Biogeographical patterns of southern African marine invertebrates

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Supervisor

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This thesis is dedicated to my husband Stephen Scott for

his faith in me and for whom greatness is a destiny.

And my parents John and Yvonne Crawford

for always believing in me.

DECLARATION

This dissertation documents the results of original research carried out at the Marine Biology Research Centre, Zoology Department, University of Cape Town. This work has not been submitted for a degree at any other university and any assistance I received is fully acknowledged. The data presented were originally collected and processed by B.P. Emmanuel and then by A. Awad. I added additional endemicity data, animal size, and life history characteristics for the purpose of this thesis.

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ABSTRACT

Biogeography is defined as the study of life, in a spatial and temporal context, with respect to the analysis and explanation of patterns for a given area.

The tendency for species richness and diversity to increases towards the equator, where both peak, is a much debated and tested pattern. Underlying mechanisms thought to cause this pattern are: gradients in temperature, stress, productivity, competition, predation, stability, effective evolutionary time, niche breadth, range size and area of occupancy. Evidence exists that both supports and negates most of these mechanisms.

In addition to the richness gradient, a latitudinal gradient in geographical range size exists, whereby species range sizes decrease with latitude, referred to as Rapoport's Rule. This has been linked to species ability to tolerate changes in climate. The latitudinal gradient in species richness is thought to be a by-product of Rapoport's Rule and the "Rescue Effect".

Thorson's Rule hinges on the fact that marine species at low latitudes are inclined to produce many small pelagic larvae, compared to high latitude species that produce fewer, large offspring. The greater dispersal ability of species with pelagic stages at low latitudes would result in the opposite of Rapoport's Rule, with larger ranges occurring at lower latitudes.

Bergman found that animal size increased with increase in latitude, and in addition larger animals are better able to disperse, facilitating larger geographic range size. Large animals are also more likely to have pelagic stages in their development. To summarise: large-bodied pelagic species with large geographic ranges should be found at greater latitudes. This combination of distributional patterns would result in latitudinal patterns that support those dictated by Rapoport's Rule. In addition the nature of a coastline, with its unique current flows, shape and other oceanographic conditions, has a significant affect on the distribution patterns and as a result, on the ranges of marine species.

Species distribution patterns for southern African marine fauna south of the Cunene River in Namibia to Ponta da Barra Falsa in Mozambique were reviewed and updated. Data were compiled recording presence or absence of species in successive 100 km units off the southern African coastline for 11 groups of marine invertebrates. Animal size, developmental mode and temperature data were collected. The data were used to investigate latitudinal and areal gradients in range size, species richness, endemicity patterns, developmental mode and animal size. I then established whether any correlations existed in an attempt to determine causality.

Areal richness was converted to latitudinal richness and diversity patterns were examined. Species richness along the coastline decreased with latitude. The overall pattern was stepped, showing changes at major geographical boundaries. The Indo-Pacific, temperature moderated, species subtraction affect, shows as the systematic latitudinal loss in non-endemic species diversity. These species were replaced by endemic fauna, resulting in a net increase in richness towards higher latitudes. Range-restricted species peaked at regions of high diversity, which coincided with biogeographic breaks.

The shape of the range size frequency distributions varied from uni-modal-right and left skewed to bi-modal distribution, with similar results evident on both linear and log scales. Large numbers of small ranged species reflect the high endemicity levels in southern Africa and the possible gaps in our knowledge on distributional patterns of marine biota in

Africa. Peaks in large ranges reflect the strong Indo-Pacific component of the fauna. Peaks in species richness and endemic species at biogeographical breaks mark the existence of a transition zones or ecotone, where species richness was inflated by the overlap of two biogeographic zones, as well as by unique species endemic to that ecotone. These may reflect regions of speciation. The peaks in range endpoints at major oceanographic features reveal the possible role of biogeographical breaks and upwelling areas as distributional barrier. Biogeographical patterns along the southern African coastline appear to vary with major oceanographic barriers, which wield a substantial affect on range endpoints, species richness peaks as well as endemicity patterns. A better understanding of the nature of these affects on the distribution patterns of species will provide a strong conservation tool for future decisions.

Mean range size of invertebrates decreased towards higher latitudes. Temperature was not limiting, unless the limiting factor was in fact anomalous temperature changes and not annual variability. There was a negative correlation between species richness and latitudinal trends in range size of groups, however, the relationship was not linear and, although significant, the correlation was weak. Biogeographic zone sizes correlated well to constituent species range sizes. Invertebrate animal size decreased from north to south, or with increase in latitude. My results showed a weakly significant or non-significant correlation between animal size and range size. Pelagic groups compared to non-pelagic groups had significantly larger animal size on east and west coasts. Range size for pelagic groups was significantly larger on east coast only. Thus animal size did not explain range size on the west coast. Temperature may not explain latitudinal trends, but it is possible that it could explain differences in west coast and east coast animal size. No single factor explained patterns latitudinaly or along the coastline for all the groups.

CHAPTER 1

GENERAL INTRODUCTION

GENERAL BIODIVERSITY

Biodiversity is the variety of life, in all its manifestations (Gaston and Spicer 2002), or more formally; biodiversity includes diversity within species, between species and of ecosystems (Convention on Biological Diversity 2009). Biodiversity concepts cover a wide spectrum of fields, varying from traditional species studies through to systematics and complex genetic studies.

The principal argument for conservation of biodiversity lies in its benefit to man, since biodiversity affects sustainable development directly and indirectly (Lovejoy 1994). An estimated 40 % of the global economy is based on biological products and processes, thus any loss in diversity impacts directly on the sustainability of sources of revenue and life (WWF-SA 2002). Ehrlich and Wilson (1991) stated three simple reasons why we should be concerned about the loss of biodiversity: 1) the immeasurable ethical and aesthetic benefits gained from a biologically diverse environment, 2) the economic benefits provided by biodiversity in the form of food, medicine and industrial products and 3) the most important, yet most poorly evaluated reason, the array of essential services provided by natural ecosystems.

Worldwide, biodiversity is threatened by human over-population, over-exploitation, invasive species, pollution, habitat destruction, poor water management, genetic engineering, pesticides, air pollution, ozone depletion, climate change and desertification (Attwood *et al.* 1999, Griffiths *et al.* 2003, Lombard *et al.* 2004). Unquestionably the greatest threat is the constant degrading effect of human activities on the planet (Culotta 1994, Aricò 1995, Herbert 1998), resulting in loss of environment and resource. Ultimately

this results in a negative impact on biodiversity, by causing extinctions of species and genetically distinct populations (Vitousek 1992, Hockey and Branch 1994, Féral 2002).

Degradation of biological diversity on a large-scale, such as that caused by deforestation or commercial fishing, threatens the preservation of essential ecological processes, on which we all depend (WWF-SA 2002). In order for scientists to foresee the cost of degradation, it is essential to understand biodiversity and the factors influencing the occurrence, distribution, biomass and biology of the species that constitute the biota. As a result, biologists are forced to rank the exploration of biodiversity as one of their main tasks (May 1988).

In recent years, the impact of biodiversity degradation on ecosystem functions and services has become an important aspect of biodiversity studies (Lovejoy 1994, Aricò 1995, Folke *et al.* 1996, Raffaelli *et al.* 2003). Subsequently, there is a worldwide drive to halt the destruction of biodiversity at global, regional and national levels. This drive has culminated in the formation of biodiversity forums and organisations with conservation of biodiversity constituting a top priority (Census of Marine Life 2009, Convention on Biological Diversity 2009)

The political boundaries imposed by man on the Earth's surface in no way correspond with the geographical distribution of animal life and this necessitates a global focus on biodiversity components and issues. Comprehensive international participation is required to complete the formidable task of mapping out large-scale biodiversity patterns. The mapping of these patterns empowers scientists with the knowledge needed to achieve adequate and representative conservation worldwide. A complete inventory of millions of

species seems impractical, and would require extensive effort and financial investment, yet this global enumeration of organisms is essential to effectively quantify and map out biodiversity (Williams *et al.* 1997).

