions. The triangular similarity matrix generated by the cluster analysis was used to perform the MDS. Groups of samples identified by clustering were superimposed on the MDS plots. Within each zone, the average Bray-Curtis similarity between sites was used as a measure of community convergence. As the number of sites sampled differed between the zones, this was done in two ways: first by using the data for all sites sampled, and then by standardizing the number of sites analysed per zone (n=13) to ensure that differences in sample size did not bias the result. For the latter approach, analyses were restricted to sites at which all four zones were sampled.

To test for significant differences in community structure between pre-defined regions, one-way ANOSIM analyses were conducted (Clarke and Green 1988, Clarke 1993). Mean covers of all species from replicate sites within each region were compared. For those regions that did differ significantly, characteristic and distinguishing species between regions were identified using similarity percentage breakdown analyses (SIMPER). Species were only considered if they contributed more than 2% to the overall similarity or dissimilarity, or cumulatively accounted for at least 80% of the overall similarity or dissimilarity within and between regions.

4. Relating biogeographic patterns to abiotic data

Temperature changes and relative riverine input were compared to observed differences in community structure along the coast. Differences in wave exposure, sand inundation and human exploitation between observed biogeographic regions were tested with hierarchically nested ANOVA conducted with STATISTICA (1999). For wave force data, times were nested within sites and sites nested within regions, because 4-15 estimates of wave forces were made at each site each time. For sand inundation and harvesting data, sites were nested within regions but only the mean volume of sand per transect or total harvesting offtake was used in the ANOVA (i.e., there were no replicate values for each time). The assumption of normality was tested visually by examination of probability plots of residuals and statistically with the Kolmogorov-Smirnoff test. Variance was evaluated by visual examination of plots of means versus standard deviation and homogeneity of variances was checked by Cochran's test (Winer et al. 1991). For the wave exposure data and the estimates of relative sand inundation, log transformations were necessary to satisfy these assumptions and estimates of harvesting offtake were root transformed (Sokal and Rohlf 1995).

Results

1. Biogeographic breaks and regional differences in community structure

Abundance estimates for 220 species (91 invertebrates and 129 algae) were used to compare community structure on rocky intertidal shores along the KwaZulu-Natal coast. ANOSIM tests between the four pre-defined regions indicated that there were significant differences in community structure between regions in the low and mid shore (Global R=0.479, p<0.01, n=39 and R=0.55, p<0.01, n=27 respectively). No significant differences in community structure were found between any of the regions in the high and top shore (R=0.027 p=0.33, n=22 and R=0.197, p=0.13, n=13 respectively).

Table 2.1 shows that the low-shore community structure in Maputaland was significantly different from that of Zululand (R= 0.783 p<0.01), Central KwaZulu-Natal (R=0.727 p<0.01) and the South Coast (R=0.810 p=0.01). There were no significant differences in low shore community structure between Zululand, Central KwaZulu-Natal and the South Coast. In the mid shore, community structure in Maputaland was similarly significantly different from that of Zululand (R=0.889 p<0.01), Central KwaZulu-Natal (R=0.754 p<0.01) and South coast (R=0.760 p=0.01). Mid shores in Zululand were also significantly different to Central KwaZulu-Natal (R=0.467 p=0.01) and the South Coast (R=0.402 p<0.02). There were no differences in mid-shore community structure between central and southern KwaZulu-Natal (R=0.041, p=0.86).

Table 2.1. Results of one-way ANOSIM tests for differences between regions in low and mid-shore community structure in KwaZulu-Natal. Tests based on Bray-Curtis similarity measures derived from root transformed estimates of mean percentage cover of all visible species from replicate sites within each pre-defined region. *= significant difference (p<0.05).

REGION	Zululand	Central KwaZulu-Natal	South Coast
Maputaland	Low-R= 0.783 (p<0.01*) Mid-R= 0.889 (p<0.01*)	Low - R= 0.727 (p<0.01*) Mid - R= 0.754 (p<0.01*)	Low - R= 0.810 (p<0.01*) Mid - R= 0.760 (p=0.01*)
Zululand		Low- R= 0.248 (p=0.10) Mid - R= 0.467 (p=0.006*)	Low- R= 0.368 (p=0.07) Mid - R= 0.402 (p=0.013*)
Central KwaZulu-Natal			Low - R= 0.061 (p=0.20) Mid - R= 0.041 (p=0.68)

Figures 2.5 to 2.8 show the results of the hierarchical cluster analyses and the two-dimensional MDS ordination plots for all four zones on the shore. The dendrogram for the low-shore sites (Figure 2.5A) showed that two sites (one from Central KwaZulu-Natal and one from the south coast) were outliers more than 75% dissimilar (<25 % similarity) to all other sites. All the Maputaland sites, along with one Zululand site (Cape Vidal Point) and one site from the south coast (Umfazazana) formed a discrete cluster, more than 70% dissimilar to the rest of KwaZulu-Natal. Sites from Zululand, central KwaZulu-Natal and the South coast did

not separate out into regional groups, with sites from different regions often more similar than sites from the same region. The MDS plot (Figure 2.5B) also indicated that Maputaland low shores were different to the rest of KwaZulu-Natal. Cape Vidal Point again grouped with the Maputaland sites, and Umfazazana, a south coast site where subsistence harvesting is undertaken, was also more similar to the Maputaland sites than other South coast or central KwaZulu-Natal sites.

The dendrogram for the mid shore (Figure 2.6A) showed that three sites (two from Zululand and one from central KwaZulu-Natal), were outliers more than 80% dissimilar to all other sites. All the Maputaland sites were again grouped together in a cluster, more than 70% dissimilar to the remaining sites. As in the low shore, sites from the three other regions did not separate out into regional groups. Cape Vidal Point grouped with the sites from central and southern KwaZulu-Natal. The MDS plot (Figure 2.6B) also indicated that the Maputaland sites were distinct.

In the high shore, there was no distinct clustering of sites into their respective regions (Figure 2.7). Two of the Maputaland sites were more than 75% dissimilar to all other sites. The remaining sites were a mix from all four regions. Sites from central KwaZulu-Natal and the south coast were the most similar with more variability between sites from Maputaland and Zululand.

In the top shore, hierarchical cluster analysis and MDS (Figure 2.8) showed that there was no separation between regions. Of all the zones on the shore, the top shore samples had the least variability between sites, with all sites more than 60% similar.

The differences between Maputaland and the three other regions (Zululand, Central KwaZulu-Natal and South Coast) indicate that there are only two distinct biogeographic regions evident in the low and mid shore in KwaZulu-Natal. Sites south of Cape Vidal can be considered as a single region, previously termed Natal (Jackson 1976).

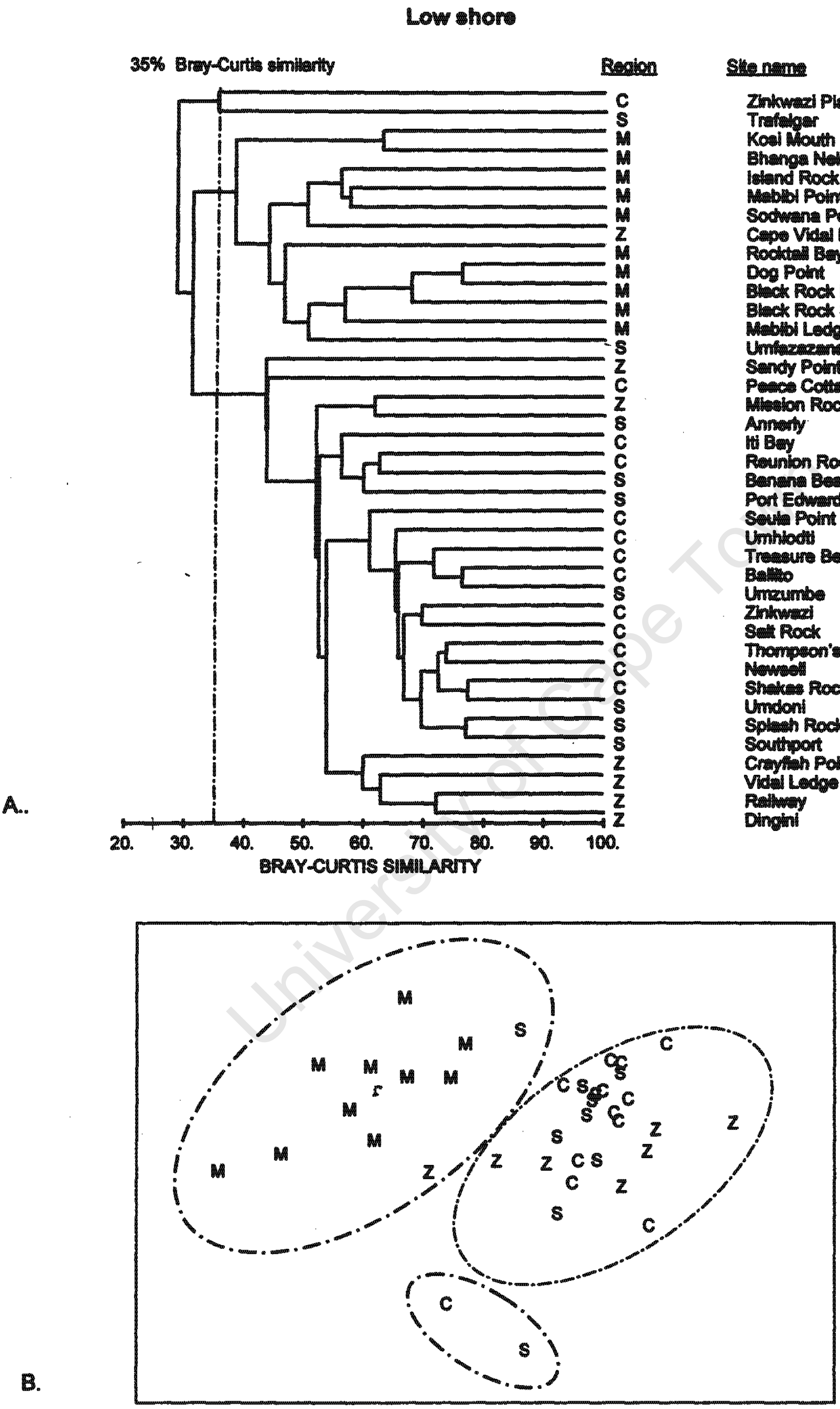


Figure 2.5. Dendrogram (A) showing results of the hierarchical cluster analysis and (B) MDS plot (stress = 0.14) based on root transformed biological data for the low shore of 39 sites within 4 pre-defined regions within in KwaZulu Natal. Region: M=Maputaland, Z=Zululand, C=Central KZN, S= South coast. -·-·-·- 35% Bray-Curtis similarity

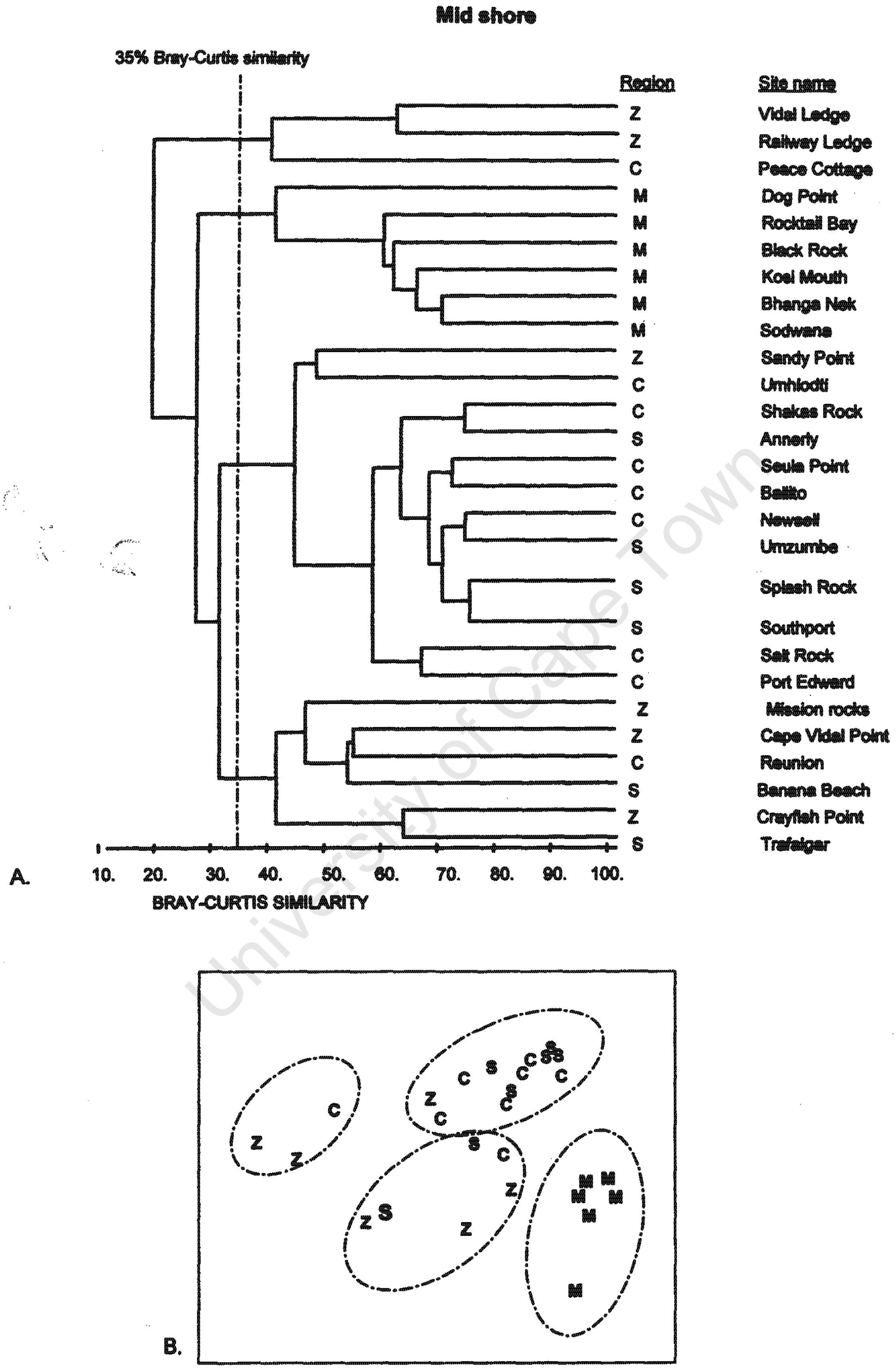


Figure 2.6. Dendrogram (A) showing results of the hierarchical cluster analysis and (B) MDS plot (stress = 0.16) based on root transformed biological data from the mid shore of 27 sites within four pre-defined regions in KwaZulu Natal. Region : M=Maputaland, Z=Zululand, C=Central KZN, S=South coast.

-·-·-·- 35% Bray-Curtis similarity

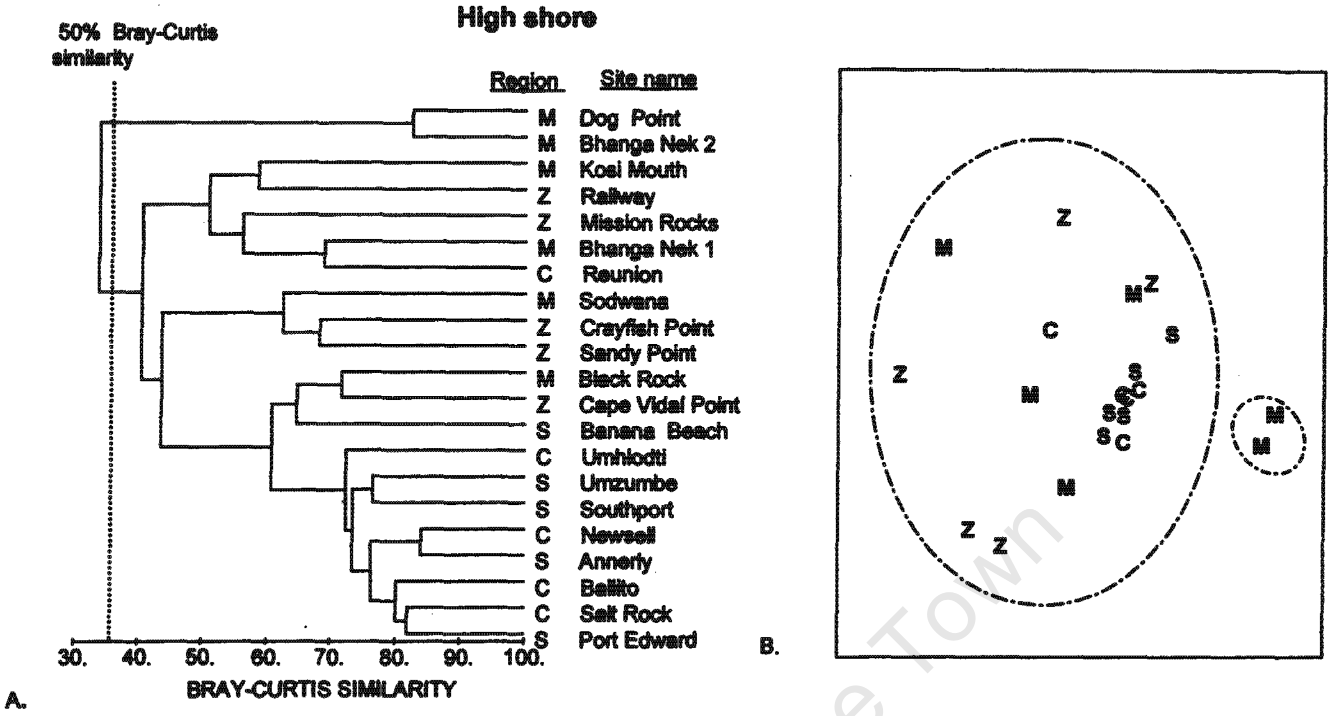


Figure 2.7. Dendrogram (A) showing results of the hierarchical cluster analysis and (B) MDS plot (stress =0.12) of root transformed biological data for the high shore of 22 sites within 4 pre-defined regions within in KwaZulu Natal. <u>Region</u>: M=Maputaland, Z=Zululand, C=Central KZN, S= South coast.

-·-·-·- 35% Bray-Curtis similarity

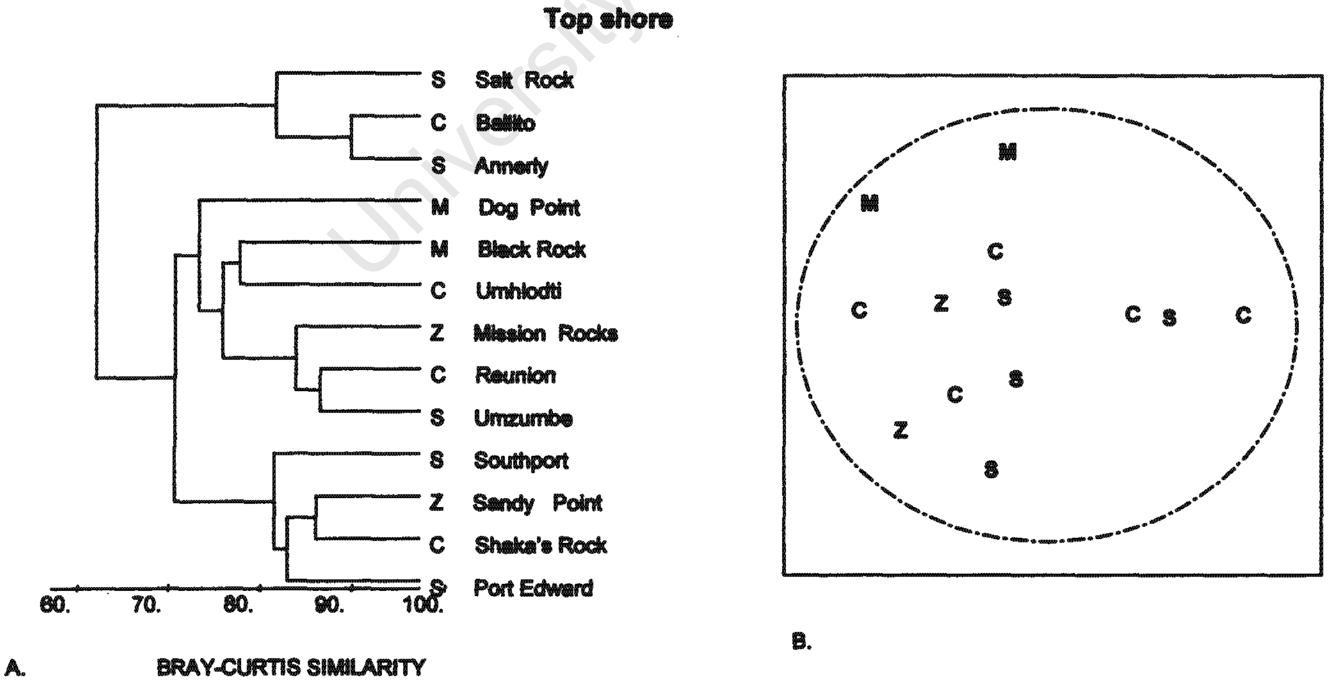


Figure 2.8. Dendrogram showing results of (A) the hierarchical cluster analysis and (B) MDS ordination (stress = 0.05) of root transformed biological data for the top shore of 13 sites within 4 pre-defined regions within in KwaZulu Natal. <u>Region</u>: M=Maputaland, Z=Zululand, C=Central KZN, S= South coast.

-·-·-·- 35% Bray-Curtis similarity

Differences between zones: divergence and convergence

There was greater between-site variability in the low and mid shore than in the top and high shore. This was also reflected in the average Bray-Curtis similarity for each zone on the shore (Table 2.2). Along the entire KwaZulu-Natal coast, the mid shore had the greatest variability in community structure between sites (S=40.51%, n=13 and S=33.29%, n=27). There was also substantial between-site variability in the low shore (S=51.46 %, n=13 and S=41.82%, n=39), but less in the high shore (S=54.95%, n=13 and S=48.23%, n=22). High similarity (S=72.79%, n=13) in the top shore indicated convergence of community structure. These differences were evident using a standard sample size in KwaZulu-Natal as a whole and when comparing all sites between zones.

Table 2.2. Average similarity (S%) between sites for each zone on the shore as determined by Simper analysis. Comparable estimates between zones in KwaZulu-Natal are indicated for a standardised sample size (n=13 sites). The average similarity for all surveyed sites is also shown, with the sample size indicated in parentheses. The average similarities within the two biogeographic regions were determined for the low and mid shore only, as no biogeographic differences in community structure were evident in the high and top shore.

ZONE	Entire KwaZulu-Natal S % (n=13)	Entire KwaZulu-Natal S % (All sites)	Maputaland S % (All sites)	Natal S % (All sites)
Low	51.46	41.82 (n=39)	47.36 (n=10)	51.14 (n=29)
Mid	40.51	33.29 (n=27)	49.73 (n=6)	39.00 (n=21)
High	54.95	48.23 (n=22)	-	-
Top	72.79	72.79 (n=13)	-	-

Characteristic species

Low shore

The low shores in Maputaland were on average 47.36% similar (Table 2.3). Of this similarity, 80% was accounted for by 19 taxa (including bare rock) (Table 2.3). The four most characteristic species were algae: *Sargassum elegans*, *Cheilosporum sagittatum*, encrusting coralline algae and *Caulerpa racemosa*, cumulatively accounting for 31.82% of the variation. The ascidian, *Pyura stolonifera*, and the brown mussel, *Perna perna*, were the two next most important species, explaining an additional 11.29 % of the group similarity. The most characteristic mobile species was the limpet *Scutellastra pica*. *Caulerpa racemosa*, *Pyura stolonifera* and the barnacle *Tetraclita squamosa rufotincta* were the most consistently characteristic species, as reflected by their high ratios of $S_i/SD(S_i)$.

The average similarity for low shores in Natal was 51.14%, with 80% of the group similarity explained by 14 taxa (Table 2.3). *Perna perna*, accounted for 30.13% of the group similarity.

Other important characteristic species were the algae *Hypnea spicifera*, *Cheilosporum sagittatum*, encrusting algae (corallines and *Ralfsia expansa*.) and *Jania verrucosa*. *Scutellastra aphanes* was the most characteristic mobile species. There was high variability in abundance between sites as reflected by the low ratio of Si / SD (Si). Encrusting coralline algae and *P. perna* were the two most consistent characteristic taxa.

Mid shore

Within Maputaland, the average similarity between mid shores was 49.73% (Table 2.3B). Ten taxa accounted for 80% of the group similarity. The barnacle, *Tetraclita squamosa rufotincta*, was the principal characteristic species accounting for 22.52% of the group similarity. Bare rock accounted for a further 18.05% and, together with the sponge *Hymeniacedon* sp., explained 50% of the group similarity. *Ralfsia expansa*, *Ulva* and *T. squamosa rufotincta* were the most consistently typical species for mid shores in Maputaland and the limpet *Cellana capensis* was consistently the most characteristic mobile species.

In the Natal region, there was substantial variability between shores with the average group similarity less than 40% (Table 2.3B). Eleven species accounted for 80% of the overall group similarity, with 4 taxa explaining 50% (Table 2.3B). The principal characteristic species were *Octomeris angulosa*, *Jania verrucosa* and *Ralfsia expansa*. *Perna perna* was the most consistently characteristic species in Natal. The most important characteristic mobile species was *Scutellastra natalensis*.

Table 2.3. Characteristic species for the (A) low, (B) mid, (C) high and (D) top shore in KwaZulu-Natal as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Maputaland and Natal were analysed separately for the low and mid shore for which significant differences in community structure were revealed between regions. The ranking is determined by S_i, the average contribution of each species to the overall similarity of the zone in each region. Av% indicates the average percentage cover of each species from all sites as based on 20 quadrats in the low and mid shore and 10 in the high and top shore of each site. Figures in parentheses for the top shore are densities.m^{-2}, not % cover. S_i/ SD(S_i) is the ratio between S_i and SD(S_i), the standard deviation of S_i. This ratio reflects how consistently the species abundance varied within each region. $\sum S_i$% is the cumulative percentage contribution of each species to the overall similarity, S. Only taxa accounting for 80% of the cumulative similarity are shown.

A. LOW SHORE

MAPUTALAND (n=10 sites) S=47.36%					NATAL (n=29 sites) S=51.14%				
Characteristic Species	%Av	S_i	Si/SD(Si)	$\sum S_i$%	Characteristic Species	%Av	S_i	Si/SD(Si)	$\sum S_i$%
Sargassum elegans	13.06	9.69	1.40	9.69	*Perna perna*	51.24	30.13	1.86	30.13
Cheilosporum sagittatum	17.84	8.99	0.98	18.67	*Hypnea spicifera*	7.34	6.90	1.25	37.03
Encrusting corallines	5.33	6.64	2.00	25.31	*Cheilosporum sagittatum*	5.75	6.28	1.36	43.31
Caulerpa racemosa	4.87	6.50	2.53	31.82	Encrusting corallines	3.30	6.22	1.99	49.53
Perna perna	11.58	6.44	1.19	38.26	*Ralfsia* sp.	2.18	5.09	1.79	54.62
Pyura stolonifera	4.70	4.85	2.16	43.10	*Jania verrucosa*	2.58	4.73	1.61	59.35
Tetraclita squamosa	2.16	4.20	2.11	47.31	*Plocamium corallorhiza*	1.93	4.36	1.29	63.71
Ralfsia sp.	1.83	4.00	1.76	51.30	*Hypnea intricata*	3.82	4.21	1.01	67.92
Chamaedoris delphinii	1.95	3.96	1.37	55.26	*Spyridea hypnoides*	1.46	2.73	1.37	70.65
Sargassum crassifolium	3.27	3.88	1.29	59.14	Bare rock	1.39	2.49	1.67	73.14
Laurencia glomerata	5.23	3.32	0.74	62.46	*Octomeris angulosa*	1.00	2.24	0.89	75.38
Idanthyrsus pennatus	7.19	3.17	0.67	65.63	*Scutellastra aphanes*	0.68	1.90	1.03	77.27
Bare rock	0.91	2.62	1.24	68.25	sand	2.10	1.69	0.62	78.96
Valonia macrophysa	1.29	2.41	1.00	70.66	*Arthrocardia* sp.	0.99	1.50	1.00	80.46
Unidentified green ascidian	2.06	2.40	1.00	73.06					
Jania adhaerens	1.55	2.27	0.86	75.34					
Hymeniacedon sp.	1.09	2.16	1.66	77.50					
Unidentified sandy ascidian	1.03	1.99	1.30	79.49					
Scutellastra pica	0.72	1.71	1.36	81.20					

B. MID SHORE

MAPUTALAND (n=6 sites) S=49.73%					NATAL (n=21 sites) S=39.60%				
Characteristic Species	%Av	Si	Si/SD(Si)	$\sum S_i$%	Characteristic Species	%Av	Si	Si/SD(Si)	$\sum S_i$%
Tetraclita squamosa	27.35	22.52	2.33	22.52	*Octomeris angulosa*	23.76	15.9	0.73	15.9
Bare rock	15.43	18.05	4.19	40.57	*Jania crassa*	20.10	14.86	0.76	30.76
Hymeniacedon sp.	7.19	8.71	1.43	49.28	Bare rock	13.30	14.71	1.1	45.47
Encrusting corallines	11.03	8.45	1.19	57.73	*Ralfsia* sp.	5.01	7.56	0.88	53.03
Palythoa nelliae	10.16	7.56	1.16	65.29	*Palythoa nelliae*	12.63	5.28	0.43	58.31
Dendropoma tholia	5.67	3.74	0.9	69.03	*Tetraclita serrata*	2.70	5.16	0.84	63.48
Ralfsia sp.	0.79	3.7	3.5	72.72	*Perna perna*	0.68	3.9	1.52	67.37
Idanthyrsus pennatus	4.84	3.01	0.97	75.74	Encrusting corallines	2.32	3.36	0.96	70.73
Cellana capensis	0.67	2.92	2.23	78.65	*Pomatoleios kraussii*	2.10	2.91	0.61	73.64
Perna perna	0.73	2.3	1.32	80.95	*Zoanthus natalensis*	2.72	2.85	0.48	76.49
Ulva sp.	0.31	2.07	2.54	83.01	*Saccostrea cucullata*	0.79	2.75	0.79	79.25
					Onikusa foliacea	1.11	2.45	0.73	81.7
					Gelidium reptans	0.68	2.32	0.75	84.01
					Scutellastra natalensis	0.49	2.14	0.7	86.15

C. HIGH SHORE (n=22 sites) S=48.23%

Characteristic Species	%Av	Si	Si/SD(Si)	$\sum S_i$%
Bare rock	37.59	19.3	1.81	40.07
Saccostrea cucullata	34.47	16.1	1.27	73.45
Chthamalus dentatus	3.05	3.2	0.92	80.06
Brown ephemeral alga	11.02	1.9	0.31	83.95

D. TOP SHORE (n=13 sites) S=72.79%

Characteristic Species	Av% (Av no.)	Si	Si/SD(Si)	$\sum S_i$%
Bare rock	51.32	37.3	4.63	51.32
Nodilittorina africana	(32.02)	23.3	2.51	83.34
Nodilittorina natalensis	(14.13)	10.3	1.22	97.47
Littoraria glabrata	(2.00)	1.5	0.99	99.48

High shore

High-shore sites were treated as an entity covering the whole KwaZulu-Natal coast because no biogeographic breaks were identified within this zone. Four taxa accounted for 80% of the average similarity (S=54.95%) in the high shore (Table 2.3C). The most consistent and most characteristic species was the sun oyster, *Saccostrea cucullata*, accounting for more than 70% of the overall similarity together with bare rock. The high-shore barnacle, *Chthalamus dentatus*, and an unidentified ephemeral brown alga were also characteristic species. The limpet, *Cellana capensis* was also relatively consistently characteristic of the high shore (Si/SD(Si) =1.4) and other characteristic species were *Siphonaria* spp., although variability of these species between sites was high (*S. capensis*, *S. concinna*, *S. serrata*; Si/SD(Si) =0.49, 0.46, 0.29 respectively).

Top shore

Top-shore sites were similarly treated as a unit covering the entire KwaZulu-Natal coast, since no biogeographic breaks were identified in the top shore. Bare rock and three littorinid snails accounted for 99% of the overall similarity (S=77.79%) (Table 2.3D). *Nodilittorina africana* was the most consistently characteristic species and was also the most abundant species (average density = 33.03.m^{-2}). Lower densities of the other characteristic species *N. natalensis* (14.13.m^{-2}) and *Littoraria glabrata* (2.m^{-2}) were recorded.

Species distinguishing between regions

Low shore

Maputaland low shores were on average 70.04% dissimilar to those in Natal. The key distinguishing species are shown in Table 2.4A. *Perna perna* was the top-ranking distinguishing species, accounting for 8.36% of this difference. The average cover of this species was far less in Maputaland (11.58%) than Natal (51.24%). The variability in species abundance between Maputaland sites and those further south was high. *Tetraclita squamosa rufotincta* and *P. perna* constituted the most consistent distinguishing species.

Table 2.4. Major distinguishing species in (A) the low and (B) the mid shore for sites in Maputaland and Natal as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. The ranking is determined by Di, the average contribution of each species to the overall dissimilarity between regions (D). Species are ranked in order of importance in contributing to the overall dissimilarity between regions. Av. % indicates the average percentage cover of each species from sites within each region. $D_i/SD(D_i)$ is the ratio between D_i (the average contribution of each species to the overall dissimilarity) and $SD(D_i)$, the standard deviation of D_i. This ratio reflects how consistently the species abundance varies within each region. $\sum D_i$% is the cumulative percentage contribution of each species to the overall dissimilarity, D. Only taxa accounting for 80% of the cumulative dissimilarity are shown.

A. LOW SHORE (D=70.04%)				
Distinguishing Species	AV% Maputaland	AV% Natal	$D_i/SD(D_i)$	$\sum S_i$%
Perna perna	11.58	51.24	1.72	8.36
Sargassum elegans	13.06	2.31	1.42	13.09
Cheilosporum sagittatum	17.84	5.75	1.22	17.74
Hypnea spicifera	0.28	7.34	1.42	21.28
Laurencia glomerata	5.23	0.00	0.96	24.21
Caulerpa racemosa	4.87	0.55	1.49	27.01
Pyura stolonifera	4.70	0.32	1.26	29.73
Idanthyrsus pennatus	7.19	0.16	0.79	32.40
Sargassum crassifolium	3.27	0.15	1.27	34.87
Hypnea intricata	0.35	3.82	1.30	37.30
Tetraclita squamosa	2.16	0.03	1.89	39.46
Chamaedoris delphinii	1.95	0.06	1.62	41.53
Palythoa nelliae	3.61	0.14	0.85	43.58
Jania crassa	0.67	2.58	1.42	45.52
Encrusting corallines	5.33	3.30	1.33	47.44
Unidentified green ascidian	2.06	0.00	1.13	49.29
Plocamium corallorhiza	0.32	1.93	1.59	51.07
Jania adhaerens	1.55	0.03	1.27	52.70
Valonia macrophysa	1.29	0.01	1.28	54.31
Sand	0.46	2.10	0.95	55.89
Laurencia pumilia	2.16	0.00	0.74	57.42
Caulerpa filiformis	0.00	2.99	0.65	58.91
Hymeniacedon sp.	1.09	0.01	1.15	60.29
Unidentified sandy ascidian	1.03	0.00	1.19	61.66
Octomeris angulosa	0.03	1.00	1.18	62.99
Spyridea hypnoides	0.20	1.46	1.20	64.28
Ralfsia sp.	1.83	2.18	1.41	65.56
Arthrocardia sp.	0.76	0.99	1.06	66.80
Bare rock	0.91	1.39	0.90	68.04
Arthrocardia carinata	0.05	1.63	0.68	69.16
Scutellastra pica	0.72	0.02	1.18	70.22
Chondria armata	0.65	0.06	1.16	71.26
Scutellastra aphanes	0.06	0.68	1.06	72.24
Laurencia natalensis	0.18	0.56	1.09	73.14
Gelidium abbottiorum	0.00	1.27	0.56	74.01
Byssus threads	0.52	0.16	0.88	74.81
Unidentified algae	0.77	0.07	0.58	75.60
Champia compressa	0.40	0.17	0.99	76.37
Cladophora rugulosa	0.00	0.44	0.77	77.07
Halimeda cuneata	0.13	0.37	1.03	77.75
Polysiphonia sp.	0.10	0.47	0.64	78.41
Callithamnion stuposum	0.21	0.28	0.97	79.05
Ulva spp.	0.06	0.41	0.72	79.69
Dictyota humifusa	0.27	0.03	1.02	80.29

B. MID SHORE (D=74.08%)				
Distinguishing Species	AV% Maputaland	AV% Natal	$D_i/SD(D_i)$	$\sum S_i$%
Tetraclita squamosa	27.35	0.44	2.69	9.71
Octomeris angulosa	0.59	23.76	1.16	17.03
Jania crassa	0.10	20.10	1.01	23.92
Palythoa nelliae	10.16	12.63	1.31	29.58
Hymeniacedon sp.	7.19	0.04	1.61	34.25
Encrusting corallines	11.03	2.32	1.24	38.72
Bare rock	15.43	13.30	1.43	43.01
Dendropoma tholia	5.67	0.01	0.98	46.39
Idanthyrsus pennatus	4.84	0.03	0.84	49.28
Ralfsia sp.	0.79	5.01	1.38	52.01
Jania adhaerens	5.59	0.25	0.63	54.63
Tetraclita serrata	0.00	2.70	1.15	57.09
Zoanthus natalensis	0.77	2.72	1.06	59.28
Pomatoleios kraussii	0.04	2.10	0.91	61.11
Onikusa foliacea	0.79	1.11	1.04	62.76
Laurencia pumilia	0.93	0.65	1.12	64.29
Neomeris sp.	1.87	0.34	0.58	65.8
Gelidium reptans	0.84	0.68	1,17	67.15
Arthrocardia sp.	0.01	1.59	0.65	68.46
Padina boryana	0.81	0.09	1.17	69.72
Dictyosphaeria versluysii	0.49	0.00	1.62	70.89
Saccostrea cucculiata	0.18	0.79	1.27	72.06
Ulva spp.	0.31	1.20	0.78	73.2
Cellana capensis	0.67	0.14	1.5	74.25
Scutellastra natalensis	0.00	0.49	1.1	75.3
Perna perna	0.73	0.68	1.2	76.33
Laurencia glomerata	1.78	0.00	0.43	77.33
Brown ephemeral algae	0.51	0.11	0.79	78.23
Hypnea intricata	0.00	1.22	0.44	79.09
Laurencia natalensis	0.00	0.46	0.67	79.91
Zoanthus parvus	0.21	0.40	0.69	80.69

Only 13 species contributed more than two percent each to the average dissimilarity between Maputaland and Natal. After *P. perna*, most of these were algal species that were more common in Maputaland e.g., *Sargassum elegans*, *S. crassifolium* and *Caulerpa racemosa*. The alga, *Hypnea spicifera*, was almost absent in Maputaland but was characteristic in Natal. Three other invertebrate species were characteristic of Maputaland low shores: the ascidian *Pyura stolonifera*, the polychaete *Idanthyrsus pennatus* and the barnacle, *T. squamosa rufotincta*.

Mid shore

The key distinguishing species between Maputaland mid shores and the rest of KwaZulu-Natal are shown in Table 2.4B. There were greater differences between regions in the mid shore (D=74%) than the low shore (D=70%). Twelve species individually accounted for more than 2% of the overall dissimilarity and, cumulatively, thirty species explained 80% of the total dissimilarity between groups. Barnacles were important distinguishing species. *T. squamosa rufotincta* was dominant in Maputaland and *Octomeris angulosa* and *Tetraclita serrata* were prevalent in Natal. *T. squamosa rufotincta* and *Dictyosphaeria versluysii* (both characteristic of mid shores in Maputaland) were the most consistent distinguishing species. The articulated coralline alga, *Jania verrucosa*, was more abundant in Natal and was the most important distinguishing alga.

2. Potential abiotic determinants of biogeographic patterns

2a. Sea-water temperature

Data collected by voluntary observing ships (V.O.S.) provided an indication of mean maximum and minimum sea-water temperatures for half-degree blocks of latitude along the KwaZulu-Natal coast (Figure 2.9). Temperatures ranged from a mean (±s.d.) winter (June-August) temperature of 21.08°C (±1.68) in the far south to a mean summer (December-February) temperature of 26.19°C (±1.35) in the far north. There was approximately four degrees difference between summer and winter for most localities. The range of mean summer temperatures was 2.43°C and the mean winter temperature ranged from 22.39°C in the far north to 21.08°C on the South coast, a range of 1.31°C.

Offshore temperatures did not change abruptly at any point along the coast (Figure 2.9). In particular, there was no indication of rapid change between Sodwana and Cape Vidal at the juncture of the Maputaland and Natal biogeographic provinces. The differences in both mean summer and mean winter temperatures between the half degrees of latitude including Cape Vidal and Sodwana respectively were less than 0.1°C. The half degree of latitude spanning sites from Cape Vidal Point to Railway Ledge and the adjacent half degree (including Sandy

Point and Dingini), differed in mean summer and winter temperatures by 0.49°C and 0.56°C respectively.

Along the KwaZulu-Natal north coast, the mean summer temperatures changed most in the vicinity of Durnford Point, 0.6°C difference between 28°30'-29°00'S and 29°00'-30°00'S. The largest difference in temperatures between half degrees of latitude in KwaZulu-Natal were evident in the vicinity of Umfazazana on the south coast with 0.94°C difference between 30°00'-30°30'S and 30°30'-31°00'S. Lowest summer temperatures in KwaZulu-Natal were evident within the latter section of coast with slightly higher summer temperatures recorded further south. Overall, temperatures declined from north to south and there was no indication of any abrupt temperature change coincident with the biogeographic break identified at Cape Vidal Point.

Comparison of offshore temperature V.O.S. data with inshore temperatures did reveal differences between localities. While the mean inshore and offshore winter temperatures differed relatively consistently (1.06, 1.05 and 1.13°C cooler inshore at Zinkwazi, Durban and Southbroom respectively), there were larger differences between offshore and inshore summer temperatures between sites. The difference at Zinkwazi was 1.36°C cooler, at Durban only 0.74°C cooler, and at Southbroom a larger difference of 2.4°C was identified, with cooler water inshore.

2.b Riverine input

The simulated total mean annual volume of riverine input was calculated per catchment and per region (Figure 2.10). Estimated river input in Maputaland was less than 100 $m^3 \times 10^6$, approximately 5% of that of the Zululand and South coast region and less than 2% of that in Central KwaZulu-Natal. Central KwaZulu-Natal had the highest riverine input, 5 906 $m^3 \times 10^6$, dominated by the contribution from the Thukela River, 3 988 $m^3 \times 10^6$, which comprised approximately 40% of the simulated total river input in KwaZulu-Natal. The St. Lucia, Mfolozi and Mhlatuze catchments in Zululand had relatively large simulated riverine outputs and the combined volume (1 991 $m^3 \times 10^6$) was similar to that of the South coast (2 023 $m^3 \times 10^6$). Southern KwaZulu-Natal has the greatest number of estuaries (51) although many are relatively small (Begg 1978), with the Mkomazi catchment dominating the riverine input. The simulated total inputs of river water in the Zululand and South Coast regions were less than that of the Thukela River. The input in Maputaland was 0.001% of that of the Natal region.

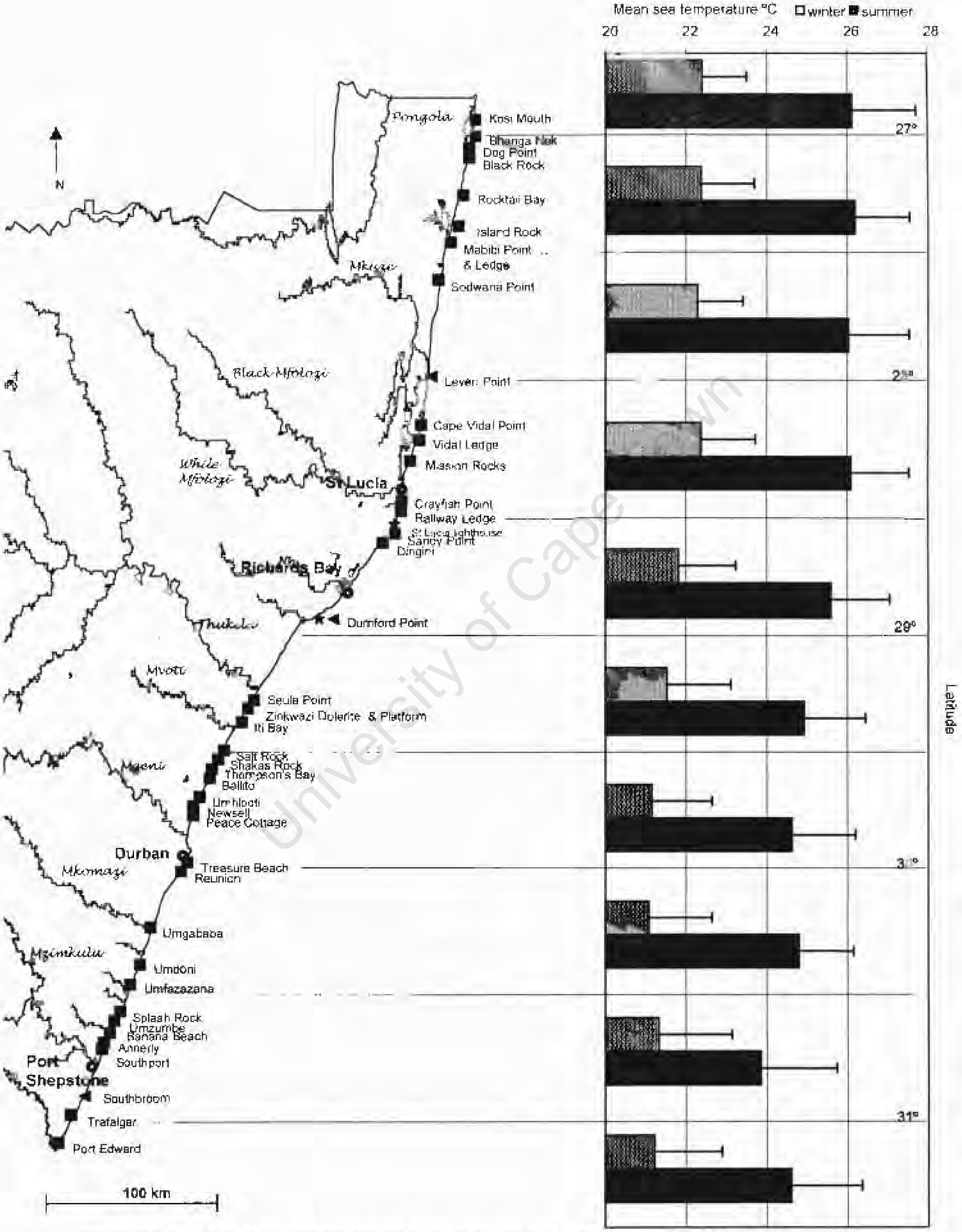


Figure 2.9. KwaZulu-Natal coast showing mean summer and winter temperature (+ s.d.) as recorded in half degrees of latitude by voluntary observing ships.

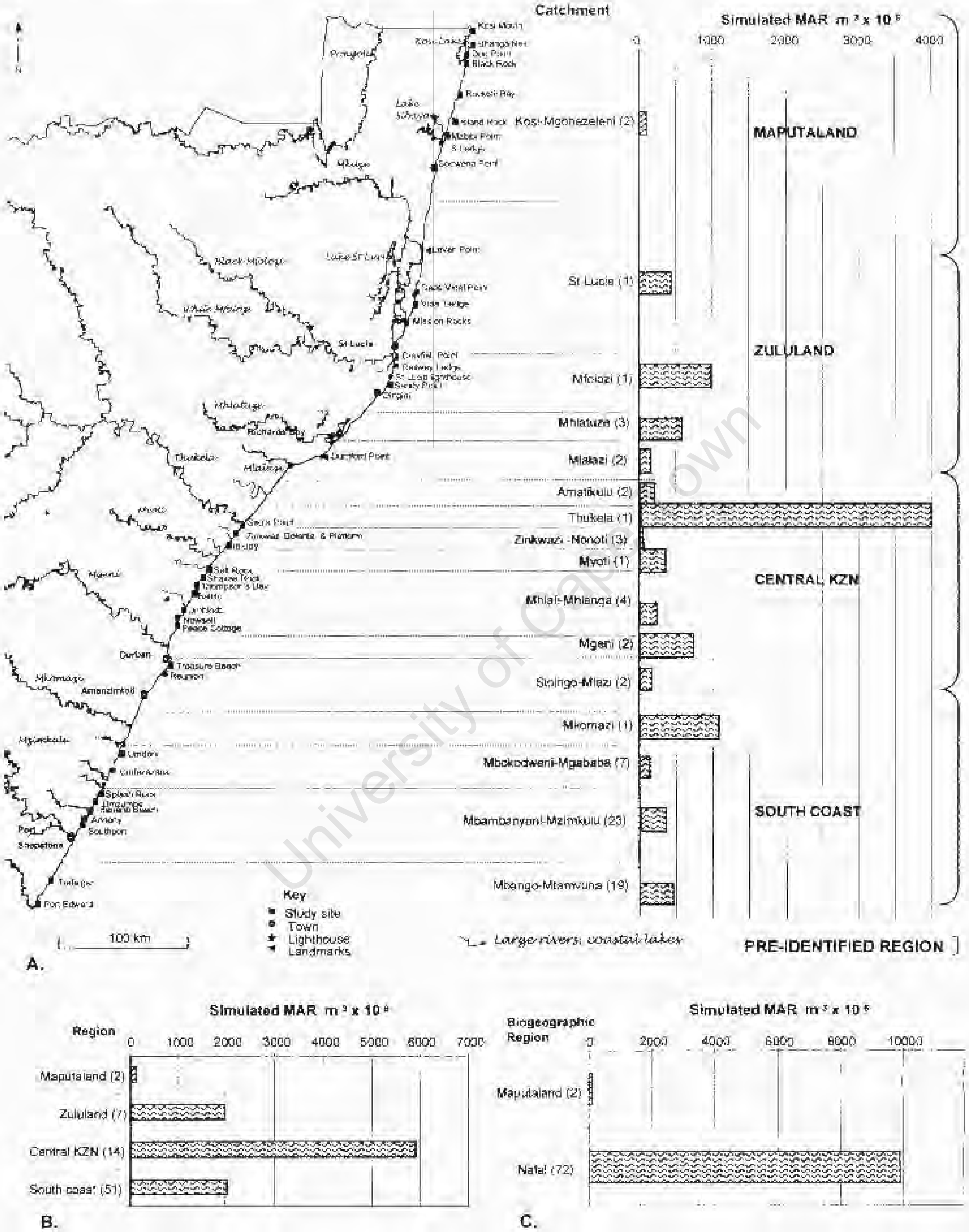


Figure 2.10. Simulated Mean Annual Runoff (MAR). (A) per catchment in KZN, (B) per pre-defined region and (C) per biogeographic region. The number of rivers for each catchment or region are shown in parentheses.

2c. Sand inundation

Sand monitoring undertaken within three zones on the shore showed that sites were subject to a large range of intensities of inundation (Figure 2.11). Sand inundation was not necessarily uniform between zones at given sites, although sites that experienced greatest volumes and frequency of inundation in the low shore, tended to experience relatively intensive inundation in all zones. In the low shore, the mean volume ranged from zero at Seula Point to 4 896 $cm^3.m^{-2}$ at Peace Cottage. In the mid shore, the total volume ranged from <2 $cm^3.m^{-2}$ at Splash Rock to 6 257 $cm^3.m^{-2}$ at Banana Beach. Total volume in the high shore ranged from zero at Black Rock to 3 672 $cm^3.m^{-2}$ at Kosi Mouth. Sand inundation was not monitored in the top shore. In all zones, relatively heavily and lightly sanded shores were found in both regions. There was no significant difference in mean volume of sand between Maputaland and Natal in the low or mid shore (p=0.5 and 0.8 respectively, nested ANOVA Table 2.5). However, there were significant differences between sites in both zones (P<0.0001).

Table 2.5 Results of nested ANOVA testing for corresponding differences in environmental factors and human exploitation between biogeographic regions. Sites were nested within regions and time was nested within sites for wave exposure data. Sand inundation was examined separately for three physically defined zones on the shore. Wave exposure was estimated by repeated simultaneous measurements of maximum wave forces within 27 sites. Mean mass of invertebrates harvested per site was recorded by ten simultaneous surveys at 30 sites. * = significant difference (P<0.01)

Factor	Sand inundation -low			Sand inundation -mid			Wave exposure			Human exploitation		
	df	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Region	1	0.47	0.50	1	0.07	0.80	1	0.04	0.85	1	20.1	<0.0001*
Site	25	10.8	<0.0001*	21	11.8	<0.0001*	30	29.5	<0.0001*	32	17.6	<0.0001*
Time							3	17.2	<0.0001*			

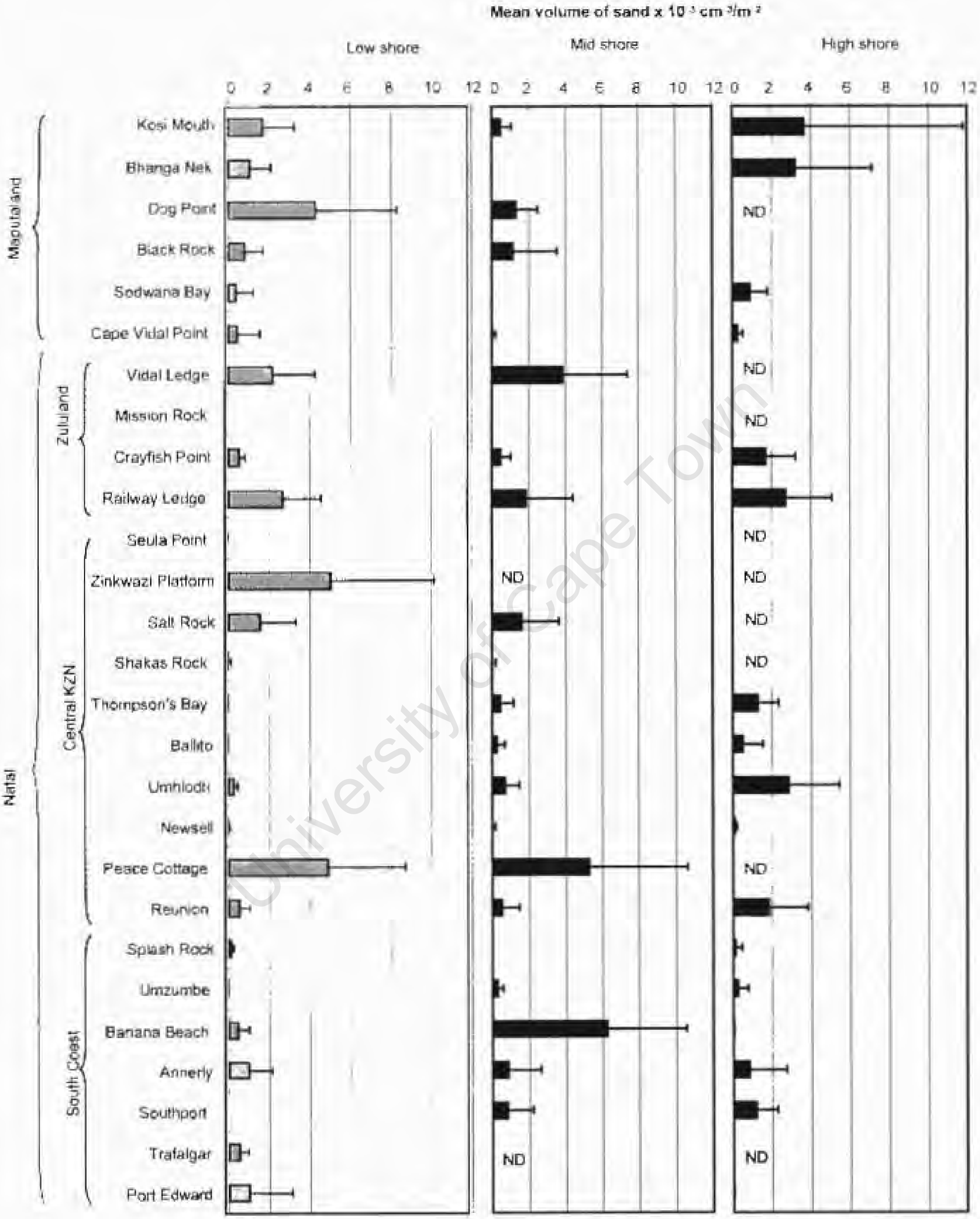


Figure 2.11. Mean volume (+s.d.) of sand. m^{-2} within the low, mid and high shore as recorded by ten simultaneously monitored 20 m transects between September 1997 and December 1999. ND = No data.

2d. Wave exposure

Mean maximum wave forces per site ranged from about 4.8×10^3 N.m^{-2} at Rabbit Rock (just south of Bhanga Nek) and Zinkwazi Platform to 18.08×10^3 N.m^{-2} at Dog Point (Figure 2.12). Exposed and sheltered sites occurred along the entire coast and there was no coastwise gradient in wave exposure evident. Nested ANOVA indicated that there were no significant differences in mean maximum wave forces between Maputaland and Natal (Table 2.5 $p=0.85$). There were however highly significant differences between sites ($P<0.0001$) and between times ($p<0.0001$). Post hoc tests showed that wave forces were significantly lower in March than those recorded on both occasions in November and on a single occasion in December. There were no significant differences between wave forces in November and December. Between-site differences in wave exposure are investigated in Chapter 3.

2e. Human exploitation

Numbers of harvesters collecting per low tide ranged widely, with 0-13 recreational collectors and 2-18 subsistence collectors operating within any one site. However as many as 83 subsistence collectors were counted at a single site (August 1998, Kosi Mouth, pers. obs. – outside of simultaneous monitoring) on a single tide. Mean numbers of collectors per site ranged from zero to 3.7 ± 8.3 recreational collectors at Crayfish Point and 7.6 ± 2.3 subsistence collectors at Black Rock.

The mean mass of invertebrates harvested per site in Maputaland ranged from 0 kg per low tide at protected or inaccessible sites up to a maximum of 85.12 kg per low tide collected by subsistence collectors at Black Rock. In Natal, the mean mass of invertebrates harvested by recreational collectors per outing ranged from 0 at Trafalgar and Zinkwazi platform up to a maximum of 8.88 kg at Crayfish Point per outing (Figure 2.13). There was substantial variability in numbers of harvesters, and therefore relative mass of harvested organisms, between monitoring times. This is reflected in the high standard deviations (Figure 2.13). There was, however, a significant difference in mean mass of invertebrates harvested per site between Maputaland and Natal ($p=0.000089$, nested ANOVA Table 2.5). The mean mass harvested per site on a single low tide in Maputaland was 40.58 ± 39.3 kg compared to 2.26 ± 2.17 kg in Natal. When only exploited sites were considered, the mean mass of harvested invertebrates per site per tide in Maputaland was 71 kg, thirty times greater than that in Natal. There were also significant differences in harvesting offtake between sites (Table 2.6, $p<0.00001$) and these are pursued in the following chapter.

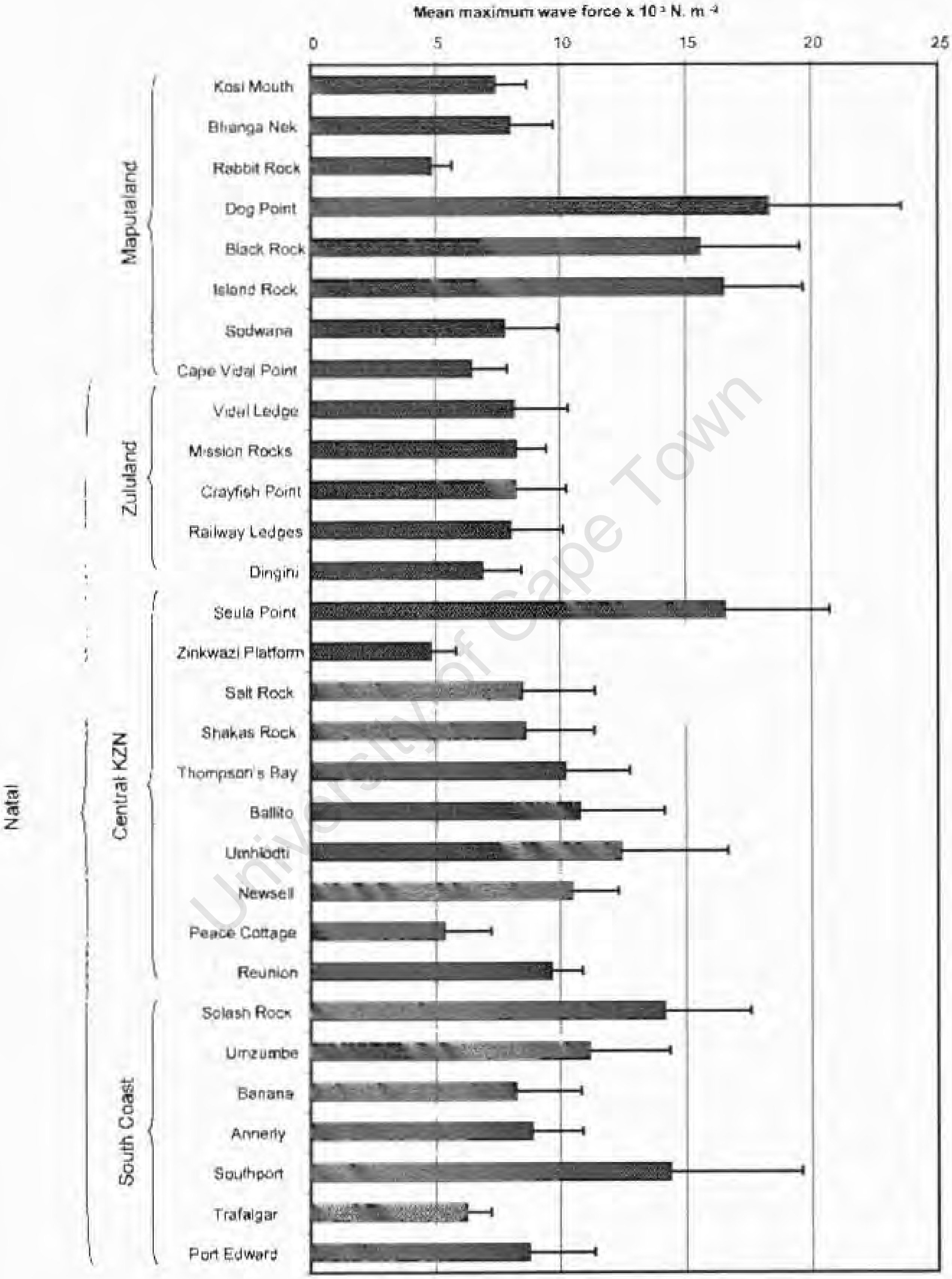


Figure 2.12. Mean maximum wave forces (+ s.d.) measured simultaneously on four occasions in the low shore as recorded by 10-15 wave drogues per site.

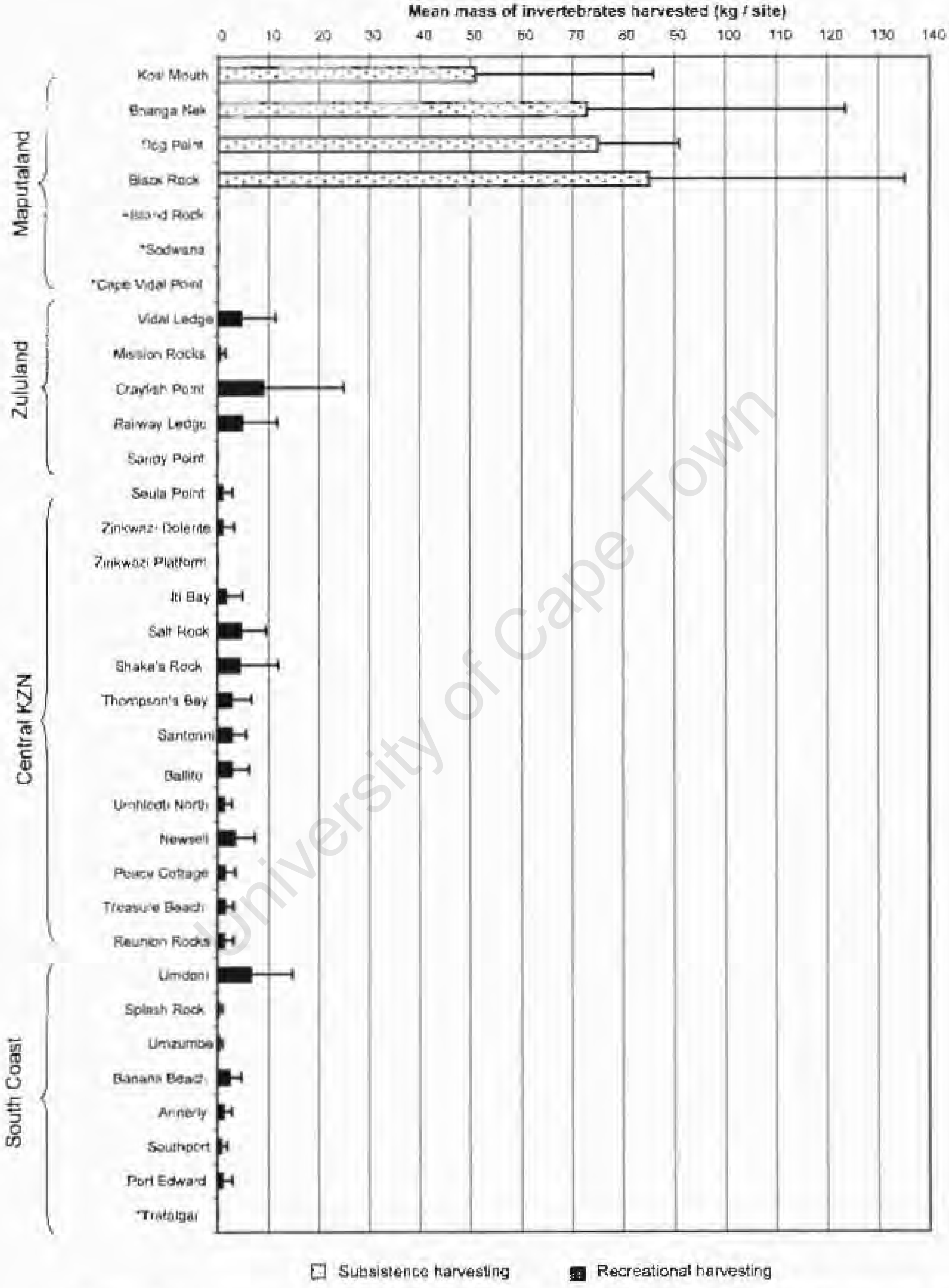


Figure 2.13. Mean mass (+s.d) of invertebrates harvested within study sites per low tide as recorded by ten simultaneous counts of subsistence and recreational collectors over a range of high and low activity periods and from published estimates of mean mass of harvested organisms per collector per outing (Tomalin and Kyle 1998). *= Unexploited site.+ = inaccessible site.

DISCUSSION

1. Biogeographic breaks and regional differences in community structure

In the low and mid shore, there were substantial differences in community structure between Maputaland sites and those from the three pre-defined regions further south. These differences were reflected in descriptive techniques (hierarchical cluster analysis and MDS) and in ANOSIM tests comparing the four pre-defined regions (Figures 2.5 and 2.6, Table 2.1). These quantitative differences justify the division of the KwaZulu-Natal coast into two biogeographic regions. This confirms the regional differences between Maputaland and Natal described by Jackson (1976), who identified the area between Mabibi and Cape Vidal as the boundary between a tropical province and a subtropical area further south. In my study, the biogeographic division was evident between Sodwana Bay and Cape Vidal. The low shore of Cape Vidal Point clustered with shores from Maputaland while the mid shore clustered with sites from Natal. Cape Vidal Point is therefore considered as the boundary between the two biogeographic regions. These two regions will hereafter be referred to as Maputaland (extending from the Mozambique border to Cape Vidal) and Natal (Cape Vidal to Port Edward), whereas KwaZulu-Natal refers to the entire coastline (Mozambique border to Port Edward) (see Figure 2.2).

Both the results presented here and Jackson's studies failed to detect a change in intertidal community structure near Durban. Stephenson (1944) traced a gradual reduction of intertidal species from the subtropical east coast to the cool temperate west, recording the subtraction of 11 species between Durban and Port Edward. Jackson (1976) attributed her failure to detect this trend to disproportionate sampling effort in different areas. The results presented here were based on equal sampling efforts and still failed to identify any break near Durban or any difference in community structure between sites in Zululand, Central KwaZulu-Natal and the South Coast. The zoogeographic analysis of Emanuel et al. (1992) divided the subtropical east coast into two distinct sub provinces with a transition just north of Durban. Unlike that analysis, my study and Jackson's analysis were based only on intertidal species but did include intertidal algae. Marine biogeographical analyses are strongly influenced by the ocean depth to which the analysis extends (Brown and Jarman 1978, Turpie et al. 2000) and greater range of depths (down to 30m) included in the analysis of Emanuel et al. (1992) may have exerted a significant influence on the observed biogeographic pattern.

My analysis was based on quantitative surveys of abundance at 39 sites along the 560km KwaZulu-Natal coast, whereas Emanuel et al. (1992) used presence or absence data at 100km intervals. Jackson (1976) used semi-quantitative measures to sample 10 sections of coast with one or more sites visited per section. Abundance ratings were recorded for a checklist of 53 species. My analysis was based on replicated samples incorporating 220 species. My central conclusion, that there is a clear biogeographic break at Cape Vidal but none south of there as far as Port Edward, is therefore likely to be robust.

Differences between zones: divergence and convergence

In the high and top shore there were no significant differences identified between Maputaland and Natal. Average similarity between sites (Table 2.2) was also much greater in the high and particularly the top shore compared to the low and mid shore, reflecting convergence of community structure, especially in the top shore. This pattern has been reflected by other studies (Stephenson and Stephenson 1972, Lubchenco et al. 1984, McGuiness 1990, Williams 1994). Convergence in the upper shore suggests that the communities there are constrained by relatively uniform stresses (Stephenson and Stephenson 1972, Bustamante et al. 1997) such as desiccation and high temperatures. In the low and mid shore, diverging abiotic conditions and stronger biological interactions (e.g., competition and predation) may lead to greater dissimilarities between sites and regions.

Maputaland and Natal were approximately 70.04% dissimilar in the low shore and 75.45% dissimilar in the mid shore, substantially greater than the 45% dissimilarity between regions identified by Jackson (1976). The most likely reason for the difference is that the two studies depended on different sampling techniques and analyses. Jackson (1976) relied on relative abundance ratings for a checklist of 53 species whereas my study depended on quantitative data. I also used equal sampling effort at all sites, whereas Jackson devoted disproportionate amounts of collecting time in different areas and sampling effort varied between sites. Jackson (1976) included pools in her study but pools and gullies were not included in the results presented here. Nevertheless, despite these differences in methodology, a similar biogeographic pattern was observed, suggesting that it is robust.