The widely recognised need to conserve remaining biodiversity is the main driving force behind global initiatives to map diversity. The culmination of the collection of this knowledge would be the selection of conservation areas representing the maximum biodiversity, while utilising the smallest possible area, thus minimising the cost associated with establishing protected areas (Emanuel 1992, Reyers *et al.* 2000, Awad *et al.*, 2002, Lombard *et al.* 2004).

This approach to conservation requires the careful consideration of adequate information on the distribution of species and other natural features of the environment being considered. The information is often spread across countless journal articles, and is difficult to access (Schalk 1998). Furthermore, the cost associated with the collection of such data often exceeds the capacity of research budgets. Consequently the selection of minimum-set conservation areas often depends on more cost-, as well as time-effective alternative methods (Reyers *et al.* 2000). A number of species-based surrogate approaches have been used: Species richness, rarity, endemism or complementarity measures of one or more indicator group are common approaches used as substitutes for complete biodiversity data (Lombard 1995, Williams *et al.* 1997, Reyers *et al.* 2000, Gladstone 2002). These approaches assume that the trends found for the indicator taxa will be the same as for other un-surveyed taxa, and thus that conservation areas identified from the survey of one or two such groups will ensure the conservation of most regional biodiversity (Reyers *et al.* 2000). Although this trend seems to be true on a global and

continental scale, results suggest that this approach has limited potential at a scale relevant to conservation (Scott *et al.* 1987, 1993, Pearson and Cassola 1992).

As another alternative to complete knowledge on the species composition and patterns of an ecosystem, several studies have proposed that it is possible to utilise diversity of higher taxa as a substitute for species level biodiversity patterns (Colwell and Coddington 1994, Williams and Gaston 1994), as diversity patterns at the genus and family level have been found to correlate with those at the species level (Roy *et al.* 1996). The choice of taxonomic rank depends on the resolution required to resolve a given problem. Regional diversity patterns have been mapped at family level for terrestrial and freshwater seed plants, beetles, amphibians and reptiles worldwide (Gaston *et al.* 1995), as well as richness patterns for a number of groups (Williams *et al.* 1997). This approach is based on the view that attempting counts among areas for 1000 families, rather than counts for 1000 species, measures variation within a larger slice of biodiversity.

Reyers *et al.* (2000) investigated the across-taxon value of indicator taxa using spatial similarity and representativeness of richness hot spots and rarity hotspots, as well as areas selected by complementarity-based richness algorithms in the Northern Province of South Africa. The results of the study supported the use of indicator-taxa in the selection of representative conservation areas, and supported the assumption that areas of conservation importance for one taxon will capture high levels of diversity for non-target taxa, although these areas exclude between` 8-50% of rare and endemic taxa. In order to represent high levels of species, specifically rare and endemic species, up to 50 % of available land would have to be conserved, an option that is simply not possible. Similar

marine studies have been done examined priority conservation areas along the coastline of South Africa (Slotow and Hamer 2000, Turpie *et al.* 2000, Awad *et al.* 2002).

The National Spatial Biodiversity Assessment (NSBA), a project led by the South African National Biodiversity Institute (SANBI) completed a comprehensive assessment of spatial biodiversity in South Africa. Thirty-four percent of the 440 terrestrial ecosystems in South Africa are considered threatened, of these 16% are vulnerable, 13% are endangered and 5% are critically endangered (Driver *et al.* 2005). The assessment resulted in the proposal of three key strategies for conserving biodiversity. Firstly, opportunities that link biodiversity to socio-economic development in priority geographic regions need to be pursued; secondly action needs to be taken to prevent further damage to threatened ecosystems and thirdly protected areas needs to be expanded.

MARINE BIODIVERSITY

In the terrestrial environment extinctions, and species hovering at the brink of extinction, are commonplace (IUCN 2009). By contrast, marine organisms rarely appear to be endangered. Many marine species have planktonic larvae that can drift long distances and thus span large geographic ranges. This was thought to reduce the chance of extinction. It is only in recent years that marine biologists have begun to realise that the resilience of marine species has been overestimated (Culotta 1994). Despite this, it is thought that only 14 or 15 marine species have been lost to extinction (Culotta 1994). However, the extent of the un-sampled area of the world's oceans, could mean that some extinctions may have been missed. Loss of biodiversity in marine ecosystem can be attributed to environmental degradation, the invasion of alien species, overexploitation of marine fauna and pollution

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(Griffiths *et al.* 2003, Occhipinti-Ambrosi and Sarini 2003, Lombard *et al.* 2004, Driver *et al.* 2005). These factors cause direct loss of the exploited species, as well as habitat loss due to damage caused by fishing gear and other anthropogenic activities. In addition to direct exploitation, over-fishing can create trophic cascades that further decrease species richness (Coleman and Williams 2002).

As with terrestrial environments, there is a pressing need to conserve marine biodiversity, as marine habitats cover more than 70 % of the Earth's surface (May 1994). The effective functioning of the marine ecosystem ensures that large-scale processes, such as primary production, carbon flow and storage, nutrient cycling and other processes are effectively maintained (Meyers 1996). On a global scale, marine ecosystem services contribute to atmosphere and climate regulation, disturbance regulation, remineralisations, waste treatment, biological control, as well as recreation and tourism. It is the current belief that any loss in biodiversity or species diversity would result in loss of ecosystem functions or services (Constanza *et al.* 1997, Duarte 2000, Raffaelli *et al.* 2003). These services are thought to be closely associated with the ecosystem's ability to withstand or resist shock (ecosystem resilience) (Meyers 1996). The potential of a species to respond to disturbances caused by human activities depends on the extent of diversity and the kind of diversity that is available (Féral 2002). The ecosystem approach to the preservation of biological diversity is the only way to ensure the conservation of processes, as well as habitats, that have not been adequately studied (Franklin 1993).

The Census of Marine Life (CoML) was officially established to encourage and fund a ten year research program to assess and explain the diversity, distribution, and abundance of species throughout the world's oceans (Ausubel 2001, CoML 2009). As part of this

mandate, CoML has established an online data management and analytical tool called: the Ocean Biogeographical Information System (OBIS). By 2009 OBIS held within its data base 19.1 million records, covering 106000 species from 643 databases. These include FishBase, CephBase, ZooGene and others. In addition CoML has a number of other biodiversity initiatives; including the History of Marine Animal Populations (HMAP), the Future of Marine Animal Populations (FMAP), genetic bar-coding and various other projects. Database driven internet guides such as OBIS have simplified the global effort to inventory species. Other examples of databases include: BIOSIS and Species 2000. BIOSIS is a site that includes lists of organisations that relate to specific topics, such as biodiversity. Species 2000 is a website that aims to synthesize existing scattered data on basic taxonomy.

South African Marine Biodiversity

The most recent comprehensive review of the state of knowledge of the marine fauna of South Africa established that 12 734 described marine animal species have been recorded from the region (Griffiths *et al.* in press). While an accurate assessment of endemism is difficult to make, Gibbons *et al* (1999) reported 36.3 % of invertebrates as endemic to South African waters. A recent COML African initiative resulted in a workshop on "Coastal and Marine Biodiversity of the Indian Ocean" held in India. Overall it appears that less than 50 % of the Indian Ocean species have been described (Griffiths 2005). Recent analysis, has shown that a number of groups in South Africa are relatively well known (fish, echinoderms, molluscs and decapods) compared to Europe (Medd 2007). However, for the lesser know groups (e.g. nematodes, copepods, platyhelminthes), in some cases we have reported as few as 1% of the number of species found in Europe. A number of

groups have not been studied at all (Griffiths *et al.* in press), while for many others (e.g. nematodes, copepods, and flatworms), no comprehensive resource guides exist, or existing guides are outdated (polychaetes, amphipods and echinoderms) (Griffiths *et al* 2003).

AIMS OF THIS STUDY

While a large body of knowledge exists around the distribution patterns of invertebrate taxa around South Africa (Barnard 1950, Day 1967a, b, Griffiths 1976, Clark and Courtman-Stock 1976, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Emanuel *et al.* 1992, Williams 1992, Bustamante and Branch 1996, Acuña and Griffiths 2002, Sink *et al.* 2005), few studies have attempted to compare distributions of different taxa. Awad *et al.* (2002) extended the invertebrate data collected by Emanual *et al.* (1992) to include endemicity. They investigated the distribution and endemicity patterns of various marine invertebrate groups in South Africa and compiled a selection of priority conservation areas. They found that there were strong peaks in species richness at the Cape Peninsula / False Bay, Port Elizabeth and Durban. These peaks coincided with areas of high sampling activity, but also with the boundaries of biogeographical provinces, where overlap in species range tends to be high. Some groups showed increases in richness from west to east, while for others; species richness was highest along the south coast. Endemicity patterns where equally variable, ranging from 19 % for echinoderms to 84 % for isopods. For the purpose of their study endemicity was defined as species endemic to the political borders of South Africa and patterns were examined within these boundaries.

To date studies have focused on composite patterns of species richness, diversity and geographic affinity within large groups of species. Little work has been done on species range size distribution, range endpoints, patterns of range-restricted invertebrate species and animal size distribution along the southern African coastline, thus creating an opportunity for this study.

This thesis aims to use the species distribution and endemicity data for 11 groups (2533 species) examined by Awad et al. (2002) to investigate at a number of key questions. There are, however, a few limitations to using the data as they stand. Endemic species are said to be species that are restricted to a predetermined geographic area. Awad et al. (2002) thus defined endemic species as those restricted to the coastline of South Africa. As a result no distinction was made between species with small or large ranges, as long as these remained confined within the politically-defined boundaries of the country.

Every study defines endemism according to the requirements of the study performed. For example, the amphipod and polychaete data included in Awad et al. (2002) defined species as endemic if they were restricted to south of the 20 °S latitude line (Griffiths 1976). The original references to isopods and molluscs (Kensley 1978, Kilburn and Ripey 1982) give the species range of occurrence, without reference to endemicity, thus allowing for different interpretations of endemicity (for example 20 °S or political boundaries of South Africa). These different definitions of endemicity are perpetuated throughout the literature and result in some confusion when reference is made to endemicity. In some senses endemicity is also an artificial, politically-defined concept, since it bears little relation to the actual range, or vulnerability, of species. For example, species whose ranges are small, but span political boundaries, would not be endemic, but those with large

ranges within a single country are endemic. For this reason it may be more useful to examine range size restriction, as opposed to endemicity. This would result in the identification of all restricted species that occupy small sections of coastline, whether they are technically endemic or not.

The IUCN lists both extent of occurrence and area of occupancy as important criteria when evaluating the status of a species (IUCN 2009). Thus a species that has a limited area of occupancy, as well as extent of occurrence, may be construed as an "endemic" to a specified area and would be more threatened than, for example, a species with a limited area of occupancy and a large extent of occurrence (not endemic to a restricted area, but limited to many areas). Accordingly restricted non-endemics are less threatened than restricted endemics, due to their wider extent of occurrence, placing a greater importance on retaining the distinction between endemic and non-endemic range-restricted species.

In an ideal world, conservation along the African coastline would be well orchestrated between neighbouring countries and endemicity would be less important. Along the west coast, management of the living marine resources of the Benguela Current has been facilitated by the Benguela Current Large Marine Ecosystem (BCLME) Programme, which was established in 2002. This initiative by Angola, Namibia and South Africa aims to protect the marine environment and manage the resources in an integrated and sustainable manner. One of the future actions of this programme is to implement measures that address trans-boundary environmental concerns, although this is not currently in place.

The data utilised in this study were originally collected to examine zoogeography and reserve selection along the southern African coastline and incorporate records ranging from the Cunene River, on the border between Namibia and Angola, to Ponta da Barra Falsa in Mozambique (Emanuel *et al.* 1992). Awad *et al.* (2002) re-arranged the data to include only species that fell within the politically defined borders of South Africa. This resulted in the re-analysis of a different suite of species according to a different definition of endemism. Distribution patterns and endemicity are known for the coast as defined by Emanuel *et al.* (1992), thus enabling me to extend the Awad *et al.* (2002) data to include an additional 1400 km along the Namibian coast, and 600 km along the Mozambique coastline.

Additionally, the Awad *et al.* (2002) data results in the inflation of the number of restricted species at the tail ends of the examined regions. Species present in these sections of coastline appeared to be restricted, whereas they may in fact have a distribution that extends, for example, northwards into the Indo-Pacific region. In order to get a more realistic picture of the actual patterns, I examined biogeographic affinity of species along the coastline.

An alternative approach for investigating species composition and patterns of an ecosystem relies on investigating diversity for higher taxa as a substitute for species level biodiversity patterns (Williams and Gaston 1994). My data enable me to examine a number of groups in different taxonomic ranks. It is thought that the problem being investigated dictates the level of resolution required and thus the choice of taxonomic rank. The purpose of this study is to examine patterns in richness, range size and animal size. The difference in taxonomic rank of available, reliable data rules out comparative

investigation to some degree, I am nonetheless able to investigate the patterns evident for the different groups.

Following this general introductory chapter, each chapter has its own introduction and literature review, specific to the questions considered in that chapter. Chapter 2 serves as a brief review of southern African marine biogeography, followed by a brief general methods section. The results for the updated and restructured Awad *et al.* (2002) data, which now includes the Namibia and Mozambique regions, are presented and discussed. Endemism is defined as species that are only found in southern Africa (from the Cunene River in Namibia to Ponta da Barra Falsa in Mozambique). This extension results in the inclusion of a greater section of the temperate, tropical and sub-tropical regions along both coastlines of southern African. Although gaps in our knowledge of species distribution pattern increase northward of the South African borders, I hope to show a clearer picture of regional patterns. Secondly, as noted above, the patterns determined by Awad *et al.* (2002) showed inflated values for range-restricted species at the borders, because these areas included species with the tail end of their distribution range extending into South Africa. By establishing the worldwide distribution status and investigating biogeographic affinities of these species I was better able to understand the observed distribution patterns. While I investigated species richness for all the groups along the southern African coastline, I am aware that this is a re-examination of the analysis that Awad *et al* (2002) performed. I, however, considered this an important and necessary starting point considering the additions to the data set. Biogeographic affinities have been examined for some of the groups in the original references and the purpose of this study is to use them to examine and explain the patterns so revealed.

Chapter 3 deals with range endpoints, range size distribution, endemicity patterns and range-restricted species within the southern African marine invertebrate fauna. Biogeographic breaks are associated with changes in environmental conditions in marine ecosystems and are often associated with the range endpoints of species. Distribution patterns of South African marine invertebrate species have shown strong peaks in species richness at the biogeographic breaks determined by Emmanuel *et al.* (1992). Peaks of species diversity manifested as a function of beta diversity for Port Elizabeth, Durban and to a greater degree the Cape Peninsula, were evident. Thus species peaks are correlated with high species turnover or range end points.

Chapter 4 considers latitudinal patterns in range and animal size of marine invertebrate species. A vast number of hypotheses have been put forward to account for changes in species richness. Palmer (1994) listed 120 named hypothesis for variation in species richness or coexistence, while Rohde (1992) identified 28 theories that specifically applied to latitudinal gradients. "Rapoport's Rule" has been proposed as a potential explanation for latitudinal, bathymetric and elevational diversity gradients. This rule states that the mean latitudinal range of species decreases towards the equator (Roy *et al.* 1994). The increase in species richness with decrease in latitude evident for numerous groups led Stevens (1989, 1992) to propose that richness can be explained by small ranged "accidental species" that maintain high species richness through the "Rescue Effect" at low latitudes.