Species characterizing and distinguishing between regions

Low shore

Both invertebrate and algal species contributed to the dissimilarity between Maputaland and Natal. The most important distinguishing species for the low shore was *Perna perna*, which was present in both regions but at much lower densities further north. Other authors have also noted the lesser abundance of *P. perna* in Maputaland. Jackson (1976) rated mussels as occasional (2/5 on her rating system) to frequent (3/5) in Maputaland, but abundant (4/5) or exceptionally abundant (5/5) in Natal. Fielding et al. (1991) reported that mussels only occurred as individuals or in small clumps in Maputaland while dense mussel beds occurred further south. In my study, high mussel densities were, however, recorded at Island Rock, a Maputaland site inaccessible to harvesters, and intermediate mussel cover was found at two protected Maputaland sites, Cape Vidal Point and Sodwana Point. Stephenson and Stephenson (1972) compared Natal shores with those of Inhaca Island in Mozambique on the basis of descriptions by Kalk (1958,1959) and Isaac (1956) and cited reduced mussels at Inhaca as a principal distinguishing feature. Studies comparing recent and abandoned shell middens in Mozambique report recent extinction of *Perna perna* on Inhaca Island and it is suggested that this local extinction is attributable to subsistence harvesting (de Boer 2000a). *P. perna* has not been recorded further north at Dar es Salaam (Hartnoll 1976).

Other invertebrates that played a prominent role in distinguishing the low shore communities of Maputaland from Natal were the solitary ascidian, *Pyura stolonifera*, and a sessile polychaete, *Idanthyrsus pennatus*. *P. stolonifera* was on average almost fifteen times more abundant in Maputaland compared to Natal despite the fact that it is an important food source for subsistence collectors in Maputaland (Kyle et al. 1997a). *P. stolonifera* is considered to be a temperate species that extends from Namibia right around the southern African coast into tropical waters in southern Mozambique (Day 1974, Berry 1982). *P. stolonifera* beds are a characteristic and dominant feature of the very low shore on the south coast (Stephenson and Stephenson 1972). This indicates that dense cover of *P. stolonifera* in the low shore is not unique to tropical shores. Large areas of *Pyura* have however been recorded at Inhaca Island (Stephenson and Stephenson 1972). Genetic sequencing of *P. stolonifera* could indicate that these tropical and temperate populations are different species (see Clarke et al. 1999). Higher cover of *I. pennatus* at Inhaca was cited as an important distinguishing feature between Mozambique and Natal (MacNae 1962, Stephenson and Stephenson 1972).

Algae were also important distinguishing species between the two biogeographic regions. *Hypnea spicifera* is the dominant alga in the low shore in Natal but was almost absent in Maputaland and is absent from Inhaca (Stephenson and Stephenson 1972). This species has however been recorded in Kenya, Madagascar and Mauritius (Silva et al. 1996). *Sargassum elegans* was more abundant in Maputaland and has been reported as replacing *H. spicifera* in Maputaland (Jackson 1976). Other algae that characterized the low shore in Maputaland, and which have also been reported in Mozambique, were *Valonia macrophysa* and *Chamaedoris delphinii* (Stephenson 1972).

Mid shore

In the mid shore, three species of barnacles were identified as important distinguishing species between regions. This conforms to the pattern observed by Jackson (1976). *Tetraclita squamosa rufotincta* was the top ranking, most consistent distinguishing species, only being recorded in any numbers in Maputaland in both my and Jackson's studies. This species is considered tropical and has been recorded at Dar-es-Salaam, Aldabra, Seychelles, Mauritius and in the Red Sea (Hartnoll 1976). *T. serrata* has previously been recorded in South Africa and Madagascar (Hartnoll 1976) and in my study was characteristic of the mid shore in Natal, along with *Octomeris angulosa*. Stephenson and Stephenson (1972) also documented *O. angulosa* and *T. serrata* as characteristic of shores in Natal.

The zoanthid community has been described as a striking feature of Natal coasts (Stephenson and Stephenson 1972). These authors commented that zoanthids were common at both Natal and Inhaca Island but that reefworm competed with zoanthids at Inhaca. The quantitative data from my study also indicated that zoanthids were common in Maputaland and Natal, with the reefworm *Idanthyrsus pennatus* and the colonial mollusc *Dendropoma tholia* competing for space in Maputaland. *Dendropoma* sp. was recorded as a characteristic species of shores at Dar es Salaam (Hartnoll 1976). The most important distinguishing algal species for the mid shore was *Jania verrucosa*, which is abundant at some sites in Natal but is uncommon in southern Maputaland and absent in the north.

Biogeographic affinities

The observed differences in intertidal species composition and abundance between Maputaland and Natal are very similar to the previously described differences between Mozambique and Natal (Stephenson and Stephenson 1972). The top five distinguishing low-shore species identified by my study were also listed as key species distinguishing Natal and Inhaca Island (Stephenson and Stephenson 1972). The similarity between the low and mid shores of Maputaland and tropical shores further north (eg. Mozambique and Tanzania) suggest that the Maputaland region of KwaZulu-Natal falls within the more tropical Indo-West Pacific region. This is a large biogeographic province which spans half the globe and extends to eastern Australia (Luning 1990). The species complement of algae in Maputaland reflects more tropical affinities while species composition in Natal is more subtropical and similar to the warm temperate south coast (Hommersand 1986, Silva et al. 1996). Bolton and Anderson (1997) considered the existence of a subtropical province in KwaZulu-Natal unlikely because the flora reflects an eastwardly decreasing number of Agulhas Province species, replaced largely by Indo-West Pacific species. The biogeographic province of Natal could be considered to form part an extended eastern overlap as Bolton and Anderson (1997) suggested. They considered this overlap to extend from East London to Mozambique including the entire KwaZulu-Natal coast. However, the results of my study suggest that Natal should more properly be classed as a separate subtropical province as advocated by Jackson (1976) because there is more than 65% dissimilarity between it and Maputaland (Figures 2.4 and 2.5).

The four and eleven most important species distinguishing between Maputaland and Natal in the low and mid shore respectively were not absent from either region, but had large consistent differences in abundance between regions. However, there were species that were confined to only one of these biogeographic regions. In the low shore, *Laurencia glomerata*, *L. pumila* and two unidentified ascidians were only found in Maputaland. *Caulerpa racemosa* was confined to intertidal shores in Natal although this species is prevalent in the subtidal in Maputaland (pers. obs.). In the mid shore, *Tetraclita serrata*, *Scutellastra natalensis*, *Hypnea intricata* and *Laurencia natalensis* were absent from Maputaland while species that were only found in Maputaland included *Dictyosphaeria versluysii* and *L. glomerata*.

Quantitative intertidal surveys north of the Mozambican border are required to establish the relationship between shores in Maputaland and tropical shores to the north. As the central and northern Mozambique coast is sheltered from wave action, Jackson (1976) suggested the exposed east coast of Madagascar as an appropriate tropical area with which to compare KwaZulu-Natal shores. This would provide more information as to the tropical affinities of Maputaland and Natal shores. Quantitative surveys of community structure along the Eastern Cape coast (including the Transkei) would indicate affinities between Natal shores and those of the temperate south coast. This would provide information as to whether Natal is part of the eastern overlap between the tropical Indo-West Pacific Province and the temperate South coast or a discrete subtropical province. One of the species that is abundant and very characteristic of the South Coast Agulhas Province is *Scutellastra cochlear* (Stephenson 1944, Field and Griffiths 1991). This species is virtually absent in KwaZulu-Natal. This suggests that Natal rocky shores do have important differences in species composition from those in the South Coast Province and are likely to fall within a discrete subtropical province.

Potential abiotic determinants of biogeographic patterns

Oceanographic influences

MacNae (1962) attributed the distribution of fauna and flora of the east coast of southern Africa to ocean currents. Warm-water species were considered to extend far south because of the southward-flowing Agulhas current while variations in the extent and strength of the northward-flowing countercurrent may explain the occurrence of cool-water species in KwaZulu-Natal and southern Mozambique (MacNae 1962). The southward-bound Agulhas current is dominant along most of the KwaZulu-Natal coast while the inshore currents are mostly northbound. Bottom current patterns can be inferred from sediment dispersal and bedform patterns. Flemming and Hay (1988) identified bedload partings just north of Cape Vidal and just north of Durban. These bedload partings suggest that there is a divergence in both inshore and offshore currents at these points. Both these bedload partings correspond with biogeographic breaks: (i) the break near Cape Vidal described by Jackson (1976) and confirmed by the present study and (ii) the biogeographic division near Durban proposed by Emanuel et al. (1992) but not supported by my results. Currents could play a role in biogeographic differences through their effects on larval transport, dispersal of spores and via their influences on other abiotic factors such as temperature. Beckley (1996) attributed the absence of a clear boundary between East and South Coast Provinces to the influence of the Agulhas current. Studies investigating benthic-pelagic coupling in KwaZulu-Natal may dramatically enhance our understanding of the dynamics of intertidal habitats (see Menge 2000), but for the present our understanding is insufficient to draw any firm conclusions about the influence of oceanic water movements on biogeographic patterns in KwaZulu-Natal.

In most biogeographic studies, historical processes (e.g. continental drift) are invoked as underlying observed biotic patterns (Myers and Guiller 1988). Along the Southern African coast, Bustamante (1994) found that large-scale variations in community structure were due to geographical differences in the physical environment, primarily temperature, nutrient supply and productivity. In KwaZulu-Natal, sea temperature changes, differences in river flow and reduced wave action in the north have previously been identified as potential factors underlying the difference between Maputaland and Natal (Jackson 1976). I additionally considered sand inundation and human harvesting as potential factors.

Sea-water temperature

The observed changes in community structure in the vicinity of Cape Vidal do not correspond with any abrupt changes in offshore sea temperature (Figure 2.9). The most rapid changes in offshore temperatures were evident on the south coast and near Point Durnford, where Jackson (1976) proposed that sea temperatures may change over a relatively short distance. The decline in temperature there is associated with a widening of the continental shelf and decreased influence of the warm Agulhas current (Schumann 1987). Jackson identified only one species (*Hypnea rosea*) whose northward limit coincided with this point and even this species was found to extend into Maputaland during the present study. I could not detect any significant changes in intertidal community structure that corresponded with the relatively abrupt temperature change at Point Durnford. However, the available V.O.S. data may not be wholly adequate for proper assessment of the role of temperature in structuring inshore communities in KwaZulu-Natal. The assumption that any discrepancy between inshore and offshore temperatures would be relatively constant along the coast was clearly validated for winter, when inshore waters were consistently approximately 1.1°C cooler. During summer, the differences covered a wider range (0.74-2.4°C). Even so, none of the differences are sufficiently large to challenge the overall conclusions drawn from the V.O.S. data. Nevertheless, the fact that the difference between offshore and inshore temperatures at one locality was more than three times that of another identifies the need for accurate inshore sea temperature measurements along the entire KwaZulu-Natal coast.

As differences in abundance of many species (e.g. *Perna perna*) contributed significantly to dissimilarity between Maputaland and Natal, some of the difference between these two regions may be accounted for by factors other than those that set distinct physiological limits for organisms. McQuaid and Branch (1984, 1985) found that seawater temperature determined species composition on rocky shores while biomass and hence trophic structure was attributed to other abiotic determinants, particularly wave action. Therefore temperature may determine the pool of available species, while variations in abundance may be explained by other factors.

Riverine input

The most conspicuous environmental difference between Maputaland and Natal was the contrast in riverine input between regions (Figure 2.10). There are 74 significant rivers and estuaries along the KwaZulu-Natal coast (Begg 1978) and only two enter the sea north of Cape Vidal, contributing less than 0.01% of the total river input in KwaZulu-Natal. The Maputaland coastal plain comprises unconsolidated to semi-consolidated rock sequence with little "hard rock", and surface run-off is almost non-existent largely due to percolation through the sandy plain (Pitman et al. 1981). Less than five percent of precipitation in Maputaland is predicted to enter streams and rivers (Begg 1978, Pitman et al. 1981). Low silt loads and clear water are consequences of reduced riverine input in Maputaland. These conditions have been thought to favour some species in Maputaland, particularly corals (McClurg 1988, Riegl and Branch 1995).

Bustamante et al. (1995b) showed that differences in nutrients and productivity explained large-scale variability in community structure around the southern African coast. Potential differences in productivity between Maputaland and Natal have not been investigated. However, differences in productivity could be related to differences in riverine input between regions, either through increased nutrients or organic matter or increased abundance of phytoplankton. Menge et al. (1997b) cited riverine input as a potential, although unlikely, mechanism underlying variability in phytoplankton concentrations and therefore community structure on the Oregon coast. Riverine dissolved organic carbon has been shown to be extensively used in plankton food webs in the Baltic Sea (Rolff and Elmgren 2000).

In some coastal areas, it has been shown that intertidal filter feeders depend on energy imported from pelagic and subtidal systems (Stuart 1982, Stuart and Klumpp 1984, Duggins et al. 1989). On the west coast of South Africa, Bustamante and Branch (1995a) demonstrated that energy used by intertidal filter and suspension feeders was to a large extent "imported" from pelagic and subtidal systems, principally by subsidies from kelp beds. Kelp beds do not occur in KwaZulu-Natal and there is not a single published description of subtidal seaweed communities (Bolton and Anderson 1997). However, the substantial riverine input in Natal may subsidise some intertidal organisms. The detritus pathway appears to play an important role in intertidal and subtidal ecosystems in KwaZulu-Natal, especially in supporting filter feeders such as *Perna perna* (Schleyer 1981, Berry 1982). Evidence suggests that primary production by phytoplankton is not potentially as important in supporting filter feeders as heterotrophic activity associated with the breakdown products of detritus (Schleyer 1981). The two principal sources of detritus along this coast are (a) allochthonous seaweed and (b) terrestrial plant matter washed into the sea by rivers (Schleyer 1981). Higher cover of *P. perna* in Natal could be attributable to the additional nutrient input of decaying plant matter supplied by riverine input. Riverine effects in KwaZulu Natal would be increased in the summer rainfall season when most of the rivers are open. In New Zealand, the absence of mussels along shores on Cook Strait has been linked to low seston quality (Gardner 2000), suggesting that reduced organic matter may limit filter feeders in some regions.

P. stolonifera is also a filter feeder, yet this species was more abundant in Maputaland than Natal where riverine input is higher. *Pyura* does compete with *P. perna* in the infralittoral and shallow subtidal (Berry 1982) and reduced mussel populations in Maputaland could favour *P. stolonifera*. Isotope studies would enable the assessment of the extent to which different filter feeders depend on riverine input or subsidy from subtidal systems (Bustamante et al. 1995a).

Sand inundation

All the sites sampled in my study were originally subjectively classed as sand-inundated or sand-free. Monitoring of depth and cover of sand (Figure 2.11) revealed surprising results as, in reality, periodic sanding proved ubiquitous. This highlights the importance of quantitative measurements of physical variables in ecological studies. The results from the sand monitoring did not, however, indicate any gradient in sand effects along the coast that could be related to the biogeographic break between Maputaland and Natal. There were shores subject to varying intensities and frequencies of inundation in both Maputaland and Natal. However, nested ANOVA failed to identify any difference in sand inundation between regions for any zones on the shore. Thus, the observed differences in community structure between Maputaland and Natal cannot be explained by differences in sand inundation between regions. Between-site differences in sand inundation are investigated in Chapter 3 and the literature regarding the influence of sand inundation on intertidal organisms is reviewed in that chapter.

Wave exposure

Elsewhere in South Africa, rocky intertidal communities have been shown to be strongly influenced by wave action, with biomass and trophic structure being largely attributable to degree of wave exposure (McQuaid and Branch 1984, Emanuel et al. 1992, Bustamante and Branch 1996). Most previous authors have not explicitly considered wave action as a factor structuring KwaZulu-Natal rocky shores, probably because almost the whole coast lacks embayments and gives the impression of being uniformly exposed. However, measurements of wave forces in KwaZulu-Natal yielded a surprising range of results (Figure 2.12). Some sites that were subjectively rates as exposed, consistently yielded low to moderate measurements of wave force. The large range in exposure values between sites in KwaZulu-Natal was unexpected, with the most exposed sites experiencing wave forces up to four times those recorded at more sheltered sites.

The magnitude of wave forces in KwaZulu-Natal were comparable to those recorded on the south and west coasts of South Africa. Bustamante et al. (1997) recorded significant differences in wave forces between sheltered and exposed sites on the west coast (1.5×10^3

versus 15 x 10^3 N.m^{-2}) and on the south coast (1.0 x 10^3 versus 10 x 10^3 N.m^{-2}). In KwaZulu-Natal, estimates of maximum wave forces at the five most exposed sites (15 x 10^3 N.m^{-2}) were similar to the highest recorded on the west coast and higher than those recorded on exposed shores on the south coast. There were no very wave-sheltered sites in KwaZulu-Natal, with the five least-exposed sites experiencing wave forces of approximately 5 x 10^3 N.m^{-2}.

It has been suggested that Maputaland may receive less wave energy than the rest of the KwaZulu-Natal coast (Jackson 1976, Berry 1978, McClurg 1988). Jackson (1976) proposed that Maputaland was afforded some protection from wave exposure by Madagascar. Results from the present study did not support this idea since the most exposed and most sheltered sites were both found within the Maputaland region. I did not expect that Madagascar would shelter Maputaland shores from wave exposure because most swells come from the south and Madagascar is situated north of the Mozambique border. The null hypothesis that there was no difference in wave exposure between regions could not be rejected (nested ANOVA Table 2.5). The presence of very exposed and relatively sheltered shores within both Natal and Maputaland indicates that the regional differences in community structure cannot be accounted for by differences in wave action. Differences in exposure within regions, however, may account for more local biological differences within regions and this possibility is investigated in the following chapter.

Human exploitation

The relative harvesting offtake between sites in Maputaland and Natal was highly significantly different despite high variability between sites (Figure 2.13, Table 2.5). Indeed, when sand inundation, wave exposure and human exploitation were compared across regions, only human exploitation was significantly different between regions. This raises the possibility that subsistence harvesting in Maputaland accounts for some of the variability in community structure between regions. All the low and mid shores in Maputaland and Natal were more than 65% dissimilar with only one exception. In the low shore, Umfazazana on the south coast of Natal was more similar in community structure to the shores in Maputaland than Natal. Umfazazana is also the only Natal site where subsistence mussel harvesting is practised (although no quantitative data are available on the magnitude of this harvesting). It grouped together with three Maputaland sites where subsistence collectors target mussels (Kyle et al. 1997a). In Chile, intertidal exploitation of invertebrates has had a considerable influence on the structure of rocky intertidal communities (Moreno et al. 1984, 1986, Duran et al. 1987, Duran and Castilla 1989, Castilla 1999). In South Africa, subsistence exploitation has modified intertidal community structure in the Transkei (Hockey and Bosman 1986, Dye 1994, Lasiak and Field 1995) with significant changes evident over large geographical scales (Lasiak 1999). The effect of intertidal harvesting in KwaZulu-Natal is the principal subject of Chapter 6, where I examine its influence at various scales.

Differences in harvesting offtake between regions cannot, however, explain the observed biogeographic pattern although they may contribute to the >70% dissimilarity between regions. Shores in Maputaland where no harvesting occurs because they are protected (Sodwana Point, Cape Vidal) or inaccessible (Island Rock) were also distinguishable from shores in Natal. Harvesting effort is concentrated in the low shore and regional differences in the mid shore exceeded those in the low shore, also indicating that human exploitation does not cause the observed biogeographic pattern. However, within Maputaland, harvested low shores were more than 50% dissimilar to those that are lightly exploited or unexploited. This indicates that human exploitation is likely to influence community structure between sites within regions. The effect of subsistence harvesting in Maputaland and in Natal is further investigated in Chapters 3 and 6.

Pyura stolonifera is more abundant in Maputaland than further south despite higher exploitation in Maputaland (Kyle et al. 1997a). However, there are three sites in Maputaland that are not subject to exploitation and these sites have high densities of *P. stolonifera* that bias the overall abundance estimate for the region. *P. stolonifera* is a common bait organism and its exploitation in Natal by anglers may account for its low abundance. Only one shore in the Natal region (Trafalgar) is not subject to bait collection. Fully protected "no take" areas are clearly a high priority in Natal and Maputaland if the role of exploitation in shaping biological community structure is to be ascertained.

Implications for conservation and management

All biogeographic regions should be represented in marine protected areas (Hockey and Branch 1994, 1997). Jackson (1976) motivated for two marine reserves along the KwaZulu-Natal coast, one in Maputaland and one in Natal. Currently, approximately 144 km of the 150km of coast included in marine protected areas in KwaZulu-Natal lies in Maputaland (i.e. north of Cape Vidal) (Figure 2.14). Only 4.8 km (about 2km of rocky shore) is conserved in Natal in the Trafalgar Marine Reserve (Mann et al. 1998). The Maputaland and St Lucia Marine Reserves only conserve rocky shores typical of the Maputaland biogeographic region. The Trafalgar Marine Reserve in Natal was established to conserve intertidal fossils and is very sheltered and not representative of the coast as a whole (see Figure 2.5) although it does host extensive subtidal seaweed communities (Mann et al. 1988). The intertidal resources that are most heavily exploited in Natal (*Perna perna* and *Pyura stolonifera*) are not present at Trafalgar, so they receive no protection anywhere in Natal.

While all Maputaland shores do fall within a marine protected area, subsistence harvesters exploit all shores in the Maputaland Marine Reserve (Figure 2.14). In the adjacent St Lucia Marine Reserve, approximately 20 km of shore (including about 4 km of rocky ledge) is unexploited and is managed as a sanctuary. At all other shores, including the Maputaland, St Lucia and Trafalgar Marine Reserves, shore angling is permitted.

Figure 2.14. Map of KwaZulu-Natal showing the current Marine Protected Areas and the types of harvesting occurring in each reserve

In the absence of representative habitats closed to all forms of fishing and harvesting, the effects of shore angling in KwaZulu-Natal cannot be unambiguously assessed. Intertidal habitats are linked to subtidal habitats, and fish and other organisms feed in the intertidal at high tide. These species are likely to play an important role in the coastal ecosystem and inshore reefs serve as nursery areas for juvenile fish, many of which are important resource species (Joubert 1981).

KwaZulu-Natal urgently requires additional marine protected areas in the Natal Province and the practice of allowing intensive subsistence harvesting throughout the Maputaland Marine Reserve, and inshore fishing along most of KwaZulu-Natal, should be re-evaluated. Without benchmark studies in fully protected areas, harvesting impacts cannot be assessed and the issue of whether harvesting is sustainable or optimal can never be adequately determined. These issues are expanded upon in Chapter 4, where the current conservation status of different biotopes in KwaZulu-Natal is considered, and in Chapter 6 where harvesting impacts are examined more specifically.

Conclusions

There are two distinct biogeographic regions represented within KwaZulu-Natal with a biogeographic break clearly evident near Cape Vidal. There were significant differences in low and mid-shore community structure between Maputaland and Natal. There were no corresponding significant differences in wave exposure or sand inundation. The most abrupt offshore temperature changes did not coincide with the observed biogeographic break although it must be recognised that offshore temperatures may not accurately reflect relative inshore temperatures. The most striking abiotic difference between regions was the much smaller riverine input in Maputaland relative to Natal, which may account for some of the observed biological differences between shores in Maputaland and Natal. Intertidal harvesting is substantially more intense at most localities in Maputaland than in Natal. This is likely to have strong local effects on community structure, but cannot solely explain the biogeographic break because unexploited sites in Maputaland have communities that are distinct from those in Natal.

The virtual absence of protected representative shores in Natal and the occurrence of subsistence harvesting on almost all Maputaland shores including those in theoretically protected areas, constitute an obvious gap in the biodiversity conservation strategy of KwaZulu-Natal. Effects of biogeography and abiotic parameters could be masked by differences in the type and intensity of exploitation. The results of this study justify re-consideration of protected areas in KwaZulu-Natal. This is critical for elucidation of the effects of anthropogenic, biotic and abiotic factors, for proper resource management, and for conservation of the full spectrum of biological diversity in KwaZulu-Natal.

Chapter 3

The influence of abiotic factors and human exploitation on intertidal community structure within Maputaland and Natal

ABSTRACT

In this chapter, differences in community structure were examined at a smaller scale, namely between sites within each of the two biogeographic regions, Maputaland and Natal. Natural experiments and multivariate analyses of species composition and abundance were used to assess the relative importance of potential abiotic determinants in the low, mid and high shore. The physical factors that were investigated were wave exposure in both Natal and Maputaland and rock type and sand inundation in Natal. Rock type and sand inundation could not be studied in Maputaland because only a single rock type exists there, and sand inundation did not differ sufficiently between sites to allow meaningful comparisons. In addition to these physical factors, the role of human exploitation in structuring rocky intertidal communities was assessed. Rock type generally had a weak influence on community structure, with large and significant differences in communities only evident in a single comparison in the mid shore, i.e., between Quaternary sandstone and dolerite shores. Sand inundation and wave exposure were identified as important determinants of intertidal community structure. The influence of sand inundation was greatest in the mid and high shore. Wave exposure exerted its greatest influence on low-shore communities, but significant effects on community structure were evident in all zones on the shore and within both biogeographic regions. Comparisons between subsistence-exploited and unexploited shores in Maputaland showed highly significant corresponding differences in community structure in the low shore. In Natal, the absence of appropriate unexploited sites prevented proper assessment of harvesting effects in this region but no differences in community structure were evident between sites with different degrees of recreational harvesting. Significant locality effects were evident in all comparisons indicating significant variability in community structure within treatments. This has important implications for studies assessing determinants of between-site differences in community structure or potential environmental impacts. Sites should be standardised so that there are no differences in other factors and site-pairs should be assessed independently if convincing evidence of an association between any factor and species composition and abundance is to be presented.

Introduction

Shores diverging in community structure invite explanation as to the processes that underpin these differences. Descriptive research on community patterns at several sites is a necessary prerequisite for the development and evaluation of general models of community structure and regulation (Foster et al. 1988, Underwood 1996, 2000a). Information about the relationships between environmental parameters and biological features is needed for management of intertidal systems as the influences of natural factors need to be separated from anthropogenic effects. Selection of sites for marine protected areas similarly depends on quantitative descriptions of sites that may then be compared in terms of a broad set of criteria (Agardy 1997, Hockey and Branch 1997, Roberts et al. in press a). Marine protected areas should represent the physical heterogeneity and associated biological variability within any biogeographic region, thus ensuring that all habitat types are conserved (Emanuel et al. 1992, Attwood et al. 1997a). As a consequence, many countries have begun characterising and classifying seashores to improve management and conservation, although some initiatives have been criticised for the lack of quantitative associations between physical habitats and biological communities (Day and Roff 1998, Zacharias et al. 1999).

Early marine ecologists focused their research on physical factors that were predicted to determine distributions of species according to their physiological tolerance (reviewed in Raffaelli and Hawkins 1996, Menge and Branch 2001). Subsequent studies refuted the idea of critical levels (Underwood 1978) and showed that few species have their distribution set directly by physical tolerance alone (Wolcott 1973). The classic work by Connell (1961a, b) and Paine (1966) demonstrated that biological interactions such as competition and predation also control the distribution and abundance of intertidal organisms. Recently, supply-side ecology has shown that recruitment processes are also major determinants of community structure (Connell 1985, Gaines and Roughgarden 1985, Fairweather 1988, Roughgarden et al. 1988, Underwood and Fairweather 1989, Raimondi 1990, Menge 1991, Grosberg and Levitan 1992, Caley et al. 1996, Robles 1997, Connolly and Roughgarden 1999).

Models of community regulation include contrasting viewpoints as to whether communities are regulated via top-down or bottom-up control (Menge 2000, Menge and Branch 2001). Hairston, Smith and Slobodkin (1960) proposed one of the first top-down models of community regulation suggesting that predators limit herbivores, which are consequently incapable of controlling plant abundance. Controlling factors were thus predicted to vary by trophic level. Menge and Sutherland (1976) predicted that controlling factors would also vary with disturbance or environmental stress. Such Environmental Stress Models (ESMs) maintain that differences in community structure are predictably related to environmental stress (Menge and Sutherland 1976, Menge and Sutherland 1987, Menge and Olsen 1990). Community structure is predicted to be controlled by the overriding direct effects of abiotic factors when environmental stress is high, but under progressively lower levels of stress, competition and predation are predicted to exert a successively dominant effect on community structure (Menge and Sutherland 1976, Menge and Sutherland 1987, Menge and Olsen 1990). Nutrient-Productivity Models (NPMs) predict that nutrients control plant productivity and community structure and dynamics via a bottom-up effect (Fretwell 1977, 1987, Oksanen et al. 1981). Recently integrated "top-down/bottom up" models incorporating both ESMs and NPMs have been developed (Menge 1992, Persson et al. 1996, Zimmerman et al. 1996, Menge et al. 1997a, Leonard et al. 1998).

The scale of observation can determine the perceived importance of any factor. Most authors agree that at larger scales, physical processes are more important than biological interactions. Barry and Dayton (1991) proposed that abiotic environmental factors should be viewed as the highest level of organisation within which other factors are subordinate. In this way, abiotic conditions are considered to set the biogeographic and physical framework within which biological interactions take place (McQuaid and Branch 1984).

In KwaZulu-Natal on the east coast of South Africa, intertidal communities differ in community structure between sites that are as little as a few kilometres apart (Jackson 1976, Harris et al. 1998, Kyle et al. 1997a, Tomalin and Kyle 1998). Physical, biological and anthropogenic factors may be implicated in these differences and the principal objective of this chapter was to determine whether sites differing in environmental factors and exploitation pressure had corresponding differences in biological community structure. To date, there are no published quantitative data describing physical conditions for any shores in KwaZulu Natal on the east coast of South Africa, and few comparative quantitative biological data (Jackson 1976, Bustamante et al. 1997).

In Chapter 2, differences in community structure were analysed at a biogeographic scale. It was demonstrated that KwaZulu-Natal is divisible into two regions, Maputaland and Natal with distinctive low and mid-shore communities. At that scale, sea temperature, sand inundation, wave exposure and human exploitation appeared unlikely causes of the biogeographic break, whereas riverine input may be a potential causative factor. This chapter focuses on a smaller scale of investigation. Various physical factors and human exploitation were examined to assess whether they can explain differences in community structure between sites within each of the two biogeographic regions. Different zones on the shore were analysed separately and characteristic and distinguishing species that reflect different abiotic conditions were sought.

Four factors: rock type, sand inundation, wave exposure and human exploitation, were selected for investigation. Biological factors are under separate investigation by other researchers (e.g., J. Harris, KwaZulu-Natal Wildlife). Variation between different zones on the shore due to differences in elevation and therefore gradients in desiccation and temperature are well described for intertidal habitats (e.g., Lewis 1964, Stephenson and Stephenson 1972, Wolcott 1973). Several authors (Jackson 1976, Branch and Branch 1981, Lambert and

Steinke 1986a) have described vertical zonation patterns on KwaZulu-Natal shores and potential causes of such zonation were not examined in this chapter. Nevertheless, three spatially defined zones on the shore, the low, mid and high shore (Figure 2.4) were investigated separately to allow comparisons between zones. Temporal variations in community structure were not examined here although they are explored in Chapter 6. Observations in California and data from control quadrats used in experimental studies in the North Eastern Pacific suggest that natural temporal variation in species composition and abundance is less than spatial variation (Foster et al. 1988). On the Southeast coast of South Africa, in the absence of disturbance, low shore community structure has been shown to remain virtually unchanged for as long as eight years (Dye 1992).

Rock type

Geological substrate has been implicated as a potential determinant of benthic community structure (Barry 1988, Raimondi 1988, Lohse 1993). Material composition, porosity, type of weathering, hardness, colour and surface rugosity of a substrate may have important consequences for intertidal organisms (Raimondi 1988, James and Underwood 1994, Schoch and Dethier 1996). The prescence or absence of quartz has been linked to differences in community structure in subtidal communities in the Mediterranean (Bavestrello et al. 2000). Rock type also determines rock topography, variations of which result in differences in habitat complexity and therefore diversity (Raimondi 1988, McQuaid and Dower 1990, Menge et al. 1991, Schoch and Dethier 1996). Rocky shores in KwaZulu-Natal are composed of numerous geologically distinct rock types. The effect of substratum has not been quantitatively examined in KwaZulu-Natal and five rock types were compared in this study: Quaternary, Ordovician and Ecca sandstone, dolerite and granite. This aspect of the work was restricted to the Natal region as all Maputaland shores are composed of a single rock type, Quaternary sandstone.

Sand inundation

On the Californian and Oregon coasts, sand movement and burial have been linked to variability in community structure within zones (Foster et al. 1988) and different community types are associated with differential sand stress (Daly and Mathieson 1977, Taylor and Littler 1982, Littler et al. 1983, D'Antonio 1986). Sand has also been reported to set lower zonational limits for mussels (Cimberg 1975, Littler et al. 1983) and limpets (Frank 1965). Engledow and Bolton (1994) showed that seaweed diversity in Namibia is related to sand inundation where sand exceeds a threshold level. In South Africa, studies in the eastern Cape indicate that sand inundation increases diversity by increasing habitat heterogeneity (Mcquaid and Dower 1990). The physiological affect of sand on a few selected South African intertidal organisms has been examined (Marshall and McQuaid 1989, 1993). A significant feature of the east coast is the shifting of vast amounts of sand (Jackson 1976, Berry 1982) resulting in alternate inundation and exposure of rocks and subjecting intertidal organisms to sand scour and burial. Prolonged sand burial of mussel beds can result in mass mortality of the brown mussel *Perna perna* (pers. obs.). Despite these facts, the potential role of sand in structuring intertidal communities in KwaZulu-Natal has never been examined. Studies examining the effect of sand inundation on community structure seldom provide quantitative assessments of sand inundation. In the previous chapter, simultaneous sand monitoring at several KwaZulu-Natal sites showed that sites were subject to a range of intensities of inundation with mean volumes of sand ranging from zero to more than 6 000 cm^3 m^{-2} (Figure 2.10).

Wave exposure

Wave action has long been recognised as an important physical factor that has significant effects on intertidal assemblages in many parts of the world (Southward 1958, Lewis 1964, 1968, Dayton 1971, Connell 1972, Menge 1976, Seapy and Littler 1978, Tsuchiya 1979, Menge and Farrel 1989, Foster et al. 1988, Underwood and Skilleter 1996). Relative abundance of common species has even been used as a biological indication of degree of wave exposure (Ballantine 1961, Lewis 1964). In South Africa, wave action has been identified as an important parameter structuring rocky intertidal communities on the west and south coast (McQuaid 1981; McQuaid and Branch 1984, 1985; Field and Griffiths 1991; Emanuel et al. 1992, Bustamante et al. 1995, 1996b, 1997). Wave forces between 1.5 x 10^3 and 15 x 10^3 N.m^{-2} have been recorded on the west coast and between 1.1 x 10^3 and 10 x 10^3 N.m^{-2} on the south coast (Bustamante et al. 1997). In response to differences in wave action, exposed and sheltered shores support different communities in these regions (McQuaid and Branch 1984, Bustamante et al. 1997). Wave exposure has never been measured on the east coast; nor has the divergence of intertidal communities been examined in relation to wave exposure. The relatively linear nature of the east coast combined with apparently continuously heavy wave action led other intertidal ecologists to assume that wave action is not a key determinant of community structure on the east coast (Jackson 1976, Douwer 1989). However, as reported in the previous chapter, simultaneous measurements of wave forces in KwaZulu-Natal revealed significant variation in wave exposure between sites (Figure 2.11, Table 2.5). Mean maximum wave forces ranged from 4.80 (± 0.34) x 10^3 N.m^{-2} at the most wave sheltered shore to 18.08 (± 5.03) x 10^3 N.m^{-2} at the most wave exposed shore.

Human exploitation

Human exploitation can transform intertidal communities (Castilla 1999). Annual shellfish harvests of 6 t.km^{-1}.year^{-1} in central Chile (Duran et al. 1987) have major effects on community structure (Moreno et al. 1984, Castilla and Duran 1985). Human exploitation of mussels at intensities reaching 14.11 t.km^{-1}.year^{-1} has radically altered communities in the former Transkei on the south coast of South Africa (Hockey and Bosman 1986, Hockey et al. 1988, Lasiak and Field 1995, Lasiak 1999). Rocky shores in KwaZulu-Natal are exploited by subsistence harvesters in Maputaland and by recreational collectors in the Natal region. Both groups harvest mussels (*Perna perna*) and subsistence gatherers also utilise the ascidian

Pyura stolonifera, oysters, limpets, chitons and whelks (Kyle et al. 1997a). The effects of both types of harvesting on community structure warrant investigation. In Maputaland, subsistence shellfish-collectors harvest between 3.74 and 88.98 t.km^{-1}.year^{-1} but their potential effects on community structure have not been examined. Recreational mussel collectors remove 1.82 to 2.27 t.km^{-1}.year^{-1} (Tomalin and Kyle 1998). Experimental removal of mussels in KwaZulu-Natal resulted in changes in community structure and mussels failed to re-establish even after eight years (Lambert and Steinke 1986b). The potential effects of human activities on community attributes should be contrasted with variability attributed to natural physical and biological factors.

Aims of this study

In this study, two-way crossed ANOSIM tests were conducted to analyse the effect of several treatments as well as locality effects. A crossed design is one in which there are replicate samples from each treatment / locality combination (Clarke and Warwick 1994). The within-shore replication allows statistical comparison of community structure between and within treatments. If sites differ in factors other than that under investigation, the locality effect test will recognise changes in community structure between sites within treatments. If the differences in community-level attributes of control and treatment sites were consistent between site pairs, such a finding would support the notion that the factor under investigation is the causative agent. Many studies examining differences in community structure have been flawed by pseudo-replication (Hurlbert 1984) because they are based on only one pair of localities (Fairweather 1991, Lasiak and Field 1995). In studies based at a single pair of localities, there may be a number of other equally plausible but entirely unaccounted-for differences between sites, besides, the factor under investigation. However, by comparing contrasting sites at several localities, the "experiment" is repeated in one or more independent settings (Underwood 1987). In this way, alternative explanations for differences in biota at control and treatment localities can be refuted by comparing multiple control and treatment localities. My approach is quantitative but observational and correlative. Independent support can be sought by experimentally manipulating the factors, as I did for human exploitation (see Chapter 6).

In this chapter, between-site differences in community structure at the scale of kilometres to tens of kilometres were examined for the low, mid and high shore of several site-pairs in KwaZulu-Natal. The two biogeographic regions identified in the previous chapter, Maputaland and Natal, were examined independently. The specific objectives were to:

1. Identify groups of sites with significant differences in the four factors (rock type, sand inundation, wave exposure and exploitation) to allow two-way crossed ANOSIM tests.
2. Determine whether there are significant differences in community structure between and within these factors.

3. Identify consistently characteristic and distinguishing species for groups of samples that were significantly different in terms of both factors and community structure.
4. Determine the relative importance of these different factors in Maputaland and Natal and in different zones on the shore.

In chapter 4, even smaller-scale (metres to tens of metre) differences in community structure are examined over large geographical scales and a biotope classification system is presented. Differences in physical factors between biotopes are investigated in Chapter 5.

Methods

1. Abiotic factors

1a. Substrate type, sand inundation, wave action and human exploitation

Substrate type was identified from geological maps and confirmed with rock samples. The characteristics of the five rock types included in this study are shown in Table 3.1. Measures used to estimate relative sand inundation, wave exposure and exploitation are described in Chapter 2 but are briefly recapitulated here. Sites were monitored simultaneously to provide comparative estimates of each factor for all sites. Repeated simultaneous monitoring of percentage cover and depth of sand within 10 quadrats (1 m x 0.5 m) along a 20 m x 1 m transect in each zone was used to estimate relative sand inundation every two months over two years (n=10 simultaneous transects) at 27 sites. The high, low and mid shore were monitored and analysed separately. The data were converted to volumes of sand per m^2. Simultaneous mean maximum wave forces were recorded overnight with 10-15 wave drogues (Palumbi 1984) at each of thirty sites, repeated four times (4 and 5 November 1988, 5 December 1998, and 18 March 1999). This was only conducted for the low shore but the same data was assumed to provide an indication of relative wave exposure between sites in the mid and high shore. Ten simultaneous counts of harvesters over a range of weather and sea conditions and during different periods of the week and year were used to estimate the relative harvesting pressure at each site.

Table 3.1. Characteristics of the five different substrates (along the KwaZulu-Natal coast) included in the analysis of the potential role of rock type in explaining between-site variability in community structure. (McBride 1963, Dawson 1993, Marshall 1994, Millar and Mason 1994).

	Quaternary sandstone	**Ecca sandstone**	**Ordovician sandstone**	**Granite/gneiss**	**Dolerite**
Rock Type	Sedimentary	Sedimentary	Sedimentary	Igneous	Igneous
Primary minerals	Calcarenite	Quartz	Quartz/arenite	Quartz/ feldspar	Basalt
Age (Ma)	<2	250	440	1100	130-160
Period	Quaternary	Permian	Ordovician	Pre-Cambrian	Jurassic
Form	Platforms	Ridges-parallel to shore	Ridge/gully - perpendicular to shore	Megaboulders	Outcrops - sills and dykes
Surface texture	Rugged	Smooth-rugged	Moderately heterogeneous	Foliated/smooth	Smooth
Grain size	Medium-coarse	Medium-coarse	Medium	Coarse	Fine
Hardness	Soft-medium	Medium-hard	Hard, resistant	Hard, resistant	Hard, resistant
Colour	Light brown	olive/grey/buff	grey-red	grey	blue-black or browns

1b. Analysis of abiotic data

To identify groups of sites differing in wave exposure, intensity of sand inundation and exploitation, the abiotic data presented in chapter 2 were re-analysed to investigate differences between sites. For the sand inundation data, each zone was analysed separately.

Differences in wave exposure, sand inundation and human exploitation between sites were tested with one-way ANOVA conducted with STATISTICA (1999). The assumptions of normality were tested with the Kolmogorov-Smirnoff test and homogeneity of variances was checked by Cochran's test (Winer et al. 1991). For both the wave exposure data and the estimates of relative sand inundation, log transformations were necessary to satisfy these assumptions (Sokal and Rohlf 1995). Harvesting offtake data were root transformed. Post hoc comparisons were conducted by means of Tukey Honestly Significantly Different (HSD) tests to determine which sites were significantly different ($p<0.05$) for each factor.

2. Identifying abiotic determinants and determining human impact

2a. Biological surveys

Biological surveys were conducted in spatially defined zones, with each shore divided into four approximately equal zones (Figure 2.4 p 32). For further details, refer to Chapter 2. In brief, 20 randomly placed quadrats were surveyed in each of the low and mid shore and ten in the high shore. The top shore was not investigated in this chapter because community structure converged strongly in this zone (Chapter 2). All sessile species were recorded as percentage cover and counts and mean size of mobile fauna were used to estimate their percentage cover.

2b. Design of natural experiments

The studies in this chapter are based on two-way crossed natural experiments. For each factor, "control" and "treatment" sites at more than one locality were identified. In this sense, the term "control" is used to define sites at which a factor is at its least intense, and the term "treatment" for sites at which it was most intense. The four factors (rock type, sand inundation, wave exposure and harvesting) were considered separately for the low, mid and high shore. For the low and the mid shore, the two biogeographic regions identified in the previous chapter, were analysed separately. In the high shore, no biogeographic differences were evident between Maputaland and Natal, so the entire KwaZulu-Natal coast was treated as a unit when processing the data from this zone.

ANOSIM tests for differences in biological community structure can only be conducted on groups of independently identified samples and not on the basis of groups defined by a cluster analysis. For this reason, sites that differed significantly in abiotic conditions or exploitation pressure were used to test for corresponding differences in community structure. Limits on the program software restricted the analyses to a maximum of 120 samples, i.e., three site pairs. Differences between paired sites were investigated using twenty (low and mid shore) or ten (high shore) replicate quadrats to test for differences between sites and groups of sites with different environmental conditions or levels of human exploitation.

Two or three site pairs of contrasting rock types were chosen to test for corresponding biological differences in each zone on the shore (Table 3.3). This was only undertaken in Natal, as all Maputaland shores are composed of the same rock type (Quaternary sandstone). Two different approaches were used to explore the potential effects of sand, wave action and exploitation on community structure. In the first approach, the three sites with the highest level of each factor and adjacent sites with significantly lower levels of each factor were selected. In this way, groups of sites experiencing the extremes of wave exposure, sand inundation and exploitation were identified (Table 3.5). For each factor, there was no standardisation of the other factors between sites. A second approach was implemented in an attempt to separate the effects of sand inundation, wave exposure and exploitation by isolating the effect of each factor as far as possible. To achieve this separation, two or where possible three groups of site-pairs differing only in sand inundation, wave exposure or exploitation respectively were selected to test if there were corresponding community differences (Table 3.5). It was not possible to isolate the effect of rock type in Natal as substrate variability was high and insufficient sites per rock type were surveyed. Only one shore in Natal was unexploited (Trafalgar) and all other Natal sites considered in this chapter were exploited at recreational intensities.

The effect of sand inundation was not investigated for Maputaland shores because there were insufficient sites with significant differences in sand inundation to conduct two-way tests. The effect of exploitation could be adequately assessed only in Maputaland because there was only one unexploited rocky shore in Natal. In an attempt to overcome this limitation, three of the most exploited localities and adjacent sites subject to low levels of exploitation, were compared (Table 3.5). Even this comparison is of questionable value, because these not all of these sites were significantly different in exploitation pressure (Tukey tests p>0.05).

2c. Analysis of Biological Data: ANOSIM and SIMPER

Biological data were root transformed and cluster analyses were computed with PRIMER (Plymouth Routines in Multivariate Ecological Research, version 4.0 1994) using Bray-Curtis co-efficients. PRIMER was used to conduct two-way ANOSIM tests to determine whether significant differences in community structure existed between two or three paired sites of different rock types and, similarly, between sites that had significant differences in wave exposure, sand inundation or exploitation. In this way, the null hypotheses that there are no differences in community structure (a) between treatments and (b) between sites within treatments were tested (Clarke and Green 1988, Clarke 1993).

ANOSIM tests compute the test statistic, *R*, reflecting the observed differences between sites, contrasted with differences among replicates within sites (Clarke 1993). The R statistic falls within the range (-1,+1). If the R statistic approximates zero, the null hypothesis is accepted, as similarities between and within sites will be the same on average. If there are many replicates at each site, *R* may be significantly different from zero but inconsequentially small

(Clarke 1993). The R statistic approximates +1 if all replicates within sites are more similar to each other than any replicates from different sites, i.e., the null hypothesis is rejected. *R* substantially less than zero indicates that similarities across sites are higher than those within sites, an unlikely scenario (Clarke and Warrick 1994). Two-way ANOSIM tests produce two R-statistics. $R_{\text{treatment}}$ indicates the degree of discrimination between control and treatment sites and R_{locality} indicates whether there are differences between localities within each treatment.

Where the R statistic revealed moderate or large significant differences in community structure, distinguishing species for groups of samples were identified using similarity percentage breakdown (SIMPER). Only species that contributed to more than 2% to the overall dissimilarity of each site pair were considered as major distinguishing species. Each site pair was analysed separately so that species showing consistent trends between contrasting conditions could be identified.

Results

1. Abiotic Data

There were significant differences ($P<0.005$) in sand inundation, wave exposure and human exploitation between sites within Maputaland and Natal in all zones of the shore in which measurements were made (Table 3.2 and see Figures 2.11, 2.12 and 2.13 p 52-55 for the data). The greatest between-site differences in any factor were for wave forces in Maputaland (Table 3.2, Figure 2.12). There were also substantial differences in harvesting offtake between sites in Maputaland (Figure 2.13). Although sampling sizes were greater in Natal (i.e., more sites were surveyed) greater between-site differences in both factors were recorded in Maputaland (Table 3.2). Between-site differences in sand inundation were greater in Natal than Maputaland but this could be attributed to the low number of sites monitored in Maputaland.

Table 3.2. Results of one-way ANOVA testing for significant differences in sand inundation, wave exposure and human exploitation between sites within the two biogeographic regions, Maputaland and Natal. * denotes significant difference ($P<0.05$).

Factor	Zone	Region	Df	MS	F	p
Sand inundation	Low	Maputaland	5	7.98	4.10	0.004009*
		Natal	20	14.56	14,14	<0.000001*
	Mid	Maputaland	4	4.79	5.59	0.001134*
		Natal	16	13.14	12.27	<0.000001*
	High	KwaZulu-Natal	18	12.31	11.86	<0.000001*
Wave exposure	Low	Maputaland	6	0.97	87.42	<0.000001*
		Natal	22	0.33	22,50	<0.000001*
Human exploitation	Low-Mid	Maputaland	6	20.15	59,41	<0.000001*
		Natal	26	1.55	2.67	0.000035*

The results of the Tukey tests are not shown here but the site pairs selected for comparison (Table 3,5) all differed significantly in terms of the factor being considered.

2. Identifying abiotic determinants and determining human impact

Two-way crossed ANOSIM tests based on similarities derived from percent cover estimates and Bray-Curtis similarities revealed significant differences in community structure ($p=0.0002$, $n=120$ or 80) between groups of sites with contrasting rock types (Table 3.3) and between sites that differed in sand inundation, wave exposure or exploitation (Table 3.5). There were also significant locality effects ($p=0.0002$, $n=120$ or 80) in every test undertaken, reflecting high variability between sites within treatments.

Although the R-statistic was significantly different from zero in all tests, some of the differences identified were inconsequentially small (Clarke 1993). Since the principal objective of this chapter was to identify key factors potentially structuring communities, only those factors for which (**1**) relatively large differences existed between control and treatment sites (i.e. large $R_{treatment}$ value), (2) $R_{treatment}$ was larger than $R_{locality}$, and (3) consistent trends were shown by several species, were considered as potential deterministic agents. R-values ranged from 0.049 to 0.875. For the purpose of this study, R-values were considered "large" if they exceeded the median value of 0.413. Values that were < 0.413 were considered "small" and factors yielding such values were interpreted as having relatively weak effects on community structure. R values less than 0.1 were considered inconsequential.

2a. Rock type

Comparisons between rock types were restricted to Natal as all Maputaland shores are composed of Quaternary sandstone. This also avoided the confounding effect of comparing sites from different biogeographic regions. In the low shore, there were weak indications of an effect of rock type on community structure (R<0.37 in all cases) but locality effects were stronger than treatment effects in all four cases (Table 3.3).

In the mid shore, there were large differences in community structure between shores of dolerite versus Quaternary sandstone (R=0.609) and the treatment effect was substantially greater than the locality effect (R=0.307). For the remaining three mid-shore comparisons, none had R-values that exceeded the critical value of 0.413 necessary for them to be regarded as key factors with the potential to structure intertidal communities. There was small differences in mid-shore communities between Ordovician sandstone and granite (R=0.354) and even smaller differences between Ecca sandstone and dolerite (R=0.197). Substrate effects between Quaternary and Ecca sandstone shores (R=0.238) were less than locality effects (R=0.356).

In the high shore, KwaZulu-Natal was treated as a unit because no biogeographic differences were detected at this level on the shore. Differences between localities (R=0.392) were greater than differences between Ordovician sandstone and granite (R=0.389). There was a weak association between high-shore community structure and contrasting dolerite and Quaternary sandstone shores (R=0.208).

Table 3.3. List of site pairs in the Natal region used to test for differences in community structure between different rock types. Other factors (e.g. wave exposure, relative sand inundation etc.) were not standardised. Only two ecca sandstone shores were surveyed and therefore only two site pairs could be investigated. As there were fewer sites surveyed higher up the shore, there were only two contrasting rock types compared in the high shore (comparisons 1 and 3). The only large significant value is indicated in bold type.

	Sites of respective contrasting rock types		**Low**		**Mid**		**High**	
1	**Ordovician sandstone**	**Granite**	$R_{treatment}$	$R_{locality}$	$R_{treatment}$	$R_{locality}$	$R_{treatment}$	$R_{locality}$
	1. Splash Rock 2. Southport 3. Port Edward	Umzumbe Banana beach Annerly	0.199	0.272	0.354	0.279	0.389	0.392
2	**Ecca sandstone**	**Dolerite**						
	1. Salt rock 2. Shakas Rock	Thompson's Bay Ballito	0.368	0.369	0.197	0.110	-	-
3	**Quaternary sandstone**	**Dolerite**						
	1. Umhlodti 2. Treasure Beach (low) Mission Rocks (mid) 3. Reunion	Ballito Thompson's Bay(low) Seula Point (mid) Newsel	0.165	0.312	**0.609**	0.307	0.208	0.181
4	**Quaternary sandstone**	**Ecca sandstone**						
	1. Umhlodti 2. Treasure Beach	Salt rock Shakas Rock	0.076	0.382	0.238	0.356	-	-

In summary, in only four of the ten comparisons made, did rock type exceed locality effects and in only one case was the influence on community structure sufficiently large enough to be considered as a potential key determinant of community structure.

Species distinguishing between rock types

In Natal, dolerite and Quaternary sandstone had corresponding differences in mid-shore community structure (Table 3.3). SIMPER analysis revealed that four taxa responded consistency between these rock types (Table 3.4). There was more bare rock and higher cover of the barnacles, *Octomeris angulosa* and *Tetraclita serrata* at sites composed of dolerite. All three dolerite shores had more than 70% cover of *O. angulosa* and bare rock while Quaternary sandstone shores had less than 25% cover of these taxa. The only species that was consistently more abundant on Quaternary sandstone shores was the short algal turf, *Gelidium reptans*. The zoanthid, *Palythoa nelliae* was more abundant on sandstone at two site pairs.

Table 3.4 ROCK TYPE – Natal: Mid shore

Major distinguishing species between dolerite and Quaternary sandstone(Q. s) mid-shores in Natal as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. SIMPER analyses were used to identify key distinguishing species, ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. Av. % indicates the average percentage cover of each species at each site. $D_i/SD(D_i)$ is the ratio between D_i, the average contribution of each species to the overall dissimilarity and $SD(D_i)$, the standard deviation of D_i and this ratio reflects how consistently the species abundance varies within each site pair. $\Sigma D_i\%$ is the cumulative percentage contribution of each species to the overall dissimilarity D. Only species that contributed more than 2% to the overall dissimilerity are shown. Species that were more abundant at dolerite sites are shaded whereas species that were more abundant at sandstone sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

	Rock type	**Dolerite**	**Q. s**				**Dolerite**	**Q. s**				**Dolerite**	**Q. s**		
	Site pair 1	Seula Point	Mission Rocks	D=91.82%		Site pair 2	Ballito	Umhlodti	D=74.51%		Site pair 3	Newsell	Reumon	D=82.64%	
	Species	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\Sigma D_i\%$**	**Species**	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\Sigma D_i\%$**	**Species**	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\Sigma D_i\%$**
*	*Octomeris angulosa*	51.08	0.00	2.00	17.12	*Jania verrucosa*	4.85	48.05	1.59	18.73	*Octomeris angulosa*	55.25	1.40	2.28	21.93
*	Bare rock	21.85	3.35	1.52	25.61	*Octomeris angulosa*	64.8	22.07	1.56	35.97	*Palythoa nelliae*	5.95	39.0	0.94	36.94
	Palythoa nelliae	0.00	21.57	0.74	33.79	Bare rock	16.6	1.90	1.73	46	Ulva sp.	0.00	18.25	0.93	45.05
	Palythoa natalensis	0.00	16.0	0.50	39.36	Encrusting corallines	0.00	13.05	1.22	54.94	Bare rock	12.85	1.75	1.29	52.67
*	*Tetraclita serrata*	7.42	0.00	1.31	44.64	*Ralfsia expansa*	9.05	0.40	1.00	61.75	*Gelidium reptans*	3.45	8.45	1.07	58.69
	Ralfsia expansa	8.50	0.70	1.20	49.87	*Pomatoleios kraussii*	0.10	2.75	0.92	65.46	*Ralfsia expansa*	0.25	6.70	0.77	63.15
	Laurencia pumila	0.00	10.85	0.77	55.06	*Gelidium reptans*	1.20	2.93	0.81	69.17	*Perna perna*	2.45	0.25	1.33	66.82
	Tetraclita squamosa	0.01	8.40	1.03	59.78	*Tetraclita serrata*	2.30	0.56	1.09	72.45	*Pomatoleios kraussii*	0.65	3.25	1.03	70.37
	Green tube	0.00	6.88	1.15	64.43	*Zoanthus natalensis*	0.80	2.80	0.45	74.79	*Tetraclita serrata*	6.50	0.15	0.47	73.68
	Zoanthus natalensis	0.00	6.53	0.87	68.83	*Perna perna*	0.55	0.83	1.10	77.05	*Saccostrea cucullata*	1.80	2.05	1.14	76.83
	Jania verrucosa	1.00	5.95	0.64	72.45	*Hypnea intricata*	0.00	1.85	0.62	79.26	*Enteromorpha* sp.	0.00	3.85	0.68	79.55
	Perna perna	3.05	0.05	0.86	75.3	*Cellana capensis*	0.25	0.80	1.44	81.36	Encrusting corallines	0.10	4.45	0.67	82.41
	Zoanthus parvus	0.00	5.42	0.50	77.87	*Laurencia pumila*	0.00	1.60	0.62	83.44					
*	*Gelidium reptans*	1.15	1.85	0.78	80.25										
	Scutellastra natalensis	1.05	0.00	1.96	82.58										

2b. Sand inundation

Using the first approach (comparing the three sites with the greatest sand inundation against three adjacent sites with significantly less inundation), there was evidence of a strong association between sand inundation and community structure in all zones on the shore (Table 3.5, low shore R=0.800, mid shore R=0.761, high shore R=0.759). The second approach, where exploitation and wave exposure were standardised by comparing only sites that did not differ in these factors, yielded lower R values in the low and high shore but the relationship between sand and community structure was still strong in all zones (low-R=0.465, mid-R=0.796, high-R=0.544).

Species distinguishing between heavily and lightly sanded shores

Natal: Low shore

When the potential effect of sand inundation was investigated at sites with equal wave exposure (approach 2), ANOSIM tests (Table 3.5) suggested a relatively weak (R=0.465) but significant relationship with community structure. However, SIMPER analyses did not support the idea of a causal relationship between sand inundation and low shore community structure because there was only one species, *Laurencia natalensis*, that showed consistent trends within the three site pairs (Table 3.6, Figure 3.1A). Even this species was ranked between 10 and 16 in terms of its contribution to differences between sites. *P. perna* did not show consistent trends between sanded and unsanded sites, with higher cover at highly sand inundated sites in two instances and at the lightly sanded site in the third case.

Natal: Mid shore

Both approaches indicated that sand inundation is a potential structuring agent in mid-shore communities in Natal. The high $R_{treatment}$ value for sand inundation (R=0.769) was supported by results from the SIMPER analysis showing six consistently distinguishing taxa between sand-inundated and less sanded sites (Table 3.7, Figure 3.1B). Sanded sites had consistently higher cover of the turf-forming algae *Jania verrucosa* and *Laurencia natalensis*. *J. verrucosa* dominated the two sites where highest volumes of sand were recorded (Railway and Vidal Ledges) with mean cover of 84.29% and 97.50% respectively. This species was the most important distinguishing species in all three site-pairs accounting for 18-25% of the dissimilarity between sites. *L. natalensis* was absent from all three less-sanded sites but was present at heavily sanded sites, although it occupied less than 4% cover.

Table 3.5 ANOSIM RESULTS : Sand inundation, Wave exposure, Human exploitation

Site pairs that had significant differences (ANOVA $p<0.05$) in each of three factors : (A) relative sand inundation, (B) wave exposure and (C) human exploitation and results of 2-way crossed ANOSIM tests for differences in community structure between and within treatments($p<0.0002$ in all cases). In the low and mid shore, the two biogeographic regions, Maputaland and Natal, were analysed separately. Two approaches were implemented. In the first approach, sites subject to the extremes of wave exposure or sand inundation were compared, as were exploited and unexploited sites. Other factors were not standardised. In the second approach, the effect of each respective factor under investigation was isolated as far as possible, i.e. sites that differed only in sand inundation, wave exposure or exploitation were compared. *In Natal, the lack of unexploited shores prevented proper assessment of the potential effect of exploitation. Adjacent sites with high and low exploitation pressure were compared although these did not differ significantly ($p>0.05$) in the intensity of human exploitation. Sites with matching numbers were compared in each case.

		APPROACH 1					APPROACH 2				
Region	**Zone**	**Sites : Treatment – high level of factor**	**Sites : Control – low level of factor**	**$R_{treatment}$**	**$R_{locality}$**	**n**	**Sites : Treatment – high level of factor**	**Sites : Control – low level of factor**	**$R_{treatment}$**	**$R_{locality}$**	**n**
A. Sand Inundation		**Heavily sand inundated**	**Lightly sand inundated**				**Heavily sand inundated**	**Lightly sand inundated**			
Natal	Low	1. Railway 2. Zinkwazi Platform 3. Peace Cottage	1. Mission Rock 2. Newsell 3. Shakas Rock	0.600	0.583	120	1. Umhlodti 2. Railway 3. Vidal Ledge	1. Southport 2. Shaka's Rock 3. Mission Rock	0.465	0.379	120
	mid	1. Cape Vidal Point 2. Peace Cottage 3. Banana Beach	1. Mission Rock 2. Newsell 3. Splash Rock	0.761	0.583	120	1. Railway 2. Vidal ledge 3. Umhlodti	1. Shaka's Rock 2. Mission Rock 3. Southport	0.796	0.474	120
KZN	High	1. Kosi mouth 2. Bhanga Nek 3. Umhlodti	1. Black Rock 2. Cape Vidal Point 3. Banana Beach	0.759	0.531	120	1. Railway 2. Umhlodti 3. Reunion	1. Newsell 2. Banana Beach 3. Umzumbe	0.544	0.495	120
B. Wave exposure		**Wave exposed**	**Wave sheltered**				**Wave exposed**	**Wave sheltered**			
Natal	Low	1. Seula Point 2. Splash Rock 3. Southport	1. Zinkwazi Platform 2. Peace Cottage 3. Trafalgar	0.634	0.875	120	1. Seula Point 2. Splash Rock 3. Southport	1. Mission Rock 2. Reunion 3. Port Edward	0.481	0.345	120
	Mid	1. Seula Point 2. Umhlodti 3. Southport	1. Salt Rock 2. Peace Cottage 3. Trafalgar	0.586	0.516	120	1. Splash Rock 2. Umzumbe 3. Southport	1. Mission Rock 2. Trafalgar 3. Annerly	0.493	0.435	120
KZN	High	1. Dog Point 2. Black Rock 3. Southport	1. Kosi Mouth 2. Bhanga Nek 3. Salt Rock	0.560	0.741	120	1. Ballito 2. Umzumbe 3. Southport	1. Cape Vidal Point 2. Port Edward 3. Annerly	0.374	0.408	120
Maputaland	Low	1. Dog Point 2. Black Rock 3. Island Rock	1. Kosi Mouth 2. Bhanga Nek 3. Sodwana	0.806	0.691	120	***A. Unexploited sites*** 1. Island Rock 2. Island Rock ***B. Exploited sites*** 1. Black Rock 2. Dog Point	***A. Unexploited sites*** 1. Sodwana 2. Cape Vidal Point ***B. Exploited sites*** 1. Bhanga Nek 2. Kosi Mouth	0.783 0.826	0.336 0.269	80 80
	Mid	1. Dog Point 2. Black Rock	1. Kosi Mouth 2. Bhanga Nek	0.576	0.561	80	-				
C. Exploitation		**Exploited**	**Protected**				**Exploited**	**Protected**			
Natal*	Low	1. Crayfish Point 2. Umdoni 3. Banana Beach	1. Mission Rocks 2. Splash Rock 3. Umzumbe	0.078	0.380	120	-				
Maputaland	Low	1. Black Rock 2. Kosi Mouth 3. Bhanga Nek	1. Island Rock 2. Sodwana 3. Cape Vidal Point	0.846	0.620	120	***A. Wave exposed sites*** 1. Dog Point 2. Black Rock ***B. Sheltered sites*** 1. Kosi Mouth 2. Bhanga Nek	***A. Wave exposed sites*** 1. Island Rock 2. Island Rock ***B. Sheltered sites*** 1. Sodwana 2. Cape Vidal Point	0.875 0.824	0.297 0.441	80 80
	Mid	1. Kosi Mouth 2. Bhanga Nek	1. Sodwana 2. Cape Vidal Point	0.049	0.488	80	-				

Less inundated sites were characterised by more bare rock and higher cover of the barnacles *Octomeris angulosa* and *Tetraclita serrata*, and the limpet *Scutellastra natalensis*. *O. angulosa* and other barnacle species were absent at heavily sanded sites (Railway and Vidal Ledges). Relatively unsanded sites had higher cover of *O. angulosa* (48.05%, 2.03% and 38.08%) and *Tetraclita* spp. (4.00%, 8.40%, 4.45%). The zoanthid *Palythoa nelliae* was always absent at heavily-sanded sites, and abundant at two of the three lightly-sanded sites.

KwaZulu-Natal: High shore

Sand inundation emerged as the most likely factor to play a key role in shaping high-shore communities as indicated by the high *R*-values obtained with both approaches (R1=0.759, R2=0.544, Table 3.4). This was further supported by the fact that five species showed consistent trends between sanded and unsanded shores (Table 3.8, Figure 3.1C). Sanded shores had higher cover of early successional ephemeral brown algae, the barnacle *Chthalamus dentatus* and several species of *Siphonaria* limpets, all of which were virtually absent from unsanded sites. Unsanded high shores were characterised by higher densities of sun oysters, *Saccostrea cucullata* and the barnacle *O. angulosa*. *S. cucullata* was consistently the most important distinguishing species between sand-inundated and less-sanded shores, accounting for more than 24% of the dissimilarity between sites in all three pairs.

Table 3.6 SAND INUNDATION -Natal: Low shore

Major distinguishing species between each of three paired Natal low-shore sites differing in relative sand inundation as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray Curtis measure of similarity. Species are ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at heavily sand inundated sites are shaded whereas species that were more abundant at less sanded sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterisk (*).

	Sand inundation	Sanded	Unsanded				Sanded	Unsanded				Sanded	Unsanded		
	Site pair 1	Umhlodh	SouthPort	D=47.00%		Site pair 2	Railway	Shaka's Rock	D=54.97%		Site pair 3	Vidal Ledge	Mission Rocks	D=78.48%	
	Species	Av. %	Av. %	Di/SD(Di)	ΣDi%	Species	Av. %	Av. %	Di/SD(Di)	ΣDi%	Species	Av. %	Av. %	Di/SD(Di)	ΣDi%
	Encrusting corallines	7.00	0.00	1.80	11.90	sand	14.25	0.00	1.20	12.04	*Perna perna*	64.95	15.25	1.54	13.63
	Scutellastra aphanes	3.54	0.00	2.04	21.67	*Perna perna*	70.80	80.10	0.89	18.45	*Hypnea spinifera*	0.00	16.90	0.98	21.56
	Cheilosporum sagittatum	4.70	1.00	1.52	30.35	*Hypnea spinifera*	2.10	2.50	1.13	23.79	*Hypnea intricata*	6.15	11.95	1.23	27.47
	Plocamium corallorhiza	2.85	1.10	1.38	37.74	*Cheilosporum sagittatum*	2.05	3.17	0.97	28.10	*Cheilosporum sagittatum*	1.30	12.37	1.06	32.84
	Ralfsia expansa	3.30	0.60	1.53	44.78	*Plocamium corallorhiza*	1.55	1.75	0.99	33.44	*Jania verrucosa*	9.10	6.65	1.33	38.13
	Perna perna	77.15	91.88	0.79	50.40	Encrusting corallines	0.55	2.50	1.10	37.76	*Spyridea hypnoides*	0.35	8.45	1.14	43.00
	Jania verrucosa	0.00	2.30	0.85	56.53	*Hypnea intricata*	2.60	1.66	0.85	42.04	*Sargassum elegans*	0.00	7.65	0.95	47.50
	Octomeris angulosa	0.50	1.53	1.44	60.59	*Octomeris angulosa*	0.00	1.55	1.00	46.09	*Sargassum crassifolium*	0.00	3.90	1.73	51.55
	Hypnea intricata	2.30	0.00	0.75	66.02	*Ralfsia expansa*	0.60	1.95	1.10	50.02	*Polysiphonia* sp.	6.05	0.00	0.84	55.73
	Gigartina minima	0.75	0.00	1.10	69.37	*Ulva* sp.	1.49	0.00	0.91	53.41	*Laurencia natalensis*	3.45	0.50	1.17	58.23
	Scutellastra natalensis	0.00	0.41	2.19	72.71	*Spyridea hypnoides*	1.93	0.20	0.78	56.74	*Arthrocardia carinata*	0.15	4.65	0.65	61.04
	Pomatoleios kraussii	0.00	0.50	0.79	75.20	*Jania verrucosa*	0.95	1.86	0.68	59.98	*Pyura stolonifera*	4.80	0.75	0.59	63.82
*	*Laurencia natalensis*	0.50	0.15	0.72	77.47	*Chthamalus dentatus*	1.35	0.00	0.78	63.12	*Plocamium corallorhiza*	3.05	0.60	0.57	66.12
	Dictyopteris ligulata	0.45	0.00	0.76	79.58	*Polysiphonia* sp.	2.70	0.00	0.64	66.19	Unidentified brown alga	1.47	0.13	1.27	68.38
	Cladophora rugulosa	0.00	0.50	0.63	81.69	*Scutellastra aphanes*	0.26	0.68	1.41	68.45	sand	2.00	0.00	0.86	70.56
						Laurencia natalensis	0.80	0.35	0.75	70.60	*Ralfsia expansa*	0.10	1.65	0.88	72.58

Table 3.7 SAND INUNDATION - Natal: Mid shore

Major distinguishing species between each of three paired Natal mid shore sites differing in relative sand inundation as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. SIMPER analyses were used to identify key distinguishing species ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at heavily sand inundated sites are shaded whereas species that were more abundant at lightly sanded sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterisk (*).