Latitudinal gradients or patterns of species richness in marine fauna are evident and varied. It has been found, that species richness for some northern hemisphere (Fischer 1960, Roy *et al.* 1996, 1998) and southern hemisphere (Buzas *et al.* 2007) marine taxa increases towards the equator, whereas species richness for amphipods, for example,

decreases (Griffiths 1976), while polychaete and nematode richness shows no latitudinal trend (Gobin and Warwick 2006). The rule does not generally apply to marine teleost fish (Rohde *et al.* 1993). For marine invertebrates, Rohde (1999) noted that the dispersal abilities of many marine invertebrates are likely to be greater at low rather than high latitudes, suggesting an opposite effect to that proposed by Rapoport's Rule. Roy *et al.* (1994) found that eastern Pacific marine molluscan species did not conform to Rapoport's Rule, but instead species diversity gradients and range magnitudes varied independently with spatial distribution of major oceanographic barriers, exerting a strong influence on latitudinal ranges. The hypotheses reviewed by Rohde's (1992), in an attempt to explain latitudinal gradients, included explanations based on the assumption that some taxa have greater diversity in the tropics. Others were supported by insufficient evidence, such as consistent correlation between species diversity and environmental stability, environmental predictability and productivity. It was concluded that greater species diversity was due to greater "effective" evolutionary time in the tropics, probably as a result of shorter generation times, faster mutation rates, and faster selection at higher temperatures (Rohde 1992). A further review of latitudinal gradients in species diversity concluded that latitudinal gradients in species diversity result from a gradient in effective evolutionary time, modulated by several other factors (Rohde 1999). It is not within the scope of this thesis to prove or disprove these theories; I merely attempt to elucidate the patterns for southern African invertebrates.

The distribution of marine invertebrates along the coast of South Africa is controlled by physical, chemical and physiological parameters (Dingle 1995, see Chapter 4 for a full discussion). Changes in distribution patterns of marine organisms seems to be more sensitive to physical processes, such as currents, on early life history stages than to

biological interactions (Hockey and Branch 1994). The marine environment, with its steep physical gradients, favours the existence of a planktonic larval stage for most species (Féral 2002). The majority of marine organisms (60 %) practicing external fertilisation and yielding free-swimming larval stages with greater potential for wide-spread dispersal (Day 1974, Hockey and Branch 1994). Dispersal, thus, generally occurs at the juvenile stage (Thorson 1946, Mileikovsky 1971, Strathmann 1985, Graham and Branch 1985). Marine invertebrates were categorised according to different reproductive traits and ranges of these groups were compared. It is hypothesized that South African marine invertebrates with pelagic development stages will have larger geographic ranges than those with non-pelagic developmental stages. Chapter 4 deals with latitudinal patterns in developmental mode and how this mode affects dispersal ability.

Finally Chapter 5 presents a summary of the results and conclusions obtained from the preceding chapters.

CHAPTER 2

BIOGEOGRAPHICAL PATTERNS OF SOUTHERN AFRICAN MARINE INVERTEBRATES REVISITED

INTRODUCTION

Cox and Moore (1993) defined biogeography as the study of biological life in a spatial and temporal context, with respect to the analysis and explanation of these patterns for a given area. Biogeographic studies are imperative, as they provide the knowledge required to ensure effective evaluation of existing conservation areas and information for future conservation efforts.

In order to adequately protect marine species, a representative set of species for each habitat type needs to be protected in each biogeographic region identified (Butchart *et al.* 2005, Sink *et al.* 2005). The geographic range of a species is the basic unit of biogeography (Brown *et al.* 1996).

This greater prospective for wide-spread dispersal in marine species is a result of the free-swimming larval stages of many marine invertebrates and the ubiquitous property of water, which ensures efficient transport and dispersal. It is thought that larval dispersal may result in species that have large geographic ranges (Féral 2002), reducing the likelihood of extinction (for review see Chown and Gaston 2000, Angel *et al.* 2006).

Species distribution patterns for South African marine species are relatively well known for a number of groups. Offshore groups analysed include euphausiids, zooplankton and fish (Gibbons *et al.* 1995, Gibbons and Hutchings 1996, Turpie *et al.* 2000). Inshore groups include molluscs, amphipods, opisthobranchs, isopods, crustaceans, octocorals, echinoderms, polychaetes, sea anemones and ascidians (Kensley 1978, Barnard 1950, Day 1967a, b, Griffiths 1976, Clark and Courtman-Stock 1976, Kilburn and Ripey 1982,

Gosliner 1987, Thander 1989, Williams 1992, Monniot *et al.* 2001, Acuña and Griffiths 2002, Primo and Vázquez 2004). The distribution patterns of these groups have been used to establish biogeographic zonation patterns along the southern African coastline (Emanuel *et al.* 1992, Field and Griffiths 1991).

Biogeographical breaks along the coastline have proven to be a contentious issue. The boundaries between zones, the existence of ecotones or overlap areas, as well as the similarity between each region, differ markedly for different taxa analysed. These disparities have been attributed to differences in the methods of analysis, sampling effort employed, ocean depth covered, extent of coast covered and conflicting opinions on definitions of overlap regions (Lombard 2004).

Based on the physical oceanographic characteristics and distribution of intertidal species, early biogeographers divided the southern African coast into three major biogeographic regions; the cool temperate West Coast Province, the warm temperate South Coast Province and the subtropical East Coast Province, each with an associated suite of organisms (Ekman 1953, Stephenson and Stephenson 1972) (Figure 2.1). These three regions have subsequently been confirmed with intertidal studies (Emanuel *et al.* 1992, Bustamante and Branch 1996). Coastal fish distribution patterns also reflect the same three biogeographic provinces (Turpie *et al.* 2000). However, taxon-specific studies have shown that the exact location of these breaks varies, depending on the taxonomic group analysed (Day 1967 a, Griffiths 1976, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992) and on the depth range studied. Day (1967 a), for example, showed that break points differ in deep versus shallow species, as one might expect, as there is little temperature difference between biogeographic zones in the deeper regions.
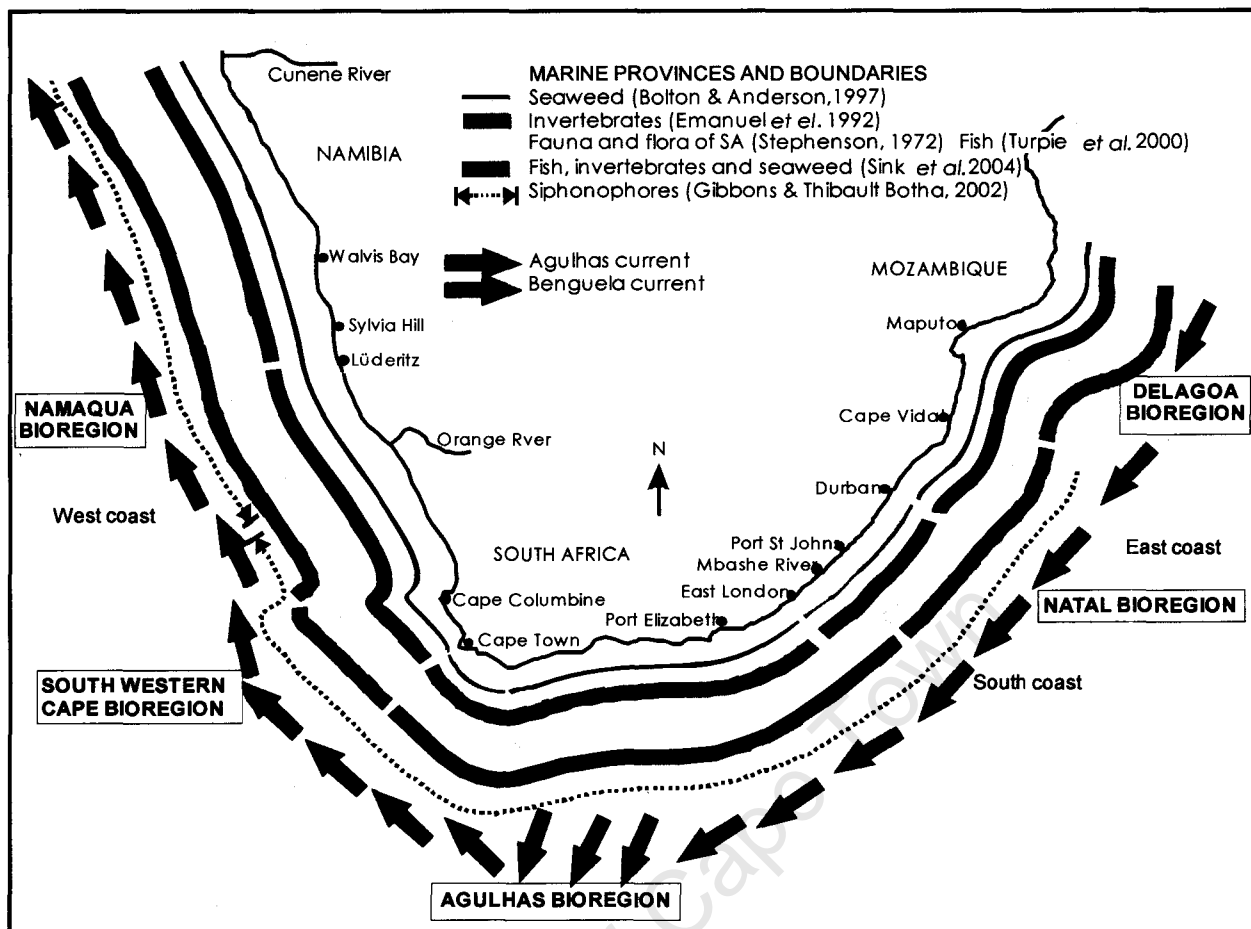
Figure 2.1 Coastline of southern Africa showing the biogeographic zones and breaks for various taxa. Bioregion names are derived from Lombard (2004).