	A. Sand inundation	Sanded	Less sanded				Sanded	Less sanded				Sanded	Less sanded		
	Site pair 1	Railway	Shaka's Rock	D=92.54%		Site pair 2	Vidal Ledge	Mission Rocks	D=91.86%		Site pair 3	Umhlodli	SouthPort	D=78.77%	
	Species	Av. %	Av. %	Di/SD(Di)	ΣDi%	Species	Av. %	Av. %	Di/SD(Di)	ΣDi%	Species	Av. %	Av. %	Di/SD(Di)	ΣDi%
*	*Jania verrucosa*	84.29	6.65	3.17	24.97	*Jania verrucosa*	97.50	5.95	2.74	28.56	*Jania verrucosa*	48.05	0.00	1.86	18.06
*	*Octomeris angulosa*	0.00	40.05	1.21	38.55	*Palythoa nelliae*	0.00	21.57	0.73	39.02	Bare rock	1.90	41.46	2.00	33.90
*	*Palythoa nelliae*	0.00	19.77	0.70	48.04	*Palythoa natalensis*	0.00	16.00	0.49	46.29	*Octomeris angulosa*	27.07	38.08	1.56	46.56
	Ralfsia expansa	0.05	6.95	0.84	53.88	*Laurencia pumila*	0.03	10.85	0.78	52.77	Encrusting corallines	13.06	0.00	1.23	54.78
*	*Laurencia natalensis*	3.37	0.00	2.55	56.87	*Tetraclita squamosa*	0.00	8.40	1.05	58.56	*Ralfsia expansa*	0.40	11.40	1.11	61.97
*	Bare rock	0.39	5.70	1.20	63.86	*Cladophoropsis sundanensis*	0.00	6.88	1.17	64.27	*Tetraclita serrata*	0.56	4.45	1.31	66.39
	Hypnea tenuis	3.79	0.00	0.87	67.71	*Zoanthus natalensis*	0.00	5.53	0.89	69.67	*Pomatoleios kraussii*	2.78	0.96	0.98	70.00
	Arthrocardia sp I	4.00	0.00	0.70	71.08	Bare rock	0.10	3.35	1.02	73.22	*Scutellastra natalensis*	0.08	1.93	2.17	73.45
	Pomatoleios kraussii	0.00	4.05	0.59	74.03	*Zoanthus parvus*	0.00	5.42	0.60	76.42	*Saccostrea cucullata*	0.00	1.40	1.14	76.10
	Encrusting corallines	1.20	0.40	1.40	76.76	*Octomeris angulosa*	0.00	2.03	0.79	78.89	*Laurencia natalensis*	1.85	0.00	0.82	78.14
	Zoanthus natalensis	0.00	5.72	0.36	79.19	*Scutellastra natalensis*	0.00	1.95	0.72	81.26	*Perna perna*	0.83	0.94	1.24	80.16
*	*Scutellastra natalensis*	0.00	0.46	0.84	81.23	*Laurencia natalensis*	1.07	0.00	0.88	83.50					

Table 3.8 SAND INUNDATION – KZN: High shore

Major distinguishing species between each of three paired Natal mid shore sites differing in relative sand inundation as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. SIMPER analyses were used to identify key distinguishing species ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at heavily sand inundated sites are shaded whereas species that were more abundant at lightly sanded sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

	A. Sand inundation	**Sanded**	**Less sanded**				**Sanded**	**Less sanded**				**Sanded**	**Less sanded**		
	Site pair 1	Railway	Newsell	D=90,93%		Site pair 2	Umhlodti	Banana Beach	D=63,84%		Site pair 3	Reunion	Umzumbe	D=45.80%	
	Species	**Av. %**	**Av. %**	**D/SD(D$_i$)**	**ΣD$_i$%**	**Species**	**Av. %**	**Av. %**	**D/SD(D$_i$)**	**ΣD$_i$%**	**Species**	**Av. %**	**Av. %**	**D/SD(D$_i$)**	**ΣD$_i$%**
*	*Saccostrea cucullata*	0.00	50.75	4.09	24.36	*Saccostrea cucullata*	21.80	60.53	1.42	30.27	*Saccostrea cucullata*	33.57	36.22	2.17	28.13
*	Ephemeral brown alga	50,45	0.00	1.30	45.22	Ephemeral brown alga	38.18	0.00	0.80	50.32	Bare rock	56.30	60.35	1.91	48.03
	Bare rock	18.15	44.00	1.93	64.17	Bare rock	24.96	9.30	1.78	63.53	*Chthalamus dentatus*	8.80	0.00	1.04	61.66
	Enteromorpha sp.	27.10	0.00	0.76	75.57	*Enteromorpha* sp.	0.80	4.00	1.14	70.45	*Octomeris angulosa*	0.00	1.08	1.17	66.73
*	*Octomeris angulosa*	0.00	3.25	1.65	80.79	*Chthalamus dentatus*	4.77	1.45	1.16	77.32	Ephemeral brown alga	1.40	0.10	0.82	71.25
	Ectocarpus sp.	2.35	0.00	0.98	84.46	*Gelidium reptans*	0.00	2.20	1.09	82.78	*Enteromorpha* sp.	1.2	0.00	1.59	75.30
*	*Chthalamus dentatus*	1.10	0.00	0.95	86.98	*Octomeris angulosa*	0.00	0.80	0.62	85.23	*Siphonaria capensis*	0.89	0.08	0.74	79.08
*	*Siphonaria capensis*	1.26	0.00	0.72	89.10	*Siphonaria concinna*	0.89	0.00	0.74	87.30	*Ralfsia expansa*	0.00	1.80	0.45	82.32
						Siphonaria capensis	0.63	0.00	0.64	89.28	*Siphonaria concinna*	0.58	0.00	0.76	85.29
											Siphonaria anneae	0.40	0.00	0.63	87.71

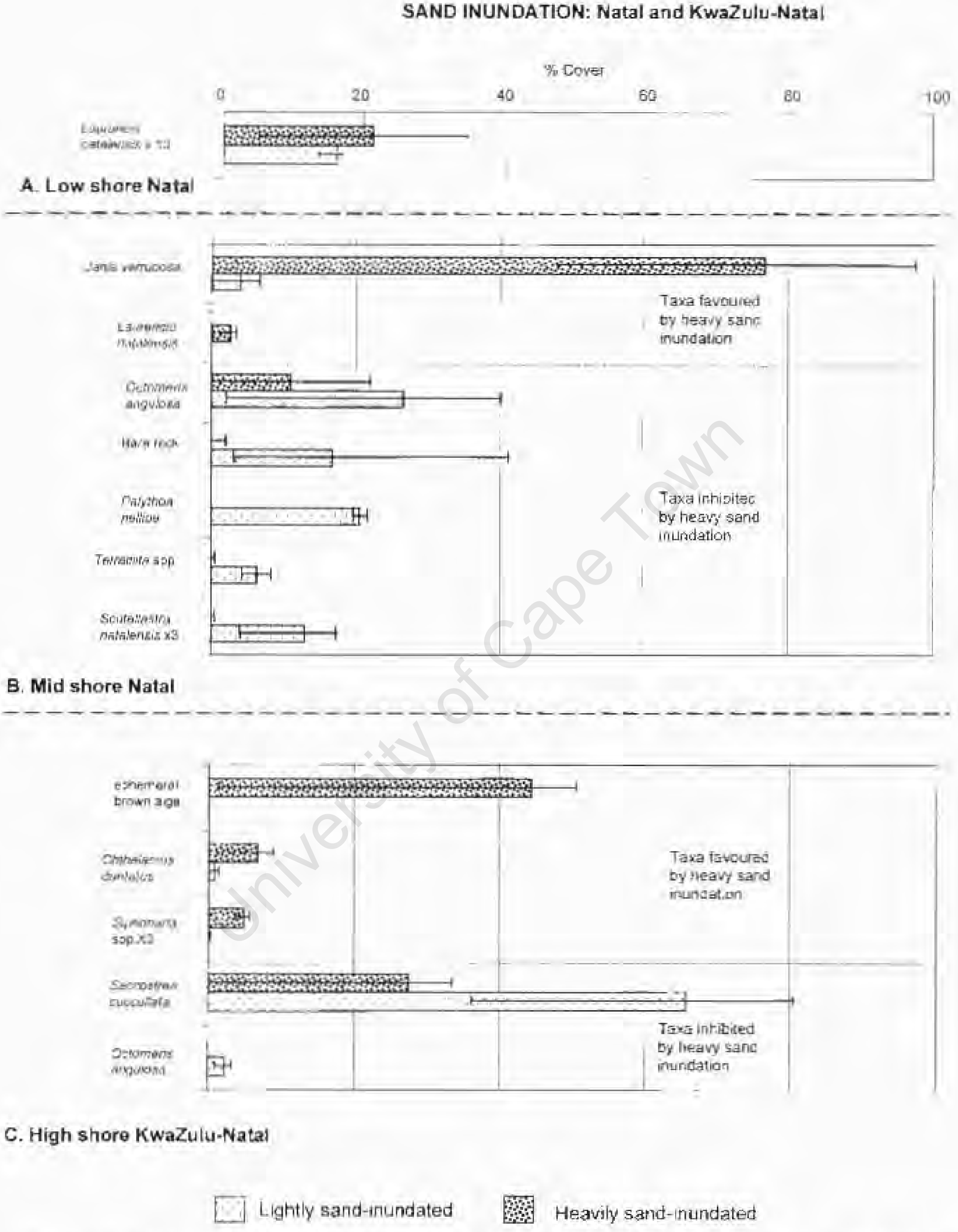


Figure 3.1. Mean cover and range of data for taxa that consistently distinguished between three pairs of rocky shores with significant differences in mean volumes of sand inundation in Natal. Three spatially defined zones on the shore were analysed separately, the low shore in Natal (A), mid shore in Natal (B) and the high shore in KwaZulu-Natal (C). Data for less abundant species have been multiplied (x3 or x10).

2c. Wave exposure

In both Natal and Maputaland, the first approach (sand inundation and exploitation not standardised) revealed large significant differences in community structure between the most and least wave-exposed shores in the low shore (Natal R=0.634, Maputaland R=0.806) and, to a lesser extent, in the mid shore (Natal R=0.586, Maputaland R=0.576,) (Table 3.5). There was also an exposure effect in the high shore but R_{locality} (R=0.741) was greater than $R_{\text{treatment}}$ (R=0.560).

The second approach, in which exploitation and sand inundation were standardised (i.e., ANOVA showed no significant difference in these factors between sites), also indicated a clear association between low shore community structure and wave exposure (Table 3.5). This was evident in the Natal biogeographic region (R=0.481) and at both unexploited (R=0.783) and exploited (R=0.826) sites within Maputaland. In Natal, differences between exposed and sheltered mid-shore communities (R=0.493) exceeded differences between localities within exposures (R=0.435). In Maputaland, tests of influence of wave exposure in the mid shore were based on only two site-pairs, all of which were exploited (i.e. exploitation was standardised) and a moderate to large influence of wave exposure was identified (R=0.576). In the high shore, the low R statistic (R=0.374) in the second approach and the consistently higher locality effect (R=0.408) suggested that wave exposure does not exert a dominating influence on high shore community structure.

Species distinguishing between exposed and sheltered shores

Natal: Low shore

In Natal, ANOSIM tests indicated a moderate association between low-shore community structure and wave exposure in the second approach (R=0.481, Table 3.5), with nine species showing consistent trends between different exposures (Table 3.9, Figure 3.2A). Higher cover of the brown mussel *Perna perna* on exposed shores was accompanied by consistently higher densities of the limpet, *Scutellastra aphanes* and higher cover of the red alga, *Plocamium corallorhiza*. At the most wave-exposed site in Natal, Seula Point, mean mussel cover was 85% while mean cover at relatively sheltered shores ranged between 15 and 54%. Sheltered shores had consistently greater cover of six types of red algae, i.e., *Hypnea spicifera*, *H. intricata*, encrusting coralline algae, *Arthrocardia cannata*, *Gelidium abbotiorum* and *Spyridea hypnoides*. The mussel *Perna perna* and the alga *H. spicifera* were respectively the two most important distinguishing species in all three site-pairs, accounting for at least 20% of the dissimilarity in community structure between exposures.

Natal: Mid shore

Mid-shore communities were relatively closely related to wave exposure (R=0.493, Table 4.3). Comparing wave-exposed and sheltered shores with equal intensities of sand inundation and equal levels of harvesting, there were seven consistently distinguishing taxa (Table 3.10, Figure 3.2B). The most important of these was *Octomeris angulosa*. This species was consistently more abundant at exposed shores, as was the limpet *Scutellastra natalensis*. Sheltered mid shores in Natal had higher cover of zoanthids (principally *P. nelliae* and *Z. natalensis*) and the turf-forming articulated coralline algae, *Jania verrucosa*. All four species of zoanthids were almost absent (highest mean cover = 0.2%) at exposed sites but were dominant at two sheltered sites (Mission Rocks and Trafalgar). The third site (Annerly) had substantial cover of *Pomatoleios kraussii*, a species that did not consistently distinguish between different exposures at the other two site-pairs. The barnacle, *Tetraclita serrata*, had more than 8% higher cover at sheltered sites within two site-pairs and differed by only 1.3% at the third site-pair.

KwaZulu-Natal: High shore

ANOSIM tests failed to identify wave exposure as a key determinant of high shore community structure (R=0.374, Table 3.5). There were only two taxa showing consistent trends between shores experiencing different intensities of wave exposure (Table 3.11, Figure 3.2C). The sun oyster *Saccostrea cuccullata* was more abundant at sheltered shores (Av%=40.15-81.88) compared to exposed shores (Av%=24.80-47.55) in all three site-pairs. There was more bare rock at all exposed sites (Av%=46.10-71.42) relative to sheltered sites (Av%=12.8-50.47). The other species distinguishing between sites with different degrees of wave action, did so in a manner that was inconsistent.

Table 3.6 SAND INUNDATION -Natal: Low shore

Major distinguishing species between each of three paired Natal low-shore sites differing in relative sand inundation as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Species are ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at heavily sand inundated sites are shaded whereas species that were more abundant at less sanded sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

	Sand inundation	Sanded	Unsanded				Sanded	Unsanded				Sanded	Unsanded		
	Site pair 1	Umhlodti	SouthPort	D=47.00%		Site pair 2	Railway	Shaka's Rock	D=54.97%		Site pair 3	Vidal Ledge	Mission Rocks	D=75.46%	
	Species	Av. %	Av. %	D/SD(D)	ΣD%	Species	Av. %	Av. %	D/SD(D)	ΣD%	Species	Av. %	Av. %	D/SD(D)	ΣD%
	Encrusting corallines	7.00	0.00	1.80	11.90	sand	14.25	0.00	1.20	12.04	*Perna perna*	54.95	15.25	1.54	13.63
	Scutellastra aphanes	3.54	0.00	2.04	21.67	*Perna perna*	70.60	80.10	0.89	18.45	*Hypnea spicifera*	0.00	18.90	0.96	21.59
	Cheilosporum sagittatum	4.70	1.00	1.52	30.35	*Hypnea spicifera*	2.10	2.50	1.13	23.79	*Hypnea intricata*	8.15	11.95	1.23	27.47
	Plocamium corallorhiza	2.85	1.10	1.38	37.74	*Cheilosporum sagittatum*	2.05	3.17	0.97	29.10	*Cheilosporum sagittatum*	1.30	12.32	1.06	32.81
	Ralfsia expansa	3.30	0.60	1.53	44.78	*Plocamium corallorhiza*	1.55	1.75	0.99	33.44	*Jania verrucosa*	9.10	6.65	1.33	38.13
	Perna perna	77.15	91.68	0.79	50.40	Encrusting corallines	0.55	2.60	1.10	37.76	*Spyridea hypnoides*	0.35	8.45	1.14	43.00
	Jania verrucosa	0.00	2.30	0.85	55.53	*Hypnea intricata*	2.60	1.55	0.85	42.04	*Sargassum elegans*	0.60	7.65	0.95	47.50
	Octomeris angulosa	0.50	1.53	1.44	60.60	*Octomeris angulosa*	0.00	1.55	1.00	46.09	*Sargassum crassifolium*	0.00	3.90	1.73	51.55
	Hypnea intricata	2.30	0.00	0.75	65.62	*Ralfsia expansa*	0.60	1.95	1.10	50.02	*Polysiphonia* sp	6.05	0.00	0.84	55.13
	Gigartina minima	0.75	0.00	1.10	69.37	*Ulva* sp	1.49	0.00	0.91	53.41	*Laurencia natalensis*	3.45	0.50	1.17	58.23
	Scutellastra natalensis	0.00	0.41	2.19	72.71	*Spyridea hypnoides*	1.93	0.20	0.78	56.74	*Arthrocardia carinata*	0.15	4.65	0.65	61.04
	Pomatoleios kraussii	0.00	0.50	0.79	75.20	*Jania verrucosa*	0.95	1.85	0.68	59.96	*Pyura stolonifera*	4.80	0.25	0.69	63.82
*	*Laurencia natalensis*	0.50	0.15	0.72	77.47	*Chthalamus dentatus*	1.35	0.00	0.78	63.12	*Plocamium corallorhiza*	3.05	0.90	0.57	66.12
	Dictyopteris ligulata	0.45	0.00	0.78	79.68	*Polysiphonia* sp	2.20	0.00	0.85	66.19	Unidentified brown alga	1.47	0.13	1.27	68.38
	Cladophora rugulosa	0.00	0.50	0.63	81.89	*Scutellastra aphanes*	0.26	0.68	1.41	68.45	sand	2.00	0.00	0.86	70.56
						Laurencia natalensis	0.80	0.35	0.75	70.60	*Ralfsia expansa*	0.10	1.65	0.88	72.58

Table 3.7 SAND INUNDATION - Natal: Mid shore

Major distinguishing species between each of three paired Natal mid-shore sites differing in relative sand inundation as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. SIMPER analyses were used to identify key distinguishing species ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at heavily sand inundated sites are shaded whereas species that were more abundant at lightly sanded sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

	A. Sand inundation	Sanded	Less sanded				Sanded	Less sanded				Sanded	Less sanded		
	Site pair 1	Railway	Shaka's Rock	D=92.54%		Site pair 2	Vidal Ledge	Mission Rocks	D=91.96%		Site pair 3	Umhlodti	SouthPort	D=78.77%	
	Species	Av. %	Av. %	D/SD(D)	ΣD%	Species	Av. %	Av. %	D/SD(D)	ΣD%	Species	Av. %	Av. %	D/SD(D)	ΣD%
*	*Jania verrucosa*	64.29	6.65	3.17	24.97	*Jania verrucosa*	97.50	5.95	2.77	28.56	*Jania verrucosa*	48.05	0.00	1.88	18.06
*	*Octomeris angulosa*	0.00	40.05	1.21	39.55	*Palythoa nelliae*	0.00	21.67	0.73	39.02	Bare rock	1.90	41.46	2.00	33.90
*	*Palythoa nelliae*	0.00	19.77	0.70	48.04	*Palythoa natalensis*	0.00	16.00	0.49	46.29	*Octomeris angulosa*	22.07	38.08	1.56	46.56
	Ralfsia expansa	0.05	9.95	0.84	53.86	*Laurencia pumila*	0.03	10.85	0.78	52.77	Encrusting corallines	13.06	0.00	1.23	54.78
*	*Laurencia natalensis*	3.37	0.00	2.55	58.67	*Tetraclita squamosa*	0.00	8.40	1.05	58.56	*Ralfsia expansa*	0.40	11.40	1.11	61.97
*	Bare rock	0.39	5.70	1.20	63.86	*Cladophoropsis sudanensis*	0.00	8.88	1.17	64.27	*Tetraclite serrata*	0.56	4.45	1.31	66.39
	Hypnea tenuis	3.79	0.00	0.67	67.71	*Zoanthus natalensis*	0.00	8.53	0.59	69.67	*Pomatoleios kraussii*	2.76	0.96	0.98	70.00
	Arthrocardia sp I	4.00	0.00	0.70	71.06	Bare rock	0.10	3.35	1.02	73.22	*Scutellastra natalensis*	0.08	1.93	2.17	73.45
	Pomatoleios kraussii	0.00	4.05	0.59	74.03	*Zoanthus parvus*	0.00	5.42	0.50	76.42	*Saccostrea cucullata*	0.00	1.40	1.14	76.10
	Encrusting corallines	1.20	0.40	1.40	76.78	*Octomeris angulosa*	0.00	2.05	0.79	78.89	*Laurencia natalensis*	1.85	0.00	0.62	78.14
	Zoanthus natalensis	0.00	5.72	0.36	79.19	*Scutellastra natalensis*	0.00	1.95	0.72	81.26	*Perna perna*	0.83	0.94	1.24	80.16
*	*Scutellastra natalensis*	0.00	0.46	0.84	81.23	*Laurencia natalensis*	1.07	0.00	0.88	83.50					

Table 3.11 WAVE EXPOSURE - KZN: High shore

Major distinguishing species between each of three paired Natal mid-shore sites differing in wave exposure as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Distinguishing species are ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at wave exposed sites are shaded whereas species that were more abundant at sheltered sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*)

	B. Wave exposure														
	Site pair 1	**Exposed**	**Sheltered**			Site pair 2	**Exposed**	**Sheltered**			Site pair 3	**Exposed**	**Sheltered**		
		Umzumbe	Port Edward	D=29.64%			Southport	Anerly	D=37.55%			Ballito	Cape Vidal	D=41.16%	
	Species	**Av. %**	**Av. %**	**D/SD(D_i)**	**$\Sigma D_i\%$**	**Species**	**Av. %**	**Av. %**	**D/SD(D_i)**	**$\Sigma D_i\%$**	**Species**	**Av. %**	**Av. %**	**D/SD(D_i)**	**$\Sigma D_i\%$**
	Chthalamus dentatus	0.00	6.30	1.15	18.50	Bare rock	71.42	41.60	1.16	20.78	Bare rock	46.10	12.80	1.51	30.60
*	*Saccostrea cucullata*	36.22	40.15	1.37	36.07	*Saccostrea cucullata*	24.80	50.90	1.41	39.46	*Saccostrea cucullata*	47.55	81.88	1.26	53.10
*	Bare rock	60.35	50.47	1.20	46.92	*Octomeris angulosa*	0.08	4.00	1.34	50.67	*Chthalamus dentatus*	3.90	0.32	1.16	63.44
	Octomeris angulosa	1.06	0.03	1.22	56.27	*Chthalamus dentatus*	2.25	0.00	1.33	59.22	*Brachidontes semistriatus*	0.40	4.00	1.18	73.36
	Tetraclita serrata	0.12	1.18	0.96	63.16	*Gelidium* sp.	0.30	1.85	1.07	66.15	*Celana capensis*	0.07	0.47	2.17	77.24
	Nodilittorina africana	0.78	0.51	1.85	69.65	*Celana capensis*	1.76	0.34	1.85	72.20	*Ralfsia expansa*	0.70	0.00	0.77	81.10
	Ralfsia expansa	1.60	0.4	0.55	75.64	*Gelidium reptans*	0.00	3.00	0.43	75.44	sand	0.00	0.40	0.64	83.96
	Scutellastra natalensis	0.01	0.69	1.20	81.54	*Nodilittorina africana*	0.45	0.06	1.52	80.00	*Tetraclita squamosa*	0.00	0.23	0.80	86.05
	Celana capensis	0.14	0.53	1.27	86.26	*Brachidontes semistriatus*	0.34	0.00	1.29	83.41					
	Gelidium reptans	0.00	0.32	0.64	89.18	*Patelloida profunda*	0.19	0.00	1.07	85.71					
	Morula granulata	0.10	0.30	0.45	91.43	*Tetraclita serrata*	0.07	0.22	0.84	87.95					
						Morula granulata	0.18	0.08	1.27	90.03					

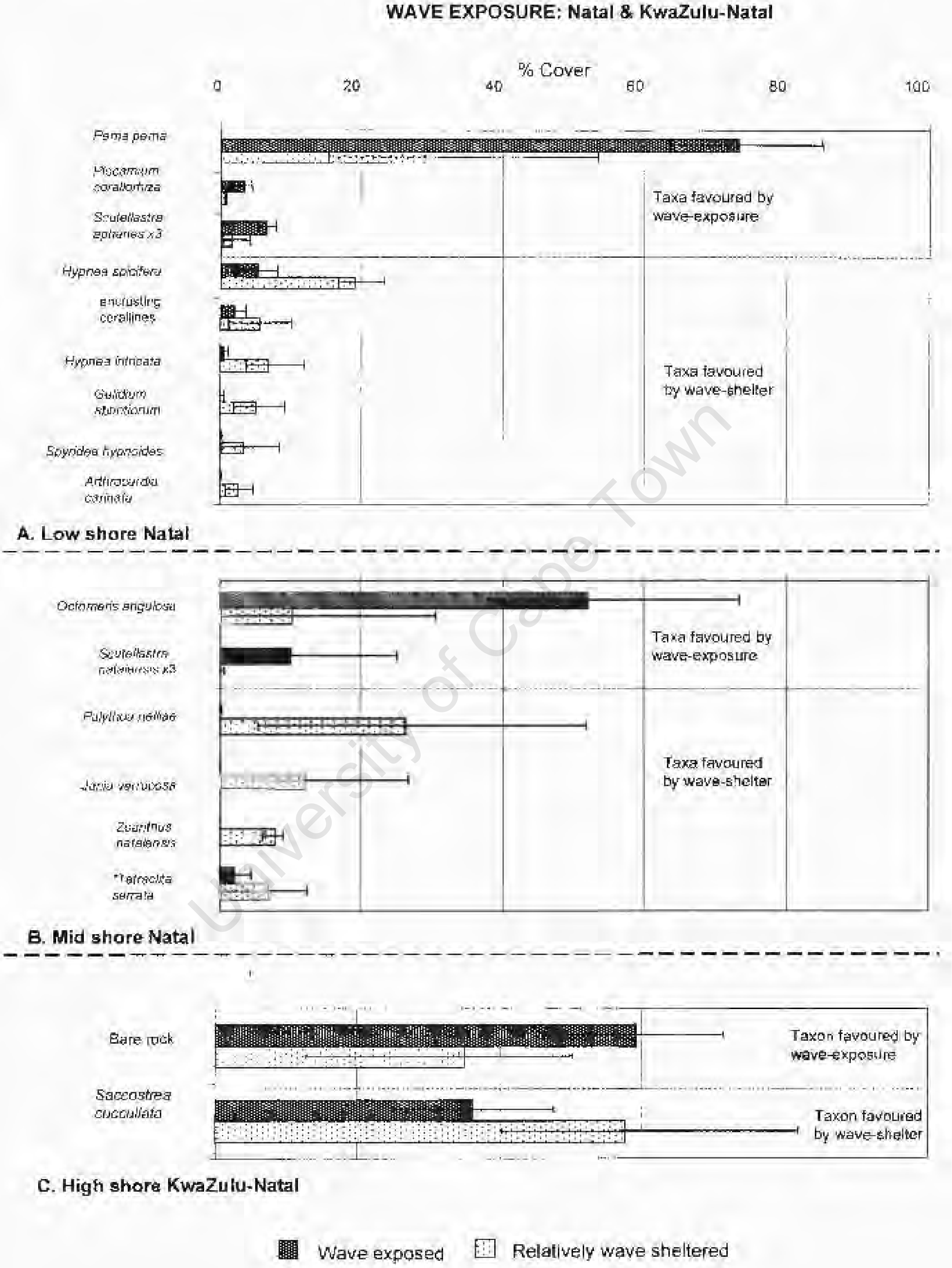


Figure 3.2. Mean cover and range of data for species that were consistently distinguishing between three pairs of rocky shores with significant differences in mean maximum wave forces in the low (A), and (B) mid shore in Natal and (C) in the high shore in KZN. * indicates consistency at only two of the three site-pairs. Data for less abundant taxa have been multiplied (x3).

Maputaland: Mid shore

ANOSIM tests revealed a relatively strong association between wave exposure and mid-shore community structure in comparison with the two sets of exploited sites in Maputaland (R=0.576, Table 3.5). Six taxa showed consistent responses to wave exposure (Table 3.12, Figure 3.3). Encrusting coralline algae, barnacles (*Tetraclita squamosa rufotincta*), bare rock and the sponge, *Hymeniacedon* sp. occupied more space on sheltered shores but mean cover of these taxa between exposures were insubstantial. *Jania adhaerens* and the reefworm *Idanthyrsus pennatus* were more abundant on exposed shores.

Maputaland: Low shore

In Maputaland, ANOSIM tests revealed that wave exposure is a potential key determinant of community structure at both unexploited (R=0.783) and exploited (R=0.826) sites (Table 3.5). SIMPER analyses indicated that there were several species that consistently distinguished sites differing in wave-exposure (Tables 3.13, Figure 3.4). At unexploited sites, *Perna perna* was the most important distinguishing species between exposed and sheltered shores, average percent cover (Av%) being 58.65% and 15.15-28.58% respectively. At exploited sites, *P. perna* was only ranked as the ninth or tenth most important distinguishing species. Unexploited sheltered shores in Maputaland were also characterised by higher percentage cover of *Pyura stolonifera* (Av% =12-25%) which only occupied approximately 5% at unexploited exposed shores. Several species of algae were identified as important distinguishing species on unexploited shores with *Laurencia glomerata* and *Chamaedoris delphinii* consistently more abundant on exposed shores. *Caulerpa racemosa*, *Jania adhaerens*, the zoanthid *Palythoa nelliae* and the barnacle, *Tetraclita squamosa rufotincta* were more prevalent on sheltered shores (Table 3.13A, Figure 3.4).

On exploited shores in Maputaland, *Cheilosporum sagittatum* was the most important of the nine consistently distinguishing species between exposed and sheltered rocky shores (Table 3.13B, Figure 3.4). This species was absent from sheltered sites but relatively common at exploited exposed sites (Av%=27.80, 27.29). *Sargassum crassifolium*, *Chamaedoris delphinii* and *Pyura stolonifera* were more abundant on exposed shores while sheltered shores had higher densities of *Idanthyrsus pennatus*, the sponge *Hymeniacedon* sp., ascidians and *Laurencia* sp.

Table 3.12 WAVE EXPOSURE - Maputaland: Mid shore

Major distinguishing species between paired exposed and sheltered exploited mid shores in Maputaland as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Key distinguishing species are ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at exposed sites are shaded whereas species that were more abundant at sheltered sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

	Wave exposure	**exposed**	**sheltered**				**exposed**	**sheltered**		
	Site pair 1	Black Rock	Bhanga Nek	D=61.45%		Site pair 2	Dog Point	Kosi Mouth	D=81.19%	
	Species	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**		**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
	Dendropoma tholia	0.15	26.53	1.32	14.05	*Idanthyrsus pennatus*	39.50	1.05	1.30	15.78
*	Encrusting corallines	19.90	20.90	1.64	25.80	Bare rock	17.50	28.18	1.72	28.28
*	*Tetraclita squamosa rufotincta*	22.55	28.40	1.26	33.51	*Tetraclita squamosa rufotincta*	3.80	26.08	1.90	40.73
*	Bare rock	12.82	16.85	1.16	40.74	*Hymeniacedon* sp.	10.30	23.05	1.36	53.18
	Laurencia pumila	12.45	0.03	0.45	46.18	*Cladophoropsis sudanensis*	14.70	0.30	0.75	62.26
	Bunodactis sp.	4.20	0.04	1.39	51.58	*Palythoa nelliae*	0.00	13.48	0.72	69.61
*	*Hymeniacedon* sp.	2.66	5.70	1.18	56.96	*Jania adhaerens*	4.40	0.05	0.96	74.50
	Palythoa nelliae	3.78	1.60	0.48	60.12	Encrusting corallines	0.30	2.90	1.48	78.87
	Brown ephemeral alga	0.00	2.35	0.73	63.00	*Dendropoma tholia*	3.60	1.85	1.21	83.03
	Dictyosphaeria versluysii	1.39	0.09	1.19	65.85	*Perna perna*	0.00	1.08	1.59	85.88
*	*Jania adhaerens*	4.20	0.10	0.45	68.68	*Ulva* sp.	0.20	0.85	1.25	88.21
	Ralfsia expansa	0.55	1.65	0.86	71.50	*Padina boryana*	1.90	0.00	0.58	90.47
	Unidentified red alga	1.55	0.00	0.66	73.81					
	Coliaria capensis	0.95	0.67	1.31	76.01					
*	*Idanthyrsus pennatus*	1.00	0.25	0.81	78.20					

Table 3.13 WAVE EXPOSURE -Maputaland: Low shore

Major distinguishing species between paired exposed and sheltered low shores in Maputaland as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Unexploited and exploited sites were analysed separately. For details of notation, see caption of Table 3.5. Species that were more abundant at exposed sites are shaded whereas species that were more abundant at relatively sheltered sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterisk (*).

	A. Wave exposure - unexploited sites	**Exposed**	**Sheltered**		
	Site pair 1	Island Rock	Seawana	D=61.45%	
	Species	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
*	*Perna perna*	58.65	15.16	2.01	11.01
*	*Pyura stolonifera*	5.00	12.25	1.57	17.48
*	*Laurencia glomerata*	8.70	0.90	1.73	23.67
	Encrusting corallines	6.26	15.92	1.41	29.16
*	*Tetraclita squamosa rufotincta*	1.56	8.05	1.35	33.95
*	*Palythoa nelliae*	0.70	9.25	0.64	38.75
*	*Jania adhaerens*	0.00	4.60	1.54	43.45
*	*Caulerpa racemosa*	1.70	6.45	1.27	48.09
	Cheilosporum sagittatum	3.70	4.65	0.88	52.49
	Unidentified green ascidian	0.75	5.15	1.37	56.46
	Ralfsia expansa	4.45	4.25	1.23	59.72
*	*Chamaedoris delphinii*	2.35	1.15	1.27	62.53
	Unidentified black ascidian	0.00	2.05	1.01	65.19
	Scutellastra pica	1.00	1.29	1.54	67.52
	Sargassum elegans	1.53	0.60	0.85	69.76
	Bare rock	0.05	1.40	0.87	71.95
	Dictyosphaeria sp.	0.03	0.95	1.43	74.04

	Exposed	**Sheltered**		
Site pair 2	Island Rock	Cape Vidal Point	D=70.87%	
Species	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
Perna perna	58.65	26.58	1.53	12.27
Pyura stolonifera	5.00	25.00	1.38	21.29
Laurencia glomerata	8.70	0.26	1.91	27.91
Palythoa nelliae	0.20	11.77	1.06	34.13
Encrusting corallines	6.28	1.60	1.43	38.18
Ralfsia expansa	4.45	1.00	1.54	42.00
Tetraclita squamosa rufotincta	1.55	5.12	1.02	45.80
Cheilosporum sagittatum	3.70	1.15	1.13	49.21
Rhodophyllis reptans	0.20	3.00	0.96	52.10
Caulerpa racemosa	1.70	1.95	1.16	54.91
Byssus threads	0.00	4.30	0.52	57.70
Jania adhaerens	0.00	2.15	1.15	60.41
Chamaedoris delphinii	2.35	0.05	0.97	63.06
Sargassum elegans	1.53	1.60	1.16	65.63
Arthrocardia sp.	0.00	2.03	1.06	68.06
Dictyota humifusa	0.10	1.33	1.41	70.36
Chondria armata	1.02	1.16	1.04	72.50

	B. Wave exposure -exploited sites	**Exposed**	**Sheltered**		
	Site pair 1	Black Rock	Bhanga nek	D=73.88%	
	Species	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
*	*Cheilosporum sagittatum*	27.60	0.00	1.81	10.47
*	*Idanthyrsus pennatus*	0.75	24.86	1.37	18.73
	Sargassum elegans	16.45	23.50	1.29	26.92
*	*Sargassum crassifolium*	16.27	2.10	0.93	33.06
	Palythoa nelliae	0.00	15.62	0.70	38.34
*	*Hymeniacedon* sp.	0.20	7.00	1.30	43.06
*	*Laurencia* sp.	6.00	13.25	1.21	47.25
*	*Perna perna*	4.85	0.05	1.37	51.20
	Caulerpa racemosa	5.60	3.63	1.11	55.10
	Unidentified sandy ascidian	1.30	5.90	0.80	58.41
*	Unidentified green ascidian	0.95	4.60	0.84	61.35
*	*Chamaedoris delphinii*	2.60	0.23	1.28	64.22
	Encrusting corallines	2.40	0.15	1.35	66.94
	Valonia macrophysa	2.55	0.00	1.12	69.66
*	*Pyura stolonifera*	2.28	0.30	1.37	72.28

	Exposed	**Sheltered**		
Site pair 2	Dog Point	Kosi Mouth	D=78.45%	
Species	**Av. %**	**Av. %**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
Cheilosporum sagittatum	27.29	0.00	2.06	10.19
Idanthyrsus pennatus	0.20	22.70	2.04	19.36
Caulerpa racemosa	3.60	22.15	1.76	26.63
Sargassum elegans	28.70	13.77	1.30	33.43
Unidentified green ascidian	0.80	9.70	1.69	38.48
Encrusting corallines	3.25	9.75	1.11	42.88
Chamaedoris delphinii	4.75	0.05	1.95	47.05
Sargassum crassifolium	8.16	0.80	0.89	50.76
Laurencia glomerata	4.66	0.80	1.44	54.10
Perna perna	4.60	0.60	1.69	57.43
Arthrocardia sp.	0.00	3.05	1.47	60.49
Laurencia sp.	0.20	2.65	1.25	63.30
Hymeniacedon sp.	0.30	1.90	1.55	65.63
Pyura stolonifera	2.05	0.90	1.30	67.70
Champia sp.	1.25	2.30	1.21	69.77

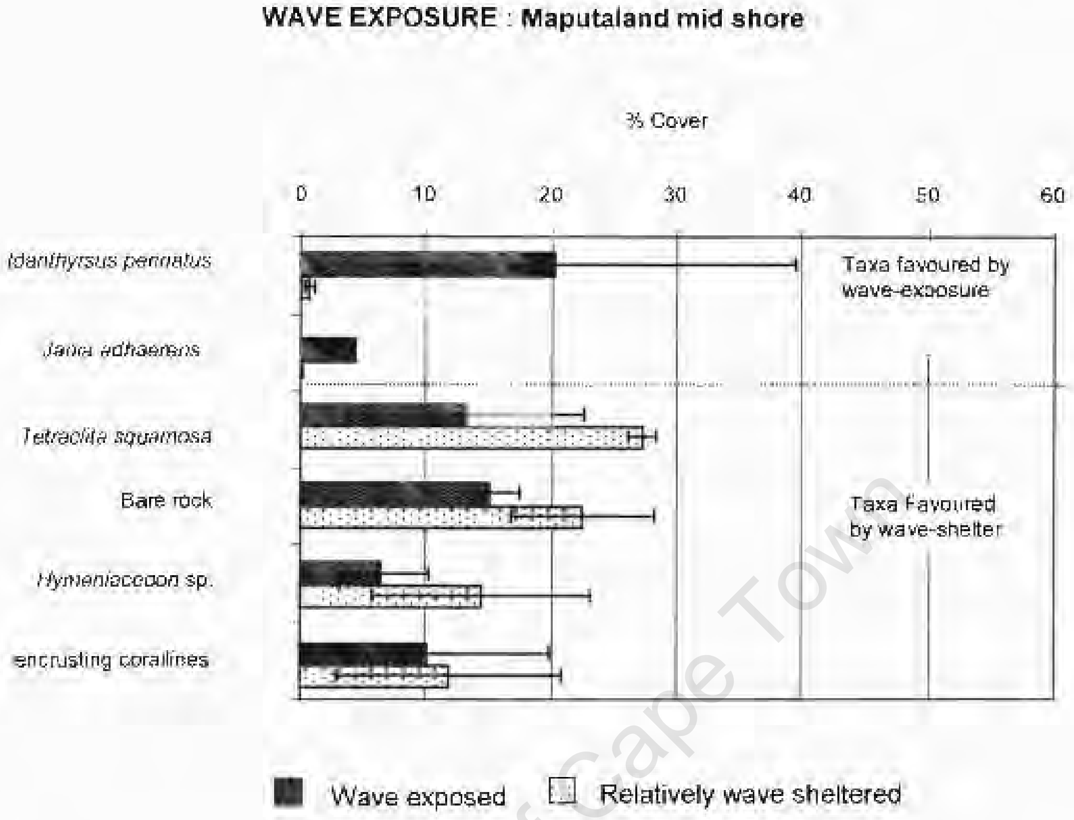


Figure 3.3. Mean cover and range of data for mid-shore species distinguishing between exposed and sheltered shores in Maputaland. Only exploited shores were examined.

2d. Human exploitation

In the Natal region, lack of unexploited sites prevented adequate testing of the effects of exploitation. Comparisons were attempted between heavily exploited and relatively less exploited sites but failed to detect any difference of consequence in community structure ($R_{treatment}$ =0.078). The $R_{locality}$ (R= 0.380) was much larger than the $R_{treatment}$. A strong significant relationship between human exploitation and community structure was apparent in the low shore of Maputaland in the first approach (R= 0.846) and in the second approach this was separately evident within wave exposed (R=0.875) and sheltered sites (R=0.824) (Table 3.5). Conversely, in the Maputaland mid-shore, the effect of exploitation was inconsequentially small (R=0.049) and far exceeded by locality effects (R=0.488).

Species distinguishing between exploited and unexploited shores

Maputaland; Low shore

SIMPER analyses revealed that seven species showed consistent trends between exploited and unexploited shores at wave-exposed sites alone, three did so at relatively wave-sheltered sites alone, and five did so at both sheltered sites (Table 3.14, Figure 3.4). Harvesting reduced mussel cover at all exploited sites. There was more than 50% difference in mean mussel cover between exploited and unexploited exposed sites (Table 3.14.A) and between 15-28% difference at sheltered sites (Table 3.14.B), with mussels nearly absent at harvested sites. Cover of *Pyura stolonifera* was most obviously reduced by harvesting at wave-sheltered sites but also at exposed sites. Mean cover of *P. stolonifera* was reduced from 12-25% to less than 1% at sheltered sites where subsistence collecting occurs.

Non-target species that were reduced by harvesting were *Tetraclita squamosa* (at sheltered sites only), encrusting corallines and the crustose brown alga, *Ralfsia expansa* (at both exposed and sheltered shores). Exploited sites had higher cover of several non-target organisms including foliar algae and the reefworm, *Idanthyrsus pennatus* (Table 3.14, Figure 3.4). Key species distinguishing between exploited and unexploited sites varied with wave exposure in a manner consistent with their relative abundance at different intensities of wave action (Table 3.12). At exposed sites, *Sargassum crassifolium*, *S. elegans* and *Cheilosporum sagittatum* were the three most important distinguishing species of seaweed, with cover increased by more than 8-20% for each species at exploited sites. At sheltered sites, *Caulerpa racemosa* was the species that contributed most to the overall dissimilarity in one site-pair comparison and *S. elegans* at the other. The reefworm, *Idanthyrsus pennatus*, was the second most important distinguishing invertebrate species at sheltered sites. Exploited sites had more than 20% cover of this species, whereas it occupied <1% cover at unexploited localities.

Table 3.14 EXPLOITATION : Maputaland; Low shore

Major distinguishing species between paired exploited and unexploited Maputaland low shores as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Exposed (A) and sheltered (B) shores were examined separately. Species are ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. For details of notation, see caption of Table 3.5. Species that were more abundant at exploited sites are shaded whereas species that were more abundant at unexploited sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

	A. Exploitation - exposed sites	**Exploited**	**Unexploited**				**Exploited**	**Unexploited**		
	Site pair 1	Dog Point	Island Rock	D=65.79%		Site pair 2	Black Rock	Island Rock	D=72.34%	
	Species	**Av. %**	**Av. %**	**Di/SD(Di)**	**$\Sigma D_i\%$**	**Species**	**Av. %**	**Av. %**	**Di/SD(Di)**	**$\Sigma D_i\%$**
*	*Perna perna*	4.50	58.65	3.05	15.22	*Perna perna*	4.85	58.65	2.71	14.39
*	*Sargassum elegans*	28.70	1.53	1.46	26.25	*Cheilosporum sagittatum*	27.80	3.70	1.51	23.53
*	*Cheilosporum sagittatum*	27.29	3.70	1.55	36.17	*Sargassum crassifolium*	16.27	1.10	0.94	30.40
*	*Sargassum crassifolium*	8.18	1.10	0.88	40.91	*Sargassum elegans*	15.45	1.53	1.14	36.98
*	*Ralfsia expansa*	0.55	4.45	1.78	45.17	*Laurencia glomerata*	0.00	8.70	2.09	43.45
*	*Laurencia glomerata*	4.65	8.70	1.32	49.26	*Laurencia* sp.	6.00	0.00	2.39	49.00
*	*Pyura stolonifera*	2.05	5.00	1.30	53.17	*Ralfsia expansa*	0.80	4.45	1.63	52.77
*	*Chamaedoris delphinii*	4.75	2.35	1.32	56.93	*Caulerpa racemosa*	5.50	1.70	0.89	56.43
*	*Caulerpa racemosa*	3.60	1.70	1.01	60.47	*Pyura stolonifera*	2.28	5.00	1.29	60.10
*	Encrusting corallines	3.25	6.28	1.28	63.61	Encrusting corallines	2.40	6.28	1.31	63.53
*	*Tetraclita squamosa rufotincta*	1.80	1.55	1.26	66.26	*Chamaedoris delphinii*	2.60	2.35	1.30	66.45
	Unidentified sandy ascidian	1.45	0.05	1.56	68.90	*Valonia macrophysa*	2.55	0.55	1.14	69.36
						Tetraclita squamosa rufotincta	2.20	1.55	0.72	71.57
	B. Exploitation – sheltered sites	**Exploited**	**Unexploited**				**Exploited**	**Unexploited**		
	Site pair 1	Kosi Mouth	Sodwana	D=69.24%		Site pair 2	Rhanga Nek	Cape Vidal Point	D=70.87%	
	Species	**Av. %**	**Av. %**	**Di/SD(Di)**	**$\Sigma D_i\%$**	**Species**	**Av. %**	**Av. %**	**Di/SD(Di)**	**$\Sigma D_i\%$**
*	*Idanthyrsus pennatus*	22.70	0.75	1.80	8.36	*Perna perna*	0.05	28.58	0.89	8.11
*	*Perna perna*	0.50	15.15	1.93	15.11	*Idanthyrsus pennatus*	24.86	0.30	1.37	15.16
	Encrusting coralline	9.75	16.92	1.63	21.73	*Pyura stolonifera*	0.30	25.00	1.35	24.13
*	*Caulerpa racemosa*	22.15	6.45	1.47	27.57	*Sargassum elegans*	23.50	1.60	0.88	30.87
*	*Sargassum elegans*	13.77	0.60	1.28	33.42	*Palythoa nelliae*	15.82	11.77	1.18	37.40
*	*Pyura stolonifera*	0.90	12.25	1.90	39.19	*Laurencia* sp.	13.25	0.00	1.41	43.52
*	*Tetraclita squamosa rufotincta*	0.00	8.05	1.95	44.70	*Hymeniacidon* sp.	7.00	0.45	1.20	47.56
	Palythoa nelliae	2.03	9.25	0.70	48.89	*Tetraclita squamosa rufotincta*	0.00	5.12	0.91	50.97
*	*Unidentified green ascidian*	9.70	5.15	1.32	52.40	Unidentified sandy ascidian	5.90	0.14	0.66	53.81
	Ralfsia expansa	0.30	4.25	1.26	55.73	Unidentified green ascidian	4.60	0.05	0.80	56.46
	Jania adhaerens	1.45	4.60	1.40	58.91	*Caulerpa racemosa*	3.63	1.98	1.22	59.15
*	*Laurencia* sp.	2.85	0.10	1.27	61.74	*Rhodophyllis reptans*	0.00	3.00	0.94	61.45
	Arthrocardia sp.	3.05	1.06	1.33	64.22	*Byssus threads*	0.00	4.30	0.52	63.71
	Champia sp.	2.30	0.30	1.18	66.59	*Jania verrucosa*	0.00	2.15	1.15	65.89
	Cheilosporum sagittatum	0.00	4.65	0.51	68.87	*Jania adhaerens*	2.22	0.30	1.07	68.07
	Bunodactis sp.	0.20	2.05	1.07	71.00					

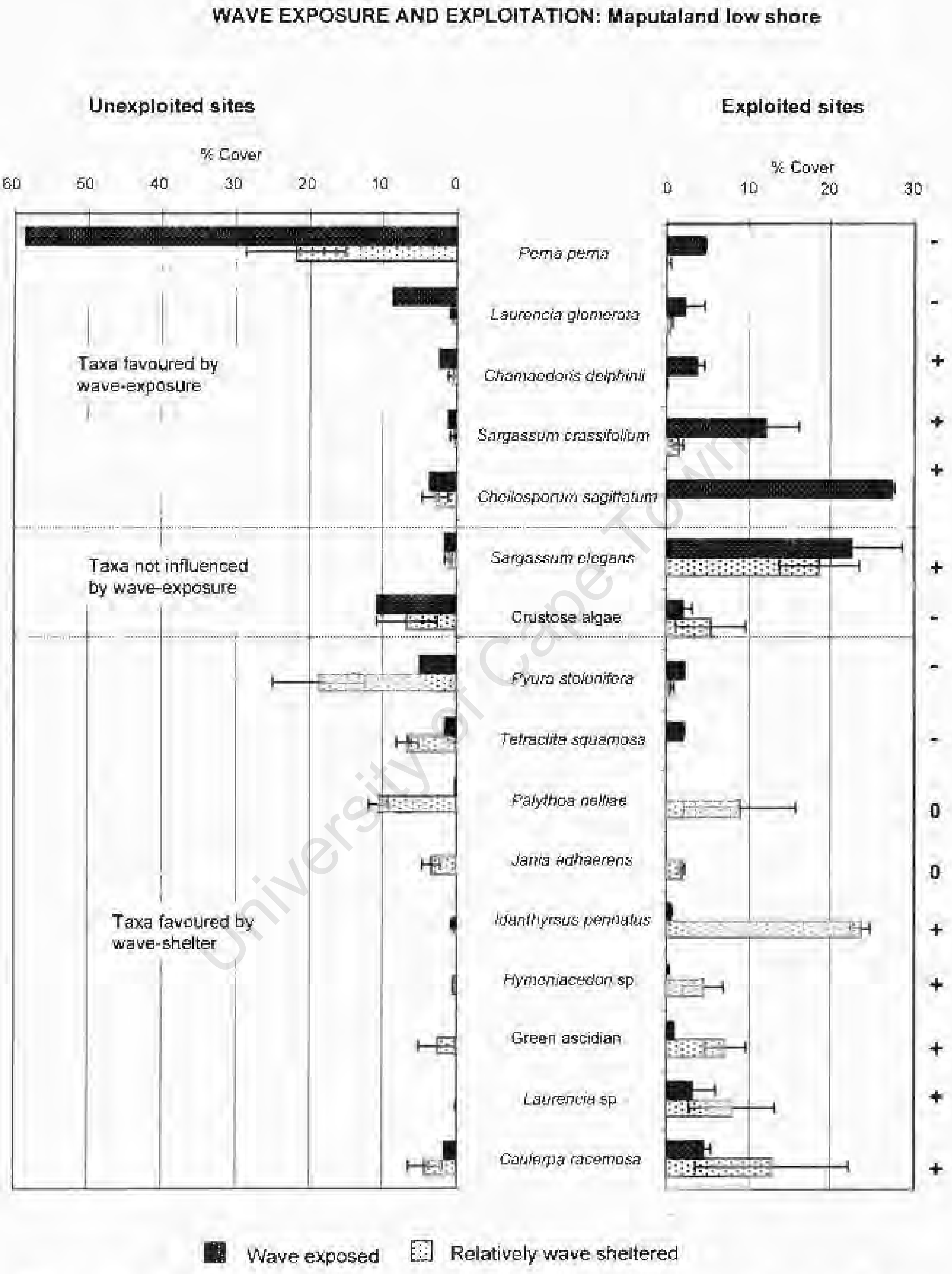


Figure 3.4. Mean cover and range of data for low-shore species distinguishing between exposed and sheltered shores in Maputaland. Exploited and unexploited shores were analysed separately to separate the effect of exposure and harvesting. Species favouring different wave regimes are grouped together.

- indicates species that were impacted negatively by harvesting, + indicates indirect effects where abundance increased at harvested shores and 0 indicates species that did not respond to harvesting.

3. Comparisons between factors

The highest R statistic (R=0.875) was obtained from comparisons between unexploited and exploited wave-exposed low shores in Maputaland (Table 3.3, Figure 3.5) and the effect of exploitation at sheltered sites was also substantial (R=0.824). Strong associations were also evident between wave exposure and low-shore community structure (R=0.826). In Natal, low-shore community structure was most closely related to wave exposure (R=0.481). Comparisons between sanded and less sanded localities yielded slightly less difference in community structure (R=0.465). The differences in low-shore community structure between shores composed of different rock types were less than differences between shores contrasting in all other factors.

In the mid shore, the relationship between community structure and sand inundation (R=0.769) was the strongest of all the factors investigated within this zone. Only in the mid shore, did shores composed of contrasting rock types have corresponding large significant differences in community structure and then only in one of the four comparisons made (dolerite versus Quaternary sandstone, R=0.609). The influence of wave exposure was less than that of rock type for these two contrasting geological substrates.

In the high shore, effects of sand inundation (R=0.544) also exceeded effects of wave exposure (R=0.374, Figure 3.5). The differences in community structure between shores composed of different rock types were less than differences between shores contrasting in sand inundation and wave exposure.

In summary, rock type only had significant effects in one instance (one of a possible ten comparisons), sand inundation had a strong influence in all zones in Natal (but could not be examined in Maputaland), exploitation had demonstrably strong effects in Maputaland in the low shore (but its effects could not be properly tested in Natal), and wave exposure had strong effects in both regions in the low and mid shore but not the high shore (Figure 3.5).

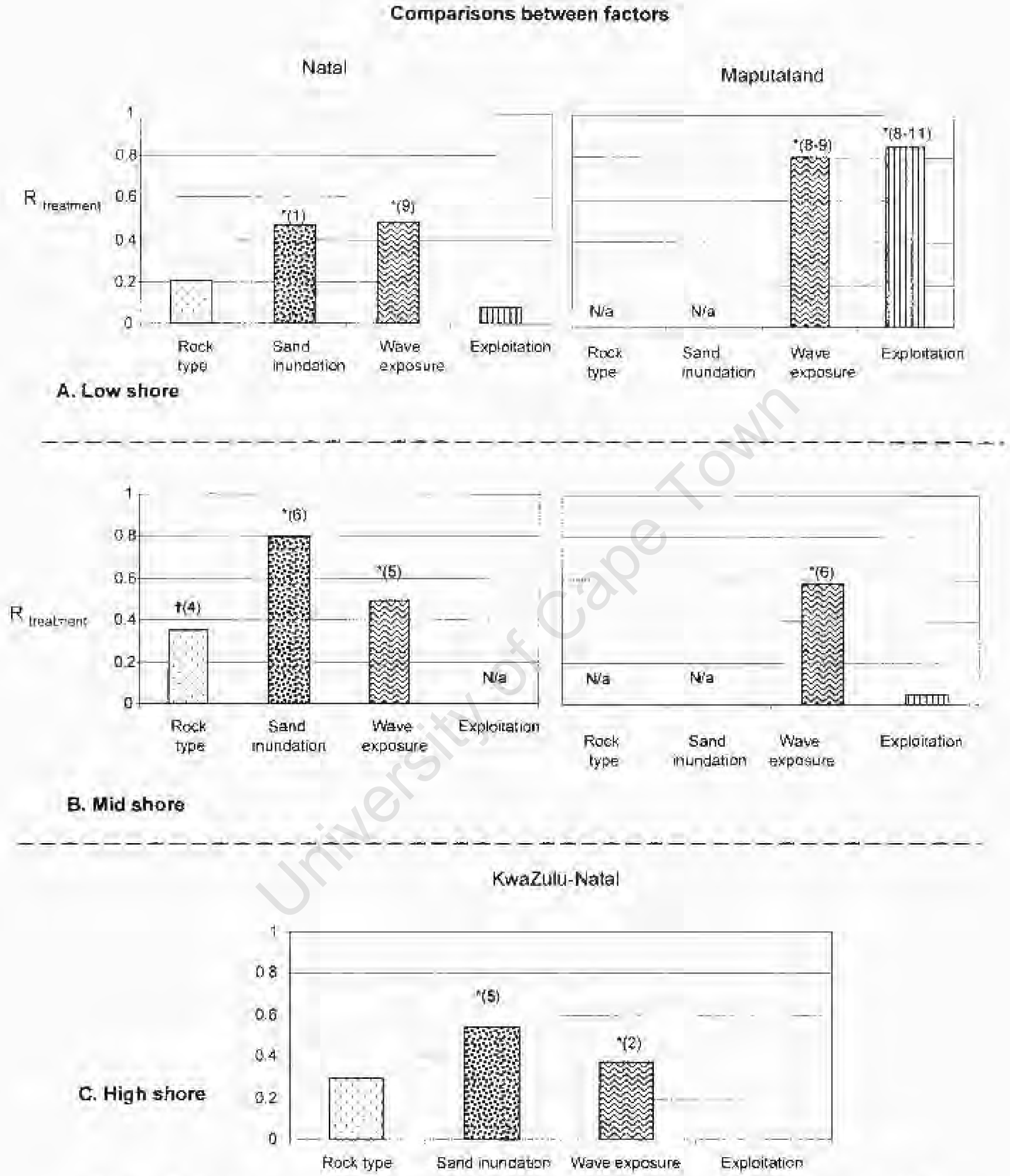


Figure 3.5. Histograms showing the mean R-values from ANOSIM tests that were undertaken to assess the relative importance of factors that potentially shape community structure in the (A) low and (B) mid shore of Maputaland and Natal and in the high shore of KwaZulu-Natal. R-values were based on approach I for rock type but approach II for other factors. † = large, significant R value in one of four comparisons, * = large, significant R-value in all comparisons. The number of species that contributed significantly (>2%) to dissimilarity in a consistent manner between site-pairs with significant $R_{treatment}$ values that were greater than $R_{locality}$ values are shown in parenthesis.

Discussion

In this chapter, the potential roles of rock type, sand inundation, wave exposure and human exploitation in structuring intertidal communities on rocky shores in KwaZulu-Natal were examined at a scale that involved comparing sites within biogeographic regions. Rock type failed to emerge as a major determinant of community structure but ANOSIM analyses (Table 3.5) did indicate significant associations between intertidal community structure and sand inundation, wave exposure and human exploitation. As treatments were not randomly allocated to experimental units, these studies are not true experiments but rather observational studies that serve as exploratory tools to identify agents that potentially determine community structure (Clarke 1993). The strict conclusion that any of these factors are causal in shaping intertidal assemblages is not valid. Any measured environmental variable identified as a potential determinant of community structure may stand only as a proxy for another unrecorded variable (Warrick and Clarke 1994). SIMPER analyses indicated species that showed consistent trends between site-pairs that contrasted extremes of each variable. These analyses supported the conclusions drawn from ANOSIM tests, with the numbers of indicator species being greatest between sites with high levels of dissimilarity and large R-values.

Background heterogeneity in community structure

The crossed ANOSIM tests compared community structure between localities both within and between the factors considered as potential determinants. These tests are independent, averaging the R-statistic for each site pair and for replicate sites within each treatment respectively. Species that show inconsistent responses between site pairs within treatments will contribute to the averaged $R_{treatment}$ statistic for effects between treatments. This has two important implications for analyses. Firstly, it is important to try to standardise all other factors when investigating the potential effect of any variable. Otherwise, differences due to other factors may result in a high R-statistic although the factor under consideration may not be related to the observed biological variability. The other implication is that site pairs should be analysed separately when employing SIMPER to identify key species distinguishing between control and treatment localities. If species show consistent responses between different site pairs, this lends support to the notions that the variable under investigation is in fact playing a role in structuring the communities, and that the distinguishing species are responding either positively or negatively to the variable.

In my study, there were significant locality effects identified for every analysis, reflecting high variability in community structure between sites. The null hypothesis that there are no site-to-site differences within a specific treatment was rejected in all cases. It is likely that many factors contribute to this heterogeneity. Within-zone variation patterns on Californian shores were in almost every case due to several factors, often interacting in complex ways (reviewed by Foster et al. 1998). Rocky shores on the Transkei coast also showed extensive variability between sites (Lasiak and Field 1995, Lasiak 1999). A crossed design allows detection of effects in a landscape that exhibits such extreme variability. A nested design would have been a valid alternative but such designs generally detect highly significant differences between sites (see Lasiak and Field 1990) and therefore require that many more sites are sampled to achieve the replication needed to obtain significant results. High between-site heterogeneity has the consequence that almost any two sites will show significant differences in community structure between sites, especially with many replicate samples (Clarke 1993). For this reason, it is essential to conduct SIMPER analyses between separate site-pairs and examine trends in species abundance independently in order to present convincing evidence of a potential association between any factor and the composition and abundance of species in a community.

I recorded several cases where the locality effect exceeded the treatment effect, indicating greater differences in community structure between sites within treatments than differences between treatments. Under these circumstances, it is likely that some other over-riding factor is the real cause of differences between sites. Factors with large $R_{treatment}$ and lower $R_{locality}$ values are strong candidates as key determinants of community structure.

Several other physical factors may account for observed variability within treatments in this study. Although vertical gradients in temperature and desiccation were taken into account by considering different zones on the shore separately, variability in elevation within zones is likely to explain some of the observed variability in community structure (Bustamante et al. 1997). Other differences may be related to topographical variability and differences in slope and aspect between sites (Menge et al. 1985, Fuji and Nomura 1991, Archambault and Borget 1996, Leichter and Witman 1997, Blanchard and Borget 1999). I did not consider slope and aspect in this analysis but I do specifically address them at a smaller scale when comparing biotopes in Chapter 5. Differences in the configuration of shorelines have also been linked to variability in benthic communities (Archambault and Borget 1999). Another factor that was not investigated in this study was potential differences in productivity between sites. Recent evidence suggests that productivity may vary at smaller scales than previously assumed (Menge et al. 1997a, Menge 2000c). Between-site differences in productivity may explain some of the observed differences between sites, both within and between factors in my study. This could be related to riverine influences or oceanographic differences between sites in KwaZulu-Natal.

Biological phenomena may also underlie some of the observed variability in community structure. Even where physical conditions are uniform, divergent communities have been attributed to differences in biological interactions between sites (Branch et al. 1987, Barkai and McQuaid 1988). Significant differences in recruitment of mussels between localities have been reported in Natal (Harris et al. 1988). This may influence community structure especially considering that recruitment is relatively low in KwaZulu-Natal. Evidence suggests that where recruitment is low, its importance in influencing community structure is amplified (Menge 1991).

Differences between two approaches in "experimental" design

Two approaches were employed to test for biological differences between contrasting sites. In the first approach, sites subject to the extremes of a given factor were compared. In the second (and more rigorous) approach, factors other than the one under consideration were standardised as much as possible. Different results were obtained by the two approaches, which is to be expected because greater biological differences are to be anticipated in the first approach. In every case, $R_{locality}$ was higher using the first approach than when using the second, indicating more variability between sites within regions. This suggests that some of the biological differences between treatments observed in the first approach may be attributable to other factors. Relative to the first approach, the second approach yielded smaller differences between control and treatment localities, due to the reduced range of the physical variables under investigation. For example, when investigating effects of sand inundation in the low shore in Natal, Approach 1 yielded a greater $R_{treatment}$ value (R=0.800) than Approach 2 (R=0.465). As some of the most sanded sites were also wave sheltered, the effect of sand was confounded with effects of wave exposure in Approach 1, leading to a strong combined effect. Higher R-values in the first approach are therefore partly attributable to other factors.

Identifying Key Determinants of Community Structure and Species distinguishing between treatments

Rock type

Rock type did not generally exert any influence on community structure in this study. In six of the ten tests, $R_{locality}$ was greater than $R_{treatment}$, indicating that the effect of rock type was overridden by other factors (Table 3.3). Of the remaining four, the $R_{treatment}$ values were relatively low in three cases with only one test resulting in a strongly significant rejection of the null hypothesis that there are no differences in community structure between rock types. This is in accordance with the findings of McQuaid and Branch (1984, 1985) who noted that the effect of substratum on the composition of rocky intertidal communities in the Cape of Good Hope were masked by the overriding influence of temperature and wave exposure. Substratum instability, however, was shown to effect species richness and evenness (McQuaid and Branch 1984, 1985). No effect of substratum was found on intertidal seaweed community composition when comparing Quaternary sandstone and Table mountain sandstone shores in the Cape (Bolton and Anderson 1990). Jackson (1976) found only minor incidental differences between communities on two adjacent shores of Ordovician sandstone and dolerite at a single location (Port Edward) in KwaZulu-Natal.

A strong substratum effect was only evident between two rock types, dolerite versus Quaternary sandstone in the mid shore of Natal. Dolerite shores had more bare rock and higher cover of barnacles and mussels whereas Quaternary sandstone shores had consistently higher cover of the red algal turf *Gelidium reptans* (Table 3.4). A weak relationship between community structure and these two rock types was also evident in the high shore but not in the low shore. Two of the dolerite shores were subject to significantly higher wave forces than their sandstone counterparts and this may account for some of the observed variability between sites. However, dolerite is a harder, smoother and darker rock than Quaternary sandstone (Table 3.1). Rock colour is significant as it influences absorption of solar radiation and therefore rock temperature which has been shown to affect settlement and recruitment of certain organisms (Raimondi 1988). Some species have been observed to attach more securely or desiccate less on harder rock than on softer substrata and variability in surface texture has implications for colonisers (Barry 1988, Lohse 1993, Raimondi 1988). Holmes et al. (1997) identified significant differences in settlement preferences for barnacles (*Balanus balanoides*) between contrasting rock types, independent of any potential effect of surface rugosity or colour cues. In South Africa, some evidence of differences in species richness and abundance of seaweed communities between smooth dolerite shores and less smooth sandstone and granite shores at False Bay has been reported (Wells et al. 1989). These differences were attributed to variability in surface relief between rock types.

Although substratum did not show strong associations with community attributes, the significant biological differences between dolerite and Quaternary sandstone shores cannot be ignored. It is likely that variability in substrate does explain some of the observed biological heterogeneity and contributes to the significant between-site differences within treatments. Different rock types differ in topography and topographic variability may result in increasing habitat complexity with features such as gullies, overhangs, caves and rockpools that may be colonised by different suites of organisms than will occur on more uniform stretches of rock. Increased heterogeneity has been correlated with increased diversity (Menge et al. 1991, Raimondi 1988, Schoch and Dethier 1996).

Sand Inundation

In Natal, sand inundation did not emerge as an overriding determinant of community structure in the low shore. However, differences in wave exposure may have obscured variability in community structure associated with differences in sand inundation. Lewis (1968) cited intolerance to siltation at sheltered sites as one mechanism that may explain patterns of spatial variation caused by differences in wave exposure. The strong association between low-shore community structure and reduced wave action combined with sand inundation may reflect this phenomenon (Table 3.5, Approach 1) as hydrodynamic conditions exert a strong influence on sediment transport and deposition (Airoldi and Virgilio 1998).

The strongest relationships between sanding and community structure were apparent in the mid and high shore of Natal (Table 3.5, Figure 3.5). These zones had high R-values and large numbers of species consistently distinguishing between heavily and lightly sanded shores compared to the low shore (Figure 3.5). Sand inundation was linked to higher cover of turf-forming algae, previously identified as a characteristic of stressful habitats (Hay 1981, Steneck and Dethier 1994, Cheroske 2000). *Laurencia natalensis* was consistently more abundant on the low and mid shore of sand-inundated sites (Figure 3.1). This species is common on sand-covered rocks in the Natal intertidal (Branch et al. 1994). The coralline turf, *Jania verrucosa*, was consistently the most important species distinguishing between sanded and unsanded mid-shores. Jackson (1976) noted that the distribution of this species was patchy and could not explain its dominance in certain areas. In the high shore, ephemeral and sand-tolerant species of algae were more abundant on sanded shores. This mirrors findings on Californian shores subject to disturbance by sand, where algae that are tolerant of sand inundation and scour, and ephemeral species that invade in the absence of sand, have been reported as characteristic (Daly and Mathieson 1977, Taylor and Littler 1982, D'Antonio 1986, Kendrick 1991). Sand has been shown to influence algal biomass through abrasion, burial and by reducing light (Rogers 1990, Kendrick 1991, Trowbridge 1996).

The reason algal turfs monopolise space on sanded shores has been attributed to their ability to accumulate sediment (Sousa et al. 1981, Seapy and Littler 1982, Stewart 1989). Sediment is proposed to interfere with recruitment of algal species that do not form turfs and some invertebrate species, thus favouring spatial dominance by turf (Sousa et al. 1981, D'Antonio 1986, Iwasaki 1994).

Increased turf on sanded shores could also be mediated by the exclusion of grazers. Sand is predicted to inhibit grazers (Sousa et al. 1981, D'Antonio 1986), although the physiological mechanisms and life history strategies of some species allow a high degree of sand tolerance (Markham 1973, Stewart 1983, D'Antonio 1986, Marshall and McQuaid 1989, 1993). Members of the Patellidae have been shown to be intolerant of sand inundation (Marshall and McQuaid 1989, 1993) and results from my study also suggest this. The patellid limpet, *Scutellastra natalensis* featured consistently as a major distinguishing species between sand-inundated and unsanded mid-shores, being absent from the mid shore of heavily sand-inundated sites. *Scutellastra granularis*, a close relative of *S. natalensis*, is unable to respire anaerobically under conditions of low oxygen tension and this may explain the absence of *S. natalensis* from sand-inundated areas (Marshall and McQuaid 1989). In the high shore of sanded sites, the sand-tolerant pulmonate limpets of the genus *Siphonaria* were characteristic. *S. capensis* has an ability to withstand smothering linked to its ability to tolerate hypoxia (Marshall and McQuaid 1989). *Siphonaria* spp. have finely toothed radulae and are unable to control the growth of foliose upright algae (Creese and Underwood 1982). They may benefit from the low-growing delicate ephemeral algae associated with sand inundation.

On the south coast of South Africa, trophic structure has been shown to be similar on heavily sand-inundated and non-inundated shores. Sand was, however, linked to a decreased biomass of filter feeders and autotrophs and increased abundance of deposit feeders (Dower 1989). My study supports the finding that sand reduces filter-feeder abundance in the mid shore and to some extent in the high shore. There was no indication of reduced cover of filter feeders in the low shore, with mussels sometimes more abundant at sand-inundated sites. Sand inundation reduced the cover of *Octomeris* and *Tetraclita* spp. in the mid shore and of the oyster, *Saccostrea cuccullata*, in the high shore (Figure 3.1). However, the barnacle *Chthalamus dentatus* was consistently more abundant in the high shore at sanded sites. This conforms with studies on the south coast (Dower 1989) where higher densities of this species were recorded on sand-inundated sandstone shores.

In summary, the influence of sand inundation on community structure was greater in the mid and high shore. Relatively unsanded shores were dominated by barnacles in the mid shore and oysters in the high shore. Patellid limpets were absent on heavily sand-inundated shores that were favoured by *Siphonaria* spp. in the high shore. Turf-forming algae, particularly *Jania verrucosa*, dominated heavily sanded mid-shore communities and ephemeral algae were dominant in the high shore of such sites.

Wave exposure

Wave exposure and hydrodynamic flow have been shown to affect various aspects of the life history of marine organisms, from rates of fertilisation (Pennington 1985, Levitan 1981, Denny and Shibata 1989), settlement (Eckman et al. 1990, Bertness et al. 1992), growth (Palumbi 1984, Brown and Quinn 1988, Koehl and Alberte 1988, Leichter and Witman 1997), productivity (Leigh et al. 1987), prey size selection (Richardson and Brown 1990) and mortality (Denny et al. 1985, Witman and Suchanek 1984, Carrington 1990). Variation in wave exposure has also been linked to variation in the relative importance of competition and predation through mediation of biological interactions (Dayton 1971, Connell 1975, Menge and Sutherland 1976, Denny 1988, Menge and Olson 1990).

My results do not distinguish between these mechanisms, but they do demonstrate differences in community structure between exposed versus sheltered shores (Table 3.5). Despite the fact that wave exposure has long been recognised as an important factor structuring intertidal communities, this relationship has not previously been investigated in KwaZulu-Natal because differences in exposure were not expected along this relatively straight exposed coastline. Many of the shores subject to significant differences in mean maximum wave exposure did not discernibly differ in wave climate when rated subjectively. This highlights the importance of quantitative measurements of wave exposure when explaining or predicting ecological patterns and processes (Jones and Demetropoulos 1968, Bell and Denny 1994, Denny 1995).

Zonation

The importance of wave exposure showed strong zonational effects, declining from the low to the high shore (Figure 3.5). This was indicated by declining R-values and decreasing numbers of species consistently distinguishing between exposures at higher shore elevations (Table 3.5, Figures 3.2, 3.3 and 3.4). The declining influence of wave forces from low to mid shore is predicted to be related to reduced wave forces in the mid shore (see results section of Chapter 5). Wave forces were not directly measured in the mid or high shore in this study but low shore measurements were presumed to reflect relative exposure in other zones. Bustamante et al. (1997) examined the relationship between shore elevation and wave exposure and found that wave forces were high in the low shore, peaked in the low to mid shore, and declined higher on the shore. Communities in the high shore are constrained by more uniform stresses, particularly high temperatures (Bustamante et al. 1997).