A further division of the cool temperate west coast at Lüderitz and the subtropical east coast at Durban was proposed for invertebrates (Emanuel *et al.* 1992). This analysis separated the west coast into the northwest Namib Province and the southwest Namaqua Province, while the east coast was divided into a northeast and a southeast Agulhas subtropical area (Figure 2.1) (Emanuel *et al.* 1992). In addition to these qualitative studies, a quantitative study has confirmed the west coast, east coast and south coast biogeographic region as separate regions (Bustamante and Branch 1996).

Seaweed data showed a division into two major biogeographic zones; a warm temperate zone with a west and south coast components and a subtropical east coast component

(Stegenga *et al.* 1997), (Figure 2.1). An overlap region at the southern portion of the Cape west coast extended from Cape Point to Cape Agulhas, where both West and South coast species reach their limits (Stegenga *et al.* 1997). Seaweed compositions north of Cape Vidal on the east coast are mostly tropical Indian Ocean species. South of Cape Vidal the seaweed composition shows a gradual overlap with the Agulhas bioregion species and Sub-Tropical Indian Ocean species (De Clerck *et al.* 2005).

Recent investigation of rocky intertidal species in KwaZulu-Natal (Sink *et al.* 2005) showed a similar break, dividing the east coast into a tropical and sub-tropical region at Cape Vidal. An additional break has been recognized at Cape Columbine along the cool temperate Namaqua Province, dividing this region into the Northern Namaqua Sub-province and the South Western Cape Sub-province (Engledow *et al.* 1992, Bolton and Anderson 1997). Tropical West and East Coast Provinces have been identified, starting in southern Angola and central Mozambique respectively (Penrith and Kensley 1970, Kensley and Penrith 1973, Bolton and Anderson 1997).

A recent workshop to determine biogeographic breaks along the coast synthesized all existing studies and examined factors that could influence breaks, such as oceanographic and geophysical features, as well as ecological processes that could underlie biotic patterns (Lombard 2004). Using this information and input from field experts, five inshore bio-regions were determined. The Namaqua Bioregion extending from Sylvia Hill in Namibia to Cape Columbine, the South Western Cape Bioregion extending from Cape Columbine to Cape Point, the Agulhas Bioregion extending from Cape Point to the Mbashe River in the Transkei, the Natal Bioregion covering the area from Mbashe River to

Cape Vidal and finally the Delagoa Bioregion that extends North of Cape Vidal into Mozambique (Lombard 2004).

The original invertebrate data collected by Emanuel *et al.* (1992) was utilised to examine the effectiveness of marine reserves on the west coast and to determine biogeographic zones. Awad *et al.* (2002) added endemicity data and investigated marine invertebrate diversity patterns along the South African coast, with the aim of highlighting potential reserves, that would adequately conserve biodiversity. Awad *et al.* (2002) restricted their study to the politically-defined borders of South Africa, resulting in the definition for endemism being constrained to include only "politically" defined endemic species. Small-ranged species restricted to the northern limits of the coastline were thus classified as non-endemics. Additionally, species with only their southern-most point of distribution penetrating the borders were considered restricted, which is clearly not the case. Sharp political delimitations of regions under investigation impose artificial borders that have no ecological significance.

As species diversity north of South Africa was not examined by Awad *et al.* (2002). I briefly examine the diversity patterns for species that are found in a wider southern African region, including Namibia to Ponta da Barra Falsa in Mozambique as a starting point for this chapter. By expanding the region to include the Namibian and Mozambique sections of the coastline, temperate and sub-tropical regions can be examined as well. The definition for endemism is changed to include species found exclusively in the defined area. Moving the borders to include a larger section of the coastline may perpetuate the problems highlighted by Awad *et al.* (2002). However, the extension of the study region results in the inclusion of a broader representative section of the coastline, with tropical to

temperate species being included. As a result I hope to get a clearer picture of the distribution patterns invertebrates along the coastline. As these data have been investigated before, I include only a very brief discussion outlining some new developments. In an attempt to understand the importance of species richness at the borders of the study area I investigated biogeographic affinities of species as well.

Perhaps one of the oldest and most debated issues in ecology refers to the latitudinal increase in species diversity towards the equator (Stevens 1989, Barbour et al. 1987, Willig et al. 2003). While the pattern holds true for numerous taxa, there are many exceptions, notably marine molluscs, polychaetes and sponges (for example see Astorga et al. 2003, Valdovinos et al. 2003). Identifying and interpreting the forces that forge this spatial variation of species diversity along latitudinal gradients remains a controversial and largely unresolved issue. Gradients in temperature, stress, productivity, competition, predation, stability (Barbour et al. 1987, Taylor and Gaines 1999, Willig et al. 2003, Gaston 2007) and recently gradients in effective evolutionary time (Rohde 1999), biogeographic boundaries and endemism (Macpherson 2003), have been ascribed as causal. However, in many cases there are exceptions that do not follow the trend.

Species diversity patterns for southern Africa have been investigated as areal richness along the coastal belt. Comparative biogeography conventionally investigates these patterns along latitudinal gradients. To facilitate comparison with previous studies I converted areal data to latitudinal data. It is my aim for this chapter to determine what the latitudinal patterns are for southern African invertebrates, and to speculate on the causal mechanism.