Distinguishing species

In my study, the most consistent species distinguishing between exposed and relatively sheltered low-shore communities in Natal and at unexploited Maputaland sites was the brown mussel, *Perna perna* (Tables 3.9 and 3.13, Figures 3.2 and 3.4). In Natal, the patellid limpet *Scutellastra aphanes*, often found on mussels, was also characteristic of exposed sites. Higher mussel cover was always observed at more exposed shores but particularly at less exploited sites. Island Rock, the only unexploited exposed shore in Maputaland, had a mean mussel cover of more than 50% (Table 3.13). Even though this was lower than the cover observed on the most exposed Natal shores, the existence of a mussel bed at Island Rock conflicts with reports that mussel beds are naturally absent in Maputaland, even at unexploited sites (Fielding et al. 1991). Tomalin and Kyle (1998) also reported high numbers of mussels at sites that I classified as wave-exposed.

Exploited shores in Maputaland also showed divergence of community structure between exposed and sheltered shores (Table 3.13B). However, algae and other unexploited species were more important distinguishing species than *P. perna*, which occupied less than five percent cover even on exposed shores. The coralline alga *Cheilosporum sagittatum* was the most important characteristic species of exploited exposed shores in Maputaland. Other algae that were characteristic of wave-exposed shores included *Laurencia glomerata* and *Chamaedoris delphinii* in Maputaland and, *Plocamium corallorhiza* in Natal.

Relatively sheltered shores in both regions of KwaZulu-Natal were characterised by higher cover of algae in the low shore. Characteristic species included *Caulerpa racemosa* and *Laurencia* sp. in Maputaland and *Hypnea* spp., *Spyridea hypnoides*, *Gelidium abbotiorum* and *Arthrocardia carinata* in Natal (Tables 3.9 and 3.13, Figures 3.2 and 3.4). This conforms with reports by Bustamante and Branch (1996) that *Gelidium* sp. and articulate corallines dominate the low shore of sheltered sites on the south and east coast. These authors cited *Hypnea spicifera* as characteristic of exposed shores on the south coast but this species was consistently the most characteristic alga at sheltered shores in my study.

In Maputaland low shores, the ascidian *Pyura stolonifera*, was more abundant on sheltered than exposed shores. This was only evident at unexploited sites, with densities being much lower and showing the opposite pattern at exploited sites. The higher densities of *P. stolonifera* on sheltered shores that are not harvested contradicts the results of Bustamante et al. (1997) who identified this species as characteristic of exposed shores. However, there are no extremely sheltered shores in KwaZulu-Natal. Bustamante et al. (1997) recorded wave forces of 1.1 and 1.5 x 10^{3} N.m^{-2} at sheltered shores on the south and west coast respectively. Semi-exposed shores on the west coast had wave forces of 7 x 10^{3} N.m^{-2} and on exposed shores on the south coast mean wave forces of 10 x 10^{3} N. m^{-2} were recorded. The two unexploited "sheltered" sites in Maputaland are probably semi-exposed by global standards, as mean wave forces were between 6.4-7.7 x 10^{3} N.m^{-2}, whereas exposed shores in Maputaland experienced forces in excess of 15 x 10^{3} N.m^{-2}. The approximately five-fold greater wave forces at "sheltered" sites in KwaZulu-Natal compared with the south coast, may explain why *Hypnea spicifera* and *P. stolonifera* were characteristic of "relatively sheltered" sites in my study but of "exposed" sites in Bustamante's studies (Bustamante and Branch 1996, Bustamante et al. 1997).

In the mid shore, the barnacle *Tetraclita squamosa rufotincta* was more abundant at relatively sheltered shores in Maputaland while in Natal, a different species of barnacle, *Octomeris angulosa*, was more abundant on exposed shores (Tables 3.10 and 3.13, Figures 3.2 and 3.3). *O. angulosa* was the most important mid-shore species distinguishing between exposures in Natal. This species was previously identified as an indicator species for exposed conditions in South Africa (Field and McFarlane 1968, Jackson 1976, McQuaid and Branch 1984). In my study, the limpet *Scutellastra natalensis* was also more abundant in the mid shore at exposed sites in Natal. In Maputaland, *Jania adhaerens* was consistently characteristic of exposed mid-shores. The sessile polychaete *Idanthyrsus pennatus* was consistently more abundant at sheltered sites that were harvested (Table 3.13).

Sheltered mid-shores had consistently higher cover of zoanthids in Natal but this pattern was not evident in the Maputaland mid shore. In tropical Brazil, zoanthids were characteristic of rocky shores that are never exposed to strong wave action (Sauer Machado et al. 1992). The within-site distribution of zoanthid-dominated communities in relation to wave exposure is investigated in Chapter 5.

Trophic structure

Wave exposure is predicted to exert a strong influence on trophic structure of intertidal communities (McQuaid and Branch 1985, Menge and Olson 1990, Emanuel et al. 1992, Bustamante and Branch 1996, Bustamante et al. 1997). I expected primary producers to have higher cover at sheltered sites because earlier work has shown this pattern (McQuaid and Branch 1985, Bustamante and Branch 1996a, Bustamante et al. 1997). In my study, several species of algae conformed to this pattern, with few algae preferring exposed sites. Zoanthids have zooxanthellae and can be considered as primary producers although they are also micro-carnivores. In Natal, zoanthids had consistently higher cover at sheltered sites thereby also conforming to the predicted pattern.

Menge and Olson (1990) predicted that all consumers would be more abundant on sheltered (i.e., less stressful) shores. However, while primary consumers conformed to this pattern, Bustamante and Branch (1996a) found that omnivores and carnivores were consistently more abundant on exposed shores. In my study, no omnivorous or predatory species emerged as important species distinguishing between exposures.

Grazers were predicted to be more abundant at sheltered shores (Menge and Olson 1990, Bustamante et al. 1997). In my study, there was no evidence in support of this prediction. In fact, the opposite pattern was observed in the low and mid shore in Natal (Tables 3.9 and 3.10, Figure 3.2). The limpets *Scutellastra aphanes* and *S. natalensis* were more abundant on exposed shores and no mobile consumers were identified as being consistently characteristic of relatively sheltered shores anywhere in KwaZulu-Natal. However, Rabbit Rock in Maputaland was historically host to high densities of limpets, particularly *Scutellastra pica* (Kyle et al. 1997a) and the lowest wave forces in KwaZulu-Natal were recorded at this site (Figure 2.12, p 54). Harvesting may have masked the effects of wave shelter at the most sheltered sites in Maputaland.

In my study, the overall pattern of filter-feeder abundance conforms with the predictions of McQuaid and Branch (1985), Bustamante and Branch (1996a) and Bustamante et al (1997). These authors showed that the biomass of filter feeders was significantly higher on exposed shores on the west and south coast of South Africa. Filter feeders, especially *Perna perna* and *Octomeris angulosa*, dominated exposed shores and, taken as a whole, were much more abundant than on sheltered shores. There were, however, several individual filter-feeding species that did not conform to the predicted pattern. In Maputaland, the barnacle *Tetraclita squamosa* and the ascidian *Pyura stolonifera* were more abundant at sheltered than exposed sites. The sponge *Hymeniacedon* sp., and an unidentified colonial green ascidian were also more abundant at less exposed sites in Maputaland, but most obviously at exploited localities (Tables 3.12, 3.13). In the high shore, the filter-feeding oyster, *Saccostrea cuccullata*, had higher cover at less exposed sites in all three site-pairs examined (Table 3.11).

The higher cover of *Tetraclita squamosa* at sheltered shores is accounted for by the fact that it needs relatively calm water to feed actively (Jackson 1976). *Tetraclita* also attaches less strongly to the substrate that *Octomeris angulosa* (Boland 1997). The reason for the higher cover of the other filter feeders at sheltered sites is unknown. I hypothesise that *Pyura* is more common at sheltered sites because of reduced competition from *Perna perna*. Similarly, at exploited sheltered sites where both *Pyura* and *Perna* have been removed by harvesting, *Hymeniacedon* sp. may achieve higher cover due to competitive release. Leichter and Witman (1997) showed that active suspension feeders (e.g., *Mytilus edulis*) grew faster than facultatively-feeding invertebrates (e.g., the sponge *Halichondria panicea*) at high-flow positions on subtidal rock walls. However, passive filter feeders often dominated high-flow sites and it was concluded that competition for space forced active suspension feeders to inhabit areas where food supply and growth rates were not maximal.

Three mechanisms have been identified as possible explanations for higher cover of filter feeders at wave exposed shores. The first relates to recruitment, with higher recruitment due to more efficient delivery of larvae predicted at exposed shores (Lenihan 1999). Leonard et al. (1998) recorded higher recruitment of mussels, barnacles and mobile species at higher flow rates in a Maine (USA) estuary. Petraitis (1991), however, found no differences in mussel recruitment between exposed and sheltered rocky shores in the same state. On the west coast of South Africa, mussel recruitment increases with increasing wave exposure, but declines at sites subject to very high wave forces (G. Branch, University of Cape Town, pers. comm.). Comparisons of mussel and *Pyura* recruitment between exposures in KwaZulu-Natal would establish the role of recruitment in structuring communities between exposures.

The second potential explanation for higher filter feeder abundance at sites with high wave exposure is that activities of herbivores and predators are constrained by strong wave forces thereby reducing consumption of algae and predation on filter feeders (Menge and Olson 1990). The results of my study offered no support for this model. In KwaZulu-Natal, there were more mobile consumers (e.g., *Scutellastra aphanes* and *S. natalensis*) at sites with higher wave forces than on sheltered shores where mobile consumers were less abundant. Predatory whelks did not feature as important species distinguishing between exposures. Fish diversity is high in KwaZulu-Natal and fish densities were not examined between exposures. Bolton and Anderson (1997) have predicted that fish are likely to have important effect in structuring intertidal and subtidal communities.

Wave-sheltered shores in KwaZulu-Natal may not conform to the predictions of Menge and Olson (1990) for two reasons. As previously mentioned, these shores can hardly be considered "sheltered" by global standards. Furthermore, wave-sheltered shores in KwaZulu-Natal may experience high physical stress from other factors. In Natal, mean wave forces ranged between 4.81 and 16.53 x 10^3 $N.m^{-2}$ with most shores subject to wave forces averaging between 8 and 12 x 10^3 $N.m^{-2}$. Only two shores, Zinkwazi Platform and Peace Cottage, had mean wave forces below 5.5 x 10^3 $N.m^{-2}$. Both of these sites were subject to extensive sand inundation. This would probably exclude benthic predators and also patellid limpets (Marshall and McQuaid 1989), the principal grazers in the low and mid shore of sheltered shores. This may account for the absence of biological control by herbivores under conditions of relatively low wave-stress in Natal.

The fact that sheltered shores in KwaZulu-Natal were dominated by macroalgae, suggests that grazers are incapable of controlling the abundance of primary producers. Experimental studies in tropical Brazil found that the roles of consumers as structuring agents in sheltered intertidal communities, were inconsistent and limited (Sauer Machado et al. 1996). In moderately exposed tropical rocky shores in Hong Kong, herbivore exclusion in the mid shore caused little alteration in community structure and physical factors were the most important structuring agents (Williams 1994). In the low shore, physical factors were also dominant but herbivory did influence community structure. These results indicate that consumers are not important structuring agents on all tropical shores.

The third possible factor underlying greater filter feeders abundance with higher wave energy is the enhanced quantity and turnover of food particles for filter feeders (Fréchette et al. 1989). Wave-beaten shores in the north-eastern Pacific receive more energy from wave action than from solar sources (Leigh et al. 1987). Detailed studies on the dominant mussel on the west coast, *Mytilus galloprovincialis*, have shown that wave action vitally increases both the concentration and turnover of particulate food (Bustamante and Branch 1996). In conditions of relative shelter, supplies of food are inadequate to sustain the stocks supported on wave-exposed shores. Energy pathways within the KwaZulu-Natal marine ecosystem are not well studied. However, evidence suggests that primary production by phytoplankton is not as important in supporting filter feeders as heterotrophic activity associated with the breakdown products of allochthonous seaweed and terrestrial plant matter washed into the sea by rivers (Schleyer 1981). The detrital pathway is predicted to play an important role in intertidal and subtidal ecosystems, especially in supporting filter feeders such as *P. perna* (Schleyer 1981, Berry 1982). It is proposed that the exceedingly turbulent surf zone and continual wave action constitute a multiplier effect breaking down material and supplying filter feeders. Evidence from other studies supports the idea that mussels predominate on exposed shores because of enhanced food supply. *P. perna*, along with three other South African species of mussels, grows more rapidly under conditions of high water circulation compared to restricted water circulation (van Erkom Schurink and Griffiths 1993). Depletion of phytoplankton over a mussel bed was shown to be faster at higher flow velocities (Butman et al. 1994). Isotope studies could be used to determine energy relationships in the KwaZulu-Natal intertidal. If mussels depend on increased food supply on exposed shores, this would imply that low shore community structure is determined principally by bottom–up effects in KwaZulu-Natal.

Human harvesting and wave exposure

My study shows that wave intensities can be predicted from harvesting patterns. A distinct spatial separation in catches of harvested intertidal organisms has persisted for many generations along the Maputaland coast (Kyle et al. 1997a). This pattern is reputed to reflect spatial differences in abundance of organisms. Results from my study suggest that differences in wave exposure underlie these differences and thereby the difference in principal target organisms between sites. Extremely high wave forces were recorded at Black

Rock and Dog Point, the most important mussel collecting sites in Maputaland (Kyle et al. 1997a). The most important *Pyura* collecting site is Kosi Mouth, where low wave forces were recorded in my study. More than half of the limpet harvest in Maputaland is gathered at the most wave-sheltered site, Rabbit rock (Kyle et al. 1997a). At the only unexploited exposed site (Island Rock), mussels were more abundant while *Pyura* had higher cover (12-25%) at unexploited sheltered sites. At exposed sites where harvesters collect mussels (Kyle et al. 1997a), mussel cover was reduced to approximately 5%. At sheltered sites (e.g. Kosi Mouth) where *Pyura stolonifera* is harvested, cover of this species was less than 1%. This indicates that harvesting may mask effects of wave exposure in Maputaland.

Human exploitation

It was not possible to meaningfully assess the influence of harvesting in Natal because there is only one unexploited site. Furthermore, only one site subject to subsistence harvesting was surveyed and virtually all localities in Natal are harvested by recreational fishers, who remove much less than subsistence fishers in Maputaland (Tomalin and Kyle 1998, Chapter 2). Differences in low-shore community structure between "highly exploited" and "less harvested" sites in the Natal region were examined, but were inconsequentially small, reflecting the fact that levels of harvesting are uniform in Natal.

In Maputaland, there was a close and highly significant association between community structure and the prescence or absence of subsistence harvesting. This was apparent at both wave-exposed and sheltered shores (Figure 3.4). Community differences were principally evident in the low rather than the mid shore (Figure 3.5), a pattern also evident in the Transkei (Lasiak and Field 1995). Of all factors examined, human exploitation yielded the highest R-value (R=0.875, Table 3.5). Large-scale modifications of rocky shore communities in response to human exploitation of intertidal organisms have been reported in other countries (Moreno et al. 1984, Castilla and Duran 1985, Oliva and Castilla 1986, Ortega 1987, Siegfried 1988, Duran and Castilla 1989).

Distinguishing species

Human harvesting in Maputaland appears to have reduced the cover of target organisms, principally *Perna perna* and *Pyura stolonifera*, at both wave-exposed and relatively sheltered sites, but particularly at more exposed sites (Figure 3.4). The cover of several non-target species, especially the articulated coralline, *Cheilosporum sagittatum*, and other algae such as *Sargassum* spp. was significantly higher at exploited sites. In the case of *C. sagittatum*, this response was limited to wave-exposed sites. Higher cover was also recorded for the reefworm *Idanthyrsus pennatus*, an unidentified ascidian, the sponge *Hymeniacedon* sp., and the algae *Laurencia* sp. and *Caulerpa racemosa*, but more specifically at sheltered sites. This indicates that wave exposure moderates harvesting impacts with different species responding differently, depending on wave action.

Cascade effects

Only four non-target species were less abundant at harvested versus protected sites, but they included two types of crustose algae: *Ralfsia expansa* and encrusting corallines (Table 3.14). Crustose algae are known to be prone to overgrowth by foliar algae (Steneck 1986, Keats et al. 1994). This suggests that increased abundance of foliar algae and colonial invertebrates such as reefworm, sponges and ascidians, had detrimental effects on crustose algae. The overall picture emerging is a cascade effect, in which subsistence harvesting substantially reduces the target species *Perna perna* and *Pyura stolonifera* leading to the expansion of a series of non-target species due to competitive release, and the diminution of crustose algae due to overgrowth (Figure 3.6). The prevalence of such cascading effects caused by harvesting is the subject of active ecological debate (Castilla 1993, Power et al. 1996, Dayton et al. 1998, Pauly et al. 1998, Sala et al. 1998, Steneck 1998, Castilla 1999).

In Maputaland, the main target species are space-occupying filter feeders (*Perna* and *Pyura*), although there are some localities such as Rabbit Rock at which limpets are also targeted. Human predation on herbivores has been linked to increased abundance of macroalgae at exploited sites (Moreno et al. 1984, Hockey and Bosman 1986, Dye 1994). The increased abundance of algae and inedible sessile species in KwaZulu-Natal does not appear to be related to changes in abundance of mobile consumers. Although the influence of grazers on intertidal communities has yet to be established in KwaZulu-Natal, current indications are that grazers do not exert a dominating influence over community structure (J. Harris, KwaZulu-Natal Wildlife pers. comm.).

In Chile, the major targets of intertidal shellfish gatherers are a predatory gastropod, *Concholepas concholepas*, and limpets (*Fissurella* spp.). The cascade effects rippling through Chilean intertidal systems are thus based on very different mechanisms. While competitive release is the mechanism proposed to increase cover of non-target species in KwaZulu-Natal, reduction of predation and herbivory accounts for cascade effects in Chile. Removal of *C. concholepas* results in a substantial expansion of its prey species, including a small inedible mussel (*Perumytilus purpuratus*) and barnacles (Castilla and Duran 1985, Duran and Castilla 1989, Castilla et al. 1994, Castilla 1999). Harvesting of herbivorous limpets, however, causes macroalgae to proliferate (Moreno et al. 1984, Oliva and Castilla 1986).

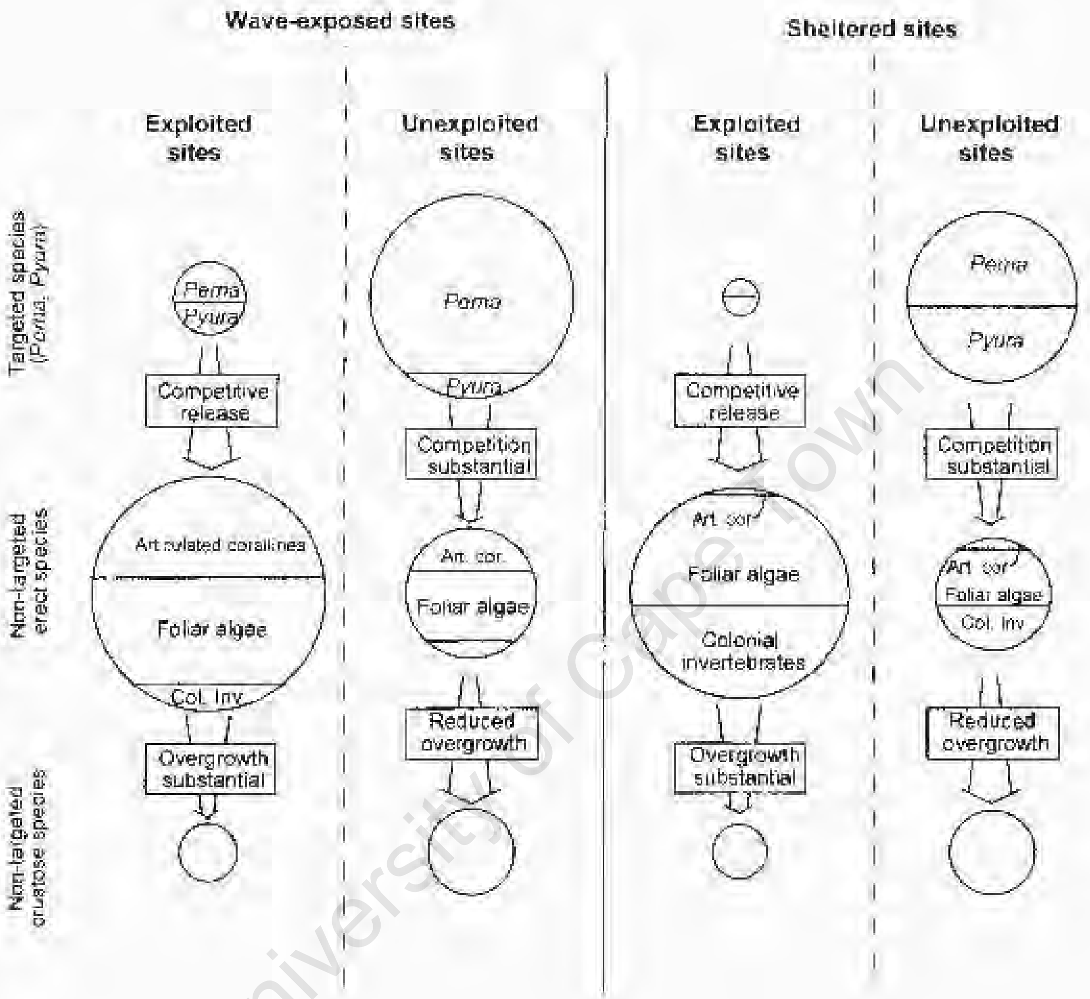


Figure 3.6. Diagram showing cascade effects in the low shore at subsistence-harvested sites in Maputaland. Harvesting reduces target species leading to increased cover of non-target species due to competitive release. This leads to overgrowth of encrusting corallines and *Ralfsia expansa*. The area of each circle is proportional to the mean percentage cover recorded in Table 3.24, with the largest circle representing 78% cover. The division of circles by lines indicates the proportional contribution of different taxa.

My results are similar to those of studies conducted in the former Transkei, on the east Cape coast, south of Natal. Heavy harvesting there has led to the disappearance of mussel beds from many previously mussel-dominated shores (Siegfried 1988, Dye et al. 1994) so that mussels now only occur as individuals amongst articulate coralline algae or in small clumps. Hockey and Bosman (1986) reported marked differences between exploited and non-exploited lower balanoid zone assemblages. At an exploited site, they recorded 50% cover of articulated corallines and foliar algae that were virtually absent at unexploited sites. Increased cover of *Caulerpa racemosa* was a consistent feature of all exploited shores in Maputaland and this species was also more abundant at exploited localities in the Transkei (Hockey and Bosman 1986). Analyses of rocky intertidal macrofaunal assemblages in the Transkei also revealed significant differences between exploited and unexploited sites although locality effects were evident (Lasiak and Field 1995, Lasiak 1999). Reduced abundance of filter feeders (particularly *P. perna*) and target organisms were recorded at all exploited sites. Unfortunately, changes in seaweeds were not examined, but increased abundance of phytal-associated species, e.g. certain crabs, brittlestars and amphipods, suggests that algal cover was higher at exploited sites (Lasiak 1999).

Experimental removal of *P. perna* in South Africa leads to rapid recolonisation by either articulated coralline algae or barnacles that may then dominate the community for several years (Lambert and Steinke 1986, Dye 1992). The increased cover of algae and inedible sessile invertebrates at exploited sites in Maputaland is cause for concern. The consistence of my results and other studies examining harvesting impacts on intertidal assemblages provides strong evidence of a causal relationship between community changes and exploitation. Experimental harvesting at unexploited localities is a logical next step to test community changes associated with exploitation (see Chapter 6).

Changes in abundance of target species on exploited shores in Maputaland are clearly linked to the direct effects of harvesting although biotic interactions may account for some of the observed biological variability. One enigma remains, however. Despite being heavily exploited in Maputaland, *Pyura stolonifera* was more abundant there than in Natal, particularly at wave-sheltered sites. *Pyura stolonifera* may be intolerant of extreme wave action or, alternatively, mussels may out-compete it under conditions of strong wave action. The near absence of *P. stolonifera* from the intertidal zone in Natal is unexplained. Experimental harvesting of *Perna* and *Pyura* would enable assessment of any competitive interaction between these species.

Implications for management and conservation

The results of this study have implications for managers and conservation authorities in South Africa. Firstly, more of the observed physical heterogeneity and associated biological diversity warrants inclusion within the marine protected area network in KwaZulu-Natal if the full spectrum of diversity is to be conserved. Hockey and Branch (1994, 1997) emphasised that a hierarchy of criteria must be examined when assessing the need for marine protected areas and the relative merits of potential sites. Heading this hierarchy is the need to identify biogeographic regions to ensure adequate representative protection. This was the central objective of Chapter 2. A second tier in the hierarchy is to identify habitat types and ensure their inclusion in marine protected areas. In this context, the present chapter shows that both wave exposure and sand inundation had significant effects on community structure, whereas rock type had negligible effects. Wave exposed versus sheltered shores and sand-inundated and less-sanded shores thus represent different habitat types in the intertidal realm. Therefore, to provide adequate coverage of rocky shore communities in marine protected areas, it will be necessary to protect shores representing the full spectrum of wave exposure and sand inundation.

In Maputaland, both exposed and sheltered rocky shores are included within the Maputaland Marine Reserve, but most of the shores in the region are subject to intensive exploitation by subsistence harvesters. Two semi-exposed shores on the southern extremity of the Maputaland Province (Sodwana and Cape Vidal Point) are closed to harvesting and one exposed site (Island Rock), although not legally protected, is generally inaccessible. As an "island", this site is not typical of an exposed shore in the physical sense and may be subject to other hydrodynamic differences. Nevertheless, this is the only exposed site in Maputaland that has not been subject to intensive harvesting and should be considered for formal protection from anthropogenic activities. In the Natal biogeographic region, only one shore (Trafalgar) is protected and this is very wave-sheltered. There are no unexploited wave-exposed sites in Natal. Exposed shores host mussel-dominated communities and, considering the exploitation pressure on this species, it would be short-sighted to allow exploitation to continue at all exposed shores in KwaZulu-Natal.

The brown mussel, *Perna perna*, has low resilience to exploitation because it is easily replaced by other species that occupy primary space (Lambert and Steinke 1986, Dye 1992). My data suggest that several species become more abundant in areas where mussels are depleted by harvesting, especially on wave exposed shores. Furthermore, mussels on the east coast of South Africa are vulnerable to harvesting effects because of relatively low stocks and low recruitment levels (Harris et al. 1998). A study comparing recent and abandoned shell middens in Mozambique found that P. perna was once harvested there but has disappeared, and this local extinction may be attributed to overexploitation (de Boer et al. 2000). In Maputaland, my study evidenced that exploitation was associated with greater differences in low-shore community structure associated than any of the other factors investigated (as reflected by the R-statistics of ANOSIM, Table 3.5, Figure 3.5). The lack of unexploited shores in Natal prevents assessment of the effects of exploitation in this region. Closed areas within representative localities where various levels of harvesting can be experimentally undertaken are required to serve as benchmarks against which the effects of exploitation and natural physical and biological factors can be assessed. Selection of closed areas depends in part on the adequate definition and recognition of the full spectrum of biotopes in KwaZulu-Natal as well as an assessment of their conservation status, and these are topics addressed in the next chapter.

Conclusions

This study has shown that diverging community structure in KwaZulu-Natal rocky shores are related to contrasting physical conditions, particularly wave exposure and sand inundation. In Maputaland, human exploitation is added to these physical factors. Quantitative evidence suggests that wave action and sand inundation are key potential determinants of community structure, the former being more important lower on the shore and the latter having a greater influence on mid- and high-shore communities. Only sand inundation emerged as a significant factor influencing community structure in the high shore in Natal. Only in a single case did rock type appear to have a significant influence, and then only in the mid shore. Dramatic effects of subsistence harvesting were evident in low-shore communities on exposed and less exposed Maputaland shores. These findings not only further our understanding of the functioning of rocky shores in KwaZulu-Natal and the impacts of human harvesting on community dynamics, but emphasise the need for an expanded "no take" network of marine protected areas. This will allow full elucidation of human impacts and the provision of adequate protection of the complete spectrum of habitat types.

Chapter 4

Development of an intertidal biotope classification system and application in conservation planning in KwaZulu-Natal.

ABSTRACT

There is an increasing need for new tools and techniques for biodiversity conservation and fisheries management. In this Chapter, intertidal biotopes for rocky shores in KwaZulu-Natal were identified and defined. An arbitrary 50% Bray-Curtis similarity was used to objectively classify 1630 samples from 38 sites spanning 560km, resulting in the recognition of 69 biotopes. These biotopes were independently validated at two additional sites by demonstrating concordance between biotopes identified using the classification system and clusters of samples objectively identified using cluster analysis and multi-dimensional scaling. Furthermore, independent ANOSIM tests indicated significant differences in community structure between different biotopes from within and between different zones on the shore at both sites. Small-scale horizontal (within-zone) and vertical (between-zone) differences in community structure were therefore captured in my biotope classification scheme. I compared my biotope classification system with other schemes that classify marine communities and habitats. I also compared diversity estimates for a range of diversity indices to assess whether different biotopes were significantly different in terms of diversity. Some biotopes that were more than 50% different in terms of community structure, did not differ significantly in terms of species richness, dominance, evenness or Shannon diversity. This shows that multivariate techniques are better for identifying different communities and for examining patterns of biodiversity. Biotopes can be used to assess the presence or absence of different biological communities and proved effective in evaluating the conservation value of existing marine protected areas in KwaZulu-Natal. Biotope surveys are more effective than labour-intensive species inventories, and do not depend on destructive sampling. They are inexpensive and can be conducted quickly and efficiently by people with minimum training. At present, only 29% of all KwaZulu-Natal biotopes are fully protected in the two existing "no take" marine protected areas i.e., St Lucia and Trafalgar Marine Reserves. An additional 25% of biotopes are covered in the Maputaland Marine Reserve but subsistence exploitation is allowed on all shores in this entire reserve. There are currently no mussel-dominated biotopes protected in Natal because of the failure to include wave-exposed sites in fully protected marine reserves. Biotope surveys were also employed to compare two proposed additional marine protected areas, demonstrating the value of biotopes in identifying conservation priorities provided a standard protocol is used for comparative assessment. The proposed Pondoland Marine Park could improve the proportion of fully protected biotopes by at least 24% whereas the proposed extension of St Lucia Marine Reserve would achieve an improvement of at least 31%. If both proposed marine reserves are established, conservation of biotopes could improve by 54% and would leave only three Natal biotopes unprotected. However, 22% of all biotopes (all confined to Maputaland) will remain exploited although they are within marine protected areas if "no take" areas are not instituted in the Maputaland Marine Reserve. Introduction of such "no take" areas would dramatically improve the conservation status of KwaZulu-Natal as a whole.

Introduction

The United Nations Convention on Biological Diversity aims to conserve and sustainably utilise biodiversity for the benefit of present and future generations. Signatories are required to make inventories of biodiversity, monitor changes in biodiversity and plan to conserve biodiversity. Gray (2000) remarked that although these requirements are commendable, for the marine environment they depend on an invalid assumption that marine scientists know how to measure biodiversity. Diversity is difficult to define because it encompasses two principal components, variety and relative abundance (Magurran 1998). Furthermore, there are several levels of organisation incorporated into the concept of biodiversity, from the genetic variability within a population or species to the diversity of ecosystems encompassed within a biogeographical province (Gray 2000).

An understanding and management of the landscape matrix is critical to sustain biodiversity over multiple human generations. In meeting this challenge, traditional management techniques, focused on individual species and populations, are insufficient (Norse 1993, Scott et al. 1993, Jennings 1995, Zacharias et al. 1998). Traditional single-species approaches need to be supplemented with new techniques aimed at conserving communities, habitats and ecosystems (Thorne-Millar and Catena 1991, Perrings et al. 1992, Franklin 1993, Norse 1993, Gray 1997). This is important because large-scale ecological processes must be incorporated into conservation planning (Margules and Pressey 2000, Cowling and Heijnis 2001). Landscape ecology is an emerging discipline that focuses on spatial patterns and the interactions among the elements of landscape mosaics (Forman and Godron 1986, Turner 1989, Wiens et al 1993). Ray (1991) refers to the marine equivalent of landscapes as seascapes and suggests that biodiversity assessments need to be made at the community, habitat and landscape level.

Inventory and analysis techniques for communities, habitats and ecosystems are proving useful as tools for conservation and management of landscapes (Scott et al. 1993, Jennings 1995, Conroy and Noon 1996). Many detailed biological data sets are geographically biased and therefore their use in conservation planning is limited (Pressey et al. 2000). For example, the Cape Floristic Region in South Africa is well studied but it still was necessary for Cowling and Heijnis (2001) to develop a classification of 102 broad habitat units to provide a consistent framework for conservation planning at a scale finer than that of national vegetation mapping. In Africa, conservation efforts have been biased towards terrestrial rather than marine ecosystems (Hockey and Branch 1994). However, principles of terrestrial conservation are not necessarily applicable to marine environments because of the physical and biological differences between these ecosystems (e.g., dispersal and transport in water result in low levels of endemism) (Hockey and Branch 1994). Effective marine conservation is therefore dependent on the development of an understanding of patterns and functioning of marine biodiversity.

In the marine realm, there are several initiatives aimed at developing inventories for seashores (Pérès and Picard 1964, Cowardin 1979, Augier 1982, Ros et al. 1985, Dethier 1992, Connor et al. 1995, Dauvin 1995, Zacharias et al. 1998, 1999, Great Barrier Reef Marine Park Authority 1999). Such classification systems support studies of biodiversity, assessments of nature conservation importance, sensitivity mapping and wider management of the marine environment (Hiscock 1995). These systems allow mapping of the distribution and extent of habitats and biological communities, thereby assisting in conservation planning, including the complex task of selecting marine protected areas and resource management. I know of no marine habitat or biological classification systems that have been applied in Africa at a scale less than that of biogeographic regions.

Indices are often employed to measure diversity and even assess changes in diversity. Species richness is the most widely used diversity index with good discriminant ability and wide empirical application (reviewed in Magurran 1988). It has been used in many studies describing diversity in rocky shore communities (e.g., Menge et al. 1991, Lohse 1993, Archambault and Bourget 1996, Seed 1996). However, diversity encompasses both variety and relative abundance and therefore an estimate of species richness should be coupled with a measure of dominance (Magurran 1988) and an index that incorporates both richness and heterogeneity (Gray 2000). The Shannon-Wiener or Shannon index incorporates species richness and evenness. Shannon Wiener indices have been used to describe biodiversity in mussel patches (Seed 1996), rocky intertidal communities in Canada (Archambault and Bourget 1996), the tropics (Menge et al. 1991), seaweed communities in South Africa and Namibia (Engeldow and Bolton 1994) and sand influenced intertidal habitats in California (Littler et al. 1983).

To achieve conservation goals, several scales of diversity should be considered and classification systems and marine protected area networks should incorporate these different scales of variability (Zacharias et al. 1999). The largest scale is biogeographic and representation of different biogeographic regions in protected area networks should be a core conservation objective (Hockey and Branch 1994, 1997). Identification of biogeographic regions in KwaZulu-Natal was the central objective of Chapter 2. Two biogeographic regions were recognised, Maputaland and Natal, with a break at Cape Vidal. Within biogeographic regions, different habitats should be recognised and representative habitat types included within marine protected areas (Underwood 1993, Hockey and Branch 1997, Roberts et al. in press a). Some of the key determinants of between-site variability in community structure on rocky shores in KwaZulu-Natal were recognised in Chapter 3. Those analyses revealed that in KwaZulu-Natal, sites covering a range of wave exposure and sand inundation should be included in marine protected areas, if the full spectrum of biological diversity is to be conserved.

Small-scale variability in both physical habitat and species composition and abundance is to be expected within any rocky shore (Archambault and Borget 1996, Benedetti-Cecchi et al.

1996, Underwood and Chapman 1996). Intertidal communities are characterised by a high degree of patchiness. Variability is associated with changes in dominance along gradients and organisms often form mosaics even within environments that appear physically homogenous (Dethier 1990). Biological variability in intertidal habitats is evident between spatially defined zones (i.e., vertical variation on the shore), but horizontal zonation patterns (i.e., within zones) are also often apparent (Foster et al. 1988, Menge and Farrell1989). Differences in elevation and associated variation in temperature and desiccation (Colman 1933, Doty 1946, Lewis 1964, 1976, Stephenson and Stephenson 1972, Underwood 1978), wave exposure (Lewis 1964, Menge and Farrell 1989, Menge and Branch 2001), topographical variability (Fuji and Nomura 1991), patchiness in settlement (Underwood and Fairweather 1989, Roughgarden et al. 1988, Menge 1991) and grazing (Lubchenco and Menge 1978, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Jara and Moreno 1984, Lubchenco et al. 1984), and even variability in behaviour of intertidal organisms (Chapman 2000) may create heterogeneity on rocky shores.

In South Africa, most quantitative descriptions of local-scale differences in intertidal communities have been conducted on the west and south coasts (McQuaid and Branch 1984, 1985, Bustamante et al. 1997). Descriptions of changes in community structure due to vertical zonation have been undertaken in KwaZulu-Natal (Stephenson 1939, 1943, 1944 1947, Jackson 1976, Lambert and Steinke 1986a), however there is little known about small-scale horizontal variability. There has been only one attempt to classify intertidal communities using quantitative data (Lambert & Steinke 1986a), and this was conducted at a single site.

Classification systems can be based on biological characteristics (e.g. Hiscock 1995, Connor et al. 1995) or physical criteria (eg. Dethier 1990, Hily and Jean 1997, Zacharias et al. 1998, 1999, Pressey et al. 2000). The Marine Nature Conservation Review (MNCR) developed one of the most comprehensive intertidal classification systems, designed for conservation objectives (Connor et al. 1997). This classification system was based on biological variability because the ultimate intended use was conservation of species (Hiscock 1995). However, environmental factors are incorporated as major determinants of community composition in the MNCR system (Connor 1994). The term "biotope" is used to combine habitat and community into the smallest physically defined unit supporting a more or less homogeneous assemblage of species (Hiscock 1995). There are several ways to classify biotopes and these ways are likely to be arbitrary and capable of construction of different hierarchies, each of which are equally valid (Hiscock 1995).

When my study was initiated, the relative importance of the physical factors that influence intertidal community structure in KwaZulu-Natal were poorly understood. Because of this, I initially distinguished biotopes on a purely biological basis. Physical differences in habitat characteristics between a subset of these biotopes were investigated at a later stage (see Chapter 5). To distinguish biotopes, I used a standardised 50% Bray-Curtis cut-off similarity value to objectively separate 1630 samples into 69 biotopes. These biotopes were then defined and listed with their characteristic species to develop a biotope classification system for KwaZulu-Natal.

The central focus of this chapter is an examination of small-scale differences in rocky-shore community structure at a scale of metres to tens of metres but covering the entire 560-km KwaZulu-Natal coast. This study represents the third and final tier in a hierarchical analysis of intertidal community structure at increasingly smaller scales. Multiple samples were classified into several biotopes, definitions of these developed, and differences in the relative abundance of different biotopes investigated between different zones on the shore and between biogeographic regions. After the classification and definition of biotopes had been completed, their validity was tested using samples from the low and mid shore of two independent sites. The classification system was first used to identify the biotopes present. These were then re-analysed using ANOSIM tests to assess if the biotopes recognised were significantly different in terms of species composition and abundance. Independent tests were also conducted to assess whether groups of independent samples that were recognised as distinct biotopes, were significantly different in terms of species richness and diversity. Finally, the conservation status of the different biotopes in KwaZulu-Natal was examined and to demonstrate the capabilities of the biotope classification system, two proposed marine protected areas were assessed for their potential to cover currently unprotected biotopes.

Objectives

In summary, the following specific objectives were addressed:

1. To objectively define biotopes within each of four zones on rocky shores in KwaZulu-Natal and to determine characteristic and distinguishing species for each biotope and develop a classification key for easy recognition of biotopes in the field.
2. To test the validity of the classification key by using it to identify selected biotopes at two independent sites and then quantitatively sampling and (i) checking for concordance of groups of samples identified using the key versus sample groupings in cluster analyses and MDS plots and (ii) testing for significant differences in species composition and abundance between different biotopes.
3. To test for significant differences in species richness and diversity between a subset of biotopes to explore the validity of such univariate indices.
4. To assess the extent to which the full spectrum of intertidal rocky-shore biotopes is currently protected in KwaZulu-Natal.
5. To test the utility of biotopes in comparing the relative value of two sites proposed as marine protected areas.

In Chapter 5, corresponding physical differences in habitat were sought between selected contrasting biotopes. In Chapter 6, a variety of approaches were used to examine the impact of human exploitation on intertidal communities including the abundance of different biotopes at experimentally harvested plots.

Methods

1. Defining intertidal biotopes for rocky shores in KwaZulu-Natal

1a. Sampling design

Surveys were undertaken at 38 sites (Figure 4.1) spanning the entire KwaZulu-Natal coastline, on shores of six different rock types, subject to different degrees of sand inundation and covering a range of wave exposure conditions (see Figures 2.11, 2.12 on p 52 and 54 for data). Analyses of biotopes were based on the same biological samples used for the biogeographic analyses in Chapter 2, except that one site was excluded (Iti Bay). Sites with varying abiotic variables were included in an attempt to incorporate the full spectrum of habitat and community diversity and therefore cover as many biotopes as possible. The biological surveys were conducted within four spatially defined zones on the shore, i.e., the low, mid, high and top shores. By surveying along the shore within these four vertical zones, both vertical (between zone) and horizontal (within zone) differences in community structure were included. The numbers of replicate samples in each zone were based on the results of the pilot study (see Chapter 2, p 28-30) and comprised 20 in each of the low and mid shore and 10 in each of the high and top shore. A total of 38 sites was sampled although fewer sites were sampled higher on the shore where variability is less. For further details, refer to the methods in Chapter 2. In total, 1630 quadrats were scored, 760 in the low shore, 520 in the mid shore and 220 and 130 in the high and top shore respectively. Each sample comprised a 1m x 0.1m quadrat in which the percentage cover of all visible species was scored.

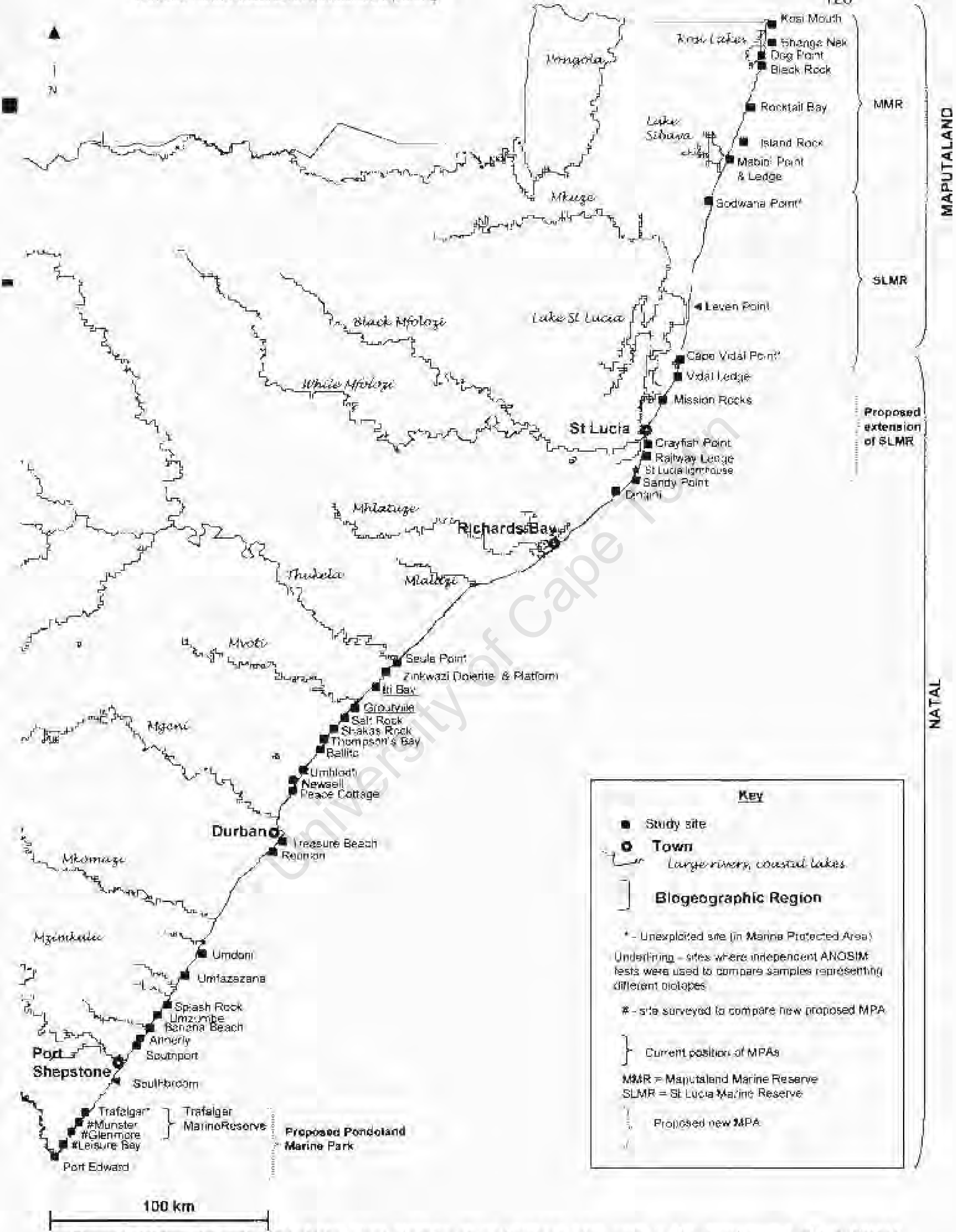


Figure 4.1 Map of the KwaZulu-Natal coast showing all rocky-shore sites used in the development of the biotope classification system, the two independent sites used to verify biotopes, the position of current and proposed Marine Protected Areas (MPAs) and the three additional sites surveyed within the proposed Pondoland Marine Park.

1b. Data analysis

To identify biotopes, data on species abundance (%cover) were analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research, version 4.0 1994). Data were root transformed to weight the contribution of less abundant species. Hierarchical cluster analyses were computed using Bray-Curtis co-efficients. The dendrograms produced by the cluster analyses were used to identify groups of samples that were similar in terms of species composition and abundance. An arbitrary cut-off value of 50 % was used to separate groups of samples objectively. The 50% level was chosen as a criterion because it yielded a practical number of groups of samples, but with sufficient samples to define the assemblages.

Ideally, every quadrat for every site along the entire coast should be included in a single analysis. Due to limitations imposed by the PRIMER software, it was only possible to compare 100 samples at any one time, necessitating the subdivision of the database. This was achieved in two ways. Firstly, each zone on the shore was analysed separately. Secondly, for the low and mid shore, groups of five sites were compared at one time (5 sites x 20 quadrats) and for the high and top shore, groups of ten sites were compared simultaneously (10 sites x 10 quadrats).

Three series of analyses were conducted, incorporating different batches of sites in each series based on different criteria:

1. In the first series, sites were grouped on the basis of similar community structure, i.e. samples from sites that displayed the greatest biological similarity in terms of total cover of all species (as determined from Figures 2.5 - 2.8, p 39-41) were compared. This analysis was aimed at identifying biotopes from similar sites spanning the entire coast. Using the dendrograms in Figures 2.5-2.8, batches of five (low and mid shore) or ten (high and top shore) similar sites were identified.
2. In the second series of analyses, sites were grouped geographically. This analysis was aimed at identifying biotopes that were specific to any region. The five or ten most northern sites formed the first group, and then working from north to south, sites were grouped into batches.
3. The third series of analyses compared samples from sites selected on the basis of the results of the first two analyses (see below). This analysis was a form of cross-checking to reconcile the results of the first two analyses into a single classification system for intertidal biotopes.

For each batch of sites within each series of analyses, all samples from the five or ten sites were analysed together by hierarchical cluster analysis. MDS plots were also constructed to verify groupings in the cluster analyses. The dendrograms from the cluster analyses were used to identify different groups of samples that were more than 50% similar. Only clusters of at least three samples were considered as biotopes.

Within each series of analyses, each cluster of samples that was more than 50% similar within each analysis was compared against every other group. The PRIMER program SIMPER (similarity percentage breakdown, Clarke 1993) was used to identify characteristic and discriminatory species for different groups of samples. Characteristic species were identified as those contributing most to the overall similarity of the group of samples. The dominant characteristic species was defined as the species that occupied the greatest percentage cover. This species was always ranked within the top four most characteristic species, being the highest ranking in most cases. Distinguishing species were those that contributed most to the overall dissimilarity between any two clusters of samples. All groups of samples with the same dominant species identified in the first two series of analyses, were compared in the third series of analyses. This was a form of cross-checking, allowing similar groups of samples from the first and second series of analyses to be compared. By comparing all groups of samples that had the same dominant species, groups of samples representing the same biotope but derived from the two different series of analyses were recognised. The most important application of this cross-checking was in the case of samples dominated by the brown mussel, *Perna perna*. During the first two series for low shore samples, 31 different groups of samples dominated by *P. perna* were identified, but these were reconciled into eight biotopes (all dominated by *P. perna* but characterised by different distinguishing species) by the third series of analyses.

Pie charts were constructed showing the relative abundance of the different biotopes in the low, mid and high shore. For the low and mid shore, separate pie charts were constructed for Maputaland and Natal so that the abundance of different biotopes could be compared between biogeographic regions. As no biogeographic break was apparent in the high or top shore (See Figures 2.7 and 2.8 respectively), the entire KwaZulu-Natal coast was considered as an entity for these zones.

2. Validating differences in community structure between biotopes

2a. Sampling design

Once biotopes had been identified as outlined in section one, classification keys were developed to allow their recognition. To test the validity of this classification scheme for biotopes, 40 independent samples (20 low shore and 20 mid shore) were collected at each of two sites, Iti Bay and Groutville, that were not used in the original development of the biotope classification system. Iti Bay and Groutville are situated on the north coast between Salt Rock and Zinkwazi (Figure 4.1). Iti Bay is a Dwyka tillite shore and is subject to recreational exploitation. The site at Groutville is composed of Ecca sandstone and is subject to subsistence exploitation.

2b. Data analysis

The root-transformed data from Iti Bay and Groutville were analysed separately. As a first step, each sample was classified as a biotope on the basis of dominant and distinguishing species (using the classification keys developed – see Tables 4.2-4.3). Then, a separate analysis of the samples was undertaken using hierarchical cluster analyses and multi-dimensional scaling (MDS). Low and mid-shore samples were analysed simultaneously so that differences within and between zones could be compared. To check if the classification system yielded the same groupings of samples as the independently undertaken MDS, the biotope names (in an abbreviated coded form) were superimposed on the MDS plot. This allowed a visual test of whether there was concordance between the classification scheme and the groupings of samples detected by MDS.

To determine whether the objectively classified samples of different biotopes reflected significant within-site differences in community structure, one-way ANOSIM tests were conducted to compare species composition and abundance between samples representing different biotopes from within and between the low and mid shore.

3. Testing for significant differences in diversity between biotopes

3a. Sampling design

To assess whether different biotopes have significant differences in diversity, three estimates (each based on 10 samples at each of three sites) were used to compare each of four diversity indices for a subset of biotopes. Only sites in the north of the Natal region (Cape Vidal Point and Ledge, Mission Rocks, Crayfish Point, Railway Ledge, Sandy Point and Dingini) were used, to avoid confounding biogeographic differences. The seven biotopes selected for investigation are shown in Table 4.1. These biotopes were selected because they were relatively common within each zone in Natal (see Figure 4.2 in Results).

Table 4.1. Biotopes that were used to test for significant differences in species richness and diversity. The dominant and distinguishing species and codes reflecting these species are indicated.

Zone	Group	Biotope		Biotope Code
		Dominant species	**Distinguishing species**	
Low	Mussels	*Perna perna*	*Octomeris angulosa*	PpO
	Red algae	*Hypnea spicifera*	-	Hs
	Articulated corallines	*Cheilosporum sagittatum*	*Hypnea spicifera*	CsH
Mid	Barnacles	*Octomeris angulosa*	-	Oa
	Zoanthids	*Palythoa nelliae*	*Zoanthus* sp.	PnZ
	Articulated corallines	*Jania verrucosa*	*Laurencia natalensis*	JvL
High	Oyster	*Saccostrea cucullata*	*Scutellastra natalensis*	ScS

For each biotope, cumulative species richness (S), Shannon diversity (H'), evenness (J') and reciprocal dominance (1/Sdi) were calculated for each of three sites. The Shannon Wiener or Shannon index incorporates both species richness and the proportional distribution of individuals amongst the species,

$H' = -\Sigma_i\, p_i\, (\log_2 p_i)$

where p_i is the proportion of the total abundance (or percentage cover) from the ith species. Evenness (J') measures the partitioning of abundance between species,

$J' = H' \log_2 (S)$

The reciprocal of Simpson's dominance index 1/Sdi is primarily a measure of dominance (Whittaker 1972),

$1/Sdi = 1/\,(p_1^2 + p_2^2 \ldots pn^2)$.

3b. Data analysis

To test for significant differences in species richness and diversity between different biotopes, one-way ANOVA was conducted with STATISTICA (1999). Normality assumptions were tested with the Kolmogorov-Smirnoff test and homogeneity of variances was tested with Cochran's test (Winer et al. 1991). Post-hoc Tukey Honestly Significantly Different (HSD) tests were used to determine which biotopes differed in terms of each respective diversity index.

4. Assessing the conservation status of intertidal biotopes

To examine the conservation status of rocky intertidal biotopes in KwaZulu-Natal, the conservation status of the sites where each biotope was identified was considered. The conservation status of biotopes was measured by their presence (or absence from) existing effective marine protected areas (MPAs), taking into account the fact that some are fully protected and others allow intertidal harvesting (Figure 2.14 pg. 66). The relative abundance of a biotope was not considered, only its presence or absence. Each biotope was then assigned a conservation status: (1) fully protected i.e., included within a fully protected MPA (i.e., Sodwana, Cape Vidal or Trafalgar), (2) partially protected, i.e., included within a MPA but subject to subsistence-exploitation (Kosi Mouth to Mabibi) or (3) Unprotected i.e., not represented within any marine protected area.

As the distribution of biotopes on every rocky shore in KwaZulu-Natal has not yet been mapped, this exercise was based only on data from the 41 shores sampled. Nevertheless, the 41 sites span the entire KwaZulu-Natal coast and all marine protected areas. To show the current conservation status of each of each biotope visually, an outer ring was superimposed on the pie charts showing the relative abundance of the different biotopes (Figure 4.2). In this way, the conservation status of the most common representative biotopes could be distinguished from that of less abundant biotopes.

5. Testing the utility of biotopes in evaluating proposed marine protected areas

Two new marine protected areas that are currently being proposed for proclamation (Figure 4.1) were considered to determine how the conservation status of intertidal rocky-shore biotopes would change if these additional marine reserves were to be established. The first is a proposal to extend the southern limit of the St Lucia Marine Reserve from the current beacon, 1km south of Cape Vidal, to the St Lucia lighthouse (KwaZulu-Natal Wildlife, St Lucia Marine Reserve Management Plan 2000). The second is the Pondoland Marine Park, which aims to combine the Trafalgar and Mkambati Marine Reserves, and the area between them, into one large marine protected area extending for approximately 80km from the Mbizana River at Southbroom in KwaZulu-Natal to the Mkozi River in the eastern Cape (Attwood and Broker 2000). Within the proposed extension of the St Lucia Marine Reserve, four sites had been surveyed in my study: Vidal Ledge, Mission Rocks, Crayfish Point, and Railway Ledge (see Figure 4.1). Within the proposed Pondoland Marine Park, only one site, Port Edward, had been surveyed. Three additional sites, Munster, Glenmore and Leisure Bay, were surveyed in March 2001 in order to constitute a comparable sampling effort. These sites are situated consecutively within a 15-km stretch of coast south of the Trafalgar Marine Reserve and just north of Port Edward (Figure 4.1). Twenty 1m x 0.5 m quadrats were surveyed in each of the low and mid shore and ten in each of the high and top shore at each site. Each quadrat was assigned to a biotope using the key developed in part 1 of this chapter (i.e., Tables 4.2 and 4.3 in Results). Biotopes that are currently unprotected or partially protected were elevated to the status of "fully protected" if they occurred at any of these proposed marine protected area sites. Pie charts comparing the relative conservation status of all biotopes in KwaZulu-Natal were then constructed for (1) the current status, (2) assuming the proposed Pondoland Marine Park is established (3) assuming the St Lucia Marine Reserve is extended to the St Lucia lighthouse, and (4) assuming both new protected areas were to be instituted.

Results

1. Defining intertidal biotopes for rocky shores in KwaZulu-Natal

There were 69 biotopes objectively identified using an arbitrary 50% Bray-Curtis similarity cut-off (Tables 4.2-4.4). Of these 69 biotopes, 40 were in the low shore, 21 in the mid shore, 7 in the high shore and only one in the top shore.

In the low shore, biotopes were dominated by foliose and articulated coralline algae, and sessile invertebrates (Table 4.2, Figure 4.2). The invertebrate-dominated biotopes were all characterised by sessile invertebrates: zoanthids, colonial reefworms, the brown mussel *Perna perna* and the ascidian, *Pyura stolonifera*. In the mid shore, biotopes were dominated by encrusting coralline and brown algae and articulated coralline turfs with one community dominated by *Ulva* sp. (Table 4.3). Invertebrate-dominated biotopes included those with anemones, zoanthids, wormshells, reefworm, molluscs and several species of barnacles. The high-shore biotopes were dominated by ephemeral algae, foliose brown algae or bare rock with limpets or the oyster, *Saccostrea cucculata* (Table 4.4A). Only one biotope was identified in the top shore, characterised by bare rock colonised by littorinid gastropods (Table 4.4B).

Algal-dominated biotopes were more prevalent in the low shore than in the mid or high shore (Figure 4.2, Table 4.2). In Maputaland, more than 60% of all samples were algal-dominated and in Natal, just less than 50% of samples were algal-dominated. In the mid shore, less than 30% of samples were algal-dominated in both Maputaland and Natal. Of the high-shore samples, 27% were algal-dominated and sessile and mobile invertebrates (Figure 4.2, Tables 4.2-4.4) dominated the remaining samples. Algal dominants were absent in the top shore.

In the low shore, distinctly different biotopes were identified in Maputaland and Natal (Table 4.2). Only one of 40 low-shore biotopes was found in both regions, that dominated by the articulated coralline alga *Cheilosporum sagittatum* and distinguished by the foliar red alga *Plocamium corallorhiza* (biotope code = CsP see Table 4.2). In the mid shore, the separation of biotopes between Maputaland and Natal was also apparent. Three of the 21 mid-shore biotopes were found in both regions, all dominated by zoanthids (Table 4.3 PnZ, Pnt and Zs). In the high shore, four of the seven biotopes occurred in both biogeographic regions. One biotope was confined to Maputaland and was dominated by the foliose brown alga *Padina boryana* (Pb): two biotopes were identified only in Natal (i.e., *Enteromorpha* sp. (EsB) and bare rock with *Siphonaria* (BrS)). The single top-shore biotope occurred in both regions.

In Maputaland, the most predominant low-shore biotopes were those dominated by the foliose brown alga, *Sargassum elegans* and the articulated coralline alga *Cheilosporum sagittatum* (Figure 4.1). Approximately 16% of samples were dominated by the brown mussel, *Perna*

perna, a striking contrast with Natal, where more than 50% of the low-shore samples were dominated by *P. perna*. In Natal, there was only one other invertebrate-dominated biotope in the low shore. This was dominated by *Pyura stolonifera* but was represented by <1% of the low-shore samples in Natal and was only found at a single site (Zinkwazi Platform). In Maputaland, 7% of the low-shore samples represented a *Pyura*-dominated biotope and reefworm and zoanthid-dominated biotopes accounted for 10 and 5.5% of the low-shore samples respectively. In Natal, the most predominant algal-dominated biotopes were characterised by both foliar red algae, particularly *Hypnea spicifera*, and articulated corallines, particularly *Arthrocardia* and *Cheilosporum* species.

In the mid shore, zoanthid-dominated biotopes were well represented in both regions but more so in Maputaland where almost 50% of the mid-shore samples represented one of four zoanthid-dominated biotopes (Figure 4.1). In Natal, 44% of the mid-shore samples represented barnacle-dominated biotopes but only 19% of samples in Maputaland were barnacle-dominated. The proportion of samples of biotopes dominated by articulated coralline algae was greater in Natal (18%) compared to Maputaland (4%) but biotopes dominated by encrusting corallines were more abundant in Maputaland (22%) than Natal (<4%).

In the high shore, three algal-dominated biotopes were identified, two dominated by ephemeral algae (EsE, EsB) and the third dominated by the *Padina boryana* (Pb). The most predominant biotopes in the high shore were dominated by *Saccostrea cuccullata*, with (ScS) or without (Scb) the patellid limpet, *Scutellastra natalensis*.

Table 4.2. List of low-shore biotopes from rocky shores in (A) Maputaland and (B) Natal. Biotopes were objectively defined on the basis of an arbitrary 50% Bray Curtis cut-off using hierarchical cluster analyses of 760 samples from 38 sites. The dominant species and, where necessary, distinguishing species as determined by SIMPER are shown. The code reflects the initials of dominant and distinguishing taxa. The relative abundance (percentage of the total number of samples) of each biotope in each biogeographic region (n%) or in KwaZulu-Natal (n%KZN) and the number of sites (N) where each biotope was identified are shown.

Group	Biotope					
A. MAPUTALAND	**Dominant taxa**	**Distinguishing taxa**	**Code**	**n%**	**n% KZN**	**N site**
Green algae	*Caulerpa racemosa*		Cr	10.20	3.17	2
Brown foliose algae	*Sargassum elegans*	*Sargassum crassifolium*	SeS	4.59	1.43	2
		Caulerpa racemosa	SeCr	3.06	0.95	3
		Cheilosporum sagittatum	SeC	15.82	4.92	3
Encrusting corallines	Encrusting corallines	*Ralfsia* sp.	EcR	3.57	1.11	2
Articulated corallines	*Cheilosporum sagittatum*	*Perna perna*	CsPp	3.06	0.95	3
		Laurencia glomerata	CsL	4.59	1.43	2
		Plocamium corallorhiza	CsP	1.02	0.32	1
		Chamaedoris delphinii	CsC	13.27	4.13	4
Red algae	*Laurencia* sp.		Ls	3.06	0.95	2
Zoanthids	*Palythoa nelliae*	*Pyura stolonifera*	PnP	2.55	0.79	1
		Hymeniacedon sponge	PnH	3.06	0.95	2
Reefworm	*Idanthyrsus pennatus*		Ip	9.69	3.02	4
Mussels	*Perna perna*	*Laurencia glomerata*	PpL	10.20	3.17	1
		Tetraclita squamosa	PpT	5.81	1.75	2
Ascidians	*Pyura stolonifera*	Zoanthids	PsZ	6.63	2.06	2
Green algae	*Caulerpa filiformis*	*Jania verrucosa*	CfJ	3.23	2.22	4
		Sargassum spp.	CfS	1.15	0.79	2
Brown foliose algae	Ephemeral brown algae		Eph	1.15	0.79	1
	Sargassum elegans	*Laurencia natalensis*	SeL	2.53	1.75	1
		Perna perna	SeP	3.69	2.54	2
Encrusting corallines	Encrusting corallines	*Cheilosporum sagittatum*	EcC	0.69	0.48	1
Articulated corallines	*Jania verrucosa*	*Perna perna*	JvP	2.07	1.43	3
	Arthrocardia sp.	*Caulerpa filiformis*	AsC	1.61	1.11	1
		Hypnea spicifera	AsH	1.15	0.79	1
		Spyridea hypnoides	AsS	0.92	0.63	2
	Cheilosporum sagittatum	*Plocamium corallorhiza*	CsP	0.92	0.63	1
		Hypnea spicifera	CsH	5.53	3.81	3
		Spyridea hypnoides	CsS	1.61	1.11	2
Red algae	*Gelidium abbottiorum*		Ga	3.69	2.54	5
	Hypnea spicifera		Hs	11.29	7.78	9
	Plocamium corallorhiza		Pc	1.84	1.27	3
	Polysiphonia sp.		Po	0.69	0.48	1
	Spyridea hypnoides		Sh	3.69	2.54	3
Mussels	*Perna perna*	Bare rock / sand	Ppb	7.83	5.40	5
		Octomeris angulosa	PpO	15.67	10.79	10
		Hypnea intricata	PpH	2.53	1.75	2
		Arthrocardia sp.	PpA	2.30	1.59	1
		Jania sp.	PpJ	11.06	7.62	5
		Cheilosporum sagittatum	PpC	12.44	8.57	11
Ascidians	*Pyura stolonifera*	*Cheilosporum sagittatum*	PsC	0.69	0.48	1

Table 4.3. List of mid-shore biotopes from rocky shores in (A) Maputaland and (B) Natal. Biotopes were objectively defined on the basis of an arbitrary 50% Bray Curtis cut-off using hierarchical cluster analyses of 520 samples from 26 sites. The dominant species and distinguishing species as determined by SIMPER are shown. For details of notation, see caption of Table 4.2.

Group	**Biotope**					
A. MAPUTALAND	**Dominant taxa**	**Distinguishing taxa**	**Code**	**n%**	**n% KZN**	**N (sites)**
Encrusting corallines	Encrusting corallines	*Tetraclita squamosa*	EcT	21.84	7.20	5
Articulated corallines	*Jania adhaerens*	*Eudistoma coeruleum*	JaE	4.02	1.33	1
Zoanthids	*Palythoa nelliae*	*Tetraclita squamosa*	PnT	5.17	1.70	4
		Zoanthus sp	PnZ	29.89	9.85	8
	Palythoa natalensis		Pnt	2,87	0.95	3
	Zoanthus spp.		Zs	10.34	3.41	4
Wormshells	*Dendropoma tholia*		Dt	6.32	2.08	3
Barnacles	*Tetraclita squamosa*	*Hymeniacedon* sp	TrH	13.22	4.36	4
		Gelidium pristoides	TrG	6.32	2.08	1
B. NATAL						
Green algae	*Ulva* spp		Us	2,32	1.52	1
Encrusting brown algae	*Ralfsia* sp.		Ra	3.19	2.08	6
Encrusting corallines	Encrusting corallines	*Jania verrucosa*	EcJ	3.77	2,46	3
Articulated corallines	*Jania verrucosa*	*Laurencia natalensis*	JvL	13.91	9.09	9
		Pomatoleios kraussii	JvP	4.06	2.65	2
Anemones	*Gyractis excavata*		Ge	2.90	1.89	1
Zoanthids	*Palythoa nelliae*	*Zoanthus* sp.	PnZ	15.07	9.85	10
	Palythoa natalensis		Pnt	1.45	0.95	3
	Zoanthus spp		Zs	5.22	3.41	5
Reefworm	*Pomatoleios kraussii*		Pk	3.19	2.08	4
Barnacles	*Tetraclita squamosa*	Zoanthids	TrZ	2.03	1.33	1
	Tetraclita serrata		Ts	3.48	2.27	4
	Octomeris angulosa		Oa	19.71	12.88	11
	Tetraclita serrata	*Octomeris angulosa*	To	17.97	11.74	9
	Chthalamus dentatus		Cd	1.74	1.14	1

Table 4.4 List of (A) high and (B) top-shore biotopes from rocky shores in KwaZulu-Natal. As no biogeographic division was evident in these zones, KwaZulu-Natal was treated as a unit. Biotopes were objectively defined on the basis of an arbitrary 50% Bray Curtis cut-off using hierarchical cluster analyses of (1) 220 and (2) 130 samples from 22 and 13 sites respectively. The dominant and distinguishing species, as determined by SIMPER, are shown. For details of notation, see caption of Table 4.2

Group	**Biotope**				
A. HIGH SHORE	**Dominant taxa**	**Distinguishing taxa**	**Code**	**N%KZN**	**N (sites)**
Green algae	*Enteromorpha* sp	Ephemeral brown algae	EsE	1.61	1
		Siphonaria spp.	EsS	13,98	6
Foliose brown algae	*Padina boryana*		Pb	10,22	2
Bare rock with Limpets	Bare rock	*Cellana capensis*	BrC	3.76	2
		Siphonaria spp.	BrS	11.29	3
Sun oysters	*Saccostrea cucullata*	bare rock / sand	Scb	30.65	8
		Scutellastra natalensis	ScS	28,49	9

Bare rock	Bare rock	Littorinid gastropods	BrL	100	13

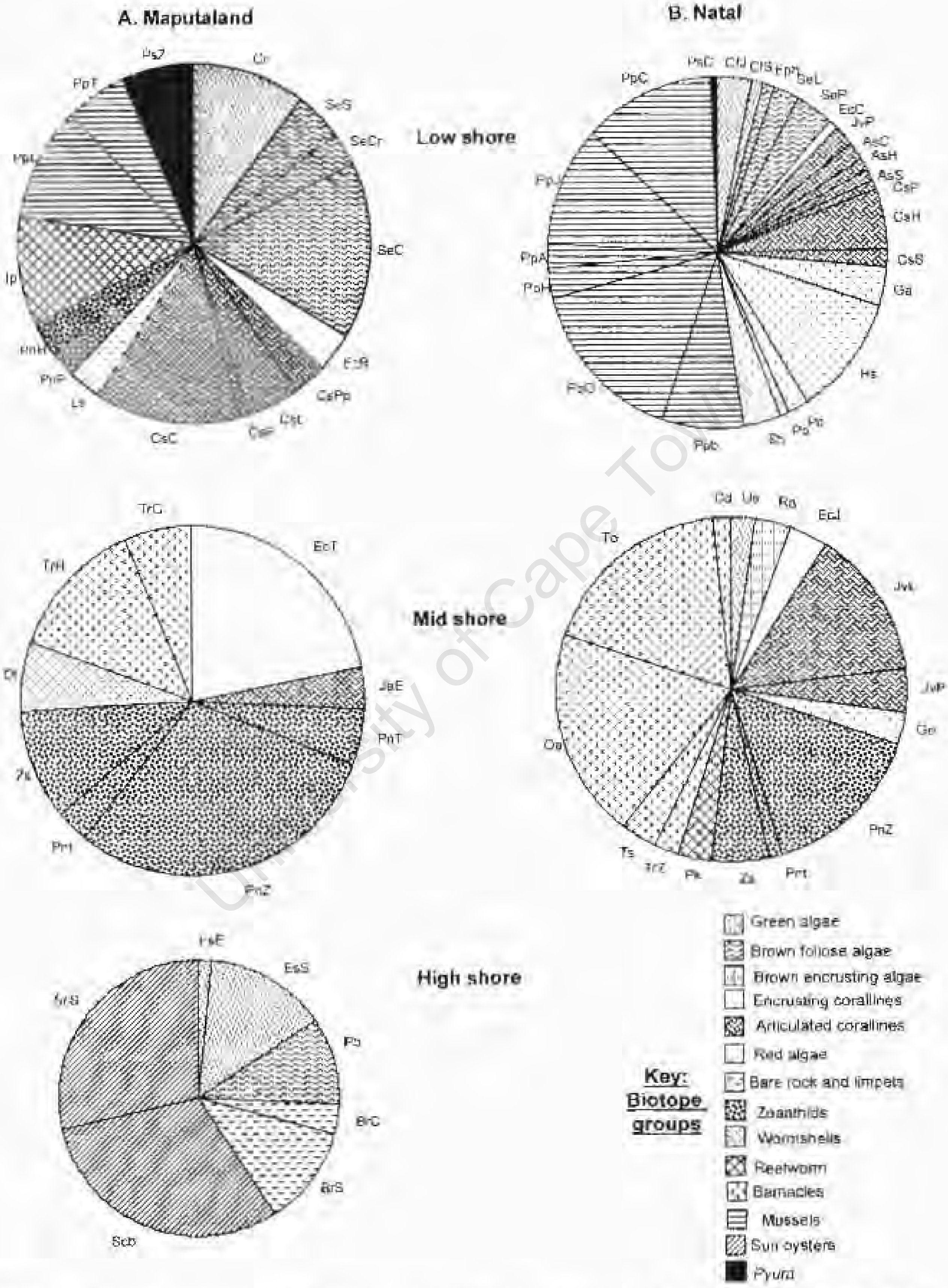


Figure 4.2. Relative abundance of different groups of biotopes in spatially defined zones in KZN. For the low and mid shore, the two biogeographic regions, Maputaland and Natal were analysed separately. As no biogeographic divisions were identified in the high shore, the entire KZN coast was treated as a unit for this zone. Codes reflect the names of specific biotopes as listed in Table 4.2-4.4.

2. Validating differences in community structure between biotopes

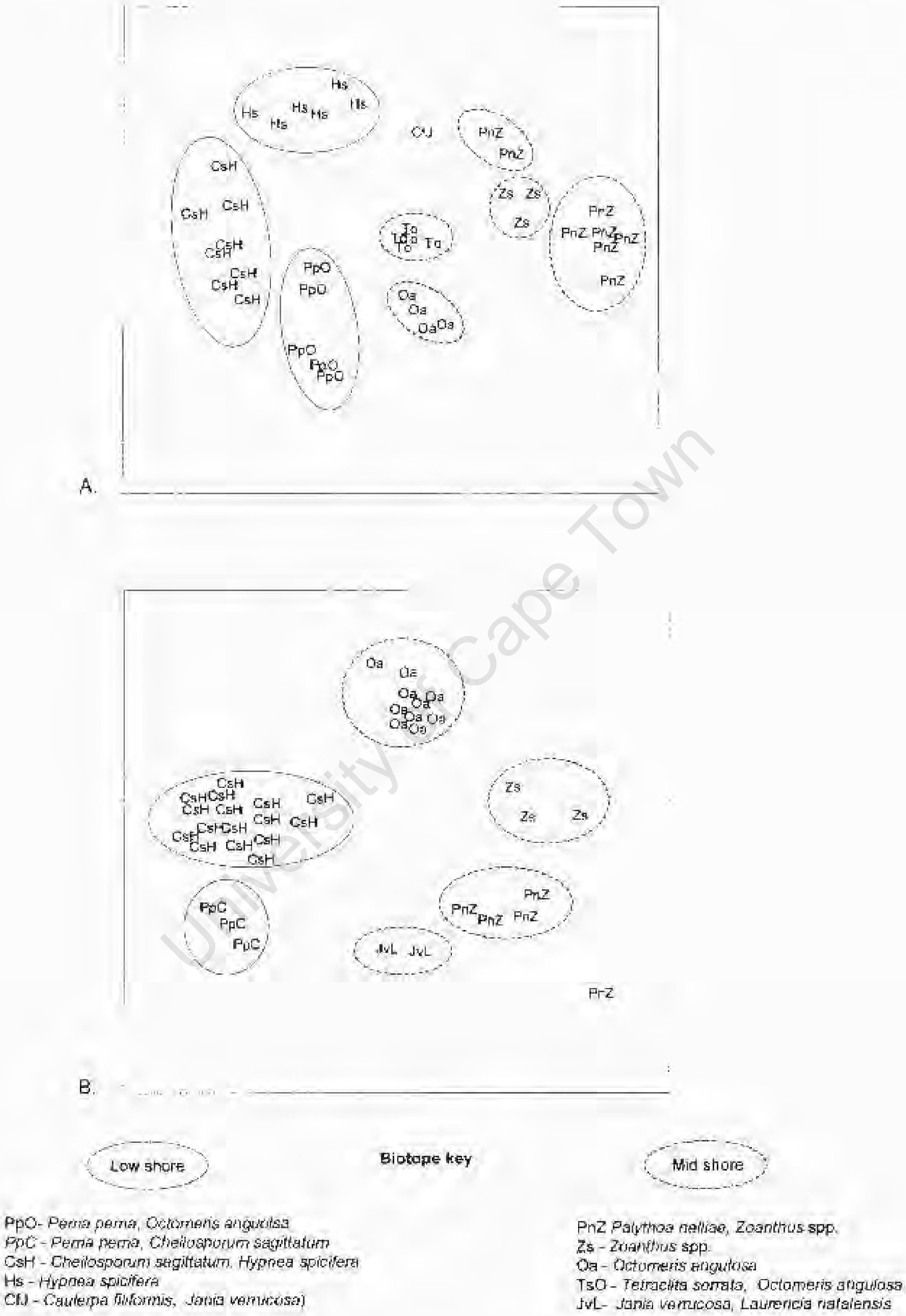
When the samples from Iti Bay and Groutville were identified by the classification system presented in Tables 4.2-4.3, ten different biotopes were recognised (Table 4.5A). In the low shore at Iti Bay, four biotopes were represented, one dominated by mussels (*Perna perna* – PpO) and three dominated by algae. Two of the latter were respectively dominated by the red alga *Hypnea spicifera* (Hs) and the biotope dominated by the articulated coralline alga *Cheilosporum sagittatum* (CsH). One sample of the biotope dominated by *Caulerpa filiformis* was identified but as there were no other replicate samples of this biotope, it was not subsequently compared with others. In the mid-shore, four biotopes were recognised, two dominated by the barnacles, *Tetraclita serrata* (Ts) and *Octomeris angulosa* (Oa), and two by the zoanthids *Palythoa nelliae* (PnZ) and *Zoanthus* spp. (Zs).

At Groutville, only two biotopes were evident in the low shore (Table 4.5B). The most common biotope was that characterised by the predominance of *Cheilosporum sagittatum*. The other biotope was dominated by *Perna perna* (PpC). The mussel-dominated biotopes at the two sites represented different biotopes distinguished by the additional presence of *Octomeris angulosa* and *Scutellastra aphanes* at Iti Bay and *Cheilosporum sagittatum* at Groutville. In the mid shore at Groutville, there were four biotopes. Two were zoanthid biotopes that also occurred at Iti Bay. One barnacle biotope was recorded, dominated by *O. angulosa* (Oa). The articulated coralline algae, Jania verrucosa dominated the final biotope, but this was not used in further analyses because of the small sample size. As there were no different biotopes dominated by the same species at either site the genus of the dominant characteristic species is used to refer to the respective biotopes hereafter.

Table 4.5. Biotopes that were identified in the low and mid-shore at (A) Iti Bay and (B) Groutville using the defined biotopes (Table 4.1). The code reflects initials of dominant and distinguishing species. The number of samples for each type of biotope is indicated (n).

Zone	**Group**	**Biotope**			
		Dominant taxa	**Distinguishing taxa**	**Code**	**n**
A. Iti Bay					
Low shore	Mussel	*Perna perna*	*Octomeris angulosa*	PpO	5
	Coralline algae	*Cheilosporum sagittatum*	*Hypnea spicifera*	CsH	9
	Red algae	*Hypnea spicifera*		Hs	6
	Green algae	*Caulerpa filiformis*		Cf	1
Mid shore	Zoanthid	*Palythoa nelliae*	*Zoanthus spp.*	PnZ	8
		Zoanthus natalensis		Zs	3
	Barnacle	*Octomeris angulosa*		Oa	4
		Tetraclita serrata		Ts	5
B. Groutville					
Low shore	Mussel	*Perna perna*	*C. sagittatum*	PpC	3
	Articulated corallines	*Cheilosporum sagittatum*	*Hypnea spicifera*	CsH	17
Mid shore	Zoanthid	*Palythoa nelliae*	*Zoanthus* spp.	PnZ	5
		Zoanthus natalensis		Zn	3
	Barnacle	*Octomeris angulosa*		Oa	9
	Coralline algae	*Jania verrucosa*	*Laurencia natalensis*	Jv	2

The classification of samples from Iti Bay and Groutville into biotopes on the basis of the classification scheme corresponded well with the grouping of samples in the MDS plot (Figure 4.3).



PpO- *Perna perna, Octomeris angulosa*
PpC - *Perna perna, Cheilosporum sagittatum*
CsH - *Cheilosporum sagittatum, Hypnea spicifera*
Hs - *Hypnea spicifera*
CJ - *Caulerpa filiformis, Jania verrucosa)*

PnZ *Palythoa nelliae, Zoanthus* spp.
Zs - *Zoanthus* spp.
Oa - *Octomeris angulosa*
TsO - *Tetraclita serrata, Octomeris angulosa*
JvL- *Jania verrucosa, Laurencia natalensis*

Figure 4.3. MDS plot based on root transformed biological data for the low and mid shore of (A) Iti Bay (stress = 0.14) and (B) Groutville (Stress =0.13). Samples were classified into different biotopes as based on dominant and distinguishing species. Groups of samples identified from cluster analyses are superimposed. For further description of biotopes refer to Tables 4.2- 4.3.

Substantial within-site differences in community structure were evident between and within the low and mid shore. There were distinct clusters of different biotopes evident at both sites and biotope samples from the low shore were completely different from those in the mid shore at both sites (Figure 4.3).

Differences within and between zones

Within each zone, there were significant differences in species composition and abundance between independent groups of samples representing different biotopes (global tests, Table 4.6). Pair-wise tests also reflected significant differences in community structure between samples recognised by the classification scheme as representing different biotopes. At both Iti Bay and Groutville, there were significant differences between all pairs of low-shore biotopes (Table 4.6). In the mid shore at both sites, all biotopes compared had large differences in community structure (R=0.63-1.00, Table 4.6), with one exception: the two biotopes dominated by different zoanthid species, *Palythoa* and *Zoanthus* were not significantly different at Iti Bay (p=0.07). At Groutville, however, there were large significant differences between the same two zoanthid biotopes (R=1).

One-way ANOSIM tests revealed highly significant differences in community structure between zones (Table 4.6) at both Iti Bay (R=0.727) and Groutville (R=0.673). Pair-wise tests revealed large differences in community structure between all biotope-pairs from different zones on the shore at both sites (R≥0.97).

Table 4.6. Results of global and pair-wise ANOSIM tests (R) between samples of different biotopes between and within the low and mid shore at (A) Iti Bay and (B) Groutville. Some biotopes were not found at Groutville as indicated by blank cells in the table. Biotopes identified at either site but represented by small sample sizes (N<3) were excluded from the analysis. * Denotes significant difference (p<0.05).

Within zones	**Contrasting biotopes**	**A. Iti Bay**			**B. Groutville**		
		R	p	n	R	p	n
Low shore	**Global test**	0.908	<0.002*	19	0.892	0.001*	20
	Perna – Cheilosporum	0.770	0.0008*	13	0.892	0.001*	20
	Perna – Hypnea	1.000	0.002*	11			
	Hypnea - Cheilosporum	0.927	0.0003*	14			
Mid shore	**Global test**	0.753	<0.001*	20	1.000	0.002*	20
	Palythoa - Zoanthus	0.382	0.07	11	1.000	0.002*	18
	Palythoa - Octomeris	0.636	0.004*	12	1.000	0.001*	14
	Palythoa - Tetraclita	0.892	0.001*	13			
	Zoanthus - Tetraclita	1.000	0.018*	8			
	Zoanthus - Octomeris	1.000	0.029*	7	1.000	0.006*	12
	Tetraclita - Octomeris	1.000	0.008*	9			
Between zones	**Global test**	0.727	<0.0002*	40	0.673	<0.0002*	40
	Perna - Palythoa	0.988	0.0008*	13	1.000	0.002*	8
	Perna - Zoanthus	1.000	0.018*	8	1.000	0.006*	6
	Perna - Octomeris	0.970	0.006*	9	0.970	0.006*	12
	Perna - Tetraclita	1.000	0.008*	110			
	Cheilosporum – Palythoa	0.996	0.004*	16	1.000	<0.0002*	22
	Cheilosporum - Zoanthus	1.000	0.006*	11	1.000	0.001*	20
	Cheilosporum - Octomeris	0.996	0.002*	12	1.000	<0.0002*	26
	Cheilosporum - Tetraclita	1.000	0.001*	13			
	Hypnea - Palythoa	0.975	0.0003*	14			
	Hypnea – Zoanthus	1.000	0.012*	9			
	Hypnea - Octomeris	1.000	0.005*	10			
	Hypnea - Tetraclita	1.000	0.002*	11			

3. Testing for significant differences in diversity between biotopes

There were significant differences between biotopes in terms of species richness and diversity as measured by the Shannon index, the evenness index and in the reciprocal of Simpson's dominance index (Table 4.7). The mean values of each index for each biotope are shown in Figure 4.4 and the results of post-hoc Tukey tests are indicated on the figure.

Table 4.7. Results of 1-way ANOVA testing for significant differences in species richness (S), Shannon diversity (H'), Evenness (J') and Reciprocal dominance (1/Sdi (Simpson's dominance index) between biotopes. * Denotes significant difference ($p<0.05$).

Index	df	Ms effect	F	p
S	6	450.27	77.51	<0.00001*
H'	6	1.40	34.31	<0.00001*
J'	6	0.51	11.91	0.00008*
1/ Sdi	6	24.23	41.16	<0.00001*

Differences within and between zones

Different biotopes from the same zone on the shore did not necessarily differ in diversity (Figure 4.4). In the low shore, all three biotopes failed to differ significantly in terms of species richness. However, the relative proportions of species did differ between biotopes within zones. *Hypnea* was more diverse than *Perna* or *Cheilosporum* according to the Shannon and evenness indices and particularly the reciprocal dominance index. In the mid shore, *Octomeris* and *Jania* biotopes were more speciose than *Palythoa* although the other indices revealed that *Octomeris* was more diverse than *Palythoa* and *Jania* because evenness was greater and there was much less dominance.

Species richness and Shannon diversity generally declined with increasing shore height but differences in evenness and dominance were less apparent between biotopes from different zones (Figure 4.3). Low-shore biotopes were more speciose than mid-shore biotopes and generally were more diverse than biotopes in the mid and high shore. Two of the three mid-shore biotopes had significantly higher species richness than the high-shore biotope. The low-shore *Hypnea* biotope was the most diverse community according to all diversity statistics and this was particularly reflected by reciprocal dominance.

The oyster biotope in the high shore was the least diverse according to estimates of species richness and Shannon diversity but estimates of reciprocal dominance indicated that the mid-shore biotopes, *Palythoa* and *Jania*, had the highest dominance and were therefore less diverse although the differences between these three biotopes were insignificant. The estimates of reciprocal dominance and evenness often failed to detect differences between the biotopes in all three zones.

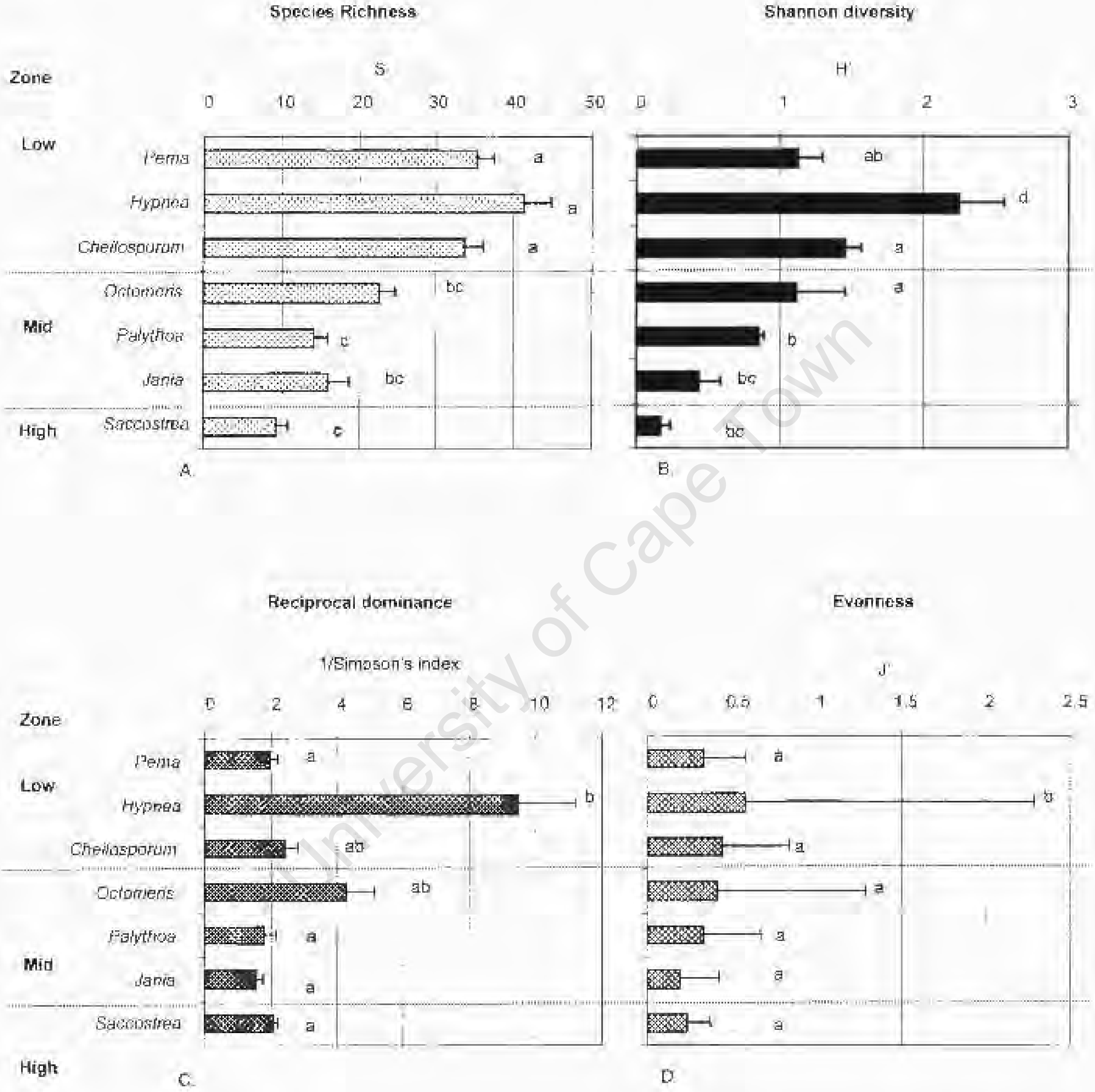


Figure 4.4. Mean and standard deviation of (A) Species Richness, (B) Shannon diversity, (C) Reciprocal dominance (Simpson's index) and (D) evenness for a subset of biotopes in KZN. Estimates are based on 3 sites, with cumulative values of diversity indices based on 10 samples from each site. Biotopes that are not significantly different (Tukey HSD test, p>0.05) share the same letter.

4. Assessing the conservation status of intertidal biotopes in KwaZulu-Natal

The current conservation status of all biotopes in KwaZulu-Natal is shown in Figures 4.5 and 4.6. Of the 69 described biotopes, only 19 occur within fully protected marine protected areas, seven of which are conserved in Trafalgar Marine Reserve and 12 in St Lucia Marine Reserve. Of the 50 remaining biotopes, 18 are "partially protected" in that they occur within Maputaland Marine Reserve, where rocky shores are subject to intensive exploitation by subsistence fishers. In the low shore, 21 of the 40 biotopes are completely unprotected and 11 of the 21 mid-shore biotopes were not included in any marine protected areas. In the high shore, three out of the seven biotopes were unprotected, two were partially protected and two were fully protected. Only one biotope was described for the top shore and was represented in fully protected marine protected areas.

5. Testing the utility of biotopes in evaluating proposed marine protected areas

On the basis of the 4 sites surveyed, establishment of the Pondoland Marine Park would yield at least a 24% improvement in the conservation status of intertidal biotopes in KwaZulu-Natal (Figure 4.6). By comparison, the proportion of fully protected biotopes could be increased by at least 31% if the St Lucia Marine Reserve is expanded. If both proposed marine protected areas are established, the combined improvement is at least 41% with only three biotopes from Natal remaining unprotected (CsP- *Cheilosporum* with *Plocamium*, PpA - *Perna* with *Arthrocardia* in the low shore and Us - *Ulva* spp. in the mid shore, Table 4.3). There are 15 biotopes in Maputaland that are partially protected but exploited and the establishment of additional marine protected areas in the Natal biogeographic region cannot protect these

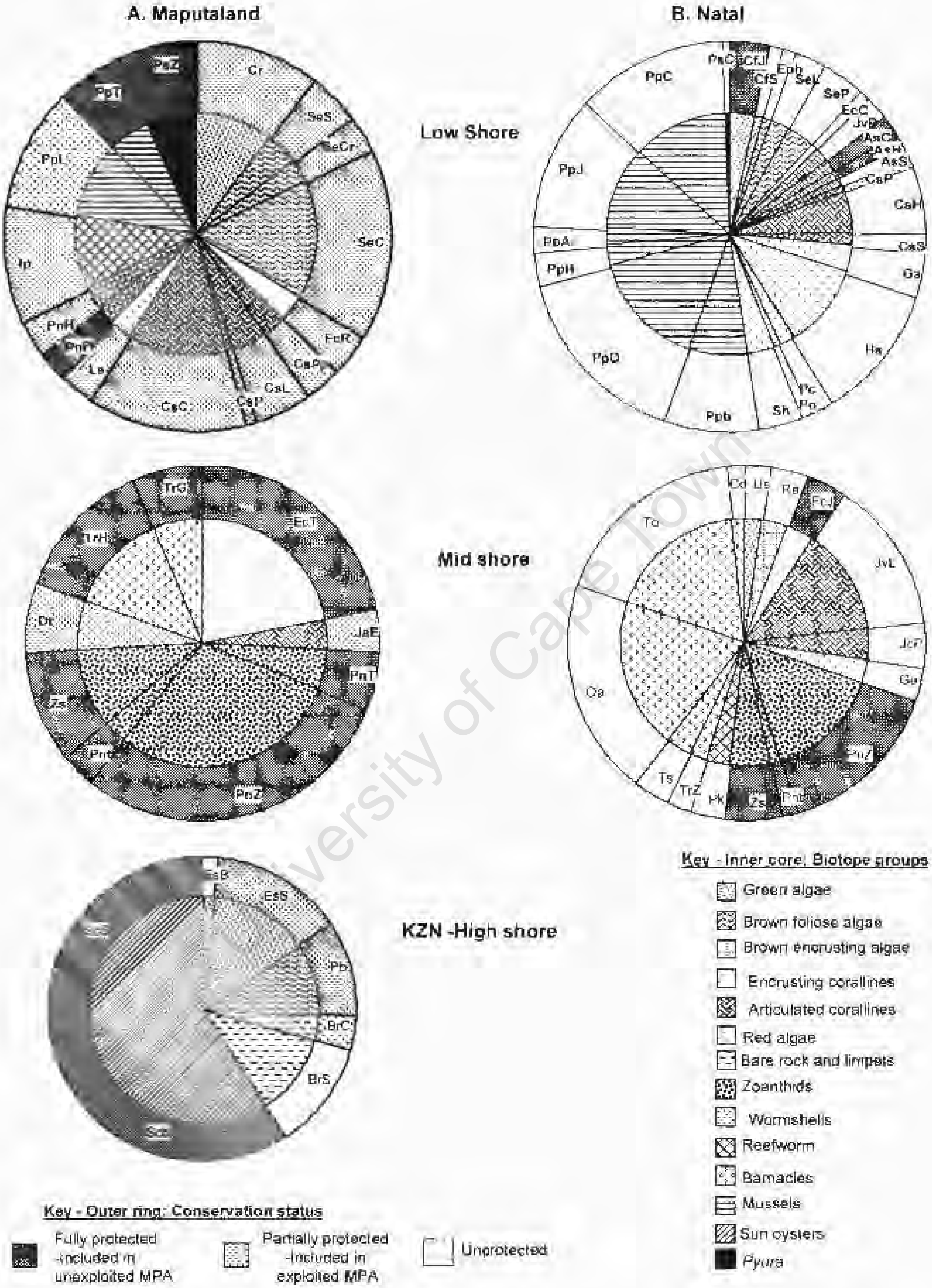


Figure 4.5 Pie charts showing the relative abundance(inner ring) and conservation status (outer ring) of the different biotope groups and specific biotopes in KZN. For the low and mid shore, the two biogeographic regions, Maputaland and Natal were analysed separately. As no biogeographic divisions were identified in the high shore, the entire KZN coast was treated as a unit for this zone. Codes reflect the names of specific biotopes listed in Tables 4.2-4.3.

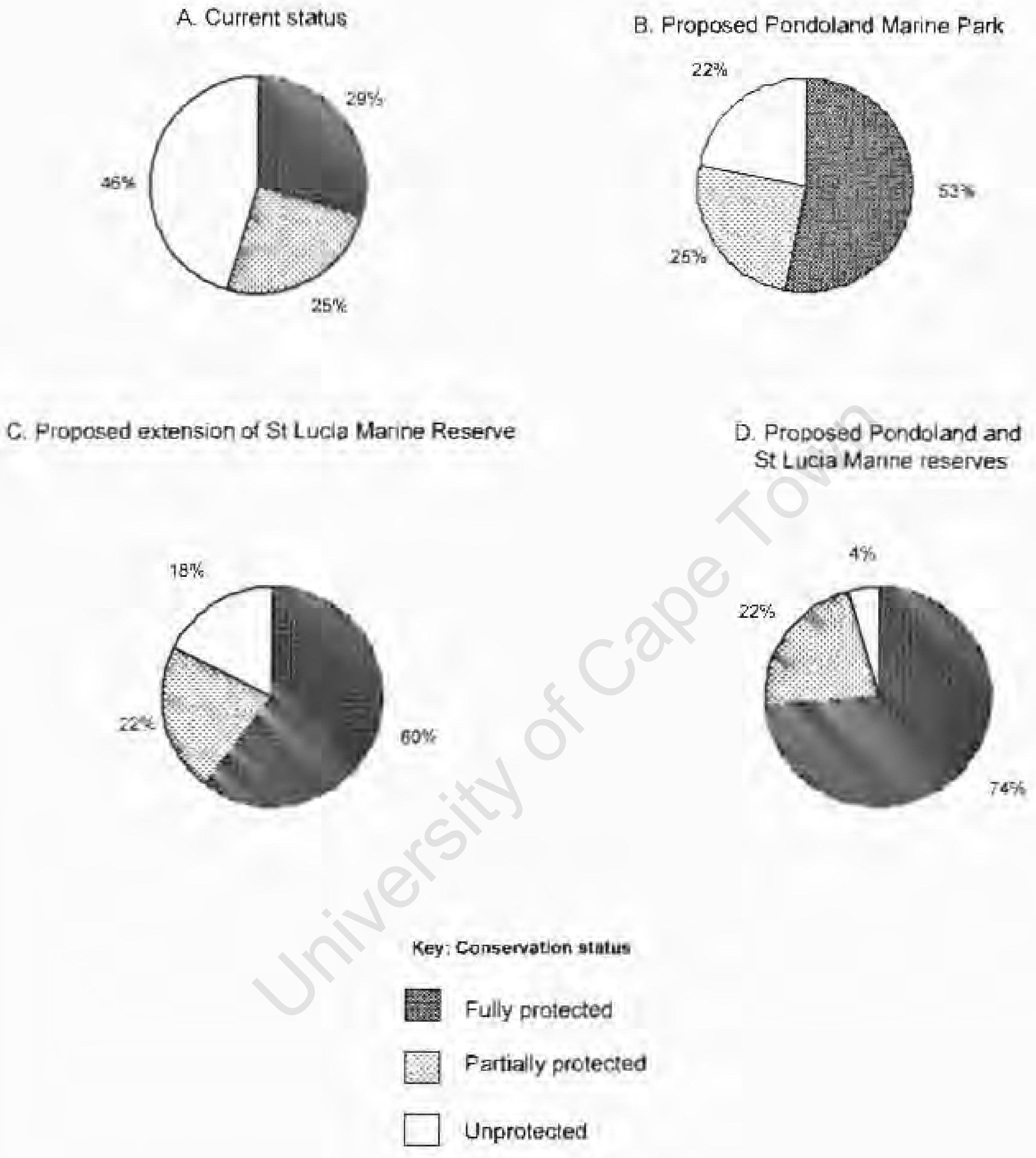


Figure 4.6. The conservation status of intertidal biotopes in KZN with (A) current MPAs, (B) if the proposed Pondoland Marine Park is established, (C) if the St. Lucia Marine Reserve is extended to the St Lucia lighthouse and (D) if both new MPAs are established. This assessment was used to demonstrate the utility of the biotope classification for conservation planning and was based on insufficient data to fully evaluate the proposed MPAs.

Discussion

The biotope classification system described by my study successfully captured small-scale (1-10 metres) differences in species composition and abundance between zones as well as within-zone horizontal variability in community structure on rocky shores in KwaZulu-Natal. This is the first set of data to provide quantitative descriptions of local-scale biological variability for rocky shores over a large geographic area in southern Africa. While multi-dimensional scaling and ANOSIM tests validated the biotope classification system at two independent sites, most biotopes failed to differ significantly in terms of four univariate diversity indices. The use of biotopes was shown to be effective in assessing the representativeness of the current system of protected areas and was also tested as a means of comparing proposed new protected areas. Clearly, biotopes can be used as an efficient tool for future conservation planning.

Patterns in biotope distribution

Biogeographic patterns

The results from this study support the biogeographic division at Cape Vidal identified during the large-scale biogeographic analysis conducted in Chapter 2 (Figures 2.5 and 2.6, see p 39-40). In the low shore, distinct biotopes were identified in the two recognised biogeographic regions, Maputaland and Natal. Only one biotope was found in both Maputaland (at Black Rock) and Natal (Umfazazana), characterised by *Cheilosporum sagittatum* and *Plocamium corallorhiza*. In the mid shore, biogeographic differences were also evident with only the zoanthid-dominated biotopes occurring in both regions. As in Chapter 2, there was little evidence of biogeographic differences in the high shore as more than half of the identified biotopes were found in both Maputaland and Natal. The single top-shore biotope occurred in both provinces.

Zonation patterns

Similar vertical zonation patterns were observed to those described by Bustamante et al. (1997) on the South African south and west coasts. Mussels and algae were characteristic on the low shore and barnacles on the mid shore. In KwaZulu-Natal, unlike the south and west coasts, zoanthids were an important component of mid shore communities (see also Chapter 3 and 4). This contrasts with the findings of Jackson (1976) who considered zoanthids part of a *Hypnea* zone below the mussel zone on the low shore. In KwaZulu-Natal, the low and mid shore is dominated by filter feeders and autotrophs, grazers become more prevalent higher up the shore. Hily and Jean (1997) observed a different trophic pattern between zones in Brittany, France. There, suspension feeders and herbivores dominate the high shore and carnivores are dominant in the low shore. The fact that the number of biotopes in the low shore was almost double that in the mid shore, which was in turn more than double that of the high shore, reflects convergence in community structure with increasing elevation. Only one biotope was recognised in the top shore, as all samples were more than 50% similar in terms of Bray-Curtis similarity. This pattern was also evident at the scale of 100's of kilometres (Chapter 2) and tens of kilometres (Chapter 3) and the reasons for high shore convergence were discussed in earlier chapters. Connor et al. (1995) also identified more biotopes in the low shore compared with the upper shore in rocky intertidal habitats in Britain and Ireland.

There were greater differences in community structure between biotopes within zones (as reflected by global tests) than between zones when all low shore samples were contrasted with all mid shore samples (Table 4.6). However, pair-wise tests indicated that differences in community structure were generally greater between samples representing biotopes from different vertical zones than those representing biotopes from within the same zone. Nevertheless, at both sites, some contrasting biotopes from the same zone had differences in community structure equivalent to those between biotopes from different zones. These results indicate that horizontal variability in community structure can equal vertical variability on rocky shores.

Comparisons with other biotope classifications

In KwaZulu-Natal, Lambert and Steinke (1986) defined five communities on the basis of 44 taxa and 200 quadrats surveyed at a single site (Umdoni Point). These communities were named according to dominant species: Coralline Community, *Perna perna*, *Ralfsia expansa*, *Tetraclita serrata* and Littorinid –Cyanobacteria and were considered to occur within separate "vertical" zones on the shore. In my study, all five of these communities were recognised along with many others. Lambert and Steinke (1986) did not describe divergence in community structure within physical zones on the shore and my study is the first to quantitatively describe small-scale horizontal differences in species composition and abundance in KwaZulu-Natal. There were 69 different biotopes described in my study (Tables 4.2, 4.3, 4.4). By comparison, the Marine Nature Conservation Review (MNCR) listed 68 littoral biotopes for rock and mixed substrata in the BioMar classification for Britain and Ireland (Connor et al. 1997). The description of many biotopes is necessitated by the complex nature of intertidal habitats which are characterised by sharp environmental gradients over short distances, a high degree of patchiness and significant differences in community structure between and within biogeographic regions (Dethier 1990, Connor et al. 1995, Hiscock 1995, Chapters 2 and 3 of my study). In order to incorporate this variation, a relatively fine sampling scale (grain) was employed.

Many classifications have drawn criticism for failure to incorporate the variability between high and low shore (Schoch and Dethier 1996). By covering four different zones in my classification, differences in community structure between zones were successfully incorporated into my classification system. However, the different biotopes described in my study do not imply that the communities are discrete in space (or time), boundaries between biotopes may be sharp or gradual.

The use of the objectively defined classification system to group samples into different biotopes was successful. This was evidenced by the close agreement between clusters of samples in the MDS plot and groups of samples that were independently recognised as distinct biotopes using the biotope classification system at two independent sites. Furthermore, ANOSIM tests (Table 4.6) revealed highly significant differences in community structure between groups of independent samples representing contrasting biotopes at both Iti Bay and Groutville. These differences were evident both within and between zones reflecting the incorporation of vertical and horizontal variability in community structure.

The strength of the classification system presented here is the rigorous, quantitative and objective approach. In my study, 1 630 quadrats from 38 shores were used to describe the biotopes. Only quantitative data were used while many other classifications are based on semi-quantitative data (Connor et al. 1995) or presence/absence data (Zacharias et al. 1998). Existing classification systems have also drawn criticism for their limited spatial extent (Day and Roff 1998). My classification covered many sites spanning 560km and therefore incorporates the entire province under the jurisdiction of KwaZulu-Natal Wildlife, the management agency responsible for conservation planning in that region.

The biotopes in my analyses were defined solely on the basis of mathematical analyses. In contrast, the BioMar biotopes were defined using a combination of ordination techniques and human expertise (Hiscock 1990). However, the BioMar classification has been criticised for subjectively defining biotopes and Zacharias et al. (1999) pointed out that some of the biotopes probably could not be identified by quantitative analysis and were artefacts of human interpretation. In my study, the arbitrary 50% dissimilarity used to distinguish biotopes avoided the rejection of groups of samples that do not correspond with pre-conceived ideas, a criticism of the BioMar system (Hiscock 1995). Furthermore, my biotopes proved identifiable in the field and were robust when independently tested. The fact that there were highly significant differences in community structure in 20 of the 21 comparisons between groups of samples representing different biotopes justified the method used to distinguish biotope groups. Only samples representing the two types of zoanthid biotopes failed to differ significantly in terms of species composition and abundance, and then only at one of the two sites where these two biotopes were compared. This indicates that the classification system may not effectively distinguish communities that include relatively high cover of the same species. In all other comparisons of species composition and abundance between samples representing contrasting biotopes, highly significant differences in community structure were evident.

Dethier (1990) remarked that the ideal classification should seek uniformity of organisms within a stand and that the only way to achieve this ideal is to make small patches of organisms the first unit of a classification system. In this study, a 1m x 0.5m quadrat was used for sampling. If a smaller quadrat had been used, a finer scale of biological communities might have been identified. Dye (1992, 1993) recognised small-scale (10-50cm) patchiness on unexploited rocky shores in the Transkei. Shores there are often characterised by mosaics of mussel clumps interspersed with patches of crustose algae and large territorial patellid limpets that maintain algal crusts and filamentous turfs (Dye 1992).

The term biotope was defined by Connor et al. (1997) as the combination of physical habitat together with its recurring associated biological community. The different biotopes presented in this chapter were not examined for corresponding differences in physical habitat. The lack of association between communities and habitat characteristics is a common shortcoming of existing classifications (Schoch and Dethier 1997, Zacharias et al. 1999). However, in Chapter 5, habitat characteristics of a subset of contrasting biotopes are investigated at three sites to test whether the biologically-defined biotopes recognised here do experience different physical conditions.

Biotopes can be used to assess the presence or absence of "communities" and thus evaluate the conservation status of different assemblages. They can also be used to monitor communities (see Chapter 6 where community changes due to experimental harvesting are captured by biotope surveys). Furthermore, biotopes can do this more efficiently than inventories of species, because the latter require a huge (and often destructive) sampling effort. Biotope surveys can be conducted quickly and are therefore an effective and inexpensive method to assess representativeness of biodiversity or monitor community change. The original surveys conducted to record species composition and cover (as described in Chapter 2 methods) took at least five hours to survey 60 quadrats (one sites), and a single site could not be surveyed over any one low tide. To survey more than one site in an area entailed several trips usually over more than one spring tide period. By comparison, biotope surveys using the classification scheme took, at most, twelve minutes for the same number of quadrats per site and three sites could be surveyed in a single low tide. Therefore biotope surveys are far less labour-intensive and cheaper to conduct because they involve much less travelling. Biotope surveys also require a relatively low level of taxonomic expertise and biotopes can be recognised by people with minimal training. Biotope surveys could also be conducted using photographic transects for later identification of biotopes.

Differences in diversity between biotopes

Although one-way ANOVA revealed significant differences in values of four diversity indices between different biotopes, there were several biotopes that failed to differ significantly in terms of diversity. These biotopes were from the same or different zones on the shore. Biotopes from the low shore were more speciose than those from the mid or high shore. This reflects the convergence of communities in the high shore, as discussed earlier. While species richness showed zonational patterns, other diversity indices did not differ between zones. Diversity as measured by the Shannon Wiener index encompasses two aspects: the number of species and the relative abundance of those species. Whereas height on the shore influenced species richness, differences in dominance (as measured by the Simpson's dominance index) were not evident between zones.

One of the central criticisms of the use of diversity indices for conservation planning is that these indices can be particularly susceptible to sampling bias (Pielou 1975, Magurran 1988, Soetaert & Heip 1990, Grassle and Maciolek 1992). In chapter 2, results from a pilot study revealed that sample size exerts a significant influence on diversity estimates for intertidal communities in KwaZulu-Natal. Cumulative estimates of species richness for macro-organisms indicated that 10 samples were insufficient and that 20 samples are appropriate for estimating species richness of low- and mid-shore communities at any one site. In this chapter, estimates were based on only 10 samples but three sites were examined for each biotope. The estimates of diversity in this study were comparable because the same sampling effort was used for each biotope.

The pilot study (Chapter 2, p 28-30) revealed that Shannon diversity oscillated with increasing sampling effort and these oscillations were related to dominance. Rocky shores typically exhibit a high degree of patchiness with variability associated with changes in dominance along gradients (Dethier 1990). This phenomenon diminishes the usefulness of some diversity indices in describing intertidal communities. It is probable that Shannon diversity curves may not stabilise even when extreme sampling intensities are applied because of the frequent fluctuations in dominance within some communities.

The indices used to explore diversity in this study are univariate measures of some aspect or aspects of community structure. In effect, these indices collapse a full set of species abundance data into a single co-efficient. This results in the loss of a great deal of information. Community data is inherently highly multivariate and is best analysed with multivariate techniques (Clarke and Warrick 1994). My study revealed that some communities that are more than 50% different in terms of Bray-Curtis similarity failed to differ significantly in terms of species richness, Shannon diversity, reciprocal dominance and evenness. Other comparisons of multivariate and univariate descriptions and tests in analysis of community data also revealed that multivariate methods are more sensitive and have superior discriminating ability to their univariate counterparts (Clarke and Warrick 1994, Gray 2000).

The problems inherent in the use of univariate indices for examining diversity highlight the need for alternative ways to measure biodiversity. Biotope classifications can capture biological variability where univariate indices fail and their value in comparing areas for conservation planning is established below.

Application in conservation planning

The future of biodiversity conservation is dismal if habitat loss and extinction continue unchecked (Pimm et al. 1995, Pimm and Raven 2000). Calls have been made for rationalisation of conservation efforts and two opposing strategies for identifying priority areas for biodiversity conservation have been recognised. The "hotspot" approach calls for protection of areas with high species diversity and endemism (Myers 1988, 1990, Reid 1998, Myers et al. 2000). Myers et al. (2000) call for a "silver-bullet" strategy where conservation efforts focus only on biodiversity hotspots and criticise the "traditional scatter gun" approach of conservation efforts. Myers (2000) excluded marine habitats from an analysis of global hotspots for biodiversity conservation priorities. However, Pimm and Raven (2000) comment that fish and other marine organisms also show an uneven and highly clumped distribution of vulnerable species and therefore advocate selection of priority areas using a hotspot approach to conserve species-rich areas (e.g., coral reefs).

The hotspot approach can be criticised on several grounds. Firstly, areas with high species diversity or endemism do not in themselves mean a region or habitat is more important to conserve than any other (Magurran 1988). In marine ecosystems the problems with such an approach are clear. More productive areas that support fisheries can have relatively low species richness (Bustamante and Branch 1996a). Failure to include such productive areas in conservation strategies is short-sighted. Secondly, many diverse marine habitats depend on trophic subsidies from other systems (Bustamante et al. 1995a, Bustamante and Branch 1996b, de Boer 2000b) and so effective conservation of the more diverse habitat may depend on conservation of less diverse habitats in an ecosystem. Incorporation of ecosystem processes in conservation planning is a major challenge for ecologists (Cowling and Heijnis 2001). Thirdly, species data sets are localised in many parts of the world and therefore cannot be used over large geographical scales for assessments of established protected areas or future conservation priorities (Margules and Austin 1994, Pressey et al. 2000). Furthermore, because a reliable estimate of the species richness of any habitat or area can only be achieved if the *entire* extent of the habitat or assemblage is measured (Gray 2000), the use of species-based approaches in determining conservation priorities is flawed. The inherent problems in assessing areas in terms of biological richness have encouraged the examination of habitat diversity as a proxy for biological diversity (Pressey et al. 2000).

Hockey and Branch (1994, 1997) and Roberts et al. (in press a, b) recommend a hierarchical approach in prioritising marine conservation efforts. Firstly, biogeographic regions should be represented within any marine protected area network, and then representative habitats within respective biogeographic regions should be incorporated. Hockey and Branch (1997) advocate the use of habitat heterogeneity to evaluate prospective marine reserves. My biotope classification, with the description of local-scale biological variability over large areas allows a higher resolution of habitats than we have been capable of in the past.

At present, only 21 of the 69 described biotopes are represented within fully protected marine protected areas. Of the remainder, 17 are included in Maputaland Marine Reserve where subsistence-harvesting is allowed on all shores. The remaining 31 biotopes, almost half of all biotopes described are not included in any marine protected areas. Most of these are biotopes that were only found in the Natal biogeographic region, where only 2 km of wave-sheltered shore is protected in the Trafalgar Marine Reserve. Of the 37 biotopes that were found only in Natal, only seven were included in the fully protected Trafalgar Marine Reserve. In Natal, the three low-shore biotopes that are conserved are relatively uncommon, comprising less than 4% of the Natal low-shore samples considered in this study. All three biotopes are algal-dominated with green foliar or articulated coralline algae constituting the dominant species. The more representative mussel and red-algal dominated biotopes were not included in any marine protected areas. Currently, no mussel communities are conserved in Natal because of the absence of protected areas covering wave-exposed shores that are the principal habitat of mussels. Similarly, in the mid shore, only zoanthid-dominated biotopes are included in Trafalgar Marine Reserve whereas the more abundant barnacle-dominated biotopes remain unprotected.

Biotopes were used to assess how additional marine protected areas may improve the effectiveness of rocky-shore conservation in KwaZulu-Natal. This revealed that the biotope classification system can serve as an effective tool for conservation planning, including between-site comparisons for protected area selection. In my study, the relative conservation status of biotopes was compared for the proposed Pondoland Marine Park and the proposal to extend St Lucia Marine Reserve (Figure 4.1). The conservation status of biotopes could be improved by 24% if the Pondoland Marine Park is established or by 31% if the St Lucia Marine Reserve is extended (Figure 4.6). The relative improvement of biotope conservation for these proposals is comparable because both were based on equal sampling effort. If only a single site had been considered in the proposed Pondoland Marine Park, the results would have indicated an improvement of conservation status of only 6%. This indicates that standardisation of number of samples and sites is vital if two areas are to be compared. The greater proportion of biotopes within the proposed expansion of the St Lucia Marine Reserve may be related to the greater habitat heterogeneity there compared to the sites examined on the south coast. The sites between the current St Lucia Marine Reserve southern boundary and the St Lucia lighthouse include heavily sand inundated and lightly-sanded shores whereas the sites within the proposed Pondoland Marine Park all appear to be uniformly lightly-sanded.

If both new marine protected areas were established, the proportion of fully protected biotopes would increase by 41% and only three Natal biotopes would remain unprotected. Two of these, dominated by *Pyura stolonifera* and *Ulva* sp. respectively, were each only found at one site, the very wave-sheltered Zinkwazi Platform and Reunion Rocks on the Durban Bluff respectively. The third, dominated by the articulated coralline alga *Cheilosporum sagittatum* (CsP), was found in Natal only at Umfazazana, a subsistence-exploited site, but is also present at subsistence-exploited sites in Maputaland. Currently, 60% of the biotopes that were found only in Maputaland are only "partially protected" (i.e., included in a marine protected area but subject to exploitation). Establishment of either or both of the proposed new marine protected areas in Natal will not change this. Only the conservation status of two high-shore biotopes will change from "partially protected" to "fully protected" if the additional protected areas are established. On the other hand, installing no-take zones within representative sites in the Maputaland Marine Reserve could protect all the low and mid-shore biotopes.

In Maputaland, only three of the 16 low-shore biotopes were represented at unexploited sites. These biotopes each constituted less than 7% of the low-shore samples in Maputaland. All three include important resources as dominant species, either *Perna perna* or *Pyura stolonifera*, and were confined to unexploited sites in the St Lucia Marine Reserve (Sodwana and Cape Vidal Points). An additional mussel-dominated biotope comprising *Perna perna* with *Laurencia glomerata* was only found at the wave-exposed Island Rock, which is generally inaccessible although harvesters have been known to collect mussels there in the past (M. Bouwer, KwaZulu-Natal Wildlife pers. comm.). Some of the more abundant biotopes in Maputaland, such as those dominated by *Sargassum elegans* and *Cheilosporum sagittatum*, were confined to sites that were heavily exploited by subsistence harvesters. The lack of mussel and *Pyura*-dominated biotopes at exploited sites suggests that human impact may have eliminated the naturally occurring mussel and *Pyura*-dominated biotopes and that at present the Maputaland Marine Reserve may be supporting communities that have been transformed by intensive harvesting. This conforms with the findings of Chapter 3 where harvesting was found to modify community structure in the Maputaland region.

In South Africa, marine protected areas collectively incorporate 17% of the South African coastline with 4.9% receiving complete conservation (Attwood et al. 1997). Ballantine (1997) recommends that 10% of any region should be fully protected to conserve biodiversity but that 20-30% is required to achieve indirect effects (i.e. stock resilience and seeding to adjacent areas). In KwaZulu-Natal, only 4% of our coastline is fully protected, highlighting the necessity of additional representative marine protected areas that are closed to all forms of harvesting. This is critical for preservation of biodiversity and for assessing human impacts on coastal ecosystems.

Protecting rocky shores without protecting adjacent subtidal systems may fail to conserve rocky shore biotopes because the ecosystem linkages between the systems will not be protected (Roberts et al. in press a). In KwaZulu-Natal, shore-angling is permitted in the whole of the Maputaland Marine Reserve. Only 22km in the St Lucia Marine Reserve is closed to all forms of harvesting (see Figure 2.14). The Trafalgar Marine Reserve is too small, only represents wave-sheltered shores and angling is permitted there as well (Mann et al. 1998 and see Chapter 3). The scarcity of fully protected areas representing the full spectrum of biotopes in KwaZulu-Natal constitutes a gap in the marine protected area network in South Africa (Hockey and Buxton 1989, Attwood et al. 1997). For a Marine Reserve to achieve any benefit to fisheries, populations of exploitable species need to be protected (Roberts et al. in press a, b). In the Natal region, populations of exploited intertidal species, particularly *P. perna*, should be included within the network of marine protected areas. The proposed extension of the St Lucia Marine Reserve and the proposed Pondoland Marine Park could both achieve this if they are proclaimed.

Conclusions

My biotope classification addressed three of the major criticisms of other marine habitat or community classification systems. The biotopes were objectively defined on a mathematical basis, the variability between and within zones in intertidal habitats was incorporated and the analyses covered a large geographical region. The validity of my biotope classification was tested at two independent sites and communities were found be recognisable in the field and robust when subject to independent tests for differences in community structure. The biotope classification scheme was effectively applied to assess the conservation status of rocky shores and to compare potential sites for further marine protected areas. Biotope surveys can achieve such goals more quickly and cost-effectively than inventories of species. The biotope classification, together with the mapping of intertidal biotopes, should facilitate more objective scientifically-based decisions on development, utilisation and conservation in the coastal zone.

Chapter 5

Testing for differences in the physical characteristics of the habitats of intertidal biotopes on rocky shores in KwaZulu-Natal

ABSTRACT

A common criticism of many marine classification systems is the failure to quantitatively associate the physical conditions of habitats with the communities they support. The focus of this chapter is centred on intra-site comparisons of selected biotopes to assess whether biotopes previously defined on biological grounds differ significantly in terms of local habitat. Five low-shore biotopes (*Perna*, *Pyura*, *Cheilosporum*, *Hypnea* and *Gelidium*) and four mid-shore biotopes (*Palythoa*, *Octomeris*, *Tetraclita* and *Jania*) were compared in terms of rock temperature, topography (slope and aspect), wave forces and sand inundation at three disjunct localities (>100km apart). All mid-shore biotopes experienced significantly higher rock temperatures than all low-shore biotopes suggesting that differences in elevation and the associated effects of temperature and desiccation are the most important abiotic factors influencing the distribution of biotopes between zones. Within zones, horizontal zonation patterns were most consistently explained by differences in wave exposure. The distributions of biotopes that support the two most important harvested intertidal species in KwaZulu-Natal, *Perna perna* and *Pyura stolonifera*, correlated with differences in wave exposure. The highest wave forces were recorded within *Perna* whereas *Pyura* occupied wave-sheltered positions. The lowest wave forces were recorded within the mid-shore biotope dominated by the zoanthid *Palythoa*. Barnacle and *Jania*-dominated biotopes did not differ in terms of wave exposure but sand inundation accounted for the distribution of these contrasting biotopes. *Octomeris* or *Tetraclita* experienced significantly less sand inundation than *Jania*, the only biotope that was clearly and consistently linked to intensive sand inundation. There was no correlation between local topographic differences and the distribution of any biotopes. All but two of the biotopes examined were associated with distinctly separate small-scale physical conditions. The two exceptions were *Perna* and *Cheilosporum*, which did not differ in terms of any of the abiotic factors examined and are therefore likely to compete for space on the shore. Human exploitation is predicted to influence the relative abundance of these two biotopes.

Introduction

A biotope is defined as a physical habitat together with an associated community of species (Connor et al. 1997). The term "biotope" therefore encompasses both physical and biological elements. In Chapter 4, a biotope classification system was presented for rocky intertidal habitats in KwaZulu-Natal but only biological elements were used in defining these biotopes. An arbitrary 50% Bray Curtis similarity value was used to objectively identify 69 biotopes. ANOSIM tests at two independent sites revealed that the biotope classification system successfully captured both vertical (i.e., between zone) and horizontal (along-shore) differences in intertidal community structure with highly significant differences in species composition and abundance between independent samples representing different biotopes. In this chapter, physical features of the habitat of a subset of these biotopes are investigated to determine whether the selected biotopes are associated with corresponding abiotic differences.

Studies estimating variability at multiple scales in intertidal habitats have shown that variation is great at small spatial scales (Archambault and Borget 1996, Benedetti-Cecchi et al. 1996, Underwood and Chapman 1996), with substantial variability within sites (Chapman 2000, Underwood et al. 2000). Such local-scale variability may mask larger-scale patterns in physical and biological factors (McGuiness 1990).

Within-site variability in abundance of intertidal organisms has been linked to physical factors including vertical gradients of desiccation and temperature (Lewis 1964, Stephenson and Stephenson 1972, Bustamante et al. 1997), physical disturbance (Sousa 1979, Paine and Levin 1981, Connell and Sousa 1983) and wave exposure (Menge and Farrell 1989, Bustamante et al. 1997). Biological factors deemed important in determining rocky intertidal community structure include predation (Connell 1961, 1972, Paine 1966, 1974, Dayton 1971), grazing (Lubchenco 1978, Lubchenco and Menge 1978, Branch 1981, Hawkins and Hartnoll 1983, Jara and Moreno 1984), complex competitive interactions among individuals (Branch 1984, Underwood and Chapman 1996) and larval supply and recruitment (Connell 1985, Gaines and Roughgarden 1985, Roughgarden et al. 1988, Underwood and Fairweather 1989, Menge 1991, Caley et al. 1996, Connolly and Roughgarden 1999, Menge 2000).

Although both abiotic and biological factors interact in determining community structure, physical variables are considered to set the stage for biological interactions (McQuaid and Branch 1985, Menge and Olsen 1990). Schoch and Dethier (1996) statistically linked abundance of organisms to intertidal geomorphology and their results served to emphasise the critical role of abiotic factors in creating patterns on the scale of metres to tens of metres. Despite the recognised importance of abiotic factors in shaping community structure at small scales, local-scale variability in physical factors within sites is seldom quantified (but see Bustamante et al. 1997).

Several classification systems including that for benthic marine biotopes of the British Isles (Hiscock 1995) have been criticised because biotopes were not objectively defined and because of the failure to establish quantitative links between abiotic habitat characteristics and community structure (Robinson and Levings 1995, Schoch and Dethier 1996, Day and Roff 1998, Zacharias et al. 1999). The biotope classification for KwaZulu-Natal was objectively defined and, in this chapter, the relationship between the distribution of a subset of biotopes and local physical variables was quantitatively examined. From the outset, the biotope classification system that I developed for KwaZulu-Natal was based on biotic analyses because the main physical factors suspected of structuring intertidal communities there were then poorly understood. Rocky shores on the KwaZulu-Natal coast have never been quantitatively analysed in equivalent detail to those of the west coast (Field and Griffiths 1991). The previously untested perception that wave exposure is unimportant in structuring intertidal communities along the relatively straight wave-exposed KwaZulu-Natal coast serves to illustrate this point. This perception was shown to be erroneous (Chapter 3). In KwaZulu-Natal, only one study (Lambert and Steinke 1986a) has previously defined biological community types but it was limited to a single site. The focus of that study was to correlate these communities with vertical gradients of emersion. No studies have ever been undertaken in KwaZulu-Natal to examine how physical factors underlie small-scale horizontal variability in community structure.

The central objective of this study was to determine whether a subset of the previously defined biotopes experience different physical conditions. In Chapter 4, some of the described biotopes were confined to sites with similar abiotic characteristics. For instance, certain biotopes were only found at very wave-exposed shores while others were confined to sand-inundated shores. Within any site, small-scale differences in abiotic factors are the norm (Dayton 1971, Sousa 1979, 1984, Foster et al. 1990, Underwood et al. 2000). For example, within a wave-exposed site, there will be areas that are sheltered from strong wave action. Similarly, within a sand-inundated shore, some areas of rock may not experience sand inundation. Because of such within-site variability at a scale of centimetres to metres in intertidal habitats, independent small-scale measurements of physical factors are required to relate potential abiotic determinants to within-site differences in the distribution of biotopes.

Abiotic Determinants

Five environmental factors were selected as potential abiotic determinants of the small-scale distribution of biotopes within shores: rock temperature, aspect, slope, wave force and sand inundation.

Rock temperature

Variability of community structure within shores has long been associated with vertical differences in elevation, emersion time and rock temperature (Stephenson 1942, Lewis 1964, 1976, Stephenson and Stephenson 1972, Underwood 1978, Menge and Farrell 1989). Broekhuysen's (1940) pioneering work established a correlation between biological zonation and the tolerance of different species to high temperature, water loss and salinity extremes. Much of Stephenson's work on universal zonation patterns on rocky shores was based on his observations in South Africa (Stephenson 1939, 1944, 1948, Stephenson and Stephenson 1972). Vertical zonation patterns in South Africa are described by Branch and Branch (1981), Field and Griffiths (1991) and Bustamante et al. (1997). Jackson (1976) described vertical zonation patterns in KwaZulu-Natal but remarked that emersion curves alone could not explain the intertidal zonation patterns in KwaZulu-Natal. Lambert and Steinke (1986a) related the distribution of five intertidal communities to differences in elevation and emersion at Umdoni in southern KwaZulu-Natal.

Topography

Topographic influences can determine community structure at small (and large) spatial scales in intertidal habitats (Foster et al. 1988, Barry and Dayton 1991). Topographic heterogeneity will also influence diversity (Burnett et al. 1998). Differences in slope and aspect have been linked to differences in community structure (Menge et al. 1985, Fuji and Nomura 1991, Archambault and Borget 1996, Blanchard and Borget 1999, Chiba and Noda 2000). In KwaZulu-Natal, Jackson (1976) remarked that aspect might influence wave action, for example, between the seaward and landward faces of a rock, and therefore influence community structure. Differences in solar radiation between rocks with different aspects could also affect intertidal communities.

Wave exposure

Wave exposure is generally considered the most important abiotic factor in determining local horizontal variability in community structure on rocky shores (Lewis 1964, Dayton 1971, Seapy and Littler 1978, Menge and Farrel 1989, Menge and Olson 1990). The biomechanical approaches employed by Koehl (1982, 1984, 1986) and Denny (1987, 1988, 1995) have been particularly successful in improving our understanding of the influence of wave action on biota. In South Africa, several authors have shown the effects of differences in wave exposure between sites (Field and Robb 1970, McQuaid and Branch 1984, 1985), but only Bustamante et al. (1997) quantitatively measured wave exposure and examined its relationship with community structure within sites. This was done at two sites, one on the west coast and one on the south coast. In Chapter 3, differences between rocky intertidal communities in KwaZulu-Natal were related to contrasting wave exposure at a scale that compared sites. As community structure was closely correlated with between-site differences in wave exposure, the relationship between even smaller-scale differences in wave forces and the distribution of biotopes within sites warrants investigation.

Sand inundation

Sand is proposed to play an important role in structuring assemblages on rocky shores with sand movement and burial linked to variability in community structure within zones and different community types associated with differential sand stress (Daly and Mathieson 1977, Taylor and Littler 1982, Littler et al. 1983, D'Antonio 1986, Foster et al. 1988, Kendrick 1991, Santos 1993). In South Africa, McQuaid and Dower (1990) examined the role of sand inundation in structuring intertidal assemblages on the south coast. By increasing habitat heterogeneity, sand inundation generally increased species richness, although local-scale reductions in species richness were attributed to extreme sand inundation (Dower 1989). Jackson (1976) and Berry (1982) predicted that sand inundation may play an important role in regulating community structure in benthic inshore habitats in KwaZulu-Natal. These predictions were borne out in Chapter 3, where sand inundation was identified as a physical determinant of community structure between sites, i.e., at a scale of tens of kilometres. Small-scale variability in sand inundation within sites has not previously been assessed in KwaZulu-Natal.

Biotopes

It was impossible to test whether these factors affected all the biotopes identified in Chapter 4, so the analysis was confined to four sites and nine groups of low or mid-shore biotopes, each biotope having been defined by a different dominant taxon. Because there is little variability in the high and top shore and because little harvesting occurs there, biotopes from these zones were not considered in this study.

The abiotic characteristics of each biotope were investigated at different sites so that general habitat differences between biotopes could be identified. Five groups of low-shore biotopes were selected to investigate potential abiotic correlates, respectively dominated by the brown mussel *Perna perna*, the ascidian *Pyura stolonifera*, the articulated coralline alga *Cheilosporum sagittatum*, and the red algae *Hypnea spicifera* and *Gelidium abbottiorum*. In the mid shore, four groups of biotopes were compared, namely those dominated by the barnacles, *Octomeris angulosa* or *Tetraclita serrata*, the zoanthid *Palythoa nelliae* and the turf-forming articulated coralline alga, *Jania verrucosa*. These biotopes are predominant on rocky shores in Natal (see Figure 4.2 p 139). Biotopes dominated by *P. perna* and *P. stolonifera* are important because subsistence and recreational harvesters (Kyle et al. 1997, Tomalin and Kyle 1998) target these species. Coralline and red-algal biotopes were selected because they often occupy space on the low shore where mussels are absent. There is a need to determine whether natural or anthropogenic factors underlie the differences in the distribution of these biotopes, and in Chapter 6, the relationship between the distribution of biotopes and human exploitation is evaluated using a variety of approaches including experimental manipulation.

Objectives

In summary, this chapter focuses on local physical habitat characteristics of different biotopes within rocky shores in KwaZulu-Natal. Three specific objectives are addressed:

1. To determine whether there are significant small-scale (i.e., within-site) differences in rock temperature, topography (aspect and slope), wave force and sand inundation between zones and biotopes.
2. To determine whether different biotopes within and between zones are consistently defined by abiotic factors.
3. To relate general biological zonation patterns (horizontal and vertical) to physical variables at a local scale.

Processes influencing community structure are often erroneously interpreted from single surveys or observations at one site (Foster 1990, Underwood and Petraitis 1993). In this study, correlations between community structure and abiotic factors were examined at sites that were more than 100 km apart (Figure 5.1) and observations were repeated at two different times at one site. Comparisons were made within sites because temporal differences in local conditions between sites (e.g., weather and sea conditions) may obscure any differences between biotopes at different sites sampled at different times.

Methods

1. Sampling design

Abiotic data were collected to identify physical factors that may underlie the distribution of different biotopes within sites. Different biotopes were only compared within respective sites although general patterns between contrasting biotope groups were examined. Abiotic data were compared between biotopes from both within and between the low and mid shore for nine groups of biotopes (two of which were each divisible into two specific biotopes i.e., *Perna* and *Tetraclita*) (Table 5.1). For simplicity, the generic names of the dominant species are used to refer to the different biotopes hereafter: *Perna*, *Pyura*, *Hypnea*, *Gelidium* and *Cheilosporum* in the low shore, *Octomeris*, *Tetraclita*, *Palythoa* and *Jania* in the mid shore.

Table 5.1. Biotopes that were investigated for corresponding differences in rock temperature, aspect, slope, wave exposure and sand inundation. Only sand inundation was examined at Salt Rock. The relevant code for each biotope (as displayed in Tables 4.2 and 4.3) is shown in parentheses. For each abiotic factor except sand inundation, n =18 for each biotope at each site. The number of sand-inundation samples for each biotope is indicated alongside the biotope code in parentheses. Due to insufficient sand monitoring samples for red-algal biotopes at Banana Beach, sand inundation of *Hypnea* was only investigated at Shaka's Rock.

Zone	Group	A. Cape Vidal	B. Shaka's Rock	C. Banana Beach	D. Salt Rock
Low	Ascidian - *Pyura*	*P. stolonifera*, zoanthids (PsZ - 20)	-	-	-
	Mussel - *Perna*	*P. perna*, *Tetraclita squamosa* (PpT - 20)	*P. perna*, *C. sagittatum* (PpC - 34)	*P. perna*, *C. sagittatum* (PpC - 30)	-
	Articulated corallines - *Cheilosporum*	-	*C. sagittatum* (Cs - 32)	*C. sagittatum* (Cs - 26)	-
	Red algae - *Hypnea*	-	*H. spicifera* (Hs -16)	*H. spicifera* (Hs)	-
	Red algae - *Gelidium*			*G. abbotiorum* (Ga)	
Mid	Barnacle - *Tetraclita*	*T. squamosa* (Tr - 20		*T. serrata* (Ts – 24)	
	Barnacle - *Octomeris*		*O. angulosa* (Oa - 31)		*O. angulosa* (Oa - 41)
	Zoanthid - *Palythoa*	*P. nelliae*, *Zoanthus* spp (PnZ – 20)	*P. nelliae*, *Zoanthus* spp. (PnZ - 21)	*P. nelliae*, *Zoanthus* spp (PnZ - 30)	-
	Articulated coralline - *Jania*	-	*J. verrucosa*, *Laurencia natalensis* (JvL - 35)		*J. verrucosa*, *L. natalensis* (JvL - 49)

The relationships between the distribution of biotopes and selected abiotic factors were primarily investigated at three sites: Shaka's Rock, Banana Beach and Cape Vidal, with additional studies of sand inundation between two biotopes at Salt Rock (Figure 5.1).

Figure 5.1. Map of KwaZulu-Natal showing the position of the three principle rocky shore sites (A-C) where abiotic conditions experienced within contrasting biotopes were examined and the site (D) where additional sand monitoring was undertaken. Cape Vidal Point is within the St Lucia Marine Reserve and was unexploited (*) while Shaka's Rock, Salt Rock and Banana Beach were subject to recreational exploitation.

Identical biotopes were not necessarily present at all the sites because of geographic differences and between-site variability in the biota and environmental factors (see Chapters 2 and 3 respectively). The *Perna* and *Tetraclita*-dominated biotope groups examined each incorporated two separate biotopes as defined by the classification system (Table 5.1). Both mussel biotopes were dominated by *Perna perna* but the distinguishing species was either *Cheilosporum sagittatum* or *Tetraclita squamosa rufotincta*. The two biotopes dominated by the barnacle *Tetraclita* also comprised two different biotopes, as *T. squamosa rufotincta* was the dominant species at Cape Vidal and *T. serrata* at Banana Beach. Biotopes dominated by the same species were investigated at different sites so that the generality of physical habitat differences between different groups of biotopes could be identified.

All nine groups of biotopes were not found at any single site. Cape Vidal was selected because it is within a fully protected Marine Protected Area where harvesting of intertidal invertebrates is prohibited, and both *Perna* and *Pyura* biotopes were present. This was the only known site in KwaZulu-Natal where sufficient samples of the *Pyura* biotope were present for adequate sampling of associated physical variables. There were no algal-dominated biotopes at that site. It was therefore impossible to compare the habitat of biotopes dominated by algae with those dominated by *Pyura*. Shaka's Rock and Banana Beach were selected because six of the selected biotopes were well represented within these sites. There were no significant differences in mean maximum wave forces between the three sites although differences in sand inundation were apparent between sites (Chapter 3).

At each site, the centre-points of 20 replicate 1 m x 0.5 m quadrats representing each biotope were marked to allow their location for measurements of abiotic factors in each quadrat the following day. Quadrats were randomly positioned and the biotopes haphazardly interspersed within either the low or mid shore, depending on which biotopes were being sampled. There was a minimum distance of 2 m between samples.

2. Measuring abiotic factors

At Shaka's Rock, rock temperatures and wave exposures were measured on two occasions. Rock temperatures were measured on 23 and 24 November 1999. Wave forces were recorded overnight on 25/26 and 26/27 October 1999. At Cape Vidal, wave measurements were made overnight on 25 November 1999 and temperatures measured on the same day. At Banana beach, wave measurements were conducted on 30/31July 1999 and all other abiotic data during 26 - 28 September 2000. Sand was monitored over a 22 month period as outlined overleaf.

2a. Rock temperature

Rock temperature for each quadrat was measured at low tide with a 30 Ga Type II thermocouple and a Bat 12 Bailey Instruments Inc. digital thermocouple reader. Rock temperatures were recorded sequentially working across the site (i.e., temperatures were recorded within different zones as biotopes were encountered). All temperatures were measured within a ten minute period over the advertised time of low tide (South African Navy 1999, 2000).

2b. Topography

Slope and aspect were measured with a compass clinometer. Aspect was recorded as a bearing and slope was measured as an angle.

2c. Maximum wave forces

To measure maximum wave forces, one wave drogue (Palumbi 1984) was attached in each quadrat for 24 hours.

2d. Sand inundation

The relative degree of sand inundation within different biotopes was assessed using the sand monitoring data (Chapter 2) from Cape Vidal Point, Shaka's Rock, Banana Beach and Salt Rock. Details of the methods appear in Chapter 2. In brief, however, cover and depth of sand were estimated within 10 quadrats (1m x 0.5m) in each of the low and mid shore at each site. Monitoring was initiated in June 1997 and data were collected simultaneously every two months until April 1999. At all four sites, cover of dominant species was recorded within the fixed quadrats used for sand monitoring. These data were used to classify samples into their respective biotopes.

The sand monitoring data from Cape Vidal Point were used to compare relative sand inundation between *Perna* and *Pyura* dominated biotopes. *Perna* and *Cheilosporum* biotopes were compared at Shaka's Rock and Banana Beach. The monitoring at Banana Beach did not incorporate sufficient samples of *Hypnea* or *Gelidium* to examine sand inundation within or between these biotopes. The *Perna* and *Hypnea* biotopes were therefore only compared at Shaka's Rock. Barnacle (*Octomeris* or *Tetraclita*) and *Palythoa* biotopes were compared at all three sites but sufficient replicate samples for the mid shore *Jania* biotope were monitored at one site only, Shaka's Rock. Sand inundation within *Jania* and barnacles (*Octomeris*) was therefore additionally examined at an adjacent site, Salt Rock.

The mean volume of sand in cm^3 within each biotope was calculated using replicate samples from the quadrats at each site. The replicates from a minimum of eight different monthly samples over the 19-month period were pooled and seasonality was not examined. The minimum sample was for *Hypnea* at Shaka's Rock, for which there were 16 samples, and the maximum sample number was 49, for *Jania* at Salt Rock.

3. Data analysis

To test for differences in rock temperature, aspect, slope and wave exposure between local habitat of different biotopes, nested ANOVA or Kruskal Wallis ANOVA was conducted with STATISTICA (1999). Biotopes were nested within zones for the parametric analysis. As some wave drogues were lost, 18 replicate samples with the full set of abiotic data were examined for each biotope at each site. Normality was tested with the Kolmogorov-Smirnoff test and homogeneity of variances was tested with Cochran's test (Winer et al. 1991). Estimates of wave exposure and temperature were log transformed to satisfy these assumptions (Sokal and Rohlf 1995). Post-hoc Tukey Honestly Significantly Different (HSD) tests were used to determine which biotopes were significantly different. Each site was analysed independently and biotopes were compared within and between zones. The data describing aspect at Banana Beach were analysed by non-parametric techniques (Kruskal-Wallis ANOVA) because the parametric ANOVA assumptions could not be satisfied.

As the sand inundation data were collected simultaneously for all sites, the data from different sampling periods were pooled for each biotope. Due to the high number of zero values and the variability in sand inundation within shores, the data were not normally distributed and homogeneity of variance was not achieved. Non-parametric Kruskal-Wallis ANOVA and Mann-Whitney U tests were therefore employed to analyse the data.