METHODS

Species richness data

For the purposes of this study, southern Africa was defined as the region south of the Cunene River in Namibia to Ponta da Barra Falsa in Mozambique, thus including Namibia, South Africa and southern Mozambique. Species were categorised as endemic if they were found only in this region and nowhere else. Data recording presence or absence of species, in 48 successive 100 km units, off the southern African coastline (Figure 2.2) were used for this analysis. The vertical range covered included the intertidal and sub-tidal region to a depth of 15 m. The units corresponded to those used by Emanuel *et al.* (1992) and Awad *et al.* (2002). The section of coastline previously examined by Awad *et al.* (2002) included units 15 to 42 of the defined area. This study added units 1-14 and 43-48, thus any changes in species richness would be visible at the front and tail ends of the area being examined. Some additional species, previously missed, were also added, resulting in possible changes in overall patterns. The data were updated to include species found in Mozambique and Namibia and endemicity status was adjusted using available literature sources (Day 1967a, b, 1974, Griffiths 1976, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992, Monniot *et al.* 2001). Endemism was added for brachyurans (Winks Emmerson, personal communication).

Eleven groups of marine invertebrates, comprising a total of 2659 species, were examined. The dataset was compiled from records of the South African Museum, surveys made by the University of Cape Town and from literature sources (Day 1967a, b, 1974, Griffiths 1976, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992, Monniot *et al.* 2001). The groups used for this analysis were octocorals, chitons, bivalves, opisthobranchs, prosobranchs, amphipods, isopods, brachyurans, polychaetes,

echinoderms and ascidians. These groups were chosen for consistency with past studies (Emanuel *et al.* 1992, Awad *et al.* 2002), and the taxonomic level of the available data. The nature of the available data results in a comparison across different taxonomic levels. However, this enabled me to investigate the highest resolution possible for the current data set. Endemicity data were updated to include the broader definition used here. A total of 121 new species were added. Species were removed from the data set if endemicity status, or distribution in Namibia and Mozambique were not known, most notably for some gastropods and bivalves.

Available distributional data for invertebrate species along the coastline are not complete. Species found in more than one unit, at irregular sites along the coastline were assumed
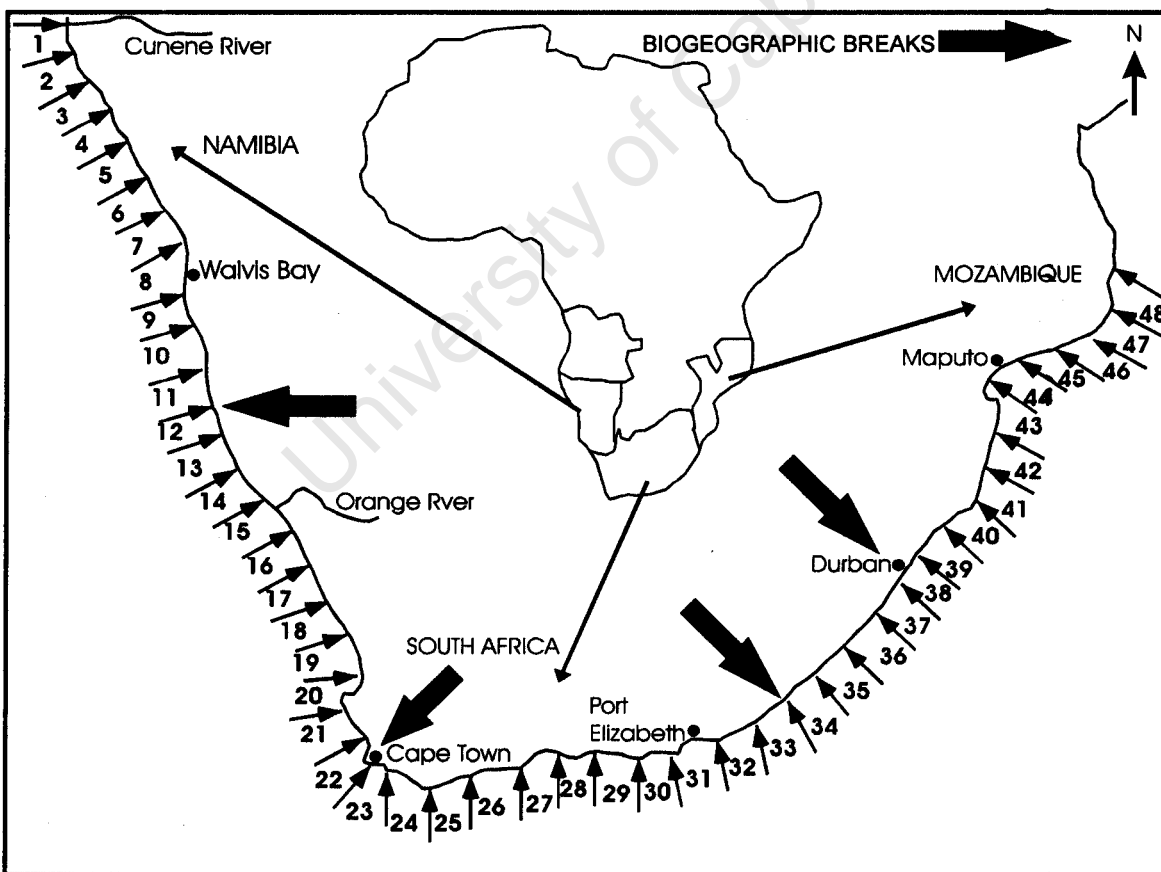

Figure 2.2 Coastline of southern Africa showing the 48, 100 km intervals used for the analysis, as well as the position of invertebrate biogeographic breaks.

to have continuous distribution. It was also assumed that suitable habitat was present in each of the 100 km zones between the two limits of occurrence. If a species found within the study area was thought to represent the southernmost point of that species's greater, worldwide distribution, the range was extended to the northern-most limit of the study area, again assuming that distribution was continuous throughout the range. Species with distributions throughout the Indian Ocean, the Indo-Pacific Oceans, the Atlantic, or widespread tropical and cosmopolitan species were handled in this manner. Species richness patterns were determined for marine invertebrates for the entire southern African region. Species richness was defined as the number of species that occurred within a single unit along the coastline.

Latitudinal richness data

The existing data points for each unit were converted to latitudinal data points and latitudinal species richness was determined for all invertebrates. Latitudinal species richness was defined as the number of species that crossed a band of latitude, computed to the nearest degree of latitude, along the coastline. Units that fell into the same latitudinal band were lumped together. In order to determine whether the patterns on the two coasts showed similar or different trends in species diversity across latitude, the west and east coast data were kept separate. The west coast was defined as species found in units 1 - 22 and the east coast included all species found in units 23 - 48 (Figure 2.2). The number of 100 km units was the same for each badn of latitude examined, to correct for this bias, I plotted a graph showing the average number of species for the units in each latitudinal band.

Biogeographic affinities

Distributional affinities where established from available literature for all the groups (Day 1967a, b, 1974, Griffiths 1976, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992, Monniot *et al.* 2001). Each species was categorised in one of the following biogeographical groups, based on their distribution:

> ➤ Endemics (E): Species found only within the region south of the Cunene River in Namibia to Ponta da Barra Falsa in Mozambique.

> ➤ Atlantic/West African (A/WA): Atlantic species, or species found along the West coast of Africa.

> ➤ Indo-Pacific (IP): Species found within the defined study area, with distribution extending into the Indo-Pacific region.

> ➤ Cosmopolitan: Species with worldwide distribution.

> ➤ Tropical species (T): Species only present in tropical waters

> ➤ Non-endemic (NE): Species with patchy or range-restricted distribution, within southern Africa, but not endemic to this region. The non-endemic category is a rather spurious grouping that lumps together the "left over" species, as it were. These are species that are found within the defined borders, as well as other parts of the world. Some of these species may in fact be cosmopolitan with continuous, as yet uncharted distribution, while others may be accidental introductions, cryptic or mis-identified species, but nonetheless need to be included.

The results were plotted for each group to show the change in biogeographic affinity of component species along the coastline, according to the 100 km units described.