To compare general patterns in physical conditions between biotopes, a matrix was compiled comparing each biotope in terms of temperature, wave action and sand inundation. Aspect and slope were not considered as they did not differ significantly between any biotopes. This matrix (Table 5.4) was then used semi-quantitatively to calculate the mean ranks of each biotope for each physical factor. High mean values indicated that the biotope experienced high levels of the factor considered (temperature, wave action or sand inundation. For example, *Perna* experienced higher wave forces than *Gelidium*, so it was given a rank of +1 (and *Gelidium* a rank of –1) in the matrix where these two biotopes were compared. The wave forces experienced by *Perna* were not significantly different from that of *Cheilosporum* so both species were ranked 0. The mean ranks for each biotope were plotted on a scatterplot to visualise the relationships of the biotopes with respect to the physical variables (Figure 5.4).

Results

1. Differences in abiotic factors within sites

Different biotopes were only compared within sites. Nested ANOVA showed that different zones experienced significant differences in rock temperature (Table 5.2 $p< 0.0002$) and wave forces ($p<0.02$) at all three sites. There were, however, no significant differences in rock temperature between biotopes at Cape Vidal or Shaka's Rock but different biotopes experienced significant within-zone differences ($p=0.0017$) in rock temperature at Banana Beach. In contrast, all three sites had highly significant within-zone differences in wave forces between contrasting biotopes (Table 5.2, $p<0.000001$). There were no significant differences in the aspect or slope of different zones or specific biotope habitats at any sites (Table 5.2, ANOVA $p>0.13$; Table 5.3 Kruskal-Wallis ANOVA $p>0.4$).

Different biotopes were also subject to significantly different intensities of sand inundation at Shaka's Rock, Banana Beach and Salt Rock but not at Cape Vidal (Table 5.3). The mean rock temperatures, wave exposures and intensities of sand inundation experienced within respective biotopes and results of Tukey HSD tests and Mann Whitney U test for each site are shown in Figures 5.2 and 5.3, and are described in more detail overleaf.

Table 5.2. Results of nested ANOVA indicating abiotic factors that were significantly different between different zones and biotopes at Cape Vidal, Shaka's Rock and Banana Beach. Measurements of rock temperature and wave exposure were made on two occasions (Time I and II) at Shaka's Rock. * Denotes significant difference ($p<0.05$).

Factor and site	**Zone**			**Biotope**		
Rock temperature	**df**	**F**	**p**	**df**	**F**	**p**
Cape Vidal	1	40.05	<0.000001*	2	2.81	0.16
Shaka's Rock I	1	155.59	<0.000001*	4	1.84	0.163
Shaka's Rock II	1	337.94	0.00016*	4	1.53	0.200
Banana Beach	1	219.56	<0.000001*	5	4.14	0.0017*
Wave exposure						
Cape Vidal	1	5.90	0.0178*	3	48.51	<0.00001*
Shaka's Rock I	1	3.03	<0.00001*	4	40.94	<0.00001*
Shaka's Rock II	1	13.58	0.00039*	4	32.13	<0.00001*
Banana Beach	1	58.66	<0.000001*	5	101.44	<0.00001*
Aspect						
Cape Vidal	1	0.57	0.45	3	1.04	0.36
Shaka's Rock	1	0.76	0.54	4	0.05	0.99
Slope						
Cape Vidal	1	2.85	0.23	3	0.08	0.94
Shaka's Rock	1	3.59	0.06	4	1.13	0.13
Banana Beach	1	0.18	0.67	5	0.08	0.78

Table 5.3. Results of Kruskal - Wallis ANOVA to determine whether contrasting biotopes were exposed to significant differences in sand inundation at all sites and in aspect at Shaka's Rock. * Denotes significant difference ($p<0.05$)

Sand inundation	df	χ^2	p	n
Cape Vidal	3	2.00	0.572	80
Shaka's Rock	3	33.24	<0.0001*	168
Banana Beach	3	21.99	<0.0001*	112
Salt Rock	1	23.70	<0.0001*	100
Aspect				
Shaka's Rock	5	5.116	0.402	108

2. Correlating biotope distribution with potential abiotic determinants

2a. Rock temperature

Comparing between zones, nested ANOVA showed highly significantly differences in rock temperature between zones at all sites (Table 5.2). Tukey tests revealed that all biotopes in the low shore (*Perna*, *Pyura*, *Cheilosporum*, *Hypnea* and *Gelidium*) experienced significantly lower rock temperatures compared to all biotopes in the mid shore (*Palythoa*, *Jania* and *Octomeris* or *Tetraclita*). This pattern was consistent at all sites (Figure 5.2).

Nested ANOVA revealed that there were no within-zone differences in rock temperature at Cape Vidal and Shaka's Rock (Table 5.2). Similarly, within zones at Banana Beach, Tukey tests revealed that most biotopes failed to experience significantly different rock temperatures, however, there were two exceptions (Figure 5.2). In the low shore, significantly higher rock temperatures were recorded within *Cheilosporum* compared to *Gelidium* ($p=0.003$). In the mid shore, significantly higher rock temperatures were recorded within samples dominated by barnacles (*Tetraclita*) compared to *Palythoa* and *Jania* ($p=0.0045$), whereas rock temperatures did not differ significantly between the latter two biotopes.

Differences in rock temperatures recorded in biotopes from different zones clearly exceeded those observed in biotopes within zones, even at Banana Beach, the only site where significant differences in temperature were recorded between biotopes within zones (Figure 5.2). Overall, differences between zones were between 1.2 and 3.0°C whereas those within zones at Banana Beach were only 0.5-0.7°C.

2b. Topography

There were no significant differences in the aspect or slope of the habitat of any biotopes at any of the sites examined (Table 5.2-5.3).

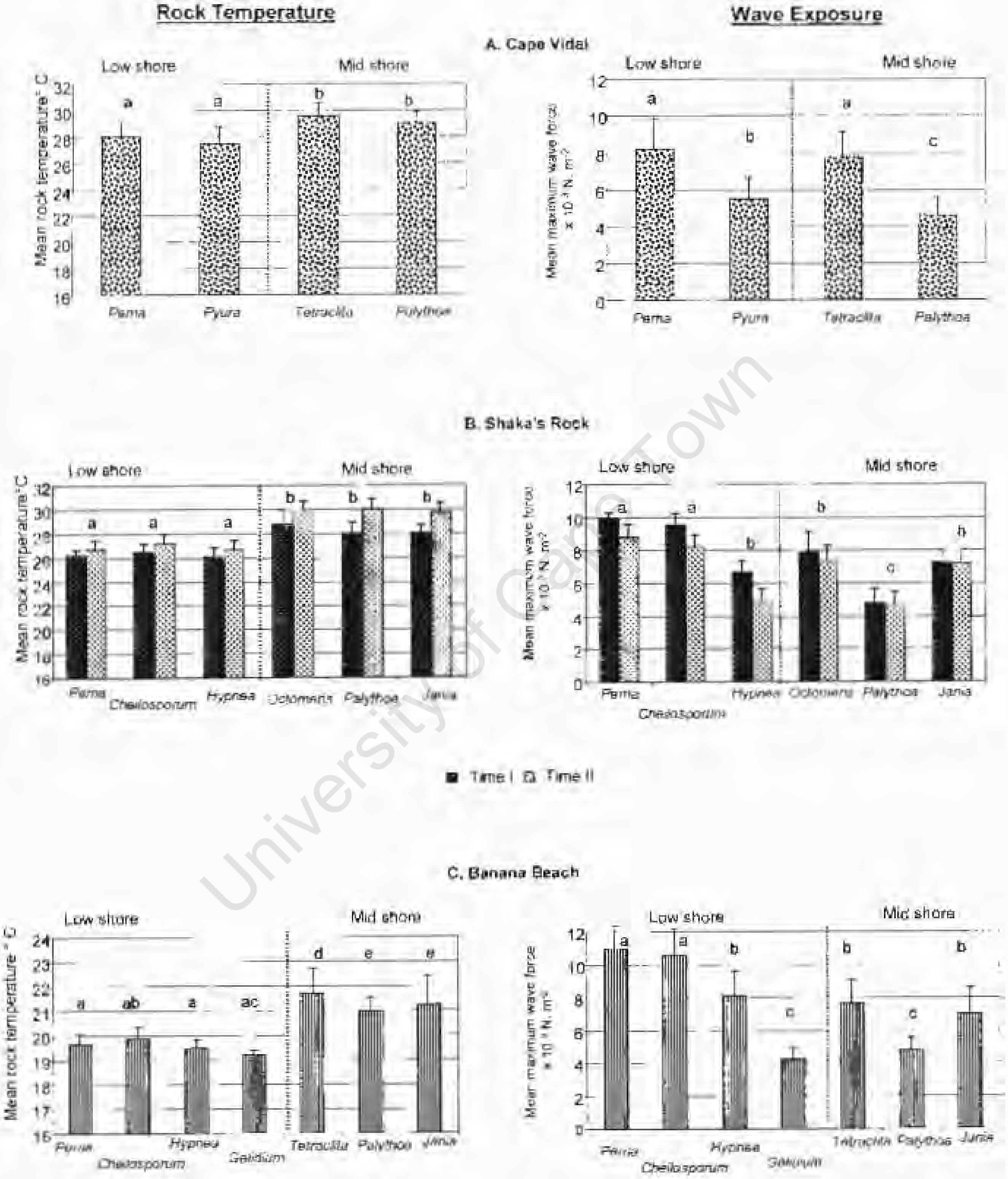


Figure 5.2. Histograms showing the mean rock temperature (+s.d) and mean maximum wave forces (+s.d) experienced within contrasting biotopes in the low and mid shore at (A) Cape Vidal Point, (B) Shaka's Rock (two sets of data for the two time periods) and (C) Banana Beach. Estimates were based on 18 replicate samples per community type and significant differences between biotopes as determined by nested ANOVA and Tukey tests (P<0.001) are shown (shared letters indicate an absence of significant difference).

2.c. Wave exposure

Nested ANOVA revealed significant differences between zones and between biotopes within the low and mid shore at all three sites (Table 5.2). Between zones, there were significant differences in mean wave forces between several of the biotopes from different zones on the shore. At Shaka's Rock and Banana Beach, *Perna* and *Cheilosporum* were subject to significantly higher wave forces than *Octomeris* or *Tetraclita* respectively ($p<0.0015$) although mean maximum wave forces did not differ significantly between *Perna* and *Tetraclita* at Cape Vidal ($p=0.08$). *Palythoa* occurred in significantly less-exposed areas ($p<0.005$) than all other biotopes except the low-shore *Gelidium* community at Banana Beach. However, Tukey tests showed that there were some biotopes from different zones that failed to differ in terms of wave forces ($p>0.05$). At Cape Vidal, mussels and barnacles experienced similar wave forces and *Hypnea*, barnacles and *Jania* did not differ in terms of wave exposure at Shaka's Rock or Banana Beach (Figure 5.2).

Comparing biotopes within zones, Figure 5.2 showed that there were large significant differences in wave exposure between different biotopes at all three sites. In the low shore at Cape Vidal, significantly higher wave forces were recorded within *Perna* compared to *Pyura*. At Shaka's Rock, *Perna* and *Cheilosporum* were subject to significantly higher wave forces than *Hypnea* on both occasions measurements were made. At Banana Beach, significantly higher wave forces were also recorded in *Perna* and *Cheilosporum* compared to the foliar-algal biotopes *Hypnea* and *Gelidium*, which also differed significantly from each other ($p<0.0001$ in all cases). The *Perna* and *Cheilosporum* biotopes did not experience significantly different wave forces at either of the sites where they could be compared (Shaka's Rock and Banana Beach, $p=0.98$ and 0.99 respectively, Figure 5.2).

In the mid shore, there were significantly higher wave forces recorded within barnacle-dominated biotopes (*Octomeris* or *Tetraclita*) compared to the zoanthid (*Palythoa*) biotopes at Cape Vidal ($p=0.00015$), at Shaka's Rock on both occasions ($p<0.00015$) and at Banana Beach ($p=0.00012$) (Figure 5.2). There were no significant differences between barnacles (*Octomeris* or *Tetraclita*) and *Jania* ($p>0.8$) but the *Jania* biotope experienced significantly higher wave forces than *Palythoa* at both sites where comparison was possible (Shaka's Rock and Banana Beach, $p<0.0002$).

The overall zonational pattern was that the highest wave forces were experienced in the low shore but that differences between biotopes within each zone far exceeded differences between zones. The mean difference in wave force recorded between zones ranged from 0.67×10^3 N.m^{-2} at Cape Vidal to 2.27×10^3 N.m^{-2} at Banana Beach. Larger within-zone differences were recorded between biotopes at all sites. For example, at Cape Vidal there was a difference of more than 3×10^3 N.m^{-2} between mid-shore biotopes at Cape Vidal and the difference in mean wave forces recorded within the low-shore biotopes *Perna* and *Gelidium* was 6.81×10^3 N.m^{-2}. Contrary to the observations for rock temperature, several biotopes from different vertical zones on the shore failed to experience significant differences in wave exposure but differences within zones were common and substantial.

2d. Sand inundation

At Cape Vidal, there was no significant difference in sand inundation experienced between biotopes (Figure 5.3A). Mean volume of sand was less than 0.1 x 10^3 $cm^3.m^{-2}$ for all biotopes. At Shaka's Rock and Banana Beach (Figure 5.3B, C), most biotopes were not subject to significant differences in the mean volume of sand inundation but Mann-Whitney U tests did indicate two mid-shore biotopes that did differ. Firstly, the *Jania* biotope at Shaka's Rock experienced significantly greater volumes of sand inundation than any of the other biotopes. The generality of this result was indicated by the fact that *Jania* was also subject to approximately five times greater volumes of sand inundation than *Octomeris* at Salt Rock (Figure 5.3). At Banana Beach, *Tetraclita* experienced the least sand inundation, although (as at Cape Vidal and/or Banana Beach) it did not differ significantly from *Cheilosporum* or *Perna*. Secondly, *Palythoa* experienced significantly greater volumes of sand inundation than any of the other biotopes at Banana Beach although this outcome is unlikely to be general, as it was not evident at Cape Vidal or Shaka's Rock.

Sand inundation

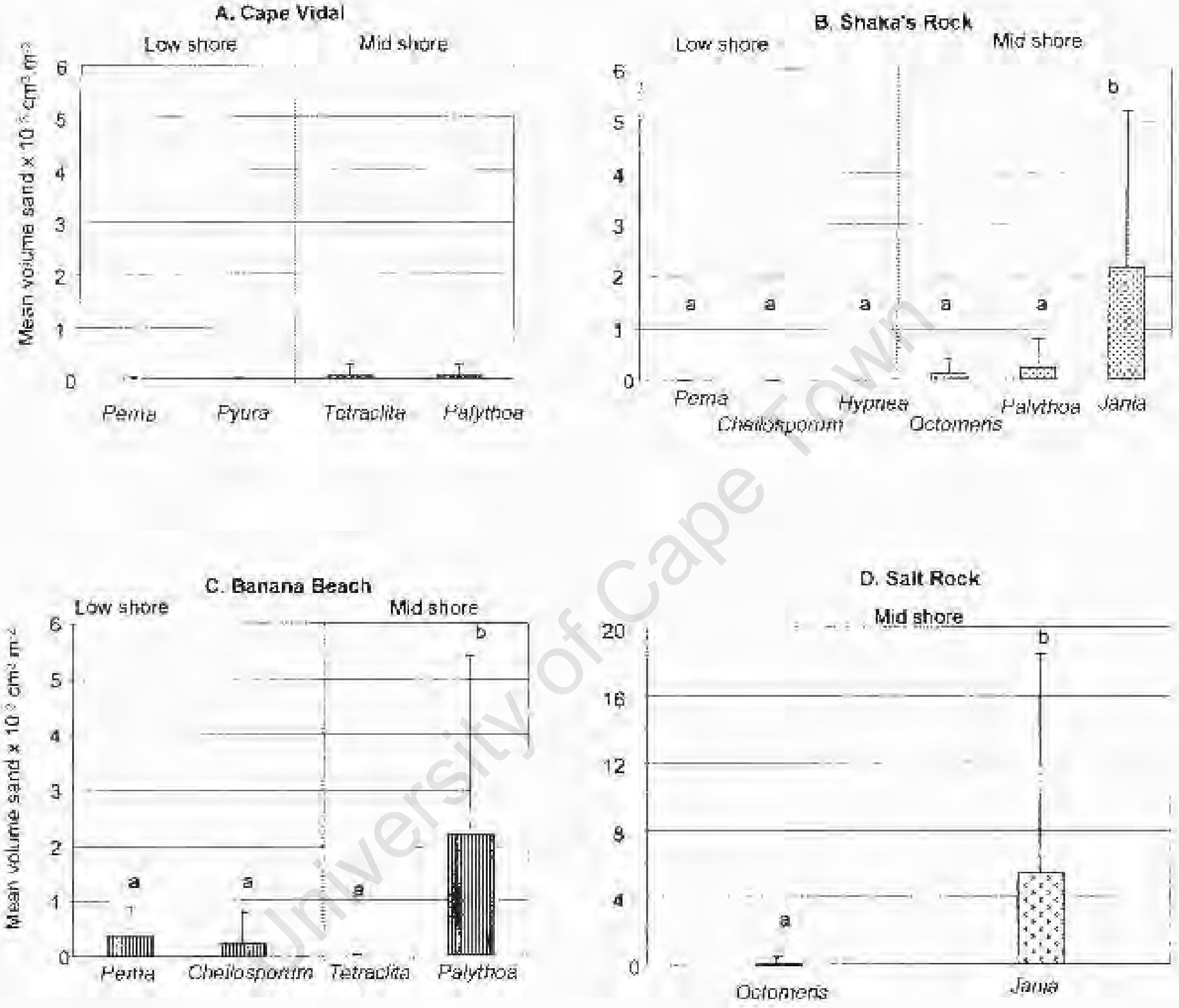


Figure 5.3. Histograms showing mean volume of sand (+ s.d.) recorded within different biotopes at (A) Cape Vidal, (B) Shaka's Rock, (C) Banana Beach and (D) Salt Rock. Kruskal-Wallis ANOVA indicated that there were no significant differences in sand inundation between community types at Cape Vidal. Significant differences between biotopes at the other three sites as determined by Mann-Whitney U tests are shown ($p<0.05$). Biotopes that were not significantly different share the same letter.

3. General habitat characteristics for different types of biotopes

Table 5.4 shows which biotopes had corresponding differences in each of the abiotic factors and Figure 5.4 summarises the general patterns. All low-shore biotopes experienced significantly lower rock temperatures compared to all-mid shore biotopes but differences between biotopes within zones were small.

Differences in wave action were substantial both within and between zones (Figure 5.4). Three groups of biotopes could be distinguished. Firstly, *Perna* and *Cheilosporum* experienced substantially greater wave forces than any other biotopes. Secondly, *Hypnea*, *Pyura*, barnacles (*Octomeris* and *Tetraclita*) and *Jania*, were exposed to moderate wave forces, with *Pyura* being slightly (but significantly) less wave-exposed than barnacles (*Tetraclita*). Finally, *Gelidium* and *Palythoa* experienced significantly lower levels of wave action than any of the other biotopes.

Most comparisons of sand-inundation revealed no differences between biotopes (Table 5.4). *Palythoa* was more sand-inundated than *Perna*, *Cheilosporum* and barnacles, but not consistently so. The most clear-cut pattern was that *Jania* was consistently more sand-inundated than any other biotope.

There were only two biotopes that did not differ in any factors examined: *Perna* and *Cheilosporum*.

Table 5.4. Summary of results testing for differences in rock temperature, wave exposure and sand inundation between contrasting biotopes. Biotopes to the left are contrasted with those listed in the top row and - or + respectively denotes that biotopes on the left experienced significantly lower or higher values for each factor. Significant differences were determined by nested ANOVA and Tukey (rock temperature, wave exposure) or Mann-Whitney U tests (sand inundation) where necessary. 0 Indicates no significant difference (p>0.05). Blank cells denote that factor could not be compared between biotopes. Each + and - were assigned a value of +1 or -1 respectively and the mean score for each factor was calculated for each biotopes and is displayed in the right hand column. Sites: C=Cape Vidal, Sh=Shaka's Rock, B=Banana Beach, Sa=Salt Rock.

Biotopes		*Perna*			*Pyura*	*Cheilosp.*		*Hypnea*		*Gel.*	Barnacle				*Palythoa*			*Jania*			Mean score
	Site	C	S	B	C	S	B	C	B	B	C	S	B	Sa	C	S	B	Sh	B	Sa	
Perna	Temp				0	0	0	0	0	+							-	-	-		-0.5
	Wave				+	0	0	+	+	+	0	+	+		+	+	+	+	+		+0.75
	Sand				0	0	0	0			0	0	0		0	0	-	0	0		0.08
Pyura	Temp	0																			-0.66
	Wave	-													+						-0.33
	Sand	0									0				0						0.00
Cheilosporum	Temp		0	0				0	0	+						-	-	-	-		-0.54
	Wave		0	0				+	+	+		+	+			-	-	+	+		+0.82
	Sand		0	0				0				0	0			0	-	-			-0.25
Hypnea	Temp		0	0		0	0			0							-	-	-		-0.55
	Wave		-				-			+		0	0			+	+	0	0		-0.08
	Sand					0						0				-		0			-0.25
Gelidium	Temp			0		-	-		0				-				-				-0.71
	Wave			-		-											0		-		-0.86
	Sand																				
Barnacle (*Octomeris* /*Tetraclita*)	Temp	+	+	+	+	+	+	+	+	+					0	0	+	0	+		+0.79
	Wave	0	-	-	-	-	-	+	0	0					+	+	-	0	0		0.06
	Sand	0	0	0	0	0	0	0	0						0	0	-	-		-	-0.23
Palythoa	Temp	+	+	+	+	+	+	+	+	+	0	0	-					0	0		+0.57
	Wave	-	-	-	-	-	-		-	0	-	-						-	-		-0.93
	Sand	0	0	+	0	0	+	0			0	0	-					-			+0.16
Jania	Temp		+	+		+	+	+	+			0	-			0	0				+0.5
	Wave		-	-		-	-	0	0	+		0	0			+	+				-0.09
	Sand		+			+		+				+		+		+					+1.00

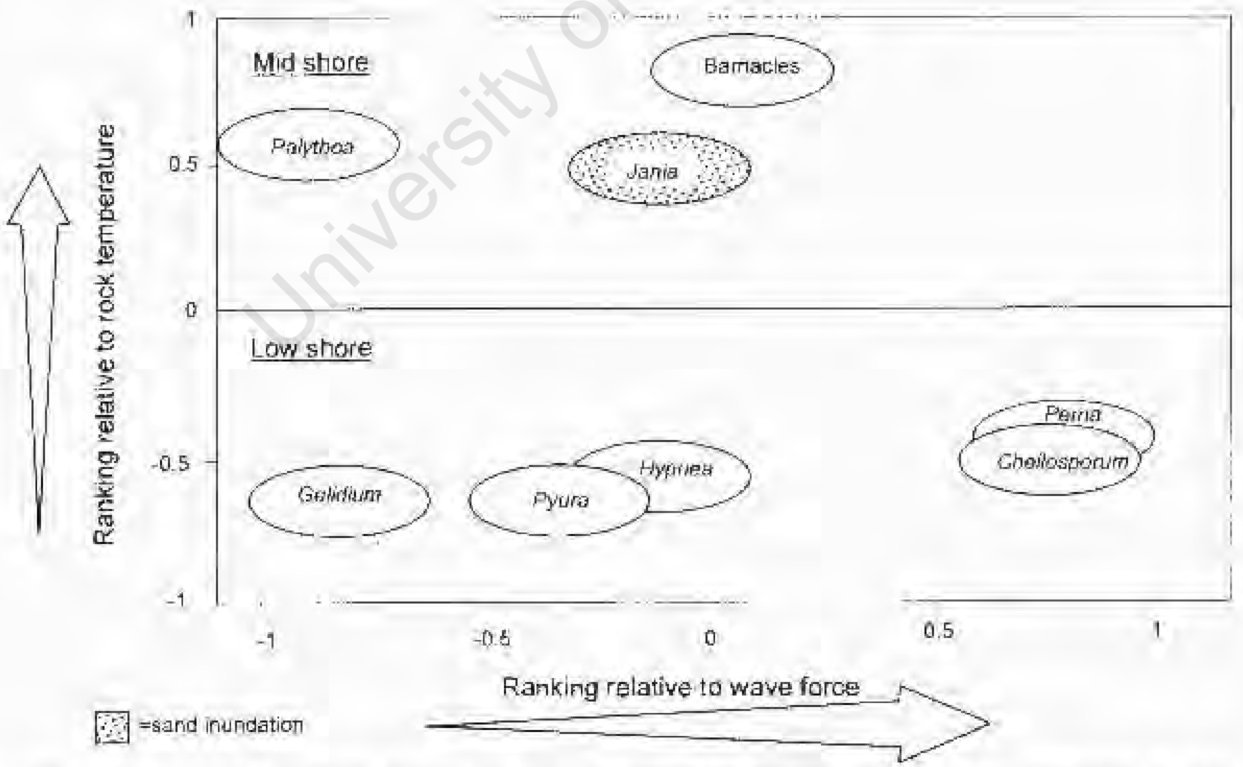


Figure 5.4. Summary diagram showing the relative ranking of biotopes based on measurements of rock temperature and wave forces at Cape Vidal, Shaka's Rock and Banana Beach. Only one biotope (*Jania*) consistently experienced greater volumes of sand inundation than all other biotopes examined at Shaka's Rock, Banana Beach and Salt Rock. The relative ranking of biotopes was based on semi-quantitative estimates derived from the information presented in Table 5.4 as described in the Methods.

Discussion

The central purpose of this chapter was to test whether biotopes recognised on an objective biological basis (Chapter 4) are also distinguishable by differences in the physical conditions they experience. It therefore addresses one of the central criticisms of some biotope classification schemes, namely, that they fail to determine whether the biotopes can be linked to physical attributes. Accomplishing this does more than simply help to define biotopes on both abiotic and biotic grounds: it pinpoints the physical factors that are most likely to lead to the development of different biological communities.

Local-scale differences in abiotic factors

Rock temperature, wave exposure and sand inundation varied significantly between at least some biotopes at a within-site scale. Topographic variability within sites was evident, but different biotopes did not consistently differ in terms of aspect or slope at any sites. The local-scale variability in abiotic factors conforms to the prediction of Dayton and Tegner (1984) that processes underlying small-scale variability in community structure act and vary at local scales. My study showed correlations between small-scale abiotic and biological patterns but causality can only be determined by experimentation. Nevertheless, efficient design of experiments requires descriptive observational data to pinpoint likely causative factors in order to formulate hypotheses that can then be tested experimentally (James and McCulloch 1990).

Correlating biotope distribution with potential abiotic determinants

The subset of biotopes selected from those defined in Chapter 4 proved to have corresponding differences in physical habitat in all but two cases (*Perna* and *Cheilosporum*). Thus, the biologically defined biotopes also differed in terms of physical conditions. This justifies the use of the term "biotope" to describe the different biological communities as both the habitat and community of species (Connor et al. 1997) are significantly different.

In general terms, most of the biotopes examined experienced significant differences in rock temperature and wave exposure. The measurements of rock temperature and wave forces were undertaken twice at Shaka's Rock and although temporal differences were apparent, the relative patterns between different biotopes were the same on both occasions (Figure 5.2). By contrast, only one of the nine biotopes was usefully distinguished by the relative amount of sand inundation (Figure 5.3) and none of the biotopes were correlated with differences in aspect or slope within any of the sites (Tables 5.2 and 5.3).

Rock temperature

There were no significant within-zone differences in rock temperature between the different biotopes at either Shaka's Rock or Cape Vidal (Figure 5.2). This indicates that the within-zone distribution of biotopes, at a scale of metres, was not related to differences in rock temperature at these sites. At Banana Beach, however, within-zone differences in rock temperature could not be eliminated as a possible determinant of the distributions of some of the biotopes (Figure 5.2C). Specifically, in the low shore, higher mean rock temperatures were experienced by *Cheilosporum* than *Gelidium*, and in the mid shore, the *Tetraclita* biotope was exposed to higher rock temperatures than *Palythoa* or *Jania*.

By contrast, all biotopes from different zones on the shore were exposed to significantly different rock temperatures at all sites (Figures 5.2, 5.4), indicating that the vertical distribution of biotopes within sites was correlated with differences in rock temperature. Significantly higher mean rock temperatures were recorded in mid-shore biotopes compared to low-shore biotopes at all three sites. These results support the common perception that elevation and the associated effects of temperature and desiccation may underlie the differences in species composition and abundance between zones on the shore (Stephenson 1942, Lewis 1964, 1976, Stephenson and Stephenson 1972, Underwood 1978, Menge and Farrell 1989, Iwasaki 1995a).

Although elevation and emersion time were not examined in this study, Bustamante et al. (1997) showed that rock temperatures were highly correlated with both. Lambert and Steinke (1986a) described five different communities for KwaZulu-Natal shores, named after characteristic taxa. A "coralline community" comprising articulate coralline algae occupied the lowest zone with the *Perna perna* community occupying scattered high ground within the coralline community. In the mid-shore a *Ralfsia expansa* community was recognised and above that a *Tetraclita serrata* community. In the high shore a *Littorina*-Cyanobacteria community was recognised. The distribution of Lambert and Steinke's (1986a) communities was therefore correlated with gradients of elevation and emersion although rock temperatures were not measured. Their results showed a separation in elevation for the coralline and mussel communities at the single site they examined, whereas no difference in rock temperature between biotopes dominated by the mussel *Perna perna* and the articulated coralline alga *Cheilosporum sagittatum* was evident at two sites where I could compare these biotopes. The results of my study correspond with Lambert and Steinke (1986a) in that barnacle-dominated biotopes experienced significantly higher rock temperatures (i.e., were found at greater elevation and were emerged for longer) than mussel-dominated biotopes.

Wave exposure

Significant differences in wave exposure existed between the biotopes compared within both the low and mid shore at all three sites examined (Figure 5.2). In the low shore, *Perna* experienced significantly higher wave forces than *Pyura* and was also more wave-exposed than biotopes dominated by red fleshy algae, *Hypnea* and *Gelidium*. Higher wave forces were recorded within *Hypnea* compared to *Gelidium*. In the mid shore, *Palythoa* consistently experienced lower wave forces than *Octomeris* or *Tetraclita* at all three sites. At the two sites where the habitat of *Jania* was investigated, significantly higher wave forces were recorded within this biotope compared with *Palythoa*, but no difference in wave exposure was evident between *Jania* and barnacle-dominated biotopes (*Octomeris* or *Tetraclita*).

Using similar wave force measuring devices to those I used in my study, Alvarado and Castilla (1996) reported considerable variation in wave exposure within rocky platforms in central Chile. Similarly, Bustamante et al. (1997) recorded significant within-site differences in wave forces on the south and west coast of South Africa. The results of my study conform with those of Bustamante et al. (1997) with local small-scale differences in wave exposure being associated with divergent community structure in the low and mid shore. Mussel and barnacle-dominated biotopes were more abundant at wave-exposed areas in my study, and the same is true for these taxa on the west and south coasts of South Africa. Considering things at a larger scale, I also showed that mussels are predominant at wave-exposed sites when I compared sites within regions (Chapter 3). Returning to the small-scale analyses covered here, *Gelidium* species showed a preference for wave-sheltered positions on the south and west coast (Bustamante et al. 1997) and in my study, *Gelidium* experienced the lowest forces of any biotopes, less than half of those measured within *Perna*.

Bustamante et al. (1997) did not identify articulated coralline algae to the level of species, but did describe articulated corallines as being most abundant at semi-exposed and sheltered sites on the west and south coast respectively. In my study, the *Cheilosporum* biotope experienced high wave forces that were indistinguishable from those experienced by the *Perna* biotope. Lower wave forces were recorded within another articulated coralline biotope, *Jania*, but these forces were not significantly different to those recorded within barnacle-dominated biotopes. There were no species of articulated coralline algae that were found to prefer wave shelter in either the low or mid shore. Both biotopes dominated by articulated corallines (*Cheilosporum* and *Jania*) were more abundant in (at least) moderately-exposed positions in my study.

Although the classification system for marine benthic biotopes of the British Isles did not establish quantitative links between contrasting biotopes and wave forces, wave exposure was recognised as one of the principal factors that determine community structure on rocky shores. Similar physical habitats were described for mussel, barnacle and algal-dominated biotopes in Great Britain (Connor et al. 1997) as identified in South Africa (McQuaid and Branch 1984, Bustamante et al. 1997) including KwaZulu-Natal (the present study). Exposed shores were animal-dominated with mussel and barnacle biotopes prevalent and sheltered shores were algal-dominated. Dethier (1990) described different communities inhabiting exposed and semi-exposed rocky shores in Washington state. Once again, similar patterns were reported with mussel (*Mytilus californianus*) dominating exposed areas whilst *Fucus* spp. and other algae were characteristic of sheltered shores.

Zoanthids were more abundant at wave-sheltered positions in my study and this pattern was also evident at the scale of between-site comparisons (Chapter 3). There are few published descriptions of determinants of zoanthid communities but in tropical Brazil, Sauer Machado et al. (1992, 1996) reported that zoanthids were present on shores that were never exposed to strong wave action.

Wave exposure has been predicted to influence trophic structure on rocky shores (McQuaid and Branch 1984, 1985, Bustamante and Branch 1996a, Bustamante et al. 1997). As on the south and west coasts of South Africa, filter feeders, principally mussels and barnacles, dominated exposed areas in the low and mid shore respectively in KwaZulu-Natal. In all areas, primary producers experienced lower wave forces. Zoanthids are difficult to place in trophic context because they are microcarnivores but depend on symbiotic algae for much of their nutrition (Branch et al. 1994). As zoanthids host zooxanthellae, I classed them as primary producers. In both the low and mid shore, sheltered areas were therefore dominated by primary producers whereas more exposed areas were dominated by filter feeders.

The small-scale relationships between wave exposure and distribution of biotopes within sites in this study were similar to the larger-scale between-site patterns in community structure covered in Chapter 3 (see Figures 3.2-3.4 on p 94-101). The proposed reasons for the success of filter feeders where wave forces are greater have already been discussed in detail in Chapter 3. In brief, however, they include (1) enhanced turnover and quantity of food for filter feeders (Berry 1978, Schleyer 1981, McQuaid and Branch 1985, Bustamante and Branch 1996a,b); (2) increased delivery of larvae (Leonard et al. 1988) and (3) reduced predation (Menge and Olson 1990).

Pyura was the only biotope dominated by filter feeders that consistently experienced relatively low wave action. This biotope experienced significantly lower wave forces than *Perna* at Cape Vidal, the only site where the habitat characteristics of these two biotopes could be compared at this scale. However, in Chapter 3, analyses of between-site differences in community structure at unexploited sites in Maputaland also revealed that *Pyura stolonifera* was more abundant at sheltered sites rather than exposed sites. Biotopes dominated by *P. stolonifera* were present at only three sites in KwaZulu-Natal (Chapter 4). Two of these were unexploited semi-exposed sites (Cape Vidal Point and Sodwana Bay, wave forces = 6-8 x 10^3 N.m^{-2}) and the third site, Zinkwazi Platform, was both wave sheltered (wave forces < 5 x 10^3 N.m^{-2}) and sand inundated. The greater abundance of *P. stolonifera* at more sheltered areas conflicts with reports by Fielding et al. (1994) and Bustamante and Branch (1996) that this species is more abundant at exposed localities. However, wave exposure is relative and all shores in KwaZulu-Natal experience wave forces exceeding 4000 N. m^{-2}. As discussed in Chapter 3 there are no very sheltered shores in KwaZulu-Natal equivalent to those on the south and west coasts (Bustamante et al. 1997).

Berry (1978, 1982) argued that recruits of *P. stolonifera* are unable to compete with those of *Perna perna* which are highly motile and are capable of smothering other organisms due to their rapid growth. He proposed that *P. stolonifera* colonies could only establish when mussel recruitment fails (Berry 1982). If mussels recruit less successfully at less exposed areas in KwaZulu-Natal, as is the case on the west coast (G. Branch, University of Cape Town pers. comm., and see Chapter 3 discussion), this may explain why the *Pyura* biotope establishes at more sheltered areas. *Pyura* and algal-dominated biotopes were not compared because there were no sites where these two biotopes co-existed in the low shore. A complicating factor in examining the distribution of mussel, *Pyura* and algal-dominated biotopes is that mussels are heavily harvested. On exposed shores, the absence of algal-dominated biotopes at unexploited sites contrasts with the prevalence of such biotopes at exploited sites. Harvesting may mask patterns in the distribution of biotopes subject to human exploitation and this issue is addressed specifically by experimental studies in Chapter 6.

Wave exposure was significantly greater in the low shore compared to the mid shore although substantial variation was evident within zones at all sites (Table 5.2, Figure 5.2). Bustamante et al. (1997) reported that at exposed and semi exposed sites, wave exposure was higher in the mid shore compared to the low shore but substantially lower in the high shore. These authors measured wave forces with increasing shore elevation at two sites. In KwaZulu-Natal, more detailed studies of the effect of elevation on wave exposure would be required to determine how wave exposure varies in relation to height on the shore. In contrast to the differences in rock temperature between all biotopes from different zones, several biotopes from different zones on the shore did not differ significantly in wave exposure (Figure 5.2), but differences between biotopes within zones were often substantial. Differences in wave exposure therefore do not easily explain vertical zonation patterns but do strongly correlate with the distribution of different biotopes within these zones.

The two contrasting barnacle biotopes in this study were not compared at any one site. However, it may be predicted that *Octomeris* should occur in relatively exposed conditions while *Tetraclita* should be more abundant within sheltered habitats as shown at a between-site scale (Chapter 3). In Chapter 3, when simultaneous wave force measurements were made at different sites, exposed mid shores had consistently higher cover of *Octomeris* than sheltered shores, where *Tetraclita* was more abundant in two of three site-pair comparisons (Table 3.10, Figure 3.2).

Sand inundation

Within the low shore, different biotopes never differed in terms of sand inundation. Within the mid shore, only one biotope consistently experienced significantly different mean volumes of sand inundation. *Jania* experienced greater inundation than any other biotopes with which it was compared.

Sand inundation has been linked to variability in intertidal assemblages in many parts of the world (Daly and Mathieson 1977, Taylor and Littler 1982, Littler et al. 1983, D'Antonio 1986, Foster et al. 1988, Dethier 1990, Kendrick 1991). On the south coast of South Africa, sand influences intertidal community structure by increasing habitat heterogeneity and through its effect on the physiology of some species (McQuaid and Dower 1990, Marshall and McQuaid 1989, 1993). Sand inundation may prevent regular feeding activity and induce physiological stress, especially by reducing oxygen availability (Marshall and McQuaid 1993).

In my study, barnacle-dominated biotopes experienced significantly less sand inundation than *Jania*. Physiological intolerance to sand inundation may exclude barnacles from sand-inundated areas. Jackson (1976), however, reported that both *Tetraclita* spp. and *Octomeris angulosa* survived up to ten days of sand burial on the Mapelane coast while only algae, including the turf-forming coralline alga, *Jania* sp., failed to survive. My results in both this chapter and Chapter 3 conflict with Jackson's observation. Barnacles were consistently less abundant and often absent at sand-inundated sites whereas *Jania verrucosa* was the most important distinguishing species characterising sanded mid-shores in three site-pairs examined (see Table 3.7 and Figure 3.1 p 87 and 89). The stretch of coast covering Crayfish Point to Railway Ledge is heavily sanded (Figure 2.11, p 52). At these two sites and adjacent heavily sanded sites (Sandy Point and Dingini, pers. obs.), no examples of barnacle-dominated biotopes were found and the mid shore at all four sites was dominated by the coralline turf, *Jania verrucosa*. Experimental studies could be used to examine the effect of different intensities of sand inundation as well as the duration of sanding events.

The proposed reasons that algal turfs monopolise space on sanded shores were discussed in Chapter 3. In brief, these include their ability to accumulate sediment (Sousa et al. 1981, Seapy and Littler 1982, Stewart 1989), the effect of sediment on recruitment of other species (D'Antonio 1986, Iwasaki 1994) and the inhibition of grazers at sand-inundated areas (Sousa et al. 1981, D'Antonio 1986, Santos 1993).

Patterns of sand inundation within sites often bear a strong relationship with topography (McQuaid and Dower 1990, Santos 1993), and wave action also influences sand inundation (Rogers 1990, Airoldi et al. 1996, Trowbridge 1996, Airoldi and Virgilio 1998). Lewis (1968) cited intolerance to siltation at sheltered sites as one mechanism that may be important in understanding patterns of spatial variation created by differences in wave exposure. Studies investigating effects of sand inundation should also consider the influence of both topography and wave exposure.

Mid-shore biotopes generally experienced greater sand inundation compared to those in the low shore (Figure 5.3). This mirrors the findings of Chapter 3 where the influence of sand inundation was greater higher up the shore (Figure 3.5). However, comparisons of biotopes between zones yielded only one consistent significant difference in sand inundation. This indicates that differences in sand inundation cannot consistently explain divergent community structure between zones. Within zones there were surprisingly few differences in sand inundation between biotopes. Only in the case of *Jania* was sand inundation clearly and consistently linked to a particular biotope.

Topography

There were no topographic differences (in slope or aspect) between areas occupied by different biotopes at any of my sites. Fuji and Nomura (1990) attributed variation in macrofaunal communities to micro-topographic characteristics but were criticised by Bustamante et al. 1997) for failure to measure wave exposure and for under-representing certain habitats in their sampling. Topography influences fluid dynamics (Denny 1988) and therefore may translate into hydrodynamic differences that could have underlain the variability observed by Fuji and Nomura (1990). Lenihan (1999) showed that habitat structure controls local physical variables, which profoundly influence biota. His work was conducted on subtidal oyster reefs and flow speed was the most important factor explaining variation in the performance of the oysters. In intertidal boulder fields, Guichard and Bourget (1998) proposed that hydrodynamic flow is a vector linking community structure and variability in topography. Topography may also influence sedimentation (Sousa 1985, Dower and McQuaid 1990) and this may also explain observed biological variability attributed to topographic variability. Santos (1993) found that substrate slope indirectly influenced subtidal algal assemblages because of reduced sedimentation on steep slopes.

Understanding horizontal and vertical variability in community structure

A limitation of my study was that physical features of biotopes could not be quantitatively compared between sites because measurements were made at different times. However relative patterns in the correlation between biotope distribution and abiotic patterns allowed semi-quantitative ranking of different biotopes to explore general principles about abiotic determinants between and within zones.

All biotopes from different zones on the shore differed in rock temperature (Figures 5.2 and 5.4). Within zones, temperature differences between biotopes were only evident at one site and even these were relatively minor. Many different biotopes from contrasting zones on the shore were not subject to significantly different wave forces or volumes of sand inundation (Figures 5.2-5.4, Table 5.4). This indicates that the vertical distribution of biotopes is most likely explained by differences in rock temperature and associated differences in thermal stress and desiccation, which correlate with gradients of elevation (Bustamante et al. 1997).

Within zones, the most consistent abiotic factor distinguishing between biotopes was wave exposure (Figure 5.2, Table 5.4). *Perna* and *Pyura* and *Perna* and *Hypnea* only differed in wave exposure. At Banana Beach, *Perna* and *Gelidium* and *Perna* and *Cheilosporum*-dominated biotopes differed in wave exposure as well as rock temperature. In the mid shore, wave exposure was the only habitat characteristic that was consistently different between the biotope groups dominated by zoanthids (*Palythoa*) and barnacles (*Octomeris* or *Tetraclita*). These results support the hypothesis that wave exposure is one of the most important abiotic determinants of horizontal variability on rocky shores, particularly within zones (Menge and Farrel 1989, Foster et al. 1998, Menge and Branch 2001).

Sand inundation also influenced variability in biotope distributions and therefore community structure within sites. In the mid shore, some of the biotopes that were not subject to significantly different wave forces, did experience significant differences in sand inundation (Figure 5.3). In particular, this was the only abiotic feature that consistently distinguished between barnacle-dominated biotopes (*Octomeris* and *Tetraclita*) and *Jania*, with *Jania* subject to significantly greater volumes of sand inundation.

The results of my study correspond with those of Bustamante et al. (1997) conducted within shores on the west and south coast of South Africa. In both studies, significant differences in rock temperature correlated with differences in community structure between zones and local-scale differences in wave action were associated with divergent community structure. The two studies, however, relied on different methodologies and analyses. Bustamante et al. (1997) conducted replicate transects (perpendicular to the sea edge) and recorded biomass of all species and then recorded shore elevation, rock temperature and wave force at two sites. In my study, abiotic data were recorded within replicate samples of selected biotopes at two shore heights at three sites (and a fourth for sand inundation). Bustamante et al. (1997) used canonical correspondence and direct gradient analyses to compare community structure and abiotic variables. Canonical correlation has been criticised as inappropriate for linking observed biological community structure to measured abiotic variables because it requires assumptions that are unrealistic for species abundance or biomass data, e.g., linear relationships between abundance and environmental gradients (Clarke & Ainsworth 1993). The validity of direct gradient analysis has also been questioned because species-environment relationships are embedded at an early stage of the analysis and may influence the observed biotic pattern (Clarke 1993). For these reasons, a simple approach testing whether biotopes differ in respective abiotic parameters was employed in the present study. Despite these differences in approach, the central conclusions concur. Temperature correlates with changes in community structure as one moves upshore; whereas differences in wave action are strongly associated with horizontal changes in community structure and its greater effect is evident lower on the shore.

Biotopes that did not differ in abiotic factors

There were only two biotopes that were compared which failed to differ significantly in any of the environmental factors examined *Perna* and *Cheilosporum*. These biotopes may experience significant differences in other abiotic factors that were not examined or may have corresponding differences in biotic factors. On present evidence, however, they have indistinguishable physical habitats, and this similarity makes them prime candidates for intense interspecific competition between their respective dominant species.

Experimental removal of mussels in Natal has been shown to result in invasion by opportunistic algae particularly articulated corallines such as *Cheilosporum*, *Arthrocardia* and *Jania* spp. (Lambert and Steinke 1986b), which then persisted. Mussels failed to return to numerical dominance in experimentally cleared areas, even over an eight year period. Human exploitation of mussels has been linked to increased cover of coralline algae (Hockey and Bosman1986, Siegfried 1988, Dye et al. 1994) and an increased abundance of phytal-associated species (Lasiak and Field 1995, Lasiak 1999). In my study, mean cover of *Cheilosporum sagittatum* at exposed sites in Maputaland was more than 25% at sites exploited by subsistence collectors and less than 5% at unexploited sites (Chapter 3, Figure 3.3). The only site subject to subsistence collecting that was surveyed in Natal had a mean cover of more than 40% of this species. At Groutville, which is also subject to intensive mussel harvesting by subsistence collectors, 85% of the low-shore samples were classified as the *Cheilosporum* biotope (see Chapter 4). Clearly the interaction between mussels and *Cheilosporum*, and the manner in which the balance is influenced by harvesting is of critical interest. Experimental harvesting studies to examine the abundance of different biotopes in relation to different levels of human exploitation are central to Chapter 6.

Abiotic versus biotic determinants

Although this study examines only a select suite of physical factors, the influence of biotic factors should not be underestimated. Competition, grazing, predation and recruitment exert significant influences on intertidal community structure (see reviews by Underwood 2000, Menge and Branch 2001). Competition for food and space has been implicated as an important process that causes and maintains ecological patterns in rocky intertidal habitats (Connell 1961, Lubchenco 1980, Branch 1984, Underwood 1996). Grazers have an important role in structuring benthic marine communities (Lubchenco 1978, Hawkins 1981, Lubchenco and Gaines 1981, Gaines and Lubchenco 1982, Hawkins 1983, Hawkins and Hartnoll 1983, Hawkins et al. 1992, Benedetti-Cecchi and Cinelli 1993, Branch and Moreno 1994, Johnson et al. 1997, Benedetti-Cecchi et al. 1998). Predators such as starfish (Paine 1966, 1974), molluscs (McQuaid 1982, Lubchenco et al. 1994), whelks (Castilla and Duran 1985, Duran and Castilla 1989, Navarette 1996), urchins (Sala et al. 1998) and fish (Anderson and Connell 1999) powerfully influence community structure of marine benthic assemblages. Larval supply and behaviour and recruitment are key biological factors that shape community structure

(Grosberg 1981, Connell 1985, Gaines and Roughgarden 1985, Menge 1991, Grosberg and Levitan 1992, Menge et al. 1993, Menge 2000a). This includes algal recruitment (Santelices 1990, Kaehler and Williams 1997).

My results show that small-scale patchiness in intertidal community structure correlates with local-scale variability in abiotic factors, particularly rock temperature and wave forces. Such patchiness is often only attributed to biological processes (Schoch and Dethier 1996) but the relationships between biotope distribution and physical factors identified in my study suggest that abiotic factors exert an important influence on biological processes. Indeed, the influence of local habitat conditions on biotic factors is an important aspect of the ongoing debate regarding the relative importance of physical versus biological determinants in marine ecosystems (Dayton 1995, Mann and Lazier 1996). Recent studies have highlighted the impact of environmental constraints on biological factors (Menge and Farrell 1989, Menge and Olson 1990, Iwasaki 1995b, Leichter and Witman 1997, Chapman 2000). For example, on rocky shores in southern Japan, distribution patterns of alternate barnacle and mussel communities are determined by recruitment (Chiba and Noda 2000) but topography and hydrodynamic flow are likely to exert a significant influence on recruitment (Guichard and Bourget 1998).

Predicting biological patterns from habitat characteristics

The first initiative towards a predictive model linking the physical features of the intertidal habitat with community composition and abundance was that undertaken by Schoch and Dethier (1996) in Washington state. The role of habitat in influencing intertidal fauna was also examined in Brittany, France (Hily and Jean 1997). There, different habitats (as described by substratum, height on the shore, wave exposure and algal cover) had significant differences in species richness, biomass and trophic structure.

Kilometre-scale intertidal biotopes in British Columbia, Canada, have been defined on the basis of physical features, namely shoreline morphology, temperature, salinity and currents, and biological surveys were conducted to examine the relationship between biological communities and these physical parameters (Zacharias and Howes 1998, Zacharias et al. 1998, 1999). Using regression tree models to identify combinations of abiotic factors required to support biological communities identified by two-way indicator species analysis (Twinspan), revealed that habitat characteristics can effectively be used to predict the occurrence of biological communities (Zacharias et al. 1999). However, these authors did find some similar biological communities in dissimilar habitats. This was attributed to their failure to include species abundance data in their analyses (only prescence/absence was considered) so that communities supporting different abundance of species were not separable. My biotope classification successfully differentiates between communities with similar species composition but different patterns of abundance. However, in my study, I did not compare habitats of biotopes with similar species composition. Many biotopes were found only at widely separate geographical localities and at this scale other abiotic factors are likely to cause differences in biological community structure (e.g., differences in sea temperature, productivity and riverine input (see Chapters 2 and 3). Nevertheless, the observed relationships between physical habitat features and the distribution of a subset of biotopes in KwaZulu-Natal indicate that abiotic parameters can be used to predict the distribution of biological communities.

Conclusions

Different biotopes experienced significant differences in rock temperature, wave forces or degrees of sand inundation (Figure 5.4). Conversely, none of the biotopes were distributed in correlation with differences in topography. Vertical zonation patterns (i.e., between zones) were most consistently explained by differences in rock temperature, which are correlated with elevation and emersion (Jackson 1976, Bustamante et al. 1997). All low shore biotopes (*Perna*, *Pyura*, *Cheilosporum*, *Hypnea* and *Gelidium*) experienced significantly lower rock temperatures than all mid-shore biotopes (*Palythoa*, *Octomeris/Tetraclita* and *Jania*). Variability in wave exposure consistently explained horizontal (i.e., within-zone) differences in the distribution of several biotopes. Sand inundation accounted for divergence of mid-shore community structure, with the *Jania*-dominated biotope consistently having greater sand inundation than any other biotope.

Perna and *Pyura* only differed in wave forces with *Perna* occupying wave-exposed positions and *Pyura* inhabiting wave-sheltered areas (Figure 5.4). *Perna* and *Cheilosporum* also experienced higher wave forces than any other biotopes. *Gelidium* and *Palythoa* occupied the most wave-sheltered positions. There were no significant differences observed in any of the abiotic factors examined between the biotopes dominated by *Perna perna* and *Cheilosporum sagittatum*. The distribution of these biotopes is predicted to relate to a competitive balance that is shifted by different regimes of human exploitation, and this hypothesis is addressed in the following chapter.

While causality between potential abiotic determinants and biological community structure may not be invoked, the consistent patterns in biological community structure and abiotic factors at the three disjunct sites studied here, and at larger scales (Emanuel et al. 1992, McQuaid and Branch 1984, 1985, Bustamante et al. 1997, Chapter 3), support the idea that these physical factors establish the framework, within which biological factors may shape intertidal assemblages. This is the first time an attempt has been made to test a biotope classification system that has been developed on biological grounds, against physical factors.

Chapter 6

The effects of exploitation on intertidal community structure in KwaZulu Natal

ABSTRACT

Using four different approaches, I uncovered evidence of direct and indirect impacts of harvesting on intertidal communities. (1) At Black Rock in Maputaland, comparisons between 1997 and 1976 revealed that numbers of mussels, the principal target species, were more than 80% lower in 1997 than in 1976. Densities of targeted limpets were also lower whereas the cover of the articulated corallines was greater in 1997. (2) Experimental harvesting at Dingini established a causative link between harvesting and community modification. Recreational and subsistence-harvested plots were compared with control plots at two sites using a two-way crossed ANOSIM. Highly significant differences in community structure were revealed between control and harvested plots with subsistence intensities of harvesting causing greater differences. Plots harvested at the two different intensities also differed in community structure. At Dingini, the changes due to harvesting were evident in patterns of biotope abundance. Mussel-dominated biotopes were almost completely lost from heavily exploited plots whereas recreationally harvested plots retained some mussel-dominated biotopes. Algal biotopes were more abundant at higher intensities of harvesting. Biotope surveys offer a simple efficient method for monitoring community structure. (3) Comparisons of subsistence versus recreationally harvested sites in central and southern Natal indicated corresponding differences in community structure. Harvesting directly reduced *Perna perna* at all exploited plots or sites and indirect effects were also evident in the form of increased cover of red algae (e.g., *Hypnea spicifera*) and articulated corallines (*Cheilosporum*, *Jania* and *Arthrocardia* spp.) at more intensely exploited areas. These changes are consistent with harvesting impacts reported in the Transkei. Cascade effects were apparent although there was no evidence of overgrowth of encrusting algae at heavily exploited sites as was seen in Maputaland. (4) Biogeographic analyses were repeated after adding additional subsistence-harvested sites from Natal. Harvesting impacts only overrode biogeographic patterns when data were untransformed, and wave exposure always exerted a stronger influence on community structure than harvesting or biogeographic patterns. By excluding all subsistence-harvested sites from biogeographic analyses it was revealed that harvesting did contribute to the observed regional differences between Maputaland and Natal, but biogeographic patterns were retained in the absence of effects of subsistence exploitation. Harvesting exaggerated biogeographic patterns and accounted for 10% of the 70% dissimilarity between regions. Implications of direct and indirect harvesting impacts are discussed in terms of conservation and management of intertidal habitats. Representative areas closed to all forms of harvesting are urgently required in KwaZulu-Natal and estimates of catch per unit effort must be supplemented with stock surveys and monitoring for changes in community structure.

Introduction

Information on the effects of human activities is critical for the management of marine biological diversity (Hiscock 1995). Two of the most prevalent human activities on rocky shores in KwaZulu-Natal are subsistence and recreational harvesting of invertebrates. The biological consequences of human utilisation of intertidal resources can be classified into two categories. The first are direct effects on resources and the second involves ecosystem impacts, where harvesting results in changes in species composition and abundance. Direct effects of harvesting include changes in stock density and size structure of populations (Lasiak and Dye 1989, Moreno et al. 1994, Siegfried et al. 1985, Hockey and Bosman 1986, Castilla and Bustamante 1989, Kingsford et al. 1991, Keough et al. 1993). Target species often become less abundant and progressively smaller when harvested because large individuals are selectively removed and young individuals may not remain on the shore long enough to reach full size (Catterall and Poiner 1987, Keough et al. 1993). This may impact on the breeding population if the larger, most fecund portion of the population is targeted (Branch 1975b, Berry 1978, Underwood 1993a). Spatial and temporal differences in population size structure should, however, be interpreted with caution as recruitment, natural mortality and growth rate also influence size structure (Lasiak 1991, Dye et al. 1994). Changes in stock are often met with corresponding changes in catch per unit effort (CPUE) (Dye et al. 1994, Kyle et al. 1997a). However, unlike most fisheries, intertidal species are easily accessible and CPUE may not provide an accurate indication of sustainability (Hilborn & Walters 1992). For these reasons, human impacts in the intertidal should also be assessed in the light of their effect on entire communities, not just on resource species. Analyses of whole communities are also important in assessing how much any change matters in terms of biodiversity conservation (Underwood 1996).

Evidence suggests that human exploitation of intertidal organisms can result in large-scale modifications of rocky shore communities (Moreno et al. 1984, Oliva and Castilla 1986, Ortega 1987, Siegfried 1988, Duran and Castilla 1989, Hockey and Bosman 1986, Dye et al. 1994). In Chile, shellfish exploitation rates of approximately 6000 kg.km^{-1}.year^{-1} (Duran et al. 1987) have drastically modified community structure on rocky shores (Castilla and Duran 1985). In the former Transkei on the south coast of South Africa, shellfish harvests ranging between 206 and 14 109 kg.km^{-1}.year^{-1} (Hockey et al. 1988) have altered the species composition and ecosystem functioning of rocky shores (Hockey and Bosman 1986, Lasiak and Field 1995, Lasiak 1999). In KwaZulu-Natal, subsistence shellfish-gatherers collect between 4 000 and 23 000 kg.km^{-1}.year^{-1} at Dog Point and 22 000 and 90 000 kg.km^{-1}.year^{-1} at Black Rock (Kyle et al. 1997a). Recreational mussel collectors harvest far less: approximately 1 800 to 2 300 kg.km^{-1}.year^{-1} (Tomalin and Kyle 1998). The potential impact of either form of harvesting on community structure in KwaZulu-Natal has never been examined although their effects on the major target species, the brown mussel, *Perna perna*, have been monitored and documented (Fielding et al. 1991, Dye et al. 1994, Kyle et al. 1997a, Tomalin and Tomalin 1997, Tomalin and Kyle 1998).

In South Africa and particularly in KwaZulu-Natal there is an urgent need to examine harvesting impacts and develop sustainable harvesting practices, as pressure on management authorities to increase access to mussel resources for recreational and subsistence collectors is escalating (Tomalin 1995, Anderson and Griffiths 1997). Studies of harvesting impacts should experimentally investigate the effects of alternative harvesting regimes as different types of harvesting may differ in terms of impact and therefore sustainability (Fairweather 1991). Profound differences between both the methods and intensities of subsistence and recreational fisheries have been reported in KwaZulu-Natal and it would be expected that they will have different impacts (Tomalin and Kyle 1998).

The effects of two types of intertidal harvesters were considered in my study: (1) licensed recreational collectors who harvest mussels south of Cape Vidal (Figure 6.1) and (2) subsistence collectors. The impact of three groups of subsistence harvesters was examined: (i) those allowed to harvest at Black Rock in the Maputaland Marine Reserve; (ii) illegal subsistence harvesters at Groutville, Umgababa and Umfazazana in central and southern KwaZulu-Natal; and (iii) subsistence mussel collectors from the Sokhulu community who participated in controlled experimental harvesting at low and high intensities at Dingini in northern KwaZulu-Natal (Figure 6.1).

In the Maputaland Marine Reserve, recreational harvesting is prohibited but approximately 200 local subsistence fishers regularly harvest the brown mussel, *Perna perna*, the ascidian *Pyura stolonifera*, limpets and other intertidal species (Kyle et al. 1997a, 1997b). Sharpened vehicle leaf-spring blades as well as cane knives, files, hoes and axes are used, and the average amounts (whole wet mass) collected are 11.2 kg of mussels or 10.86 kg of *Pyura stolonifera* per person per outing (Kyle et al. 1997a). Subsistence harvesting of intertidal resources in northern KwaZulu-Natal became a controversial issue when the Maputaland Marine Reserve was proclaimed in 1986 (Kyle et al. 1997b) but harvesting was allowed to continue and monitoring of CPUE was initiated in 1988 (Kyle et al. 1997a).

Over the past 25 years, there has been conflict between local people who have been allowed to harvest, visitors who are denied access to resources and conservation agencies that have to enforce regulations (Kyle et al. 1997a). Concern has been expressed that resources are overexploited and that harvesting may be unsustainable (Heydorn and Hughes 1969).

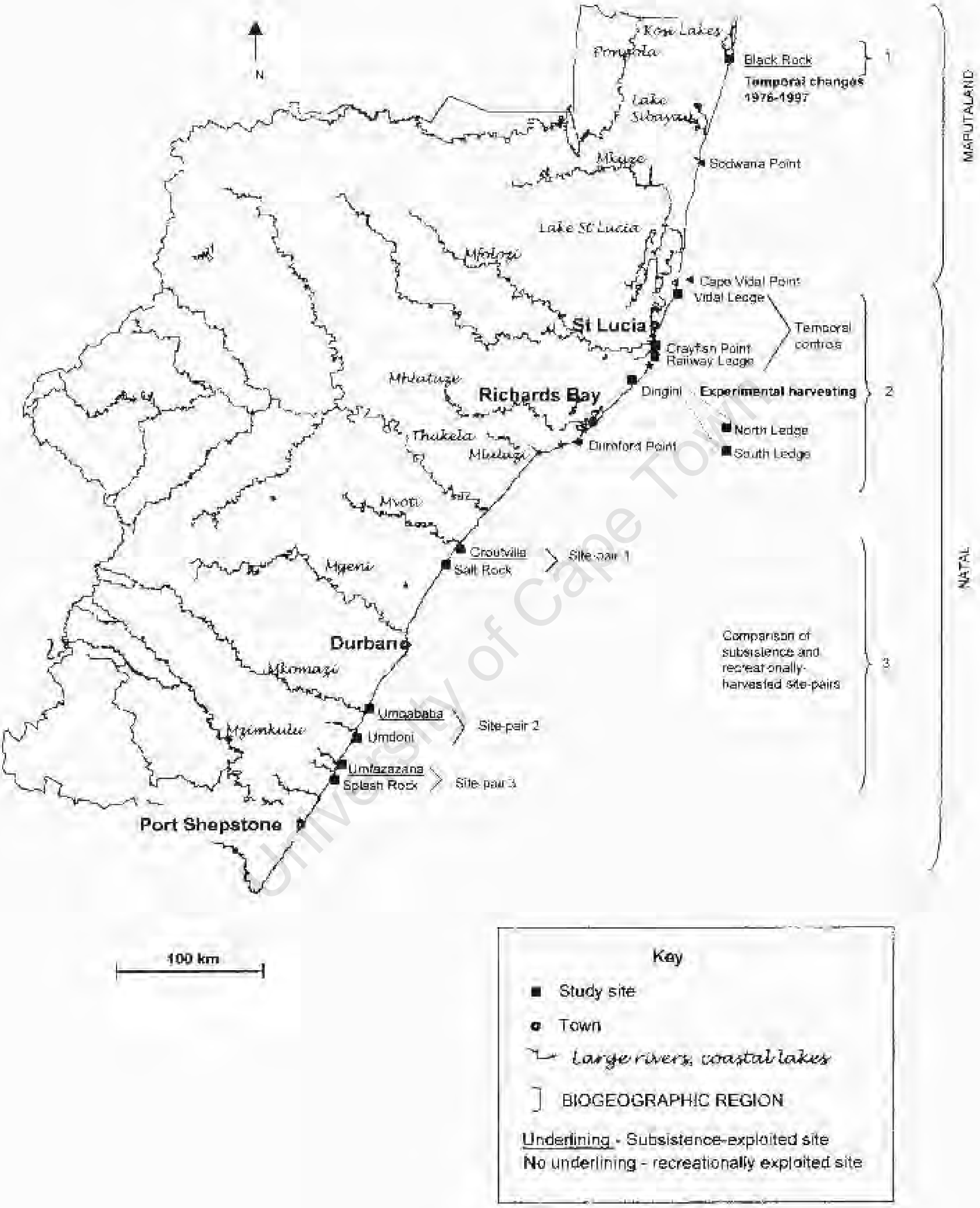


Figure 6.1. Map of KwaZulu-Natal showing rocky shore sites surveyed during the first three approaches (1-3) to assess the impact of human exploitation on community structure. All sites included in the fourth (biogeographic) approach are shown in Figure 1.2.

The earliest intertidal survey conducted in Maputaland was a single transect at Black Rock, conducted as part of a series of semi-quantitative surveys in ten sections of the KwaZulu-Natal coast (Jackson 1976). Jackson remarked that it would be short-sighted to continue to allow the type of harvesting she observed in Maputaland. However, analysis of CPUE data (1988 - 1994) for Maputaland led Kyle et al. (1997a) to the conclusion that subsistence harvesting of mussels and *Pyura* in Maputaland is occurring at a constant level and is therefore sustainable. However, without baseline and benchmark data it is difficult to ascertain whether the resource is fished at levels that are close to the maximum or are overfished. Kyle et al. (1997a) showed that the CPUE of limpets has declined substantially, implying overfishing.

In the past, the activities of subsistence fishers have been regarded as illegal. They were entitled to remove 50 mussels per day in KwaZulu-Natal if they had bought a recreational licence to do so. These amounts were inadequate to subsist on, and subsistence fishers invariably took more (Harris et al. 2000). Licences were difficult to obtain (they cost money and were often only obtainable considerable distances away from subsistence communities) and therefore subsistence fishers were often not licensed, even for a recreational take. Because subsistence fishers were not formally recognised, management systems (including monitoring, permit systems, allocation procedures and research to ensure sustainability) were not developed to cater for these fisheries (Harris et al. 2000).

In line with South Africa's new political climate after the democratic elections of 1994, a new Fisheries Policy was developed over the years 1996-1998, and the case of subsistence fishers was reviewed (van der Elst et al. 1998). An Access Rights Technical Group recommended that a new category of harvesters - subsistence fishers - be recognised and defined and that management schemes be developed to ensure that they be given preference in certain areas, and that their harvesting should be at a sustainable level (Branch et al. 1996, Martin and Nielson 1997, van der Elst et al. 1998). These recommendations were brought into law with the promulgation of the Marine Living Resources Act of 1998. Actions necessary to implement the act are currently underway, following recommendations by a Subsistence Fisheries Task Group (Harris et al. 2000). In the interim, subsistence fishing that was (and still is) technically illegal continues to be reported adjacent to human settlements in KwaZulu-Natal. Kyle et al (1997a) describe subsistence-harvesting activities in the Maputaland region but for the Natal biogeographic region, there is no documented information regarding which sites are harvested, the details of harvesting, methods or the types and quantities of organisms collected by subsistence collectors. Anecdotal evidence suggests that mussels are principal target species and cane knives are used to scrape clumps of mussels off the shore (L. van Schoor, A. Millar, KwaZulu-Natal Wildlife, pers. comm.)

Harvesters from the Sokhulu community have for many years illegally harvested mussels at Dingini (see Figure 6.1) using wide-bladed instruments such as cane knives (T. Ferguson, KwaZulu-Natal Wildlife, pers. comm.). As part of a co-management project to legalise their activities, rural Zulu women from this community participated in experimental harvesting at Dingini with the aim of developing sustainable harvesting practises (Harris et al. 1996, Attwood et al. 1997b). In this experiment, mussels were harvested using a screw driver and set numbers of bags of mussels approximating both recreational and subsistence harvesting levels were collected from replicated plots at two sites.

South of Cape Vidal, licensed recreational harvesters may gather mussels and bait organisms from all shores except approximately 2km of rocky shore in the Trafalgar Marine Reserve, and at the experimental harvesting site at Dingini. Approximately 11 000 license holders (Tomalin 1995a) collectively harvest 200-250 mt of mussels per year from about 110 km of rocky shore in the Natal region (Tomalin and Kyle 1998). Concern over recreational harvesting has also been reported with a reduction in harvesting pressure being advocated for some areas in this region (Tomalin and Kyle 1998), although these authors also claim that calls for reduced subsistence harvesting effort in Maputaland are unfounded.

Significant differences in community structure between exploited and unexploited shores in Maputaland were uncovered in Chapter 3. In addition, the results of the biogeographic analysis in Chapter 2 showed that Umfazazana, the only surveyed Natal site that was subject to subsistence exploitation, was more similar in terms of community structure to Maputaland sites than to other sites in Natal, indicating that harvesting may cause convergence of community structure. The significantly higher harvesting offtake per site in Maputaland also suggests that harvesting may influence biogeographic patterns. In this chapter, the impact of human exploitation on low-shore community structure on rocky shores in KwaZulu-Natal is investigated more specifically. Four approaches, each operating at a different scale, were implemented to examine whether harvesting by recreational and subsistence collectors influences community structure (Figure 6.1).

1. Temporal changes in community structure between 1976 and 1997 were investigated at Black Rock in Maputaland.
2. Temporal and spatial differences in community structure within and between sites was examined in northern KwaZulu-Natal. Replicated experimentally harvested plots and unexploited control plots were surveyed to determine whether there were significant differences in community structure between and within treatments, and whether there were any temporal changes between 1996 and 1998 at control sites. Changes in biotope abundance between treatments were also investigated.
3. The role of subsistence harvesting in structuring intertidal communities was further examined by surveying two additional sites in the Natal biogeographic region where rural

people practice subsistence harvesting. Three site-pairs were analysed to determine whether sites subject to subsistence versus recreational harvesting have consistent differences in community structure.

4. Inter-regional comparisons were made to test whether intense (subsistence) harvesting had any influence on the biogeographic break detected in Chapter 2 between Maputaland and Natal.

These four approaches were used to compare harvesting impacts between different types of fisheries and between biogeographic regions. Species and biotopes that consistently reflect changes in community structure associated with harvesting in KwaZulu-Natal were sought. Finally, the implications of the results of the present studies for management and conservation were assessed.

Methods

Four approaches were employed to examine the effect of harvesting on intertidal communities, all were restricted to the low and mid shore, as most harvesting is concentrated in the lowest quarter of the shore (Hockey and Bosman 1986, Lasiak and Field 1995, Kyle et al. 1997a, Tomalin and Kyle 1998). (1)Temporal changes in abundance of mussels were examined between 1976 and 1996/7 at a scale of metres at Black Rock. (2) At Dingini, the site of a harvesting experiment on the Zululand coast, spatial differences in community structure between replicated unexploited control plots and plots subject to different harvesting treatments were investigated at a larger scale of metres to tens of metres. To explore temporal changes in community structure over the same period at the scale of tens of kilometres, data from Dingini were compared with data from three other sites where no changes in harvesting effort took place. (3)To test whether subsistence harvesting plays a role in spatial variability in intertidal communities between sites in Natal (at a scale of tens of kilometres) and (4) between the biogeographic regions of Maputaland and Natal (hundreds of kilometres), two additional subsistence-harvested sites in Natal were surveyed. The data were added to the matrix of sites previously analysed in Chapter 2 for biogeographic trends, and the total data set re-analysed to test if these sites showed affinities with other sites in Natal (the biogeographic region in which these sites are situated), or with subsistence-harvested sites in Maputaland.