RESULTS

Areal species richness

Awad *et al.* (2002) data set: Species richness and endemicity patterns along the southern African coastline for the 11 groups examined are shown in Figure 2.3. Peaks in species richness were found at the three biogeographic breaks (Cape Point, unit 22; East London, unit 33 and Durban, unit 38) for isopods, echinoderms, chitons, octocorals, bivalves, opisthobranch and prosobranch-gastropods and for all the fauna combined. Amphipods and polychaetes had richness peaks at all the breaks, except for Durban and East London respectively. Brachyurans and ascidians richness peaks occurred only at Cape Point and Durban. In addition to these peaks there were peaks at St Lucia (unit 41) for polychaetes, opisthobranchs and octocorals.

Along the west coast at Torra Bay (unit 6), species richness increased by 30 % for polychaetes. The Lüderitz region (unit 12) showed clear peaks in richness for isopods, echinoderms, amphipods, brachyurans, opisthobranchs (to a lesser degree) and the whole group's distribution. Polychaetes showed a peak at unit 11. Richness also peaked at Kosi Bay (unit 42) for ascidians and isopods, and at Baia De Maputu (unit 43) for amphipods, echinoderms and brachyurans. Species richness appeared to plateau along the Mozambique coastline and plateaud, or showed a gradual decrease northward, along the Namibian coastlines for all groups except octocorals. This group showed a sudden drop in species richness at units 42 and 43, followed by a peak of non-endemics.

Endemicity for all the groups combined more than doubled from 26 % endemicity found by Awad *et al.* (2002) to 54 % found here (Table 2.1). Octocorals, chitons, polychaetes,
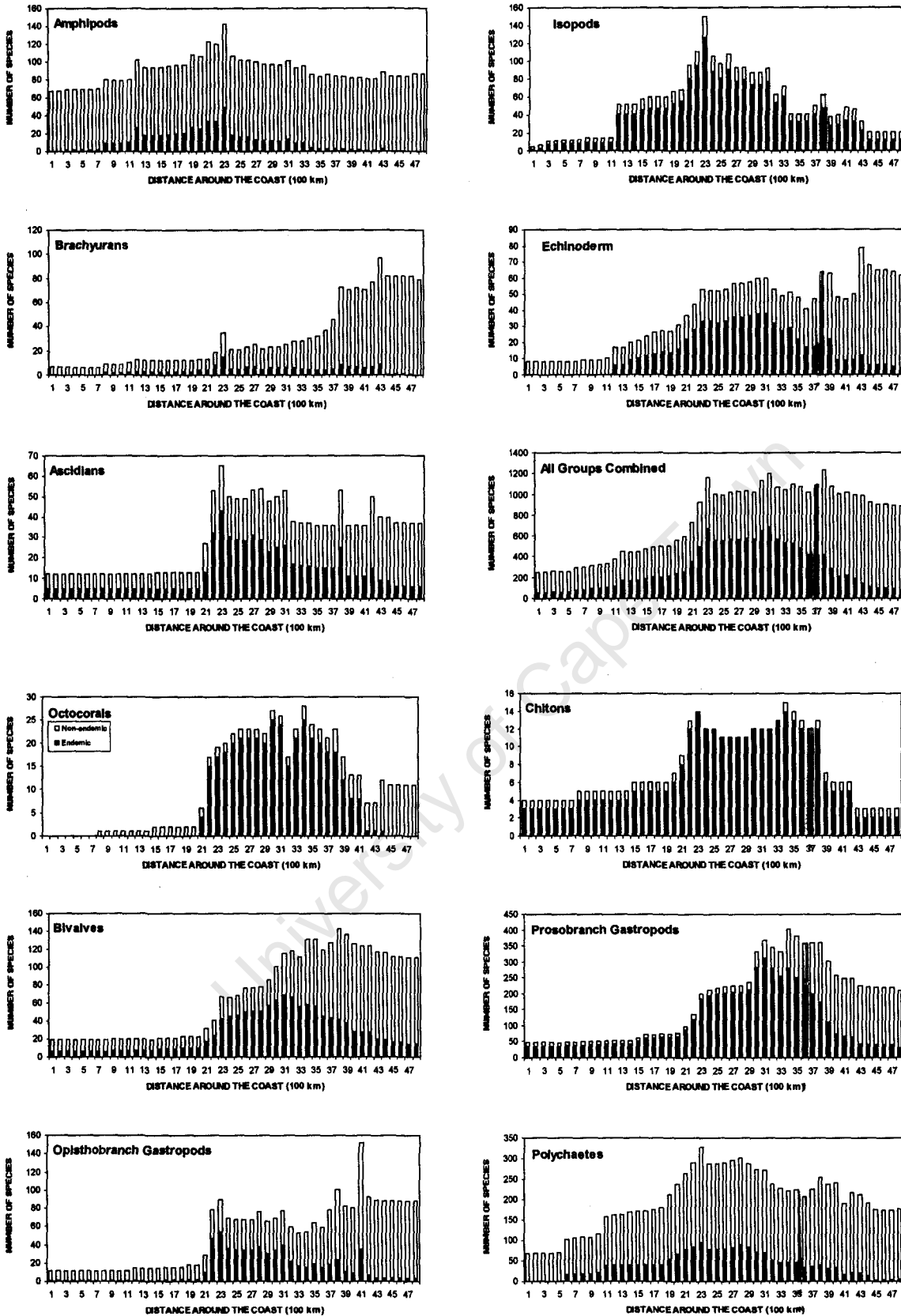
Figure 2.3: Distribution for invertebrate groups showing non- endemic species richness (white bars) and endemic species richness (black bars) along the southern African coastline.

echinoderm and ascidians endemicity increased notably, thus contributing most to this change. The proportion of endemic echinoderm species more than doubled from 19 % to 44 %. Prosobranch gastropods and polychaetes endemicity increased from 62 % to 70 % and 21 to 34 % respectively. These two groups represent the groups with the greatest number of species and would thus have the greatest affect on overall endemicity. The number of endemic chitons increased from an already high 78 % to 92 %, while octocorals endemicity increased from 30 % to a staggering 81 %. The figure for these groups has little effect on the overall endemicity, as they only have 25 and 68 species respectively. Interestingly, though, some group's endemicity remains the same or even decline.

Table 2.1: The percentage endemism for all the groups analysed in the Awad *et al.* (2002) study compared to the new updated data.

Group name	Awad *et al.* (2002)	This study
	Percent endemic	Percent endemic
Octocorals	30	81
Chitons	78	92
Bivalves	45	45
Prosobranchs	62	70
Opisthobranchs	48	48
Polychaetes	21	34
Amphipods	40	40
Isopods	84	84
Brachyurans	Not completed	24
Echinoderms	19	44
Ascidians	54	64
All groups	26	54

Latitudinal species richness

Figure 2.4 shows species richness expressed in terms of the latitudinal gradient. Investigation of all the groups combined showed that species richness increased with increasing latitude along both coastlines. Diversity was notably higher on the east and south coast, compared to the west coast. The east coast richness peak at 29 °S represents the Durban biogeographic break, where richness reaches 1200 species. The

34 °S peak of 1500 species, represents 800 km of south coast falling along the same latitude, and also includes the species-rich Cape Point biogeographic break. For both coastlines, richness increases sharply between 25 and 26 °S and again at 32 to 34 °S. In each of these cases a number of units on the same latitude were lumped together.

Prosobranch gastropods, polychaetes, isopods, amphipods and to some degree bivalves, show an increase in richness with latitude on both coasts. Octocorals, chitons, opisthobranchs, brachyurans, echinoderms and ascidians all show an increase in diversity with latitude for the west coast, but for the east coast, very little change occurs until 27 °S (just south of Mozambique), where opisthobranch richness spikes and all the other groups dip, richness continues to decrease until 32 °S (The Wild Coast) and then increases again for all groups.