1.Temporal changes at Black Rock, Maputaland

To determine whether community structure differed between 1976 and 1997 at Black Rock (Figure 6.1), survey results from these periods were compared. Jackson (1976) used a single vertical transect to quantify the distribution of dominant plants and animals across the shore, using permanently identifiable physical features as reference points. She defined eight physical zones (see Figure 6.3 in the Results) and scored the abundance of organisms, including *Perna perna*, within each. In 1997, I surveyed six vertical transects (30m apart) in the same area as Jackson's transect, scoring 1 m X 0.5 m quadrats every 0.5 m between the high and low water mark. Biotopes (as defined by dominant species) and the abundance of mussels were recorded for each quadrat. During these surveys, I identified Jackson's zones (Figure 6.3 A-H) on each transect and calculated the mean number of mussels per zone. To estimate the abundance of mobile organisms in the low and mid shore, mean numbers of these species were calculated based on data from 20 random quadrats surveyed in each zone in 1997.

2. Experimental harvesting of mussels at Dingini.

2a. Experimental design

Data from an experimental mussel fishery (Harris et al. 1996) were collected for a detailed investigation of changes in community structure following harvesting at two different intensities. The experiment was conducted at two localities at a single site, Dingini (Figure 6.1), near Mapelane on the Zululand coast. This is the site of a five year co-management project, at which rural Zulu women from the local Sokhulu community participated in experimental harvesting with the aim of developing sustainable mussel harvesting practices (Harris et. al. 1996, Anderson and Griffiths 1997, Attwood et al. 1997). Dingini was surveyed in February 1996, before experimental harvesting was initiated. Cover of all species was recorded in twenty random quadrats in the low shore, using methods described in Chapter 2.

There are two rock ledges at Dingini, separated by approximately 500 m of sandy beach, and the experimental treatments were replicated by conducting harvesting at recreational and subsistence intensities on both ledges. Each ledge was divided into three 40-m wide plots and treatments of different intensities of harvesting were randomly assigned to individual plots (Figure 6.2). For this study, one control and two treatments in an orthogonal design were examined for differences in community structure. As each treatment was replicated at the two separate localities, this constitutes a crossed design. The control plots were left unexploited and the two treatments comprised two different intensities of harvesting, respectively approximating recreational and subsistence levels of utilisation (J. Harris and B. Tomalin pers. comm.). Harvesting was initiated in June 1996 and all plots were re-surveyed in April 1998. F-values measuring fishing intensity were estimated every 6 months by stock assessments of mussels and catch records per plot using standard yield per recruit analysis. The mean F-values between June 1996 and April 1998 for the recreational harvesting treatments were 0.29 and 0.35 and for the subsistence harvesting treatment, 0.56 and 0.63 (J. Harris, KwaZulu-Natal Wildlife, pers. comm.).

Before experimental harvesting was initiated, the middle of the mussel bed was marked with six nails across each plot at both localities. Twenty two months after harvesting was initiated, six perpendicular (vertical) transects were surveyed at each plot with five quadrats surveyed per transect (Figure 6.2). Data could not be obtained for one transect in the recreationally-exploited plot on the south ledge, so only five transects were included for this plot. The experimental plots were contiguous but the transects were centrally positioned in the plots leaving a 10-m buffer zone at the edge of the plots (i.e., 20 m between plots) to ensure spatial independence of samples from different treatments. A non-destructive visual method was used to score percentage cover of sessile species and numbers and sizes of mobile species within each quadrat.

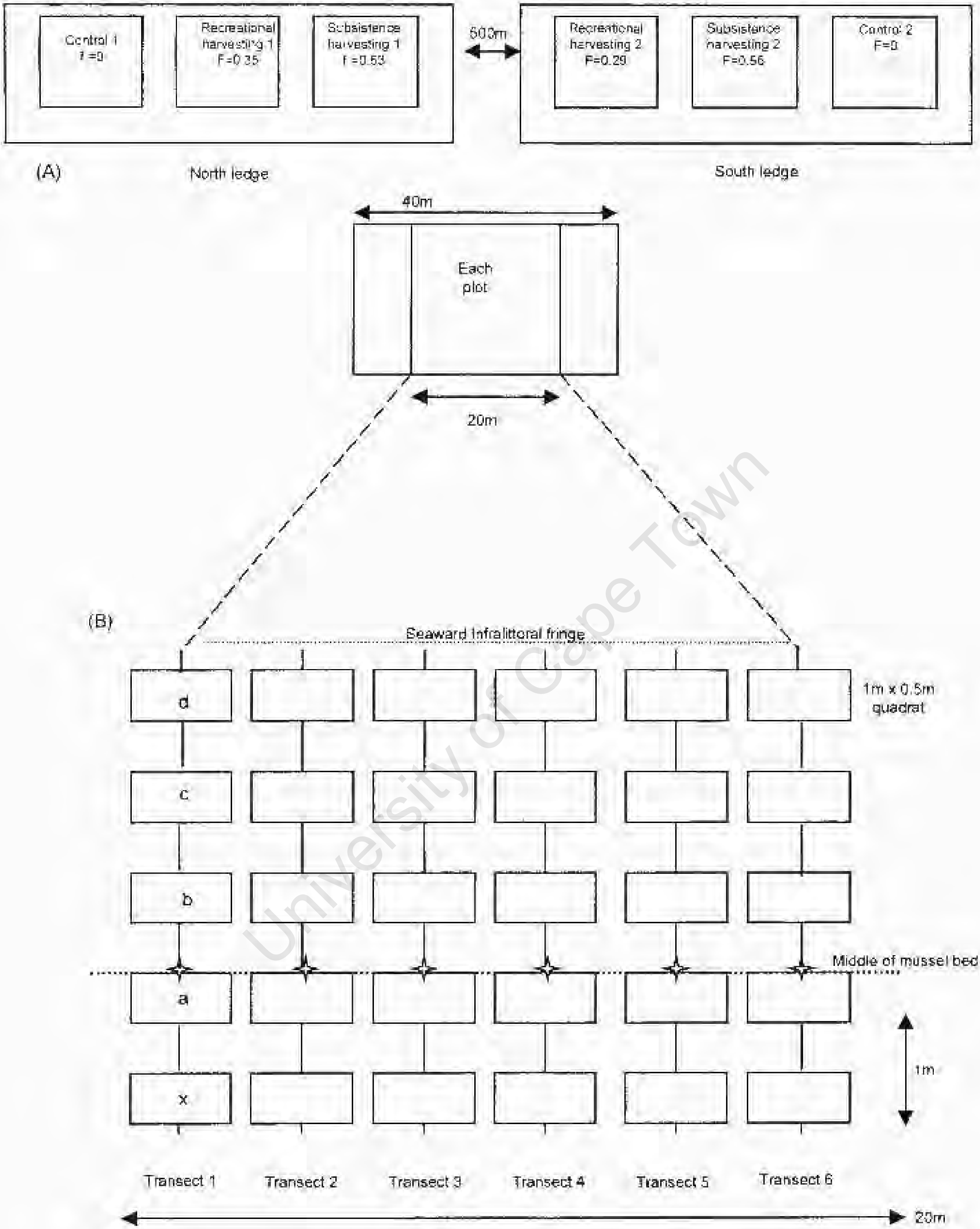


Figure 6.2. Diagram illustrating the position of (A) the experimental localities and plots and, (B) the quadrats within the 6 transects within each plot at Dingini.

✧ = marker indicating position of the middle of the original mussel bed before harvesting.

2b. Dingini experiment: Data analysis

PRIMER (Plymouth Routines in Multivariate Ecological Research, version 4.0 1994) was used for analysis of community structure (Clarke and Warrick 1994). The data were root-transformed to downweight the contributions of abundant species. Hierarchical cluster analysis and multi-dimensional scaling (MDS) were performed using the replicate transects for each treatment.

A two-way crossed ANOSIM was conducted to determine whether there were significant differences in community structure between localities within treatments and between treatments (controls and the two different intensities of harvesting). Similarity percentage breakdown (SIMPER) was used to identify discriminatory and characteristic species between and within treatments (Clarke 1993). Species that contributed more than 2% to the overall dissimilarity between samples were considered as major discriminating species. The two ledges were analysed separately to determine whether consistent differences were apparent between treatments.

To explore the effect of harvesting on biotopes, pie charts were constructed to compare the abundance of different biotopes at Dingini in 1996 before harvesting (n=20 quadrats) and at each of the six plots (two controls and four treatment plots, n = 30 quadrats per plot) surveyed in 1998, after harvesting had been operating for 22 months. Sample numbers were higher in the experimental study because the stratified sampling design included 30 quadrats whereas the 1996 data from Dingini were collected as part of a coastwise survey in which 20 random quadrats were routinely surveyed (see Chapter 2). The biotope classification system (Chapter 4) was used to identify the biotope present in each quadrat. A biotope was assigned to each quadrat, based on the dominant species characteristic of each of the biotopes in the low shore (Chapter 4, Table 4.1).

2c. Temporal changes within Dingini and adjacent control sites in Zululand

To determine whether significant temporal changes occurred at unharvested plots at Dingini over the duration of the survey period, data from surveys at Dingini 1996 before the experiment started were compared with those from the unexploited control plots from the two localities at Dingini in 1998. Twenty quadrats scored in 1998, ten at each of the Dingini control plots, were compared with the twenty quadrats scored in the same zone (quads b and c, Figure 6.2) in 1996.

In addition, three recreationally-exploited sites adjacent to Dingini, i.e., Railway Ledge, Crayfish Point and Vidal Ledge (Figure 6.1), which had previously been surveyed in 1996, were re-surveyed in 1998 to determine whether significant temporal changes had occurred over the duration of the harvesting experiment. These sites were selected because the surveys in 1996 established that the community structure at these sites was more similar to the pre-harvesting condition at Dingini than any other sites in Natal (Figure 2.5, p 39). They were re-surveyed in 1998 in an identical manner to that employed in 1996, with percentage cover of all visible species being recorded in 20 random 1m x 0.5m quadrats in the low shore. To test for temporal variation in unexploited plots at Dingini, one-way ANOSIM tests were conducted to compare the twenty pre-harvest samples from 1996 with the twenty samples from the unexploited control plots surveyed in 1998. Independent 1-way ANOSIM tests compared data between these years at Railway Ledge, Crayfish Point and Vidal Ledge.

3. Comparing recreationally and subsistence-exploited sites in Natal

To compare community structure at subsistence versus recreationally exploited sites in Natal, three sites subject to subsistence harvesting (Umfazazana, Groutville and Umgababa) were compared with the closest sites that were exploited only by recreational collectors (respectively Splash Rock, Salt Rock and Umdoni, Figure 6.1). The analysis was based on data in Chapter 2, but additional data were obtained for Groutville and Umgababa. The low shores of these sites were surveyed in September 2000 in an identical manner to all previously surveyed sites, with twenty random quadrats scored for percentage cover of all visible species. A crossed design was used to compare community structure within and between sites subject to recreational versus subsistence harvesting using a two-way ANOSIM test to compare differences between and within the two levels of harvesting. SIMPER analyses were undertaken to identify characteristic and distinguishing species. Average similarities of sites subject to different types of exploitation were compared to determine whether subsistence exploitation led to convergence of community structure.

4. Assessing the influence of subsistence harvesting on biogeographic patterns

The data gathered to compare subsistence and recreational harvesting in Natal also allowed an examination of whether harvesting offers any explanation for the biogeographic break between Maputaland and Natal, as documented in Chapter 2. The data set was based on that for the entire KwaZulu-Natal coast, which was used for biogeographic analysis in Chapter 2, but data from the Dingini experiment and from the two additional Natal sites at which subsistence harvesters collect mussels (Groutville and Umgababa) were added.

If subsistence harvesting influences biogeographic patterns in community structure, it was expected that these subsistence-harvested sites would be more similar to those in Maputaland than to other sites from the Natal region. At Dingini, only data from shore-heights equivalent to the original low shore surveys (i.e. quadrats b and c Figure 6.2) were used for comparisons. Mean cover of each species was calculated from twenty samples per site.

Hierarchical cluster analyses were undertaken to compare community structure at all sites surveyed in 1996 together with the control and subsistence-harvested localities at Dingini (surveyed in 1998) and the two additional subsistence-harvested sites, Umgababa and Groutville (surveyed in 2000). Cluster analyses were performed first using untransformed data and then root-transformed data. Using untransformed data emphasises the importance of abundant species; with root-transformed data all species contribute more uniformly to the observed pattern. By undertaking both analyses, comparisons of emergent patterns were possible. To determine whether the biogeographic pattern documented in Chapter 2 (Figure 2.5, p 39) was related to regional differences in harvesting intensity or would persist in the absence of subsistence exploitation, a third hierarchical cluster analysis was performed comparing only subsistence-harvested (heavily exploited) and recreationally-harvested (lightly exploited) localities. SIMPER was used to identify characteristic and distinguishing species within and between regions. Only species that contributed more than 2% to the overall similarity or dissimilarity were considered.

Results

1. Temporal changes at Black Rock, Maputaland

Comparison of abundance estimates for *Perna perna* at Black Rock in 1997 and 1976 (Jackson) indicated that mussel stocks were substantially lower within the low and mid shore zones in 1997 (Figure 6.3). Transects surveyed in 1997 showed that although variability within zones (i.e., between transects) was apparent, the abundance of *P. perna* was more than 80% lower within each zone. In both Jackson's study and the present study, the abundance of *P. perna* increased down-shore. In the lowest part of the shore, Jackson (1976) estimated approximately 500 mussels.m^{-2} whereas a mean of 68 ± 91 mussels.m^{-2} was recorded in 1997. In zones E and F, mussels had decreased from approximately 240 to less than 40.m $^{-2}$.The percentage reductions were lowest in the low shore.

The densities of mobile organisms also appeared to be much lower in 1997 than in 1976. The abundance of limpets in 1997 was substantially lower than the figures reported by Jackson (1976). Jackson recorded combined densities of *Cellana capensis* and *Scutellastra* sp. of 40 to 80.m^{-2} whereas in 1997 the mean densities of *Scutellastra pica* were 1.4 ± 3.2 .m^{-2} (n=20 quadrats) and those of *C. capensis*, 25.2 ± 8.3 .m^{-2}.

Articulated coralline algae achieved higher cover in 1997 than in 1976. Jackson recorded an abundance of 5-7% for the coralline alga *Cheilosporum* sp. in zone G and none of this species in zones F and G. In 1997, the mean cover of *Cheilosporum sagittatum* in zones E-G, was 37 ± 29 % and coralline algae community was scored as the primary biotope in 73% of quadrats in zone G and 64% of quadrats for zone F.

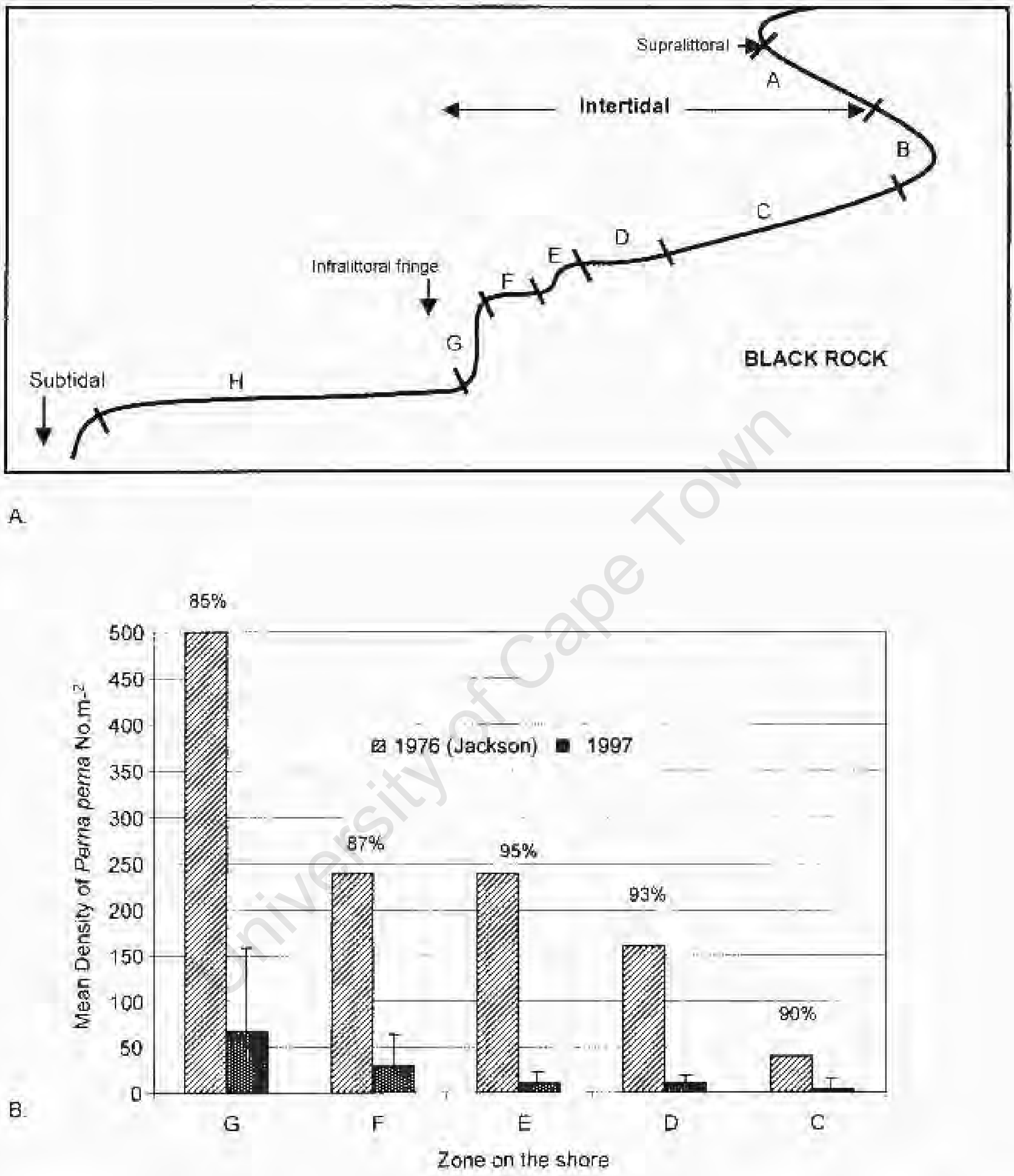


Figure 6.3. Profile of Black rock showing (A) Jackson's (1976) physical zones A - H, and (B) histogram showing the relative abundance of mussels per zone on the shore as recorded by Jackson (1976) and in 1997 (present study). The percentage difference between 1976 and 1997 is indicated per zone.

2. Experimental harvesting of mussels at Dingini.

2a. Spatial changes

The experimental harvesting at Dingini produced clear changes in community structure. The dendrogram and MDS plot (Figure 6.4) indicated a distinct separation of communities in exploited plots from those in unexploited controls, but none between localities. Transects from exploited plots were approximately 56% dissimilar to those from unexploited controls. Five of the transects from the subsistence harvesting treatment were relatively distinct from those of the recreational harvesting treatment (subgroups IIa versus IIb in Figure 6.4); but the remaining six transects were grouped with samples from subsistence-harvested plots (subgroup IIc). There was no clear indication of convergence in community structure due to harvesting. The average similarity of transects within each treatment indicated that recreational levels of harvesting led to less similarity at both localities (Table 6.1). Similarity within transects from plots subject to subsistence harvesting was less than that of the control at the south ledge and virtually identical to the control at the north ledge.

Table 6.1. Average Bray-Curtis similarity of transects within controls and experimental harvesting treatments at Dingini as based on root transformed estimates of percentage cover.

Treatment	North ledge	South ledge
Controls	75.29%	76.90%
Recreational harvesting	69.40%	73.03%
Subsistence harvesting	75.32%	71.53%

The results of the two-way ANOSIM tests revealed highly significant differences in community structure between control and exploited plots (Global R=0.817,Table 6.2a). There were also significant differences in community structure between localities within treatments (Global R=0.523. Table 6.2a), but differences between treatments were greater than locality effects, as evidenced by the higher R-statistic. Pairwise-tests revealed that subsistence intensities of harvesting led to greater differences in community structure from the controls (R=0.984) compared to recreational harvesting (R=0.850). There were also significant differences in community structure between the two harvesting treatments although they were of smaller magnitude (R=0.502).

Table 6.2. Results of two-way crossed ANOSIM test based on Bray-Curtis similarity measures derived from root transformed estimates of percentage cover of all visible species. Tests were conducted between and within control plots and replicate plots subject to two levels of experimental harvesting at two localities at Dingini in northern KwaZulu-Natal. * denotes significant difference (p<0.05).

	$R_{treatment}$	P-level	n	$R_{locality}$	P-level	n
a.Global test of effect of treatment	0.817	<0.0002*	36	0.523	<0.0002*	36
b. Pairwise tests between treatments						
Control vs Recreational harvesting	0.850	<0.0002*	24	-		
Control vs Subsistence harvesting	0.984	<0.0002*	24	-		
Subsistence vs Recreational harvesting	0.502	<0.0002*	24	-		

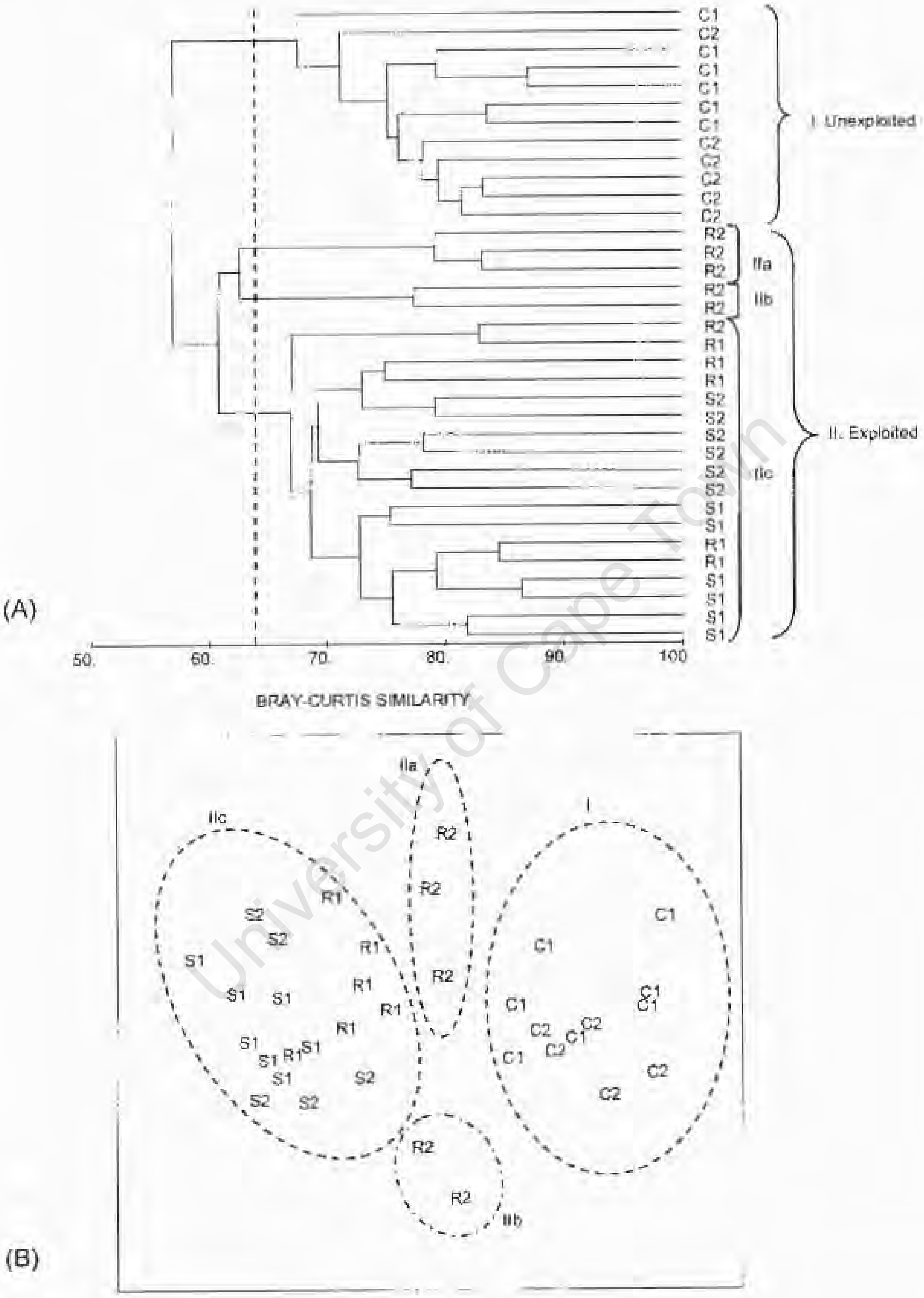


Figure 6.4. Experimental harvesting at Dingini: (A) Dendrogram and (B) MDS ordination plot (stress =0.17) based on Bray-Curtis indices of similarity derived from root transformed estimates of percentage cover of all species within replicate transects at control (C), recreationally exploited (R) and subsistence harvested (S) plots at Dingini. 1=North ledge, 2= South ledge.

SIMPER analysis also indicated greater average dissimilarities between control and subsistence levels of harvesting (north ledge D=47.31% and south ledge D=43.61%) than between control and recreational levels of harvesting (north ledge D=42.01% and south ledge D=39.47%) (Table 6.3). Differences between the two harvesting treatments (north ledge D=39.40% and south ledge D=30.71%) were less than differences between controls and treatments (Table 6.3).

SIMPER analyses identified several taxa that accounted for the differences between control and harvested treatments and between the subsistence and recreational harvesting treatments (Table 6.3, Figure 6.5A). *Perna perna* was consistently the most important distinguishing species between all three treatments. Exploitation reduced mussel cover, particularly at the higher levels of exploitation associated with subsistence harvesting. *P. perna* accounted for more than 17% of the average dissimilarity between controls and heavily exploited sites at both localities. At these heavily exploited sites, densities of the limpet *Scutellastra aphanes* (a patellid usually found on mussel shells) were consistently lower than at unexploited control sites. It did not, however, consistently distinguish between control and recreationally-harvested plots. Major distinguishing species that were more abundant at exploited plots compared with controls, were the upright coralline algae, *Jania verrucosa* and *Cheilosporum sagittatum*, and the foliar red macroalgae *Hypnea spicifera*, *Spyridea hypnoides* and *Plocamium corallorhiza*. *Laurencia natalensis* and *Arthrocardia* sp. were more abundant at recreationally-harvested plots relative to controls. Only four species showed consistent trends between the two levels of exploitation: *P. perna*, *J. verrucosa* and *S. hypnoides* had higher cover at lightly-exploited sites and *H. spicifera* was more abundant at heavily-exploited sites (Table 6.3). The most striking patterns were that *P. perna* was substantially reduced by harvesting, whereas several foliar and articulate coralline algae increased in abundance (Figure 6.5).

Table 6.3. Major distinguishing species between paired control and exploited plots at Dingini as determined by SIMPER analyses. Species are ranked in order of importance in contributing to the overall dissimilarity (D) between samples from contrasting plots. Average percentage cover of each species (Av%) at each site is based on the mean of 30 samples. $D_i/SD(D_i)$ is the ratio between D_i, the average contribution of each species to the overall dissimilarity and $SD(D_i)$, the standard deviation of D_i. This ratio reflects how consistently the species abundance differed within each site pair. $\sum D_i\%$ is the cumulative percentage contribution of each species to the overall dissimilarity, D. Species that were more abundant at more exploited sites are shaded while species that were more abundant at unexploited or less exploited sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*) and mean cover of these species are shown in Figure 6.5A. H-rec = recreationally harvested plots. H-sub = subsistence-harvested plots.

	North ledge	**H-rec**	**Control**	**D=42.01%**		**South ledge**	**H-rec**	**Control**	**D=39.47%**
	Distinguishing species	**Av%**	**Av%**	**Di/SD(Di)**	**$\sum D_i\%$**	**Distinguishing species**	**Av%**	**Av%**	**Di/SD(Di)**	**$\sum D_i\%$**
*	*Perna perna*	24.17	57.36	2.58	11.96	*Perna perna*	21.61	64.72	3.62	16.46
*	*Jania verrucosa*	11.07	7.83	1.90	21.46	*Plocamium corallorhiza*	13.64	1.75	1.34	26.83
*	*Arthrocardia sp.*	10.10	4.06	1.88	30.36	*Jania verrucosa*	12.17	2.93	1.72	36.05
*	*Hypnea spicifera*	10.13	1.31	1.70	39.19	*Cheilosporum sagittatum*	7.17	1.88	2.14	42.80
	Ralfsia verrucosa	4.93	0.14	2.50	47.79	*Hypnea spicifera*	11.61	4.22	1.70	49.50
	Encrusting corallines	6.70	0.61	3.22	56.26	*Arthrocardia sp.*	5.00	3.22	1.55	55.77
*	*Plocamium corallorhiza*	4.33	1.89	1.55	61.50	*Caulerpa filiformis*	0.97	0.00	3.36	60.23
*	*Laurencia natalensis*	1.20	0.14	2.62	65.18	*Spyridea hypnoides*	4.83	3.17	1.20	63.22
*	*Spyridea hypnoides*	4.00	2.45	1.32	68.57	*Polysiphonia sp.*	0.58	0.22	1.27	65.80
	Gelidium abbottiorum	0.63	0.08	1.19	71.40	*Laurencia natalensis*	0.50	0.06	1.27	68.34
*	*Cheilosporum sagittatum*	2.61	2.57	0.95	73.63	*Hypnea rosea*	0.56	0.20	1.38	70.76
	Zonaria subarticulata	0.20	0.42	0.95	75.92	*Zonaria subarticulata*	0.53	0.22	1.21	73.10
	Halimeda cuneata	0.47	0.17	0.87	77.99	*Dictyopteris macrocarpa*	0.64	0.25	1.55	75.38
	Sargassum elegans	0.43	0.17	0.84	80.00	*Scutellastra aphanes*	0.68	1.51	1.80	77.46
		H-sub	**Control**	**D=47.31%**			**H-sub**	**Control**	**D=43.61%**	
	Distinguishing species	**Av%**	**Av%**	**Di/SD(Di)**	**$\sum D_i\%$**	**Distinguishing species**	**Av%**	**Av%**	**Di/SD(Di)**	**$\sum D_i\%$**
*	*Perna perna*	11.28	57.36	3.35	17.71	*Perna perna*	16.11	64.72	3.24	17.28
*	*Hypnea spicifera*	23.06	1.31	5.61	32.87	*Hypnea spicifera*	28.31	4.22	3.20	31.32
*	*Plocamium corallorhiza*	17.56	1.89	2.74	45.27	*Arthrocardia sp.*	7.42	3.22	1.42	38.58
*	*Jania verrucosa*	10.50	7.83	1.44	51.32	*Polysiphonia sp.*	4.11	0.22	2.43	45.62
*	*Cheilosporum sagittatum*	6.67	2.57	1.12	55.45	*Plocamium corallorhiza*	7.67	1.75	1.66	52.05
*	*Scutellastra aphanes*	0.07	1.28	2.84	59.20	*Jania verrucosa*	7.33	2.83	1.61	57.95
	Zonaria subarticulata	1.81	0.42	1.38	62.67	*Scutellastra aphanes*	0.35	1.51	2.27	60.85
	Arthrocardia sp	3.78	4.06	1.30	66.13	*Cheilosporum sagittatum*	2.50	1.86	1.21	63.71
	Encrusting corallines	2.14	0.61	1.66	69.25	*Laurencia natalensis*	0.86	0.05	1.15	66.35
*	*Spyridea hypnoides*	3.75	2.45	1.32	72.25	*Dictyopteris macrocarpa*	1.00	0.25	1.07	68.79
	Melobesia sp	0.56	0.00	2.72	75.09	*Spyridea hypnoides*	3.58	3.17	0.97	71.01
	Ralfsia verrucosa	0.95	0.14	1.63	77.92	*Caulerpa filiformis*	0.45	0.00	0.89	73.05
	Ulva sp.	0.08	0.40	2.32	80.16					
	Champia compressa	0.47	0.00	1.33	82.39					
		H-sub	**H-rec**	**D=39.40%**			**H-sub**	**H-rec**	**D=30.71**	
	Distinguishing species	**Av%**	**Av%**	**Di/SD(Di)**	**$\sum D_i\%$**	**Distinguishing species**	**Av%**	**Av%**	**Di/SD(Di)**	**$\sum D_i\%$**
*	*Jania verrucosa*	10.50	11.07	1.60	9.30	*Hypnea spicifera*	28.31	11.51	1.67	10.63
	Plocamium corallorhiza	17.56	4.33	2.19	18.48	*Arthrocardia sp.*	7.42	5.00	1.69	18.66
	Arthrocardia sp	3.78	10.10	2.31	26.66	*Plocamium corallorhiza*	7.67	13.64	1.26	26.56
*	*Hypnea spicifera*	23.06	10.13	1.98	34.52	*Polysiphonia sp.*	4.11	0.58	1.86	33.92
*	*Perna perna*	11.28	24.17	1.39	41.74	*Jania verrucosa*	7.33	12.17	1.37	40.81
	Ralfsia verrucosa	0.95	4.93	1.75	47.27	*Perna perna*	16.11	21.61	1.41	45.69
	Encrusting corallines	2.14	6.70	2.24	52.01	*Cheilosporum sagittatum*	3.50	7.17	1.76	50.41
	Zonaria subarticulata	1.81	0.20	1.49	56.47	*Spyridea hypnoides*	3.58	4.83	1.23	54.58
	Cheilosporum sagittatum	6.67	2.61	1.14	60.91	*Laurencia natalensis*	0.86	0.50	1.43	58.18
	Laurencia natalensis	0.42	1.20	1.76	64.32	*Caulerpa filiformis*	0.45	0.97	1.58	61.41
	Scutellastra aphanes	0.07	0.82	1.17	67.30	*Zonaria subarticulata*	0.36	0.53	1.20	64.22
	Gelidium abbottiorum	0.00	0.63	1.15	70.22	*Dictyopteris macrocarpa*	1.00	0.64	1.21	66.95
	Ulva sp.	0.08	0.60	1.01	72.80	*Hypnea rosea*	0.33	0.56	1.52	69.30
*	*Spyridea hypnoides*	3.75	4.00	1.01	75.35	*Amphiroa bowerbankii*	0.17	0.33	1.32	71.48
	Halimeda cuneata	0.00	0.47	0.87	77.56	Encrusting corallines	1.33	1.17	1.23	73.56
						Champia compressa	0.32	0.14	1.02	75.63
						Amphiroa anceps	0.36	0.03	0.87	77.69

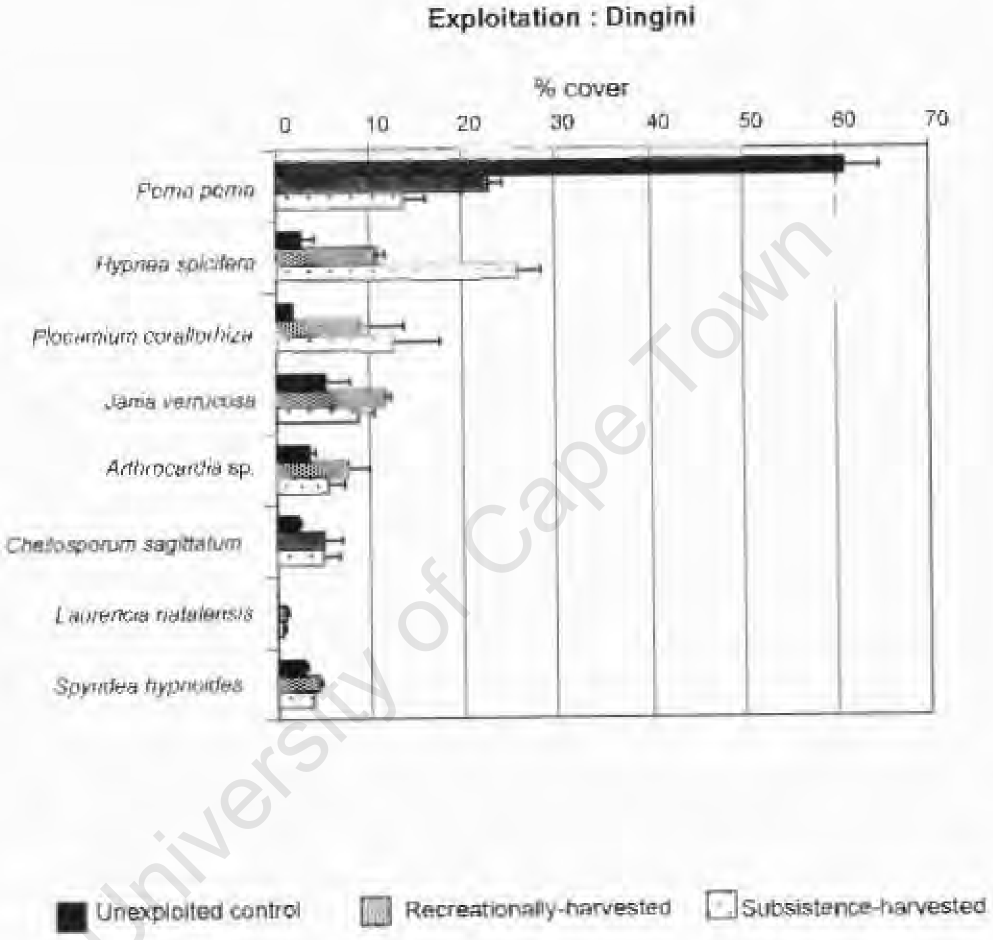


Figure 6.5. Mean cover and range of data for species that were consistently distinguishing between control and harvested experimental plots at Dingini.

2b. Patterns in biotope distribution

Ten biotopes were identified at Dingini (Figure 6.6) including five mussel and five algal-dominated communities. Comparison of the relative abundance of biotopes between control and exploited localities indicated substantial changes in the biotope composition between treatments (Figure 6.5). In 1996, 19 of the 20 samples comprised the dense mussel biotope. In 1998, control plots were also characterized by dense mussel biotopes or mixed mussel and algal assemblages in which *Perna perna* was the dominant species. The control plots at Dingini contained no samples of any algal-dominated biotopes in 1998. By then, the recreationally-harvested plots mainly comprised mixed mussel-and-algal biotopes or biotopes dominated by coralline and red algae. Almost half of the dense mussel bed that existed prior to harvesting, was transformed to algal-dominated biotopes (Figure 6.5). Both ledges had approximately equal proportions of communities dominated by mussel and algae.

Subsistence-harvested plots at both localities had few or no samples of mussel-dominated biotopes and were characterized by red and coralline algal-dominated biotopes (Figure 6.6). Within the plots harvested at subsistence levels, there were differences between the two localities. At the north ledge, the most prevalent biotope was that dominated by *Jania verrucosa*, although a band of mussel-dominated biotope remained on the extreme low shore. At the south ledge, no mussel-dominated communities remained and the two most prevalent biotopes were dominated by *Hypnea spicifera*. Although there were no samples of mussel-dominated biotopes, scattered individuals and small clumps of *Perna perna* were present and mean cover per transect was actually greater than at the north ledge.

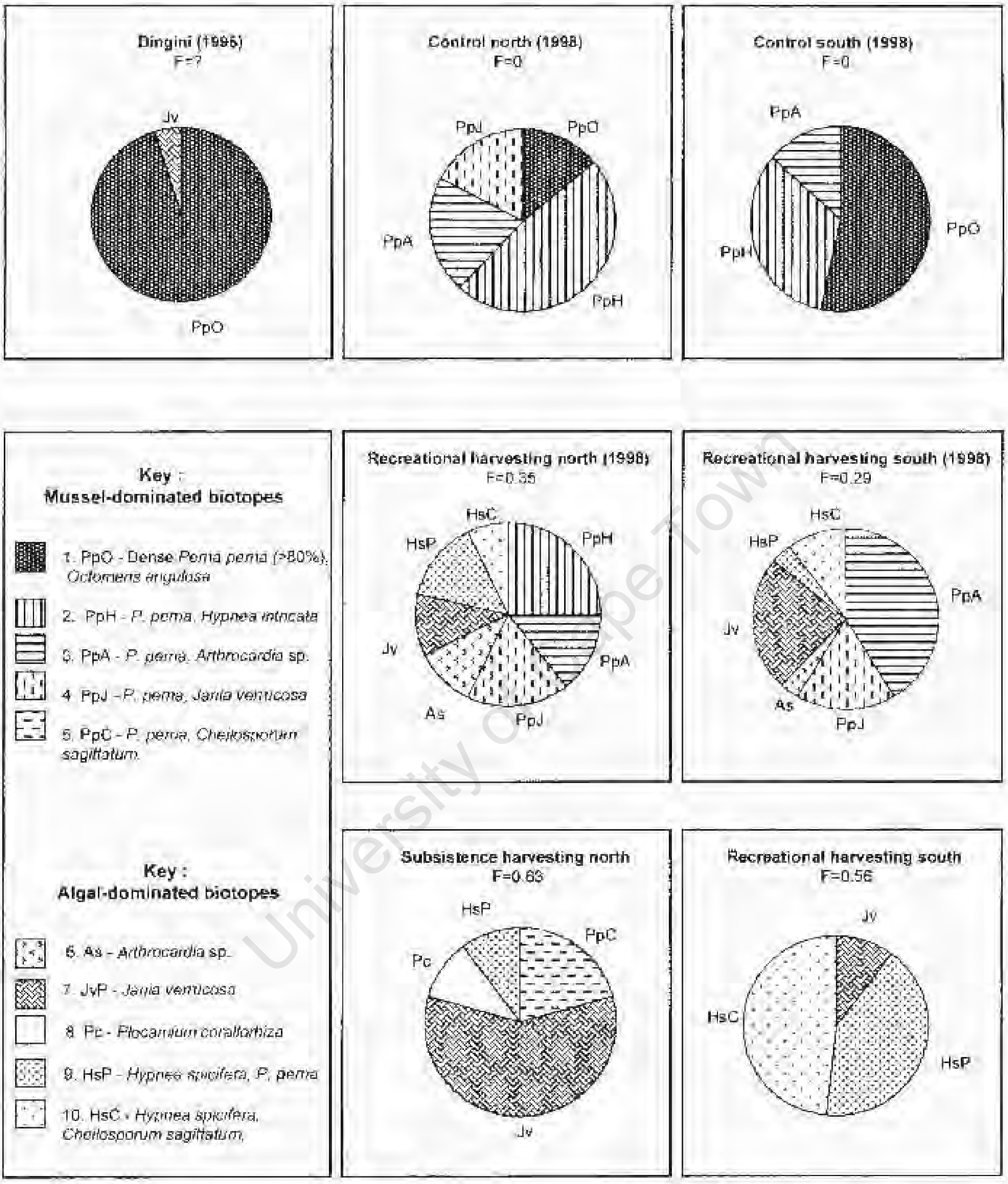


Figure 6.6. Pie charts showing the relative abundance of biotopes in 1996 (i.e. before harvesting) and in 1998 at unexploited controls and at localities subject to recreational and subsistence levels of harvesting at Dingini. For further description of biotopes, refer to Chapter 4 (Table 4.1 and Appendix I.).

2c. Temporal Changes

To resolve whether the changes in community structure in the harvested plots at Dingini could be ascribed to harvesting rather than simply being due to temporal changes of unknown cause, community structure in unexploited plots at Dingini and also at three adjacent recreationally-exploited sites were compared between 1996 and 1998.

A one-way ANOSIM test failed to detect any differences in the community structure at Dingini between samples taken in 1996 and those taken within the unexploited controls in 1998 (Table 6.4). There were also no significant differences in community structure between years at Vidal Ledge or at Crayfish Point (Table 6.4). A significant difference in community structure between years was found at Railway Ledge, but this was relatively minor (R=0.122). SIMPER analysis indicated that the amount of sand was the most important distinguishing factor between years there; mean cover of sand was approximately 14% in 1998 but <2% in 1996 (Table 6.5). There was <1% difference in mean mussel cover between 1996 and 1998, so temporal changes in mussel cover were minor. Algae cover was generally lower in 1998 compared to 1996 but differences were again minor (<3%).

Table 6.4. Results of one-way ANOSIM tests for differences between years (1996 and 1998) at four Zululand sites. Tests based on Bray-Curtis similarity measures derived from root transformed estimates of percentage cover of all visible species from twenty replicate quadrats surveyed in 1996 and 1998. * indicates significant difference (P<0.05).

Sites	R_{years}	p	n
Dingini (controls)	0.068	0.630	40
Vidal Ledge	0.042	0.917	40
Crayfish Point	0.055	0.070	40
Railway Ledge	0.122*	0.001	40

Table 6.5. Major distinguishing taxa between 1996 and 1998 at Railway Ledge as determined by SIMPER analyses. Taxa are ranked in order of importance in contributing to the overall dissimilarity, D=33.30%, between years. For details of notation, refer to Table 6.3.

Distinguishing species	**1998- Av %**	**1996 - Av%**	**Di/SD(Di)**	**$\sum D_i\%$**
Sand	14.25	1.30	1.23	12.58
Perna perna	70.80	71.45	0.78	21.47
Jania verrucosa	0.95	4.75	0.60	27.34
Hypnea intricata	2.60	4.65	0.61	32.97
Hypnea spicifera	2.10	2.10	1.05	38.59
Cheilosporum sagittatum	2.05	1.68	1.26	43.71
Spyridea hypnoides	1.93	2.10	0.98	48.79
Plocamium corallorhiza	1.55	1.50	0.98	53.39
Polysiphonia sp.	2.20	1.50	0.66	57.95
Ulva sp.	1.49	1.50	1.16	62.29
Chthalamus dentatus	1.35	0.00	0.78	65.71
Caulerpa filiformis	3.50	3.85	0.32	69.12
Encrusting coralline algae	0.55	1.25	0.81	72.43
Chnoospora minima	0.85	0.20	0.60	75.03
Dictyopteris macrocarpa	0.55	0.54	0.73	80.03

3. Comparing recreationally and subsistence-harvested sites in Natal

Comparisons of community structure were made between three subsistence-harvested sites (Groutville, Umgababa and Umfazazana) in Natal and three nearby recreationally-exploited sites with which they were paired (respectively Salt Rock, Umdoni and Splash Rock, see Figure 6.1 for locations). The average Bray-Curtis similarity of each site was used as a measure of community convergence. Average within-site similarity for subsistence-exploited sites was less than that of adjacent recreationally-harvested sites in two of the three site-pairs examined (Table 6.6). This does not support the prediction that subsistence harvesting causes convergence of community structure.

Table 6.6. Average Bray-Curtis similarity (S%) of sites subject to recreational and subsistence intensities of harvesting in Natal. Similarity is based on root transformed estimates of percentage cover from twenty replicate 1m x 0.5 m quadrats random placed in the low shore.

Recreationally harvested sites	S%	Subsistence harvested Sites	S%
Salt Rock	50.38%	Groutville	55.81%
Umdoni	66.23%	Umgababa	43.17%
Splash Rock	52.04%	Umfazazana	41.95%

A two-way crossed ANOSIM test yielded significant differences between ($R=0.558$, $p<0.0002$, $n=120$) and within recreational and subsistence-harvested treatments ($R=0.142$, $p<0.0002$, $n=120$). Differences in community structure between harvesting treatments were far greater than the differences between localities within treatments. SIMPER analyses revealed relatively consistent differences between sites exploited by recreational mussel collectors and those subject to subsistence exploitation of intertidal invertebrates (Table 6.7, Figure 6.7). Six of the major species distinguishing between sites exploited by recreational versus subsistence harvesters showed consistent trends between site pairs. *Perna perna* was consistently more abundant at sites that were subject to lower (recreational) harvesting intensities. The other five species were the articulated coralline algae, *Cheilosporum sagittatum* and *Jania verrucosa*, two types of encrusting algae (coralline and *Ralfsia* sp.), and the red alga *Hypnea spicifera*, all of which were more abundant at sites harvested by subsistence fishers.

Table 6.7. Major distinguishing species (D_i >2%) between paired localities exploited at recreational and subsistence levels as determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity. Species are ranked in order of importance in contributing to the overall dissimilarity between samples from contrasting sites. Average percentage cover of each species at each site is based on the mean of 20 replicate 1m x 0.5m quadrats. For details of notation, please refer to the caption of Table 6.4. Species that were more abundant at sites subject to subsistence exploitation are shaded while species that were more abundant at recreationally exploited sites are not shaded. Species that showed consistent trends between site pairs are indicated with an asterix (*).

		Subsistence Exploitation	Recreational exploitation				Subsistence Exploitation	Recreational exploitation				Subsistence Exploitation	Recreational exploitation		
	Site pair 1	Groutville	Salt Rock	D=71.58		Site pair 2	Umgababa	Umdoni	D=59.47		Site pair 3	Umfazazana	Splash Rock	D=59.47	
	Species	**Av. %**	**Av. %**	Di/SD(Di)	ΣDi%	**Species**	**Av. %**	**Av. %**	Di/SD(Di)	ΣDi%	**Species**	**Av. %**	**Av. %**	Di/SD(Di)	ΣDi%
*	*Cheilosporum sagittatum*	52.60	1.95	2.02	19.55	*Perna perna*	28.85	84.52	1.86	18.05	*Perna perna*	8.47	70.9	1.91	21.08
*	*Perna perna*	16.75	71.21	1.61	38.05	*Cheilosporum sagittatum*	21.6	4.23	1.18	30.6	*Cheilosporum sagittatum*	40.17	11.2	1.36	35.39
*	Encrusting corallines	10.90	1.25	1.80	47.25	Encrusting corallines	13.0	3.80	1.48	40.04	Encrusting corallines	16.15	1.65	1.14	44.42
*	*Hypnea spicifera*	6.45	4.65	1.18	52.18	*Hypnea spicifera*	7.20	2.15	1.14	47.42	*Hypnea spicifera*	10.15	8.24	0.94	52.05
*	*Jania verrucosa*	3.75	2.72	1.19	56.67	*Sargassum elegans*	8.55	0.00	0.88	54.59	*Sargassum elegans*	14.35	0.08	0.5	58.22
	Hypnea intricata	0.50	6.30	0.81	60.83	*Ralfsia verrucosa*	6.00	2.00	1.15	60.65	*Ralfsia verrucosa*	3.50	1.05	0.89	62.31
*	*Ralfsia verrucosa*	2.35	1.70	1.34	63.87	*Octomeris angulosa*	1.45	1.18	1.03	64.43	*Plocamium corallorhiza*	2.25	0.96	0.86	65.48
	Plocamium corallorhiza	1.25	1.70	0.92	66.85	**Bare rock**	1.33	0.30	1.07	67.67	*Scutellastra aphanes*	0.06	1.37	1	68.37
	Bare rock	2.20	0.89	0.56	69.2	*Caulerpa racemosa*	4.45	0.08	0.41	70.74	*Octomeris angulosa*	0.10	1.47	0.66	71.22
	Spyridia hypnoides	0.85	0.5	0.91	71.25	*Jania verrucosa*	1.10	0.90	0.71	73.75	*Jania verrucosa*	1.20	0.30	0.76	73.49
	Scutellastra aphanes	1.05	0.01	0.77	73.3	*Scutellastra aphanes*	0.94	1.24	1.11	76.49	byssus	2.00	0.00	0.56	75.72
	Octomeris angulosa	0.20	0.76	0.83	75.29	*Hypnea intricata*	1.00	0.60	0.83	79.16					
						Dictyota sp.	1.50	0.00	0.62	81.54					

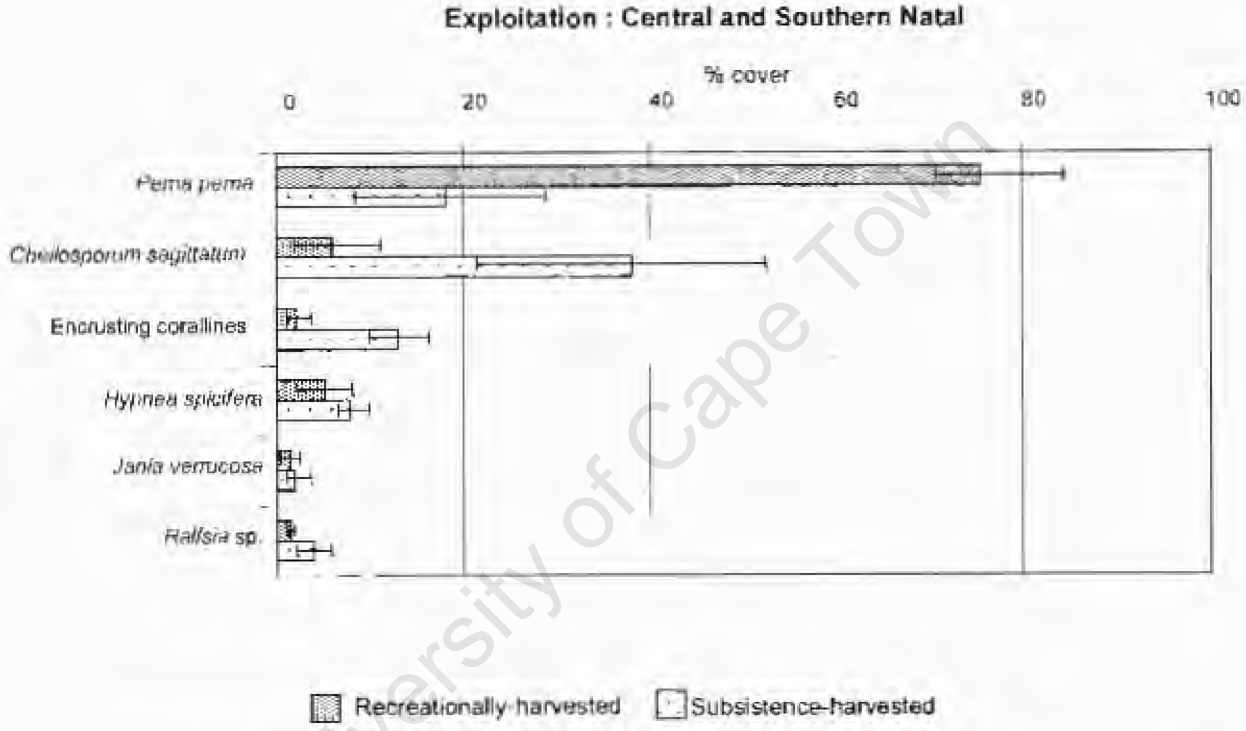


Figure 6.7. Mean cover and range of data for species that were consistently distinguishing between recreationally and subsistence-exploited sites in central and southern KZN.

4. Assessing the influence of subsistence harvesting on biogeographic patterns

Hierarchical cluster analyses revealed that sites subject to subsistence exploitation showed clear differences in community structure from other sites within both Maputaland and Natal (Figure 6.8). In the cluster analysis based on untransformed data (Figure 6.8A), four distinct groups of sites were evident. Three wave-sheltered exploited sites in Maputaland (group II) and two wave-sheltered Natal sites (group I) were distinct from all other sites. Group III comprised the three unexploited Maputaland sites and all semi-exposed and exposed sites subject to recreational harvesting in Natal. Data from the control plots at Dingini clustered with these recreationally harvested sites in the Natal region. All remaining subsistence-harvested sites in both Maputaland and Natal clustered together, including the experimental subsistence-harvested plots at Dingini (group IV) although those in Natal formed a discrete sub-cluster (group IVa). The cluster of subsistence-exploited sites (group IV) was more than 70% dissimilar to all other sites from both biogeographic regions.

Root transformation of the data allowed all species to contribute more uniformly to the similarity matrix, rather than domination by the most common species. Then, cluster analysis yielded three distinct groups (Figure 6.8B). Group I comprised the two extremely wave-sheltered Natal sites (as in Figure 6.8A). All the Maputaland sites grouped together in group II, with the two most wave-sheltered sites being 60% dissimilar to the rest (sub-group IIa). There were two other sub-clusters in group II: exploited wave-exposed sites (sub-group IIb) and exposed, mostly unexploited sites (sub-group IIc) which were more than 50% different to their subsistence-exploited counterparts (sub-group IIb). Group III comprised only sites from Natal. Two out-liers were evident, but apart from them, three sub-groups were apparent: recreationally-exploited semi-exposed sites (IIIa), recreationally-exploited exposed sites including the Dingini pre-experimental sample and controls (IIIb) and subsistence-exploited sites from Natal, namely Groutville, Umgababa, Umfazazana and the experimentally-harvested plots at Dingini together with two recreationally-harvested sites (Mission Rocks and Annerly) (IIIc). Together, these sites were more than 50% different to the rest of the sites in the Natal region, and were equivalent to sub-group IVa recognised in Figure 6.8A.

These cluster analyses revealed that the influence of wave exposure was greater than biogeographic and harvesting effects. In both analyses, unexploited sites from Maputaland (Island Rock, Cape Vidal and Sodwana) and Natal (Trafalgar) did not group together but rather clustered with other sites of similar exposure. When data were untransformed, sites then grouped according to the type of exploitation, with harvesting effects overriding biogeographic patterns. However, when the data was transformed, biogeographic differences exceeded those due to harvesting type although subsistence harvested sites were still nearly all distinct from unexploited sites within Maputaland and from recreationally-exploited sites in Natal.

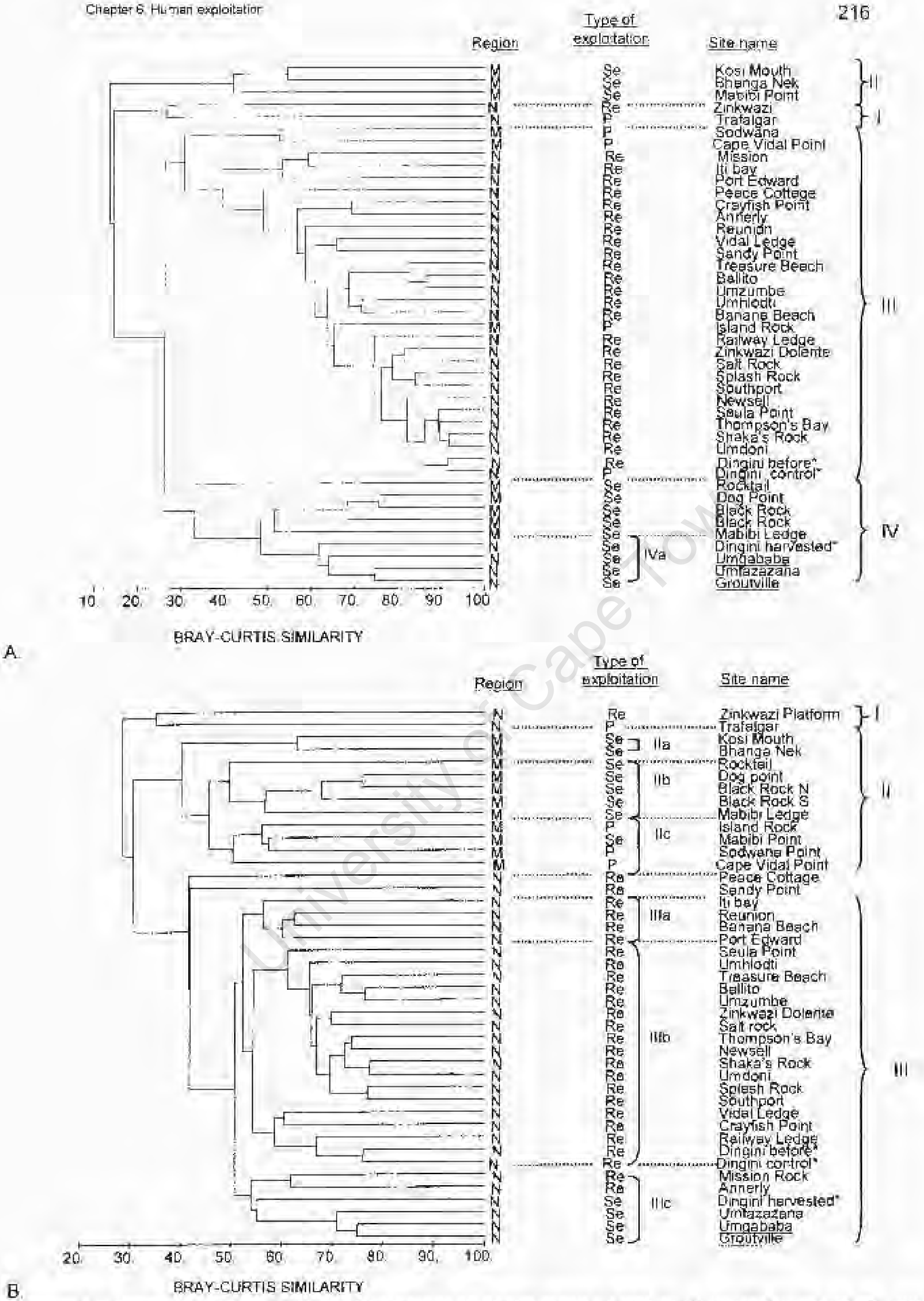


Figure 6.8. Dendrograms showing results of the hierarchical cluster analysis based on (A) untransformed and (B) root transformed low-shore biological data from sites subject to recreational (Re) and subsistence exploitation (Se) and unexploited sites in marine protected areas (P). M=Maputaland and N=Natal. Asterisks highlight the Dingini site before initiation of the harvesting experiment, its controls and the harvested plots after the experiment. Underling indicates the two subsistence-harvested sites added to the original data set.

In Chapter 2, results suggested that subsistence-harvesting may have contributed towards biogeographic differences (eight of 11 Maputaland sites versus one of 28 Natal sites were subsistence-exploited). To examine biogeographic patterns in the absence of the effects of subsistence harvesting, a separate hierarchical cluster analysis was performed using only those sites at which subsistence utilization has not been practiced in recent history (Figure 6.9). Three major groups of sites were apparent. In group I, Zinkwazi and Trafalgar, the two most wave-sheltered sites in Natal, were approximately 70% dissimilar to all other sites in KwaZulu-Natal. This follows the pattern evident even when subsistence-exploited sites were included in analyses (Figure 6.8, 6.9). However, the previously observed biogeographic division persisted amongst the remaining sites, with the three Maputaland sites (group II) more than 60% dissimilar to all the remaining Natal sites (group III).

SIMPER analysis revealed that the two most important distinguishing species between regions were *Pyura stolonifera*, which was consistently more abundant in Maputaland and *Perna perna*, which was more abundant in Natal (Table 6.8). *P. stolonifera* was almost absent in Natal (Av%=0.3%) but at unexploited Maputaland sites had an average cover (Av%) of 14%. *P. perna* was less abundant on unexploited shores in Maputaland (Av%= 34.13%) than in Natal (Av%=52.82%). *Hypnea spicifera* was absent at unexploited sites in Maputaland but was characteristic of Natal low shores (Av%=7.23). The zoanthid *Palythoa nelliae*, the barnacle *Tetraclita squamosa* , and the algae *Laurencia glomerata* and *Caulerpa racemosa*, were also identified as major distinguishing species, all being more abundant in Maputaland.

Table 6.8. Major distinguishing species in the low shore between unexploited sites in Maputaland and unexploited or recreationally-exploited sites in Natal. Major species were determined by SIMPER analyses based on root transformed percentage cover estimates and the Bray-Curtis measure of similarity for all sites that were not subject to subsistence harvesting. The ranking is determined by Di, the average contribution of each species to the overall dissimilarity between regions (D=63.83%). Av. % indicates the average percentage cover of each species from sites within each region. For other details of notation, please refer to Table 6.3.

Distinguishing Species	**AV% Maputaland**	**AV% Natal**	**D_i/ SD(D_i**	**$\sum D_i$%**
Pyura stolonifera	14.06	0.33	2.61	6.15
Perna perna	34.13	52.82	1.49	10.82
Hypnea spicifera	0.00	7.23	1.46	14.9
Palythoa nelliae	7.08	0.14	1.7	18.88
Tetraclita squamosa rufotincta	4.91	0.03	3.47	22.67
Laurencia glomerata	3.28	0.00	1.21	25.62
Caulerpa racemosa	3.37	0.57	1.92	28.16
Hypnea intricata	0.18	3.96	1.33	30.68
Encrusting coralline algae	7.93	2.63	1.44	33.19
Plocamium corallorhiza	0.00	1.92	1.67	35.47
Unidentified green ascidian	1.98	0.00	1.38	37.55
Jania verrucosa	0.75	2.63	1.33	39.58

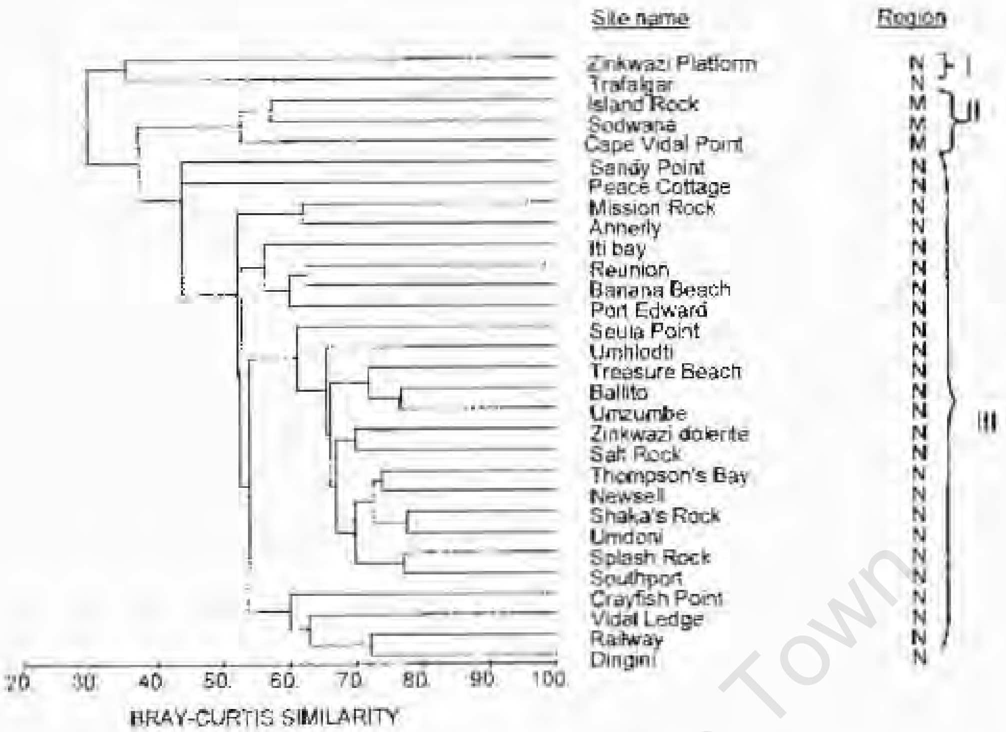


Figure 6.9. Dendrogram showing the results of a hierarchical cluster analysis based on root transformed biological data from the low shore of sites that are not subject to exploitation by subsistence harvesters. M=Maputaland and N=Natal.

Discussion

Differences in low-shore community structure were evident over a range of temporal and spatial scales within and between sites subject to different intensities of human exploitation. Temporal changes were observed at Black Rock in Maputaland. At Dingini, on the northern Natal coast, spatial and temporal changes were clearly related to experimental harvesting. In central and southern Natal, differences were evident between sites subject to different harvesting regimes. Finally, inter-regional differences in community structure could also be linked to harvesting intensity.

1. Harvesting and temporal changes at Black Rock, Maputaland

At Black Rock in Maputaland, it appears that patterns of community structure and zonation have changed between 1976 and 1997 (Figure 6.3). It is true that this conclusion relies on an unreplicated survey by Jackson (1976). Nevertheless, in all six transects surveyed in 1997, the abundance of the mussel *Perna perna* was less than 20% of that estimated by Jackson in 1976, and numbers of limpets, particularly *Scutellastra* spp. were also substantially lower in 1997. Both mussels and these limpets are reported as principal species targeted by collectors in Maputaland (Kyle et al. 1997a). The limpet *Cellana capensis* was relatively abundant in the mid shore in both 1976 and 1997 and this species is apparently not harvested by collectors (Kyle et al. 1997a). The reduced densities of *Perna perna* and mobile organisms that are harvested by members of the local community (Kyle et al. 1997a), do suggest that harvesting was responsible for the changes in community structure. However, because of the absence of any benchmark surveys at protected sites, other causes cannot be ruled out. Jackson's data do not allow comparisons of overall community structure between 1976 and 1997. Nevertheless, the articulated coralline *Cheilosporum* sp. was more abundant in 1997 than in 1996. As this is a non-target species, this suggests that that it increased in cover due to competitive release following harvesting of competitive dominants. A similar response to intensive mussel harvesting has been documented in the Transkei (Hockey and Bosman 1986, Dye 1992, Dye et al. 1994, 1997, Lasiak 1999). I also noted greater abundance of foliar and articulate coralline algae at heavily harvested sites when comparing sites in Maputaland (Chapter 3, Figure 3.4, p 101).

The fact that mussels were more abundant lower on the shore at Black Rock and depletion between 1976 and 1997 was most evident higher up the shore, suggests that harvesting influenced patterns of vertical zonation. Tomalin and Kyle (1998) reported that mussels seem to occur lower on the shore in Maputaland than in Natal. Furthermore, Jackson (1976) reported that *Cheilosporum* sp. was mostly confined to the infratidal fringe and subtidal zone at Black Rock in 1976, whereas it was a significant component of the low-shore community in my study. Therefore, studies of harvesting impacts should consider that changes in biological zonation patterns could result from harvesting. Because of this phenomenon, biologically defined zones should not be used for stock assessment and fixed transects across the shore are required to examine changes in zonation.

The documentation of change in abundance of mussels within all zones at Black Rock is also important because it contradicts reports by Kyle et al. (1997a) that the abundance of *Perna perna* appears not to have declined within Maputaland. The observed reduction of harvested mobile consumers is however consistent with the marked decline in catch per unit effort (CPUE) of limpets reported by Kyle et al. (1997a), who also noted that densities of *Chiton salihafui* may have been seriously impacted by collection. As this species is relatively uncommon and is a range-restricted endemic, it should be excluded from any subsistence fishing rights.

Monitoring of shellfish harvests in Maputaland in terms of catch and effort has led researchers to conclude that the mussel and *Pyura* fisheries are sustainable (Kyle et al. 1997a). Effort was assessed from catches and numbers of people per day collecting from the intertidal zone at different localities. The time taken to collect organisms was not documented. The multi-species nature of the fishery did not allow effort to be determined for most individual species (Kyle et al. 1997a). Any changes in effort unrelated to numbers of harvesters or actual catches would therefore not be reflected in the CPUE. One of the changes in effort that has occurred in Maputaland is the wearing of shoes during collecting outings. In 1999, more harvesters were wearing shoes while harvesting than there were four years previously (K. Sink unpublished data) and this may improve the efficiency of harvesters. Other changes in effort that may have occurred include increased collecting times per outing and that harvesters may be venturing or concentrating collecting effort lower on the shore. During opinion surveys (K. Sink, unpublished data) many of the harvesters complained that "the tide does not retreat as much as it used to", that mussels now occur lower on the shore, that harvesters get wetter while collecting nowadays, and that it is more dangerous and takes longer to collect their catch than it did 20 years ago. Kyle et al. (1997a) reported a decrease of more than fifty percent in harvesting effort between 1988 and 1994. Although this may be attributable to the development of a cash economy and return of refugees to Mozambique following the cessation of civil war there (Kyle et al. 1997a), discussions with the local community revealed that some women no longer collect because it has become more difficult to achieve a worthwhile harvest. In the Transkei, reduced harvesting effort at some sites was also attributed to the fact that it was no longer economical for harvesters to collect seafood in the face of diminishing catches (Siegfried 1988).

Unlike most fisheries, intertidal rocky-shore species are readily visible, easily accessible and their handling time exceeds search time. Consequently, crude measures of CPUE may not be a reliable indicator of stock size or sustainability until stocks have almost disappeared (Hilborn and Walters 1992). This phenomenon is known as hyperstability. To resolve this, CPUE data should be supplemented with other information. Several aspects of my study provide evidence that sustained subsistence harvesting can change community structure in that the densities of key harvested species decline and non-target species increase. Although other factors may have contributed to the observed changes over the past twenty years at Black Rock, the potential link with subsistence harvesting cannot be ignored. Other authors have shown that long-term harvesting can reduce the abundance of target organisms by an order of magnitude, and that this may lead to indirect changes in the abundance of non-target species (Lasiak and Dye 1989, Moreno et al. 1984, Castilla and Duran 1985, Siegfried et al. 1985, Hockey and Bosman 1986, Fairweather 1990, Lasiak 1991, Underwood 1993a, Dye et al. 1994a). It is therefore plausible that sustained intensive harvesting may have caused the observed temporal changes in Maputaland.

These results serve to illustrate that intertidal fisheries should not only be monitored in terms of CPUE. Stock surveys and impact studies on entire communities should be conducted with the awareness that biological zonation patterns may be influenced by harvesting. Two critical requirements for proper monitoring emerge: (1) replicated, quantitative data collected at fixed points at harvested localities to monitor target species and community structure and (2) fully protected reference sites with comparable monitoring. Taken on their own, the changes at Black Rock cannot be conclusively linked to harvesting. Nevertheless, they are important because they constitute the only comparison that can be made for an intensely harvested site in Maputaland over a relatively long period of time. The patterns of change also parallel differences between harvested and unharvested sites in the region (Chapter 3), supporting the conclusion that harvesting was responsible for the changes. Controlled experiments constitute much stronger evidence of the effects of harvesting.

2. Experimental harvesting of mussels at Dingini

Temporal and spatial changes in community structure were examined at the experimentally harvested sites at Dingini and at three adjacent sites over the duration of the harvesting experiment. The control plots at Dingini and two of the three monitored sites did not change significantly over the two-year period. The third monitored site (Railway Ledge) did change, but the changes were almost an order of magnitude less (R=0.122) than changes observed at the harvested plots at Dingini (R=0.81-0.98) and were principally attributed to changes in the amount of sand cover, not differences in the abundance of biota. At Dingini differences in mussel cover between control and harvested plots were large (20-50%) whereas <1% difference in mussel cover was observed between years at Railway Ledge. Background temporal changes over the duration of the experiment were therefore non-existent or very limited in comparison with changes in the experimentally harvested plots. Dye (1992) also reported that in the absence of disturbance, intertidal community structure in the former

Transkei did not change appreciably over an eight-year period (Dye 1992). In conclusion, the substantial changes in the experimentally harvested plots were thus directly attributable to harvesting and were unlikely to have been confounded by background temporal changes due to other factors.

Experimental harvesting at Dingini established a causative relationship between changes in community structure and mussel harvesting. The changes in harvested plots were reflected by differences in community structure (Figures 6.4 and 6.5) and biotope abundance (Figure 6.6). At Dingini, reductions of mussel abundance at exploited plots evidenced the direct effects of harvesting. The patellid limpet, *Scutellastra aphanes*, was also reduced at heavily harvested plots because this species is associated with mussels as a substratum (Robson 1986). Indirect effects of harvesting were also apparent as reduced mussel cover was accompanied by increasing cover of foliar red and articulated coralline algae. Among the species that flourished in heavily harvested plots was the articulated coralline *Cheilosporum sagittatum*, which in terms of rock temperature, wave forces, sand inundation, aspect and slope shares habitats with the same physical conditions as the mussel *P. perna* (see Chapter 5, Figure 5.4 p 176). It is thus a prime candidate for competition with this mussel (Branch 1984). The most likely explanation for the increased cover of upright algae in harvested plots is competitive release following the reduction of mussel cover.

Other studies have also detected indirect effects of harvesting including proliferation of algae (Branch 1981, Hawkins and Hartnoll 1983, Moreno et al. 1984, Hockey and Bosman 1986, Oliva and Castilla 1986, Underwood 1993a, Branch and Moreno 1994). The replacement of mussels with articulated corallines has been documented at harvested sites in the Transkei (Hockey and Bosman 1986, Siegfried 1988, Dye 1992, Dye et al. 1994, Lasiak 1999), and in response to experimental clearing of mussels in KwaZulu-Natal (Lambert and Steinke 1986b).

Under conditions of experimental harvesting at Dingini, larger differences in community structure were recorded between control plots and those subject to subsistence harvesting (R-statistic=0.984) than between control and recreationally-harvested plots (R=0.850). Seven or eight major discriminating species showed consistent responses to subsistence or recreational intensities of harvesting respectively (relative to unexploited controls at both localities) (Table 6.3). Only four species showed consistent trends between the two harvesting treatments and the differences between harvesting treatments (R=502) were less than those observed between controls and either treatment. These results indicate that the impact of subsistence harvesting was greater than that of recreational harvesting and that harvested plots of either type were more dissimilar to unexploited controls than they were to each other.

In Chapter 4, intertidal biotopes were identified and defined for KwaZulu-Natal. In this chapter, the use of these biotopes proved effective in detecting changes in community structure between harvesting treatments (Figure 6.6). At Dingini, harvesting intensities simulating recreational collecting resulted in complete loss of the dense mussel biotope although other mussel biotopes with lower cover of *Perna perna* (50-75%) still remained. More intense harvesting (simulating subsistence-gathering) resulted in the disappearance of all mussel-dominated biotopes on the south ledge and drastic reductions on the north ledge. The implications of this are discussed later in this chapter. Indirect effects of harvesting were also evident when using biotopes to compare treatments. Algal-dominated biotopes (particularly those characterised by articulated corallines or foliar red algae) became prevalent in plots subject to high-intensity subsistence-harvesting.

In the Transkei, no changes in species richness were associated with harvesting because losses of species associated with mussels were offset by increased abundance of phytal-associated species (Lasiak and Field 1995, Lasiak 1999). Lasiak (1999) was able to demonstrate changes in community composition and abundance in response to harvesting by intensive sampling using destructive methods to extract infauna. My biotope classification however clearly reflected community changes without the need for destructive sampling. Furthermore, biotopes effectively monitor changes in community structure more quickly and efficiently than species inventories (see Chapter 4 discussion) and can be conducted by anyone with a little training. Therefore, biotope surveys can serve as a time-saving, inexpensive and simple method to monitor ecosystem impacts of shellfish fisheries on rocky intertidal shores, and harvesters could be trained to undertake this task in partnership with management.

The intermediate disturbance hypothesis predicts that species richness is greater under conditions of intermediate or moderate disturbance (Connell 1978). Sousa (1979) showed that numerical dominance and diversity may also respond in a similar manner. Species richness was not examined in my study, but in the Transkei, disturbance in the form of selective predation by subsistence-fishers led to increased species richness at exploited sites (Hockey and Bosman 1986).

At Dingini, the abundance of different biotopes at the experimental plots can be compared to assess whether community diversity responded to exploitation in accordance with the intermediate disturbance hypothesis (Figure 6.6). At unexploited plots, all samples were mussel-dominated and only three to four different biotopes were represented. At intermediate (recreational) harvesting intensities, six to seven biotopes were represented and there was less dominance by any one biotope. At heavily harvested plots, only three and four biotopes were represented, dominated either by *Hypnea spicifera* or articulated coralline algae. These patterns of biotope diversity indicate that the responses of community diversity to human exploitation conformed with the intermediate disturbance hypothesis.

3. Comparing recreationally and subsistence-harvested sites in Natal

Highly significant differences in community structure existed between sites subject to recreational versus subsistence exploitation (>60% dissimilarity) in all three site-pairs in Natal indicating that the two types of harvesting do yield divergent communities. Six species consistently distinguished between sites subject to the two types of harvesting. The two most important were *Perna perna* and *Cheilosporum sagittatum* which respectively reflected the direct and indirect effects of harvesting. Mussel cover was consistently less at subsistence-harvested sites than recreationally harvested sites (Av% difference = 56%), whereas the articulated coralline alga *Cheilosporum sagittatum* was always more abundant at sites subject to subsistence harvesting compared to recreationally-harvested sites (Av% difference = 30%). A comparable comparison could not be undertaken in Maputaland because no intertidal recreational harvesting occurs there.

The differences between the sites subject to subsistence versus recreational harvesting in central and southern Natal (Figure 6.7) had parallels with differences between control and exploited plots at Dingini (Figure 6.5) and between unexploited and subsistence-harvested sites in Maputaland (Chapter 3). *P. perna* and *C. sagittatum* showed consistently similar responses in all these comparisons. *Hypnea spicifera* and *Jania verrucosa* were also consistently more abundant where exploitation was intensive, both at the three subsistence-harvested sites (Groutville, Umgababa and Umfazazana) from the three site-pairs compared in Natal and at subsistence-harvested plots at Dingini.

The differences in community structure between the recreationally-harvested and subsistence-harvested site-pairs in central and southern Natal were similar in pattern but exceeded the magnitude of the differences between the two types of experimental harvesting at Dingini. Two factors could underlie these differences. First, the effects of harvesting at Dingini were assessed only 22 months after experimental harvesting began. At the three subsistence-harvested sites in Natal (Groutville, Umgababa and Umfazazana), details of the duration and extent of harvesting are undocumented but it has certainly persisted much longer (>10 years) (C. Coetzee, A. Millar, R. Broker and L. van Schoor, KwaZulu-Natal Wildlife, pers. comm.). Second, there were differences in collecting methods between the treatments imposed at Dingini and those used at traditional sites for subsistence harvesting. At Dingini, narrow-bladed screwdrivers were used to remove individual mussels or small clumps. At other sites, subsistence collectors use cane knives, vehicle leaf-spring blades, hoes, axes and even spades (C. Coetzee, A. Millar and L. van Schoor, KwaZulu-Natal Wildlife, pers. comm.). These collecting tools have wider blades and create larger areas of bare rock than a screwdriver. A greater impact on community structure would be expected from the use of such implements, and unwanted bycatch of juvenile mussels is considerable (J. Harris, KwaZulu-Natal Wildlife, pers. comm.).

In comparing recreationally-harvested and subsistence-harvested site-pairs in the Natal region, the assumption was made that there were no other extraneous factors causing differences between sites (or, at least, that their influence was insufficient to obscure patterns caused by harvesting). In particular, it was assumed that all sites experienced approximately equal wave exposure. Wave exposure was, however, not recorded at the three subsistence-exploited sites and therefore cannot be ruled out as contributing to between-site differences in community structure. However, the species composition of the sites suggested that differences in exposure were unlikely. The two most important species distinguishing between recreationally and subsistence exploited sites in Natal, *Perna perna* and *Cheilosporum sagittatum*, favour strong wave exposure both in Natal (Figure 3.2, p 94) and in Maputaland (Figure 3.4 p 101). However these two species displayed opposing responses at sites subject to recreational versus subsistence exploitation. *P. perna* decreased and *C. sagittatum* increased at subsistence-exploited sites. These opposite trends would not be expected if differences in wave exposure were driving the observed differences between recreational and subsistence-harvested sites in Natal. The fact that *P. perna* and *C. sagittatum* also showed these same opposite responses at the subsistence-harvested plots under experimental conditions at Dingini lends confidence to the assertion that harvesting is the factor causing these trends.

In Chapter 5, both *Perna* and *Cheilosporum*-dominated biotopes could not be distinguished in terms of wave exposure, sand inundation, aspect or slope when intra-site comparisons were made (Figure 5.4, p 176). Thus, although other physical variables cannot be eliminated as potential causative agents explaining differences between the site-pairs, they seem unlikely explanations. Differences in harvesting remain the most tenable explanation.

4. The influence of harvesting on biogeographic patterns

In Chapter 2, a clear biogeographic break was evident between Maputaland and Natal (Figure 2.4 p 32). Only one site, Umfazazana, did not conform with the biogeographic break. This was the only subsistence-harvested site surveyed in Natal and it clustered with other subsistence-exploited sites in Maputaland rather than with other sites in Natal. The two regions had significant differences in harvesting intensity. As a result, regional differences in exploitation could not be discounted as a potential explanation for the biogeographic differences. In this chapter, two additional subsistence-harvested Natal sites and data from the experimentally harvested plots at Dingini were added to the biogeographic analysis to help resolve the potential role of subsistence exploitation in determining biogeographic differences.

Inclusion of these samples showed that the effects of harvesting exceeded biogeographic differences when the data were untransformed (Figure 6.8A). The effects of wave exposure were, however, even greater than differences related to exploitation, as sheltered sites from Maputaland and Natal were most dissimilar to all other sites (Groups I and II, Figure 6.8). When the data were root transformed (Figure 6.8B), biogeographic differences were then greater than differences related to harvesting, but exploitation continued to exert a dominant influence within each of the regions. Subsistence-exploited sites tended to cluster separately from recreationally-exploited or unexploited sites, but only within wave exposure regimes and biogeographic provinces. The powerful influence of wave exposure on a coastline that was previously thought to be uniformly wave-exposed shows that abiotic factors can exert an overriding influence on community structure, often masking the influence of other factors.

When all subsistence-harvested sites were excluded from the biogeographic analysis, the break separating Maputaland and Natal still persisted (Figure 6.9). Thus, the observed biogeographic pattern cannot be solely attributed to differences in harvesting offtake between the two regions. Certain species differ naturally in their abundance between the regions, and consistently contributed generously to the overall dissimilarity between regions in both this study and in Chapter 2. For example, *Hypnea spicifera*, *H. intricata* and *Plocamium corallorhiza* were always more abundant in Natal, and *Tetraclita squamosa*, *Laurencia glomerata*, *Caulerpa racemosa* and *Palythoa nelliae* had consistently higher cover in Maputaland.

Some species failed to consistently distinguish between regions depending on whether subsistence-harvested localities were excluded (as here) or included (as in Chapter 2). *Sargassum elegans* and *Cheilosporum sagittatum* were the second and third-ranking major distinguishing species between regions when subsistence-exploited sites were included in biogeographic analyses, being more abundant in Maputaland (Chapter 2, Table 2.4A, p 46). However, when exploited sites were excluded these species failed to contribute significantly to the overall dissimilarity between regions (Table 6.8). The mean cover of *C. sagittatum* in Maputaland was reduced by 15% and that of *S. elegans* by 12% when exploited sites were not considered (Table 2.4A versus Table 6.8). The colonial reefworm, *Idanthyrsus pennatus*, similarly contributed less to the dissimilarity between regions when subsistence-exploited sites were excluded from the analysis. In concordance with this, *S. elegans*, *C. sagittatum* and *I. pennatus* were identified as major distinguishing species between subsistence-exploited and unexploited sites in Maputaland (Chapter 3, Table 3.14, p 100).

Perna perna and *Pyura stolonifera* consistently distinguished between regions with higher cover of *P. perna* in Natal and higher cover of *P. stolonifera* in Maputaland. However, for both species, subsistence harvesting reduced their mean cover within Maputaland. When subsistence-harvested sites were excluded from the biogeographic analysis in this chapter, regional differences in mean mussel cover were reduced by 20% and those of *Pyura* by 10%. This demonstrates that although there is naturally a lower cover of *P. perna* in Maputaland compared to Natal, this effect has been exaggerated by intensive subsistence mussel-harvesting in Maputaland. Conversely, harvesting obscured the fact that the mean cover of *Pyura* is naturally three times more abundant in Maputaland than Natal.

In conclusion, these results show that intensive mussel harvesting at eight of the eleven sites sampled in Maputaland exaggerated underlying biogeographic differences. In chapter 2, Maputaland low-shore sites were more than 70% dissimilar to those in Natal. Exclusion of subsistence-harvested sites from the analysis reduced the dissimilarity to 60%. The 10% difference indicates that subsistence harvesting did contribute to observed differences in community structure between regions. The magnitude of the effect was however too small to have been responsible for the recognition of the biogeographic break between Maputaland and Natal. This was confirmed by the perpetuation of this break when subsistence-harvested sites were excluded from the analysis (Figure 6.9).

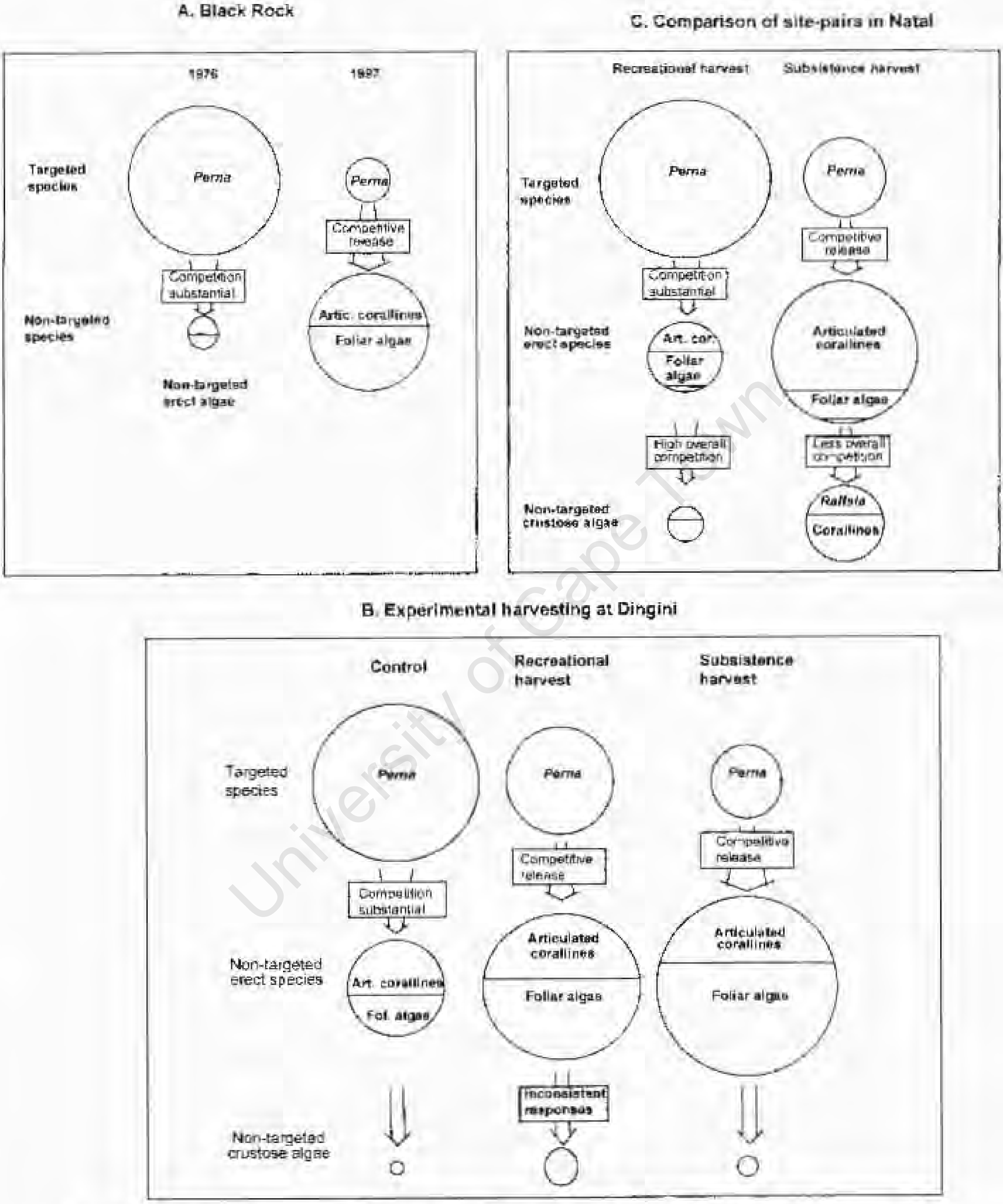
5. General effects of harvesting on intertidal communities

The direct effects of the removal of target organisms were evident in all four approaches adopted here. Mussel numbers were 88-95% lower at Black Rock in 1997 than in 1976 and declines in the targeted limpet were evident. At Dingini, mean cover of mussels declined by approximately 30-40% in experimental plots harvested at recreational intensities and by approximately 50% in subsistence-harvested plots. In Natal, mussel cover was 55-62% less at sites exploited by subsistence collectors than at adjacent sites harvested by recreational collectors. Other studies have shown how intensive intertidal harvesting causes stock depletion (e.g., Moreno et al. 1984, Castilla and Duran 1985, Hockey and Bosman 1986, Moreno et al. 1986, Lasiak 1991, Keough et al. 1993). In southern Mozambique, *Perna perna* was present in old harvesting middens but their absence from modern middens led de Boer (2000a) to the conclusion that local extinction may have resulted from human exploitation. Evidence of overexploitation of shellfish by prehistoric humans exists in New Zealand (Anderson 1979). Therefore, the possibility that human exploitation could cause local extinction of shellfish should not be dismissed (Poiner and Catterall 1988).

Indirect effects due to human exploitation in my study included increased abundance of other species due to reduced competition and reductions of a species dependent on the prescence of a target species. The clearest pattern emerging was that algal abundance increased in heavily harvested areas. The proliferation of algae can be considered a cascade effect although the mechanism (reduction of filter feeding mussels) is different from that observed in other regions where grazers or predators are principle target species. Increased abundance of articulated coralline and foliar algae was recorded in all of the studies, and was probably an indirect effect of reducing competitive target species. Such indirect effects of exploitation are likely to be substantial wherever target species are abundant and interact competitively with many other species (McClanahan 1989).

The indirect harvesting impacts reported in my studies were also consistent with those recorded in several reports covering the former Transkei. First, Hockey and Bosman (1986) documented higher cover of articulated corallines and foliar algae at exploited than unexploited localities in the Transkei. They reported approximately 50% cover of algae at exploited sites but their virtual absence from unexploited sites. Second, Siegfried (1988) reported that areas that previously supported large mussel populations became dominated by coralline algae in the low shore. Third, there are records of mussel beds disappearing in harvested areas, with mussels now only occurring as individuals amongst coralline algae or in small clumps (Dye 1992, Dye et al. 1994). Fourth, changes in macrofaunal communities in all regions of the Transkei indicate reductions of mussels and other target species and increased abundance and biomass of seaweed-associated species (Lasiak and Field 1995, Lasiak 1999). Finally, in KwaZulu-Natal, Lambert and Steinke (1986) showed that when *Perna perna* was experimentally removed, it was replaced by articulated corallines and mussels did not reappear in cleared areas even after eight years.

In Chapter 3, based solely on correlations between exploitation and community structure in Maputaland, it was suggested that cascade effects arise from harvesting. Communities dominated by consumers, principally filter feeders, were transformed to communities dominated by primary producers, mainly foliar and articulated coralline algae. The two main target species, *Perna* and *Pyura*, were diminished at harvested sites but this appeared to indirectly benefit non-target species, including foliose algae, articulated corallines and sessile invertebrates (Figure 3.6 p *). This general conclusion now seems robust in the light of the results from the approaches presented in this chapter, and summarised in Figure 6.10.



A. Black Rock

C. Comparison of site-pairs in Natal

B. Experimental harvesting at Dingini

Figure 6.10. Diagram showing indirect direct effects and cascade effects in response to subsistence harvesting at (A) Black Rock in Maputaland, (B) Dingini in northern KwaZulu-Natal and (C) at Groutville, Umgababa and Umfazazana in the Natal region.The areas of the circles are proportional to the abundance of taxa and division of circles by horizontal lines reflects the relative contribution of taxa. In (A), abundance of *Perna* reflects numbers.m^{-2}, the large circle being equivalent to 500.m^{-2}. All other circles indicate % cover, with the largest circle equivalent to 77%. The data are averages, derived from Tables 6.3 and 6.7 and Figure 6.3.

There were however differences of detail between responses observed in the different studies (Figure 6.10). When comparing sites in Maputaland (Chapter 3, see Figure 3.4 p 101) harvested sites had greater abundance of several non-target sessile invertebrates than unharvested sites. However, in neither the Dingini experiment or the site-pair comparisons in Natal did sessile invertebrates emerge as indirect beneficiaries of mussel harvesting. Furthermore, there was no hint that proliferation of non-target foliar or articulate coralline algae led to a reduction of crustose algae as suggested in Chapter 3 (See Figure 3.6 p 117). In fact, both *Ralfsia expansa* and encrusting corallines were more abundant at subsistence-harvested sites than recreationally-harvested sites (Figure 6.10C) and their responses were inconsistent in the Dingini experiment (Figure 6.10B). The responses of crustose algae were thus ambivalent.

In other areas, removal of molluscs by shellfish gatherers has resulted in proliferation of algae (Branch 1981, Hawkins and Hartnoll 1983, Moreno et al. 1984, Hockey and Bosman 1986, Oliva and Castilla 1986, Underwood 1993a, Branch and Moreno 1994). In these cases, the molluscs were grazers and their removal caused increased abundance of their food. Researchers on the Transkei coast suggest that the selective removal of patellid limpets caused increased cover of foliar macro-algae thereby reducing the availability of primary space for other species (Lasiak and White 1993, Dye 1995). This pattern is general, but not universal. Experimental removal of limpets of the genus *Cellana* in south eastern Australia increased abundance of microalgae but macroalgae did not increase (Sharpe and Keough 1998).

The removal of predatory or herbivorous molluscs in intertidal habitats often results in increased abundance of their prey or food source. In southern Chile, removal of key grazing gastropods, *Fissurella* spp. led to increased cover of macroalgae (Moreno et al 1984, Branch and Moreno 1994, Castilla 1999). Removal of the predatory gastropod *Concholepas concholepas* by harvesters in Chile resulted in cascade effects rippling through the intertidal ecosystem. Prey species, particularly the mussel, *Perumytilus purpuratus*, which is too small to be harvested, increased substantially (Duran and Castilla 1989, Castilla et al. 1994, Castilla 1999).

In KwaZulu-Natal, the major exploited species are not grazers or predators but space-occupying filter feeders. Mussels (*Perna perna*) are the primary target organisms along the entire coast and in Maputaland, *Pyura stolonifera* is also intensively exploited. Although mussels harbour limpets, particularly *Scutellastra aphanes* and harvesters also gather patellid limpets in Maputaland, the proliferation of upright algae at harvested sites is not necessarily linked to the removal of grazing limpets. No limpet-dominated communities were apparent in the low shore of KwaZulu-Natal, even where harvesting is prohibited (Chapter 4). At Dingini, mobile organisms were not harvested except as by-catch. Nevertheless, macro-algae became established in previously mussel-dominated areas within a relatively short time. In KwaZulu-Natal, the change in community structure when mussels are removed therefore appear to be more closely related to the provision of space than removal of grazers. On rocky shores, space is an absolute, non-renewable resource (Branch 1985). Changes in community structure in response to exploitation may be related to changes in competitive interactions. Removal of dominant species makes space available for less competitive species and non-target species and algae can increase in abundance. Other authors have also documented indirect harvesting impacts mediated by competitive interactions (Moreno et al. 1984, Godoy and Moreno 1989).

In my study the only non-target species that was consistently reduced by mussel harvesting was *Scutellastra aphanes*, a patellid limpet that occurs most frequently on mussel shells. However, beds of *Perna perna* and *Pyura stolonifera* constitute structurally and functionally complex habitats that provide refuge for many other organisms and often support high species richness (Suchanek 1979, 1980, Tsuchiya and Nishihira 1985, 1986, Underwood and Fairweather 1986, Fielding et al. 1994, Seed 1996). If destructive sampling had been undertaken, the impacts on infauna might have been detected. In Australia, removal of *P. stolonifera* had deleterious effects for many species (Fairweather 1991, Underwood 1993a). Lasiak (1999) also showed significant differences in the composition of macrofaunal communities between exploited and unexploited sites in the Transkei (R=0.65-0.87). Species that were adversely affected by exploitation included those targeted by collectors, such as *P. perna*, *P. stolonifera* and patellid limpets, as well as species dependant on primary substrate for food supplies (e.g., the winkles *Oxystele* and the keyhole limpets *Fissurella* spp.). Most of the species that benefited from harvesting were those associated with seaweeds such as the crab, *Dehaanius undulatus*. These studies demonstrate that species dependant on target species, e.g., for shelter or as a substratum, may become less abundant in their absence.

Convergence of community structure has been cited as a predictable response to human exploitation (Hockey and Bosman 1986, Fairweather 1990, Sharpe and Keough 1998). In my study, the average within-site Bray-Curtis similarity was used as a measure of convergence. However, in both the experimentally harvested plots at Dingini and the studies comparing recreationally and subsistence-harvested sites in Natal, I failed to detect convergence of community structure even at high harvesting intensities (Table 6.1). For comparative purposes, the average similarities of samples within unexploited sites and sites exploited by subsistence harvesters in Maputaland were also calculated (Table 6.9). Wave-exposed and relatively wave-sheltered sites were examined separately. Again, there was no indication that harvesting caused convergence at either wave-exposed or less-exposed sites. Sites showing highest and lowest similarity between samples were both unexploited. Trends in similarity between exploited and unexploited sites were also inconsistent between site pairs. Of the three wave-exposed sites, the unexploited site (Island Rock) had greater convergence of community structure than either of the subsistence-exploited sites. The two pairs of relatively wave-sheltered sites showed the opposite trend with higher similarity at the subsistence-exploited sites, but in both cases the difference in average similarity was marginal.

Table 6.9. Average Bray-Curtis similarity (S) of unexploited and subsistence-exploited sites in Maputaland. Similarity is based on root transformed estimates of percentage cover from twenty replicate samples. *= sites exposed to significantly higher wave forces ($P<0.05$).

Unexploited sites	S	Subsistence-exploited Sites	S
*Island Rock	60.23%	*Dog Point	53.97
		*Black Rock	47.95
Sodwana	52.07	Kosi Mouth	53.18
Cape Vidal Point	37.09	Bhanga Nek	38.54

Some analyses of macrofaunal communities in the Transkei have also failed to observe convergence in community structure at exploited sites, despite the detection of other significant changes in community attributes (Lasiak and Field 1995, Lasiak 1999). Convergence of community structure is clearly not a uniform response to harvesting.

Considering things at a larger scale, Sharpe and Keough (1998) remarked that in areas where harvesting is prevalent, differences between regions will be reduced due to convergence of community structure. In my study, the opposite pattern emerged. There were greater differences between regions when subsistence-exploited sites were excluded from analyses (Figure 6.9). As discussed earlier, this reflects the concentration of intense (subsistence) harvesting in Maputaland which emphasised the differences and thereby diversity between regions.

ANOSIM tests for the Dingini harvesting experiment and between shores subject to subsistence and recreational exploitation in central and southern KwaZulu-Natal indicated significant locality effects within treatments. Nevertheless, under experimental conditions at Dingini and in matched comparisons of site-pairs in central and southern KwaZulu-Natal, locality effects were considerably less than the effects of exploitation.

Substantial variability in community structure was also reported between three unexploited sites in the Transkei (Hockey and Bosman 1986) and between shores in other studies of human impacts in the same region (Lasiak and Field 1995, Lasiak 1999). This variability in community structure is probably ascribable to differences in physical and biological factors between sites. For example, differences in wave exposure between localities are associated with differences in community structure both between sites (Chapter 3) and within sites (Chapter 5). Recruitment of mussels in KwaZulu-Natal is patchy at small scales (Harris et al. 1998) and this may also contribute to variability within treatments. Sala et al. (1998) also cautioned that other human impacts and effects of natural events can cloud studies of harvesting impacts (Sala et al. 1998). This reflects the highly heterogeneous nature of intertidal communities between sites at a scale of tens of kilometres and highlights the need for careful experimental design in studies of human impact.

Implications for management and conservation

There are three principal aspects of harvesting impacts that are pertinent to managers: (1) the implications of stock reduction, (2) the relevance of indirect effects in terms of the protection of biological diversity and ecological processes and (3) the necessity for long-term monitoring and 'no-take' benchmark areas. These are discussed below, and specific management recommendations for KwaZulu-Natal are put forward.

Implications of stock reduction

Understanding the impacts of harvesting is central to management of stocks of target species. Exploitation may influence recruitment success by depletion of adult stocks, thereby reducing reproductive output (Catterall and Poiner 1987, Underwood 1991, Sharpe and Keough 1998). Concern has been expressed that depletion of mussels along the Transkei coast may have reduced populations to a degree that even protected populations are too small to be viable (Dye et al. 1997, Harris et al. 1998). A reduction in the output of larvae could also jeopardise the recolonisation potential of sessile marine invertebrates. For example, like most ascidians, *Pyura stolonifera* has a short larval stage (1-3 days) that restricts dispersal to local areas (Griffiths 1976, Clarke et al. 1999). If stocks are completely eradicated from a site, the brevity of the larval stage may prevent re-seeding from more distant stocks. In KwaZulu-Natal, substantial unexploited subtidal *Pyura* stocks may ensure a constant supply to adjacent intertidal shores, and these subtidal populations should continue to enjoy protection from exploitation.

The two most important target species in KwaZulu-Natal are both filter feeders and, as such, play an important role in littoral food chains because they capture phytoplankton and particulate matter that is inaccessible to other trophic groups (Gili and Coma 1988). They are therefore responsible for a large share of the energy flow from pelagic to benthic systems and harvesting them could have serious consequences for shallow-water food webs.

Kyle et al. (1997a) argue that mussel harvesting in Maputaland is "sustainable" because the CPUE has been relatively constant over the seven-year monitoring period. However, whether this equates to sustainability depends on the definition of the term (see Castilla 1995, Struhsaker 1998). Constancy does not necessarily imply that the harvest is near to the maximum sustainable yield. If harvesting exceeds the maximum sustainable yield and CPUE remains at a stable but less-than-optimal level, then management has failed. Controlled harvesting at known fishing effort is needed to resolve the issues of what levels of harvesting yield best returns. Castilla (1999) has challenged marine scientists to incorporate humans into experimental studies to improve our understanding of marine ecosystem functioning and thereby management of fisheries. This was the approach adopted at Dingini where experimental harvesting provided information on direct and indirect impacts at specific harvesting intensities (Harris et. al. 1996, Attwood et al. 1997).

Relevance of indirect harvesting impacts

Changes in community structure revealed in my study could have far reaching implications for the sustainability of intertidal fisheries. Intensive harvesting of *Pyura stolonifera* in Australia resulted in complete elimination from many areas (Underwood 1993a). In my study, the loss of mussel-dominated communities and their replacement by algal-dominated communities in exploited areas is cause for concern. Evidence from other studies suggests that *Perna perna* is unable to recolonise cleared areas even after long time periods (eight years) and that unlike other mytilids, this species is not a competitive dominant (Lambert and Steinke 1986, Lasiak 1991, Dye 1992, Dye et al. 1997). The algal communities that became established wherever intensive mussel harvesting occurred are reported to be stable and persistent, particularly those dominated by coralline algae (Lambert and Steinke 1986, Dye 1993, Dye et al. 1997). These coralline communities are persistent but for two reasons they are unlikely to represent a scenario of 'alternative stable states' (sensu Sutherland 1974). The first relates to the fact that the switch is induced by human harvesting, and a condition cannot be considered stable if it is maintained by artificial control (Connell and Sousa 1983, Sousa and Connell 1985). Secondly, waves and sand inundation periodically clear gaps within mussel beds in KwaZulu-Natal yet these do recover, although recovery may be slow (J. Harris, pers. comm.).

Another potentially serious consequence of reduced cover of mussels is that mussel spat prefer to settle among established mussels (Paine 1989). On the west coast of South Africa, the spat of *Mytilus galloprovincialis* settle amongst adult mussels at densities 20-100 times greater than they do on bare rock or primary colonising algae (G. Branch, University of Cape Town, pers. comm.). On the east coast *Perna perna* similarly preferentially recruits among mussels as opposed to articulated coralline algae (Lasiak and Barnard 1995, Harris et al. 1998). If *P. perna* does require adequate stocks of adult mussels for successful recruitment, diminishing the stocks at harvested sites may result in recruitment failure. In KwaZulu-Natal, however, there are reports of intensive intermittent mussel recruitment onto all rocky intertidal surfaces in some years (e.g., in 1978 - Berry 1978; and in 1994 -Tomalin and Kyle 1998).

The sea mussel, *Mytilus californianus*, has a similar ecology to *Perna perna* (Tomalin and Kyle 1998). Concerns about harvesting of *M. californianus* have been expressed, particularly when large gaps are created within mussel beds (Paine 1989). Paine and Levin (1981) reported that large cleared areas take many years to recover because mussel spat preferentially settle on mussels and because gaps in mussel beds are filled mainly by the encroachment of adult mussels from the periphery of cleared areas. The same is true for *P. perna* in KwaZulu-Natal and Transkei, where larger gaps in the mussel bed take longer to recover than smaller gaps (Dye 1992, Tomalin and Kyle 1998). This fact is pertinent to the control of harvesting equipment. In my study, subsistence harvesters exerted a greater impact on intertidal communities than recreational fishers. This is partly attributable to the different instruments used for harvesting by these two sectors. Other authors have reported that improvements in harvesting equipment, particularly the introduction of modern gear in artisanal fisheries, can have negative repercussions for inshore fisheries and the biotic communities that support them (May 1984, Underwood 1993a, Fanelli et al. 1994, McClanahan et al. 1997). Therefore, the equipment used during harvesting should be an important consideration when managing intertidal fisheries. Wide-bladed implements unselectively clear large gaps on rocky shores, which are likely to recover only over very long time periods, if ever. Furthermore, wide-bladed implements remove a substantial unwanted bycatch of the juveniles of target species and of other non-target species. Consequently, only narrow-bladed tools should be permitted for harvesting by all user groups.

Monitoring and the necessity of closed areas

Stock assessments and monitoring of community structure should be conducted over entire shores because harvesting may alter biological zonation patterns. Tomalin and Kyle (1998) compared mussel stocks and then subsistence and recreational fishing effort in Maputaland and Natal respectively. Greater average available densities of mussels were recorded at Dog Point and Black Rock in Maputaland (1 400–1 500.m^{-2}) than on shores in central Natal (670–865.m^{-2}). This is opposite to the pattern observed by Fielding et al. (1991) and in my studies, in which mussel cover was far lower in Maputaland than Natal (Chapters 2 and 3). Tomalin and Kyle (1998) used different stock-survey methods in Maputaland and Natal. In Maputaland, stocks were estimated using transects that were perpendicular to the shore and ran from "above" the mussel zone to the low-water slack. In Natal, a single 20-m transect running parallel to the shore within a biologically defined 'mussel band', was conducted and an estimate of the width of the mussel bed was recorded. Furthermore, the Maputaland surveys were conducted when spring tides were "exceptionally" low and Natal surveys during unexceptional spring low tides. Their results may thus simply reflect differences in sampling procedures and conditions. Standardised procedures are essential when making comparisons, and whole-shore estimates are more accurate than estimates made within subjectively defined zones. This is particularly important when harvesting may have shrunk the biological zones of resource species as suggested by the comparison of the mussel zone at Black Rock in 1976 and 1997 and demonstrated more conclusively in the harvesting experiment at Dingini.

The results in this chapter reflect the absolute necessity of unexploited "no-take" areas to serve as benchmarks against which human impacts can effectively be assessed. Without such areas, human impacts cannot be identified (Ballantine 1991, 1997, Adessi et al. 1994, Ward et al. 2000). In Chile, the dramatic modification of intertidal communities by harvesting was only revealed when closed areas were implemented (Castilla and Bustamante 1989, Castilla and Duran 1985, Oliva and Castilla 1986, Castilla 1999). Similarly, marine reserves in New Zealand revealed increased primary and secondary productivity in response to protection (Babcock et al. 1999). Representative intertidal rocky shores should be fully protected in marine protected areas in which all harvesting (including angling) is prohibited. Such areas serve not only as benchmarks but can re-seed adjacent exploited areas (Ballantine 1991, Underwood 1993a, 1997).

Core functions of marine protected areas include conservation of species and habitats, and management of fisheries (Hockey and Branch 1997). Margules and Pressey (2000) stress that reserves should separate biological diversity from the processes that threaten its persistence. Subsistence or recreational exploitation within a marine reserve, including angling (Underwood 1993a), compromises these core functions of protected areas. In marine protected areas with high visitor numbers in Australia, 25% of people actively collected intertidal molluscs despite regulations prohibiting their removal (Keough et al. 1993) and 34% of anglers foraged for bait while fishing (Underwood 1993a). Therefore, all types of collection should be banned and educational initiatives and active law enforcement are necessary to ensure compliance.

With respect to selecting Marine Protected Areas, my study demonstrates the importance of understanding the influence of natural abiotic factors on communities. For example, wave exposure exerts a powerful influence on community structure and different target species favour exposed or sheltered shores. In particular, dense mussel beds were only found on wave-exposed shores. As discussed in Chapter 3, wave action increases the concentration and turnover of particulate food (Bustamante and Branch 1996) and sheltered shores may be incapable of supporting dense mussel stocks due to limited food supply. However, in my study *Pyura stolonifera* was more abundant on sheltered shores, possibly because of reduced competition from mussels. The relevance of these observations is that representative shores covering the full range of abiotic conditions must be included in closed areas if benefits are to be incurred for both fisheries and if harvesting impacts are to be distinguished from the effect of wave action.

Management options

One management option that has been considered for inshore fisheries is rotational cropping (Hockey and Bosman 1986, Siegfried 1988, Dye et al. 1994, Bradbury and Pfister 1996). However, rotational cropping is not a viable management strategy for fisheries that modify community structure, particularly if these changes take long time periods to be reversed. Stock enhancement by the seeding of mussels is, however, an appropriate management technique that has had some success in the Transkei (Dye et al. 1997).

McClanahan et al. (1997) emphasise that traditional practices should not be used as a justification for ecologically-destructive methods of harvesting, particularly considering that many artisanal fisheries now use modern equipment (also see Underwood 1993a). Effective resource management is critical to the long-term success of small-scale fisheries, and subsistence fisheries are no exception. Co-management arrangements have been identified as a potential way forward (Hauck 1999, Harris et al. 2000). The essence of co-management is that user groups and government share the responsibility for managing a resource (Hutton and Pitcher 1998). The benefits of co-management include greater participation of the user-groups and therefore a broader source of information (Jentoft and Mikalsen 1994). In turn, the legitimacy of regulations and therefore compliance should increase, resulting in a more efficient management system and reduced costs (Jentoft and Mikalsen 1994, Hutton and Lamberth 1997, Talepa et al. 1997, Sowman et al. 1997). Hutton and Pitcher (1998) review co-management and its applicability in South African fisheries, and identify critical factors for the establishment of successful co-operative management systems. However, they do caution that even when all critical factors are met, the process can be derailed due to culture-specific situations e.g., a history of inequitable resource allocation.

Co-management has generally been a positive development in the management of nearshore fisheries. Castilla and Fernandez (1998) highlight the success of co-management initiatives in small-scale benthic fisheries in Chile, where management is not only more equitable and efficient but sustainable exploitation is also being achieved. The experimental mussel fishery at Dingini in KwaZulu-Natal has been cited as one of the most comprehensive co-management initiatives in South Africa (Hutton and Pitcher 1998) illustrating the potential for this management option for intertidal fisheries.

Management Recommendations for KwaZulu-Natal

The KwaZulu-Natal coastline should be zoned into different areas allowing for different levels of resource utilisation. No-take benchmark areas and unexploited areas allowing for experimental work must feature in such a zonation scheme.

At present only 4% of the KwaZulu-Natal coastline is closed to all foraging activities (see Figure 2.14, p 66). Ballantine (1997) recommends that 10% of any region should receive complete protection to conserve biodiversity, but that 20-30% should be closed to ensure indirect benefits (e.g., resilience to overexploitation and seeding of recruits to adjacent areas). In KwaZulu-Natal, representative fully protected areas are needed in both biogeographic regions. Harvesting at all shores within the Maputaland Marine Reserve jeopardises intertidal communities in that area. Island Rock (currently seldom exploited due to its inaccessibility) should receive formal protection as it is presently the only relatively unexploited wave-exposed site. Communities with moderate mussel cover are legally protected at Cape Vidal and Sodwana Bay, but stocks have declined at these sites (K. Sink unpublished data) and measures are required to improve compliance of regulations prohibiting harvesting. The presence of anglers at these sites particularly hinders efforts to prevent harvesting of intertidal resources (Attwood et al. 1997). In the Natal biogeographic region, there are no fully protected areas. Trafalgar Marine Reserve does conserve approximately 2 km of rocky shore, but is representative of only one extreme of wave action, being wave-sheltered. The biological community structure there is not typical of most rocky shores in Natal, as shown in hierarchical cluster analyses (Figures 2.4 (p 32), 6.7, 6.8). Representative "no take" areas are required as a matter of urgency in Natal and these should include wave-exposed sites that support dense mussel beds.

The monitoring of stock and catch per unit effort in KwaZulu-Natal can be improved upon. Stock surveys should cover entire shores as harvesting may alter biological zonation patterns and monitoring of community structure (at sites exploited at different intensities and unexploited benchmark sites) should be incorporated into fisheries management. Biotope surveys are an efficient way to achieve this and they can be conducted by people with minimal training.

Two other considerations pertinent to management of subsistence fisheries are control over effort and incentives. In Maputaland, at present, subsistence-harvesters are not licensed and catches are not regulated. Each harvesting trip entails an approximately 12-km round trip, taking about four hours on foot (Kyle et al. 1997a). Tidal cycles limit access to the low shore. Tomalin and Kyle (1998) attributed the sustainability of harvesting in this region to the restricted mobility of subsistence collectors and the fact that there are unexploited stocks in the inaccessible infratidal and subtidal zones. Gear limitations should persist (e.g., ban of use of SCUBA) and subtidal exploitation of mussels and *Pyura* should continue to be banned. The Subsistence Fisheries Task Group (Harris et al. 2000) recommends that subsistence fishers should be obliged to collect resources *personally*, using low-technology gear, and that the catch should be for local use or local sale only. It is proposed that a permit system should be implemented and community monitoring of resource harvesting is encouraged. These recommendations are aimed at development of sustainable harvesting practises.

Aquaculture of *Perna perna* could be investigated in KwaZulu-Natal as Vakily (1989) considered it as a promising mariculture species for the tropics. Aquaculture output is usually directed at the luxury market and is unlikely to relieve pressure on wild stocks by subsistence gatherers (Van Erkom Schurink and Griffiths 1990). However, if local communities could develop a cash economy based on aquaculture, this might reduce their dependence on wild mussels as a protein source. Important limitations are the shortage of suitable sheltered embayments and the restricted number of estuaries where aquaculture would be viable in KwaZulu-Natal. One of the most promising strategies for aiding the recovery of shores denuded of mussels by harvesting is the transplantion of juvenile mussels to re-seed impacted areas (Dye et al. 1997).

Conclusions

The effects of exploitation may be difficult to identify where humans have been exploiting marine resources for thousands of years at unknown intensities (Castilla and Paine 1987). The absence of adequate historical records makes it difficult to speculate about the pristine state of the rocky shores in KwaZulu-Natal and the size of the original unexploited stocks. Assessment of the effects of harvesting in the intertidal is also hampered by the scarcity of representative unexploited sites, especially in Natal. Despite these limitations, the evidence presented in this chapter shows that exploitation has modified community structure within and between sites in both Maputaland and Natal. Important changes due to exploitation were reduced cover of mussels and *Pyura* and increased cover of articulate corallines and foliar algae. These changes are consistent with the effects of exploitation observed in the former Transkei on the eastern Cape coast. Greater changes in community structure were observed at sites subject to intensive harvesting by subsistence gatherers than at sites harvested at lower intensities by recreational fishers. Changes in abundance of biotopes in the experiments at Dingini indicate that using biotopes as a means of monitoring can efficiently detect changes in community structure associated with human exploitation. Fully protected areas, controlled harvesting at predetermined levels, and in-situ monitoring of stocks and community structure at fixed sites should be pursued as a priority, both to protect representative sections of the coast and to allow an adequate evaluation of optimal offtake. Co-management systems and re-seeding of over-exploited mussel stocks may serve as viable management options but, in the long term, the dependence of local people on intertidal resources should be reduced.

Chapter 7

Synthesis

1. Introduction

This thesis was undertaken in the interest of improved conservation and resource management in rocky intertidal habitats in KwaZulu-Natal on the east coast of South Africa, a region that was previously little studied. It includes quantitative descriptions of patterns in community structure and diversity, an improved understanding of community regulation and the identification of the effects of harvesting. To achieve this, sampling of biological communities (including 220 species) was undertaken at 42 rocky shores spanning the entire KwaZulu-Natal coastline, and measurements made of selected physical factors to test the extent to which they correlated with community structure at different scales. A biotope classification scheme was also developed to provide a consistent framework for conservation planning. Finally, four different approaches were applied to test the effects of human exploitation.

2. Biogeographic patterns

In Chapter 2, I addressed patterns of community structure at a biogeographic scale covering the entire KwaZulu-Natal coast. Prior to my research, there was a range of opinions about where (and if) the region is divisible into biogeographic provinces, and no replicated sampling at standardised intensities had been undertaken at a sufficiently fine scale to resolve the issue. Furthermore, no quantitative comparisons of possible physical factors underpinning biogeographic patterns had been made. Analyses of this nature are important for two reasons. First, the selection of marine protected areas depends on a hierarchy of criteria, the first of which is to ensure adequate coverage of all biogeographic regions. Second, unless an understanding is gained of the probable abiotic factors influencing biotic patterns, it is impossible to separate the influences of natural factors from human impacts such as harvesting.

Biogeographic patterns in intertidal rocky-shore communities within KwaZulu-Natal were resolved by my analyses. Two biogeographic regions and a clear biogeographic break at Cape Vidal were recognised, separating Maputaland in the north from Natal in the south. These two regions were approximately 70% dissimilar and had significant differences in low and mid-shore community structure. Both of the recognised biogeographic regions require adequate representation in the marine protected area network of South Africa. At present, there are no fully protected shores in the entire Natal region and subsistence harvesting at all shores in the Maputaland Marine Reserve compromises the functioning of this protected area.

Correlations between the biogeographic patterns and five potential causative factors (sea temperature, riverine input, wave action, sand inundation and intensity of human harvest) were sought. Riverine input clearly emerged as a factor that may explain the biogeographic break between Maputaland and Natal. Of KwaZulu-Natal's riverine input, 99% enters the sea south of Cape Vidal and therefore influences intertidal communities in only the Natal biogeographic region. It is suggested that the input of particulate and dissolved organic matter from river water in Natal may explain the greater abundance of filter-feeding mussels there. The role of riverine inputs on inshore productivity and nutrient supply warrants further investigation.

Sea-water temperatures could not be linked with the observed biogeographic pattern. Latitudinal differences in sea temperature were minimal at the biogeographic break. Low levels of wave action in Maputaland were previously proposed as an explanation for regional differences in marine benthic communities, but my study showed that there were no significant differences in wave forces between regions, so that biogeographic patterns cannot be explained by wave exposure. Levels of sand inundation were also not statistically different between the two regions. The only other factor that differed between Maputaland and Natal was the intensity of human exploitation. The mean mass of invertebrates harvested per site per low tide was eighteen times greater in Maputaland than in Natal. Thus, regional differences in the intensity of human exploitation may contribute to the observed biogeographic pattern. Additional biogeographic analyses in Chapter 6 were able to resolve the role of human exploitation at a biogeographic scale.

3. Intertidal community regulation: abiotic determinants and harvesting impacts

In Chapter 3, I examined biotic and abiotic patterns between sites within the two biogeographic regions at a scale of kilometres to tens of kilometres. This was necessary to satisfy the next criteria in the hierarchy of criteria required for the selection of marine protected areas, which is to cover the physical and associated biological diversity between habitats within biogeographic regions. Identification of between-site patterns in community structure and their potential abiotic determinants is also important for the development and evaluation of general models of community structure and regulation, and is critical for managers with jurisdiction over inshore habitats. Identification of human impacts impinges upon an understanding of how natural physical factors influence intertidal communities and this necessitates that the roles of abiotic and anthropogenic factors are examined concurrently.

The relative importance of four factors (rock type, wave exposure, sand inundation and intensity of human exploitation) that potentially shape intertidal communities within each of the biogeographic regions of Maputaland and Natal were investigated. The influence of rock type and sand inundation on community structure could only be investigated in Natal, but the effects of wave exposure and harvesting were examined in both biogeographic regions. In Maputaland, unexploited sites were compared with sites harvested by subsistence gatherers but in Natal, the scarcity of unexploited sites limited my analyses to comparisons of sites subject to different intensities of recreational harvesting.

Sand inundation and wave exposure were identified as potential abiotic determinants and the relative importance of these factors in shaping communities varied between zones on the shore. In both Maputaland and Natal, wave exposure powerfully influenced communities in the low shore but had less effect in the mid shore and virtually none in the high shore. Conversely, sand inundation had little influence on low-shore communities but exerted a strong influence on community structure in the mid and high shore. Rock type generally had a weak influence on intertidal community structure, with only dolerite and quaternary sandstone shores showing consistent differences in community structure, and then only in the mid shore.

Wave exposure has long been recognised as an important determinant of community structure. However, until now, it had never been measured in KwaZulu-Natal and was considered unimportant by previous researchers because the KwaZulu-Natal coastline appears uniformly wave exposed and it could not be imagined that any significant differences in wave forces existed along the relatively linear coast. However, measurements of wave forces showed that wave-exposed sites experienced wave forces that were almost four times greater than those at sheltered sites. This serves to emphasise that quantitative comparable measurements of abiotic factors are critical to ascertain their potential role in regulating intertidal communities. In my study, the general pattern that emerged was that filter feeders (particularly mussels and barnacles) were more abundant at wave-exposed sites and primary producers (algae and zoanthids) dominated more wave-sheltered sites. However, some filter feeders did not conform to this pattern. Notably, the ascidian *Pyura stolonifera* was more abundant on sheltered shores. In Maputaland, both *Pyura* and the brown mussel *Perna perna* are targeted by subsistence harvesters. Despite this, *Pyura* is more abundant there than in Natal, but mean mussel cover is lower. *Pyura* may reach its greatest abundance in Maputaland and at sheltered positions because of reduced competition from *Perna perna*. Unexpectedly, grazers were more abundant on wave-exposed than sheltered shores. This does not conform to the prediction of Menge and Olson (1990) that consumers will be less abundant at sites exposed to strong wave action.

The data from 19 months of sand monitoring revealed that sand inundation is ubiquitous, even on shores initially subjectively rated as sand-free. Although sand inundation has been recognised as a disturbance that can impact on littoral communities, long-term monitoring of sand-inundation has rarely been undertaken anywhere in the world, and never before in KwaZulu-Natal. Furthermore, the influence of sand inundation has seldom been examined concurrently with other factors. In KwaZulu-Natal, sites with significant differences in the intensity of sand inundation had corresponding differences in community structure. In the mid shore, heavily sand-inundated shores were consistently distinguished from lightly sanded shores by greater cover of the articulated coralline turf, *Jania verrucosa*, and reduced cover of barnacles (*Octomeris* and *Tetraclita* spp.). In the high shore, lightly sanded shores had greater cover of the oyster *Saccostrea cucullata* whereas heavily sanded shores were characterised by greater cover of ephemeral algae and higher densities of pulmonate limpets (*Siphonaria* spp.).

The influence of subsistence harvesting on low-shore community structure in Maputaland was greater than that of any other factor examined in either region. Similar comparisons in Natal were thwarted by the absence of representative "no-take" benchmark areas. However, comparisons of sites subject to different intensities of recreational harvesting failed to detect any difference of consequence in terms of community structure. My study is the first to uncover convincing evidence of the impacts of subsistence harvesting on intertidal communities in KwaZulu-Natal. Previously, monitoring of catch per unit effort in Maputaland led Kyle et al. (1997a) to the conclusion that subsistence harvesting there was sustainable and Tomalin and Kyle (1998) remarked that calls for reduced harvesting in Maputaland were unfounded. However, my study uncovered direct and indirect effects of harvesting. Direct harvesting impacts included reduced cover of target species, i.e., the mussel *Perna perna* and the ascidian *Pyura stolonifera*. Indirect effects were also evident in the form of increased cover of algae and non-target sessile invertebrates due to competitive release. Encrusting algae also seemed to be indirectly affected by harvesting, as overgrowth by erect algae and invertebrates appeared to reduce their cover at exploited compared to unexploited sites. This constitutes a cascade effect arising from human exploitation.

Rocky intertidal habitats are highly heterogeneous and throughout my study background variability was evident in tests of community regulation and harvesting impacts. This has important implications for other studies aimed at identifying natural abiotic determinants and anthropogenic effects. Sites should be standardised as far as possible to prevent other variables confounding patterns in communities. For example, in Maputaland, wave exposure determined the distribution of the two most important target species, with the mussels *Perna perna* occurring predominantly on wave-exposed shores and the ascidian *Pyura stolonifera* being more abundant at sheltered sites. Unless exposed and sheltered shores had been examined separately, the influence of harvesting would have been difficult to detect. The taxa that increased in response to harvesting also reflected differences in wave exposure, with wave or shelter-loving species replacing *Perna* and *Pyura* respectively.

In my study, almost any two sites had significant differences in community structure because sample sizes were large and because there was so much variability between sites within regions. Most authors group sites according to treatment when conducting SIMPER analyses and fail to establish whether species responses are consistent between site-pairs. I showed that it is possible for ANOSIM to indicate a significant treatment effect even when species responses were inconsistent between site-pairs. Therefore, to provide convincing evidence of an association between any factor and community structure using a two way crossed

ANOSIM, site-pairs should be analysed separately to detect whether community responses are consistent.

4. Biotope classification

Chapter 4 represents the third and final tier in a hierarchical analysis of intertidal community structure at increasingly smaller scales. A biotope classification scheme was developed as a new tool for assessing the conservation status of intertidal communities, evaluating conservation priorities and monitoring change in intertidal habitats. This is the first time anywhere in Africa that such an intertidal classification scheme has been developed at a sufficiently fine scale to allow conservation planning.

Community data in four zones (low, mid, high and top shore) were analysed to distinguish distinct biotopes, using an arbitrary 50% Bray-Curtis dissimilarity to objectively separate samples. These biotopes were defined and then objective tests at independent sites showed that they are easily recognisable in the field and are robust when analysed by tests of differences in their community structure. To determine whether different biotopes were significantly different in terms of diversity, univariate indices were calculated for a subset of biotopes. My study revealed that univariate indices (i.e., species richness, Shannon diversity and reciprocal dominance) can fail to capture significant variation in biological community structure. This fact, together with the recognised sampling difficulties in estimating species richness and diversity, indicates the necessity of using habitat-based approaches in conservation monitoring and planning.

My biotope classification addressed common criticisms levelled at existing intertidal classification schemes by (1) using objective mathematical methods to distinguish biotopes, (2) incorporating the variability between the low and high shore, (3) covering a large geographic area (two biogeographic regions) and (4) quantitatively linking biologically recognised biotopes with physical features of their habitats (Chapter 5). Biotopes were effectively used to assess the current conservation status of intertidal communities in KwaZulu-Natal and to evaluate proposed new marine protected areas. Biotopes can fulfil these functions more quickly, cheaply and efficiently than inventories of species, do not depend on destructive sampling and require lower levels of taxonomic expertise.

5. Habitat characteristics of biotopes

A biotope is defined as a physical habitat together with an associated community of species (Connor et al. 1995). To validate the use of the term "biotope" for the communities identified in Chapter 4, a subset of these was examined to test for quantitative associations between these biotopes and the physical habitats that support them. To do this, the habitat characteristics of nine low and mid-shore biotopes were examined in Chapter 5 to test for differences in rock temperature, topography (aspect and slope) and wave forces.

In all cases but one, biotopes were demonstrated to have corresponding differences in physical habitat conditions, thus justifying the use of the term biotope to describe contrasting community types. Measurements revealed that differences in rock temperature (which correlate with elevation and desiccation) correlated with the distribution of contrasting biotopes between zones. This supports the traditional assumption that elevation and the associated influences of high temperatures and desiccation underlie vertical zonation patterns on rocky shores. The horizontal distribution of different biotopes within zones was best explained by variability in wave exposure or sand inundation. In contrast with other studies, there was no evidence of any correlation between the distribution of any biotopes and local topography (aspect and slope). This was the first time that quantitative links have been established between biologically-defined intertidal biotopes and their physical habitat characteristics.

The within-zone patterns of biotope distribution in relation to wave exposure and sand inundation mirrored the larger-scale patterns documented in Chapter 3. In the low shore, biotopes dominated by the mussel *Perna perna* experienced higher wave forces than those dominated by the ascidian *Pyura stolonifera*, or than biotopes dominated by foliar red algae (*Hypnea* or *Gelidium* spp.). In the mid shore, barnacles occupied more exposed positions than zoanthids. Two of the mid-shore biotopes were only separable in terms of the relative degree of sand inundation they experienced. Specifically, the articulate coralline turf, *Jania verrucosa*, consistently experienced significantly greater intensities of sanding than barnacles (*Octomeris* and *Tetraclita* spp.).

Only two biotopes failed to differ in terms of any abiotic characteristics, i.e., those dominated by *Perna perna* and *Cheilosporum sagittatum*. As these biotopes share the same physical habitat, it is possible that they compete strongly for space. In Chapter 3, subsistence harvesting in Maputaland depleted *P. perna*, but *C. sagittatum* increased in response to harvesting. Furthermore, the *Cheilosporum* biotope reached its greatest abundance at subsistence-exploited sites in both biogeographic regions. It was therefore hypothesised that human harvesting influences the relative abundance of these contrasting biotopes, and this was examined in Chapter 6.

6. Harvesting impacts

The sixth chapter of my thesis constituted a specific investigation of the effects of human exploitation on rocky shores in KwaZulu-Natal. Harvesting could not be eliminated as a potential factor contributing to the biogeographic pattern identified in Chapter 2. In Chapter 3, using a correlative approach, large differences in community structure were evident between unexploited sites and sites subject to subsistence harvesting in Maputaland. In Chapter 6, four approaches were implemented to examine the impact of recreational and subsistence harvesting within and between sites in the Natal biogeographic region, and to ascertain the extent to which subsistence harvesting contributes to biogeographic differences between Maputaland and Natal.

The first approach was to compare community structure at Black Rock between 1976 drawn on information in Jackson (1976) and 1997. This is the only site for which data exists to allow a comparison of an intensely harvested site over a relatively long time period. The abundance of mussels in 1997 was 80% lower than in 1976, numbers of harvested limpets had declined substantially and the cover of articulated coralline algae had increased. These changes mirror the observed differences between harvested and unharvested sites uncovered in Maputaland in Chapter 3. This supports the assertion that harvesting was responsible for the observed temporal changes. However, stronger support for this conclusion was provided by the second approach, in which experimental harvesting established a causative link between human exploitation and changes in community structure.

Experimental harvesting at two localities at Dingini established clear spatial and temporal changes in intertidal communities that were directly attributable to recreational and subsistence harvesting. These changes were reflected by differences in community structure and patterns in biotope abundance. Target species declined and foliar red algae and articulated corallines increased in exploited plots relative to unexploited controls. Changes were greater at subsistence-exploited plots than at recreationally-exploited plots. Unexploited control plots were characterised by a prevalence of mussel-dominated biotopes whereas recreationally-harvested plots supported a more diverse mixture of both mussel and algae-dominated biotopes. Subsistence harvesting caused an almost complete loss of all mussel-dominated biotopes, which were replaced by biotopes dominated by foliar red and articulated coralline algae. These patterns conformed with the predictions of the intermediate disturbance hypothesis. The replacement of mussel biotopes by those dominated by coralline algae provides strong support for the assertion that the abundance of these two biotopes is related to the intensity of human exploitation, and that in the absence of harvesting *Perna* outcompetes *Cheilosporum*. The successful demonstration of harvesting impacts using biotopes shows that biotope surveys could be used as an effective and efficient technique to monitor community structure in addition to traditional fisheries monitoring aimed at single species.

The third approach compared community structure at sites subject to recreational versus subsistence harvesting in Natal. Sites harvested in these two ways were more than 60% dissimilar, indicating that divergent communities occur on shores subject to the two types of harvesting. Mussel cover was consistently lower at subsistence-harvested sites whereas the articulated coralline alga *Cheilosporum sagittatum* was always more abundant at sites subject to intensive subsistence-exploitation. These patterns had parallels with the comparisons of unexploited and subsistence-exploited sites in Maputaland (Chapter 3) and with differences between unexploited control plots and experimentally-harvested plots at Dingini.

The fourth approach was employed to resolve the role of subsistence harvesting in determining biogeographic patterns. In Chapter 2, the only subsistence-harvested site surveyed in Natal (Umfazazana) clustered with other subsistence-harvested sites in Maputaland rather than with other sites in Natal. The two regions also had significant differences in harvesting intensity and therefore regional differences in exploitation could not be discounted as a factor underlying biogeographic differences. Data from two additional subsistence-harvested Natal sites and from the experimentally-harvested plots at Dingini were added to the data used in Chapter 2 and biogeographic analyses were then repeated. Harvesting impacts exceeded biogeographic effects when the data were untransformed. Root transformation of the data allowed all species to contribute more uniformly to community patterns and harvesting impacts then failed to override biogeographic patterns. At this scale, the influence of wave exposure on community structure was always greater than patterns attributable to harvesting or biogeography. When all subsistence-harvested sites were excluded from the biogeographic analysis, the biogeographic break separating Maputaland and Natal persisted, indicating that the biogeographic pattern cannot be solely attributed to differences in harvesting offtake between regions. However, subsistence harvesting did exaggerate biogeographic patterns although the magnitude of this effect was small. Of the 70% dissimilarity between regions, 10% could be accounted for by differences in the exploitation intensity in Maputaland and Natal. Species that differ naturally between regions were separated from those that showed exaggerated regional differences due to intensive harvesting in Maputaland. This is the first study that I know of that documents harvesting impacts at a biogeographic scale.

My study uncovered significant changes in community structure due to human exploitation in all four approaches and therefore at all three scales examined – a biogeographic scale covering hundreds of kilometres, a between-site scale of tens of kilometres, and a within-site scale of metres to tens of metres. These harvesting impacts closely paralleled those in Maputaland, as revealed in Chapter 3. The general pattern that emerged was that harvesting directly reduced the cover of target species (*Perna perna* or *Pyura stolonifera*) and that of organisms that depended on such target species (e.g., the limpet *Scutellastra aphanes*, which lives on mussel). General indirect effects were also evident, with all studies showing increased cover of algae, particularly articulated corallines, at harvested sites. In Maputaland, non-target sessile invertebrates also increased in response to harvesting but this did not happen in Natal. In Chapter 3, encrusting algae seemed to be indirectly affected by harvesting as overgrowth of upright algae appeared to reduce their cover at exploited versus unexploited sites in Maputaland. This pattern was not observed at Dingini or at intensively harvested localities in Natal.

7. Implications for resource management and conservation planning

The impact of harvesting on intertidal communities has important implications for management of resources. In Maputaland, where seven years of monitoring indicated no change in catch per unit effort, analyses of community structure yielded significant harvesting impacts. In Natal, comparisons of community structure at three exploited and unexploited pairs of sites, and between 1976 and 1997 at Black Rock, indicated that harvesting transforms intertidal community structure. Experimental harvesting at Dingini confirmed that the community differences observed in Maputaland were consistent with harvesting impacts. The most important lesson here is that fully protected areas are critical for assessing harvesting impacts. Without benchmark areas and monitoring, there would have been no indication of any problem in this fishery. In situ monitoring of stocks and entire communities should form part of the fisheries management process. With a little training, harvesters could conduct biotope surveys in partnership with scientists and management as part of a co-management arrangement. The changes revealed in my study indicate that exploitation also alters biological zonation patterns on the shore. Therefore, it is important that whole-shore estimates are used for stock assessments and that fixed monitoring transects are installed. Furthermore, estimates of catch per unit effort should also incorporate the time taken to gather resources and should reflect any changes in gear or efficiency.

The impacts of subsistence intensities of harvesting were greater than the impacts of recreational intensities of harvesting. This was attributed partly to the larger quantities required by subsistence harvesters but also to the different methods usually employed by these two user groups. Subsistence harvesters often clear large areas in mussel beds because wide-bladed implements are employed. This results in a large by-catch of juvenile mussels and other species and creates bare space where other competitors can invade. This may have serious implications for mussels because recruits preferentially settle amongst adults. Large gaps in mussel beds recover slowly because juveniles may fail to recruit into the algal communities that become established following intensive mussel harvesting. This means that narrow-bladed tools should be mandatory for all user-groups in intertidal habitats. Slow recovery times also mean that rotational cropping is not recommended as a viable management option for intertidal rocky shores.

Changes in community structure and disappearance of dense mussel biotopes at intensively exploited sites show that harvesting can impact on biodiversity and this is why all forms of harvesting should be prohibited in fully protected components of marine protected areas that are to serve as benchmark localities. Beds of mussels and *Pyura* constitute complex three-dimensional habitats and harbour many other species that may be lost when algae or other invertebrates replace these resources after harvesting. Heavy harvesting can also modify trophic patterns on rocky shores. Filter feeders play an important role in marine foodwebs by coupling benthic and pelagic systems and may regulate primary and secondary production in littoral foodchains (Gili and Coma 1998). Harvesting substantially reduces the abundance of filter feeders, so this could have serious consequences for energy flow in marine foodwebs. It is because of such linkages between species and ecosystems that there are limits to the value of single-species approaches in management, and ecosystem processes need to be incorporated in conservation planning.

A hierarchical approach is advocated in developing conservation strategies for marine habitats (Hockey and Branch 1997, Roberts et al. in press a). Firstly, all biogeographic regions should be represented in protected areas, then within regions, habitat heterogeneity should be used to prioritise conservation efforts. Biotopes offer a finer resolution of habitat heterogeneity than we have been capable of in the past.

In KwaZulu-Natal, both Maputaland and Natal urgently require fully protected "no take" areas. The range of communities associated with different abiotic conditions showed that protected areas must include both wave-exposed and sheltered shores and sites subject to different intensities of sand inundation if the full spectrum of biological diversity is to be conserved. By including shores that host resource species, benefits to fisheries can also be incurred.

At present, only 4% of the KwaZulu-Natal coastline is fully protected but this is situated in only a single biogeographic region and covers only wave-sheltered shores. A further 14% of the coastline is protected from invertebrate harvesting, but shore-based angling is permitted there. These partially protected areas do span both biogeographic regions but fail to cover any wave-exposed shores that support mussel biotopes. In fact, only 29% of all the rocky-shore biotopes identified are currently represented in partially protected areas. This could be improved to 53% if the proposed Pondoland Marine Park is promulgated, to 64% if St Lucia Marine Reserve is extended, or to 74% if both new proposed protected areas are established in Natal. To protect the remaining biotopes, fully protected wave-exposed and sheltered sites are needed in the Maputaland Marine Reserve, where subsistence harvesting currently occurs. Some biotopes may be products of intensive harvesting and we do not need to conserve such transformed communities. Instead, closed areas where undisturbed representative biological communities can become established, and which can serve as benchmarks for assessing harvesting impacts, are urgently required.

8. Conclusion

Castilla (2000) highlights the need to improve linkages between marine ecology, marine conservation, fisheries management and social sciences. It is in this spirit that my thesis has attempted to bridge these disciplines in a holistic study of community regulation and harvesting impacts which is relevant to management of resources and conservation planning in KwaZulu-Natal.

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