The number of 100 km units is not equal for each degree of latitude examined, especially the higher latitudes. To correct for this bias, I included figure 2.5 to show the average number of species for the units in that latitude. The latitudinal increase along the west coast shows very clearly, while the east coast shows no trend at all.

Biogeographic affinity

The biogeographic affinities for each group are highlighted in Table 2.2. This table shows the distributional affinities of species, expressed as a percent of the total number of species found in southern Africa for each defined group. The percent composition of endemics was the largest component for all groups, except brachyurans and polychaetes, where non-endemics and Indo-Pacific's dominated. More than 80 % of chitons, octocorals
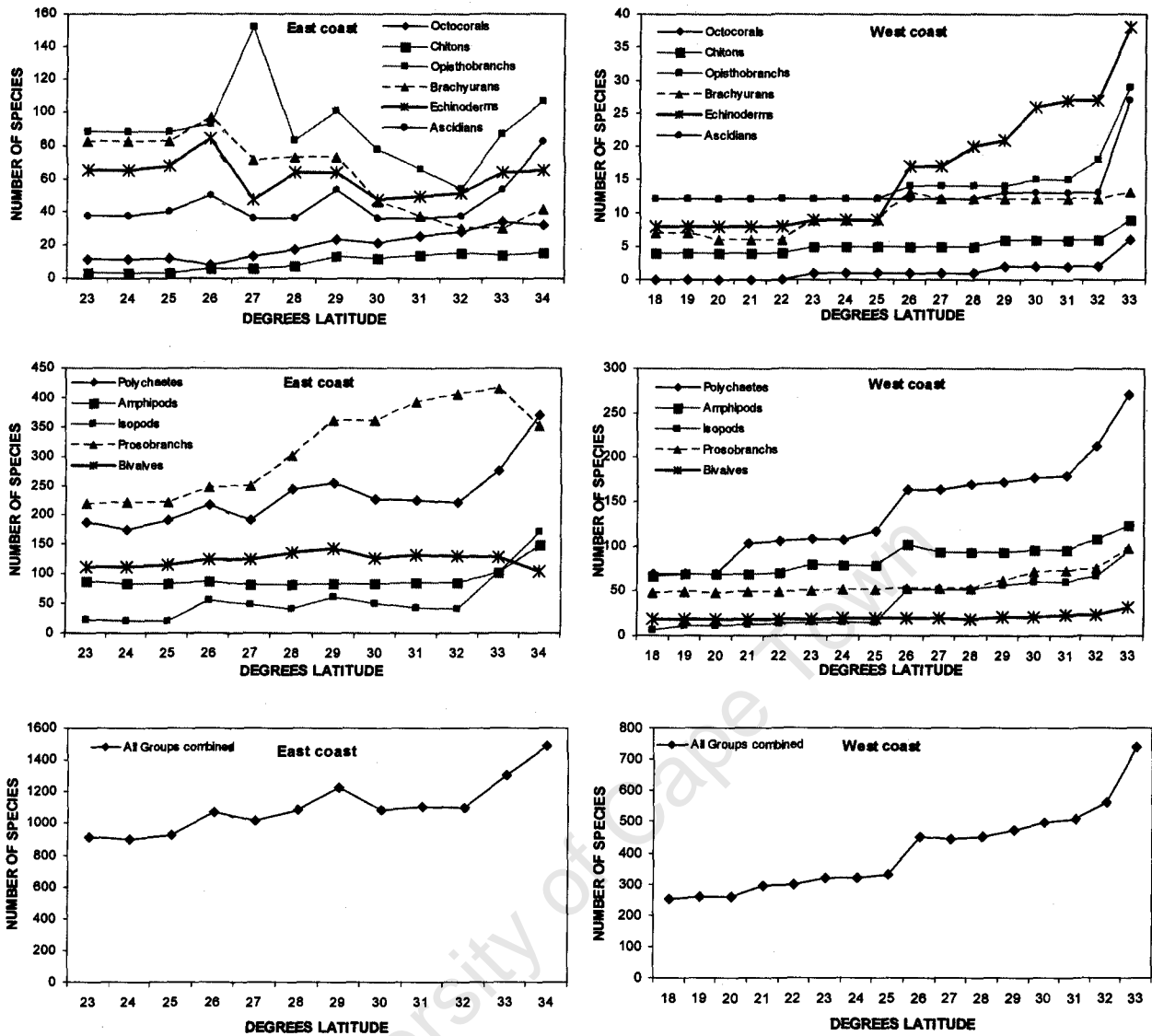
Figure 2.4: Latitudinal invertebrate species richness gradients along the west and east coast of southern Africa
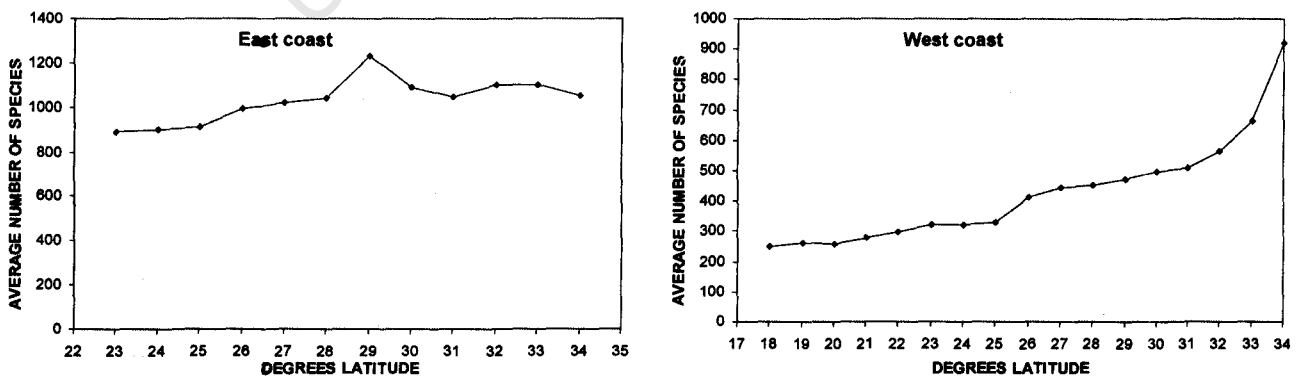

Figure 2.5: The average number of species for the unit found in each latitude.

and isopods were endemic. The Indo-Pacific and tropical biogeographic category represented the second most species-rich distributional affinity for most of the groups. Polychaetes, opisthobranchs and ascidians also had a large component of non-endemic range-restricted species (species with scattered distribution).

Table 2.2: Comparison of the biogeographic affinities of species, expressed as a percent of the total number of species found in southern Africa for each group

	Octocorals	Bivalves	Opisthobranchs	Chitons	Prosobranchs	Polychaetes
Atlantic	0	4	0	0	1	5
Endemic	81	45	48	92	69	31
Indo-Pacific	15	21	16	4	16	5
Cosmopolitan	1	1	3	0	1	8
Non-endemics	1	13	23	4	3	41
Tropical	1	18	9	0	10	9
Total	100	100	100	100	100	100
	Amphipods	Brachyurans	Ascidians	Isopods	Echinoderms	All Groups
Atlantic	11	2	1	1	3	3
Endemic	39	24	63	83	43	53
Indo-Pacific	12	53	4	0	7	13
Cosmopolitan	23	4	5	0	2	5
Non-endemics	8	14	16	15	19	17
Tropical	8	4	10	0	26	9
Total	100	100	100	100	100	100

Figure 2.6 shows the distribution of species, along the southern African coastline according to their biogeographic affinities. Endemic species consistently formed the largest component for all the groups except brachyurans, and to lesser an extent polychaetes. The peaks in the total number of species along the coastline (Figure 2.3) are reflected in the peaks in number of endemics for most groups. For brachyurans, which are dominated by Indo-Pacific species (53 %), the distribution pattern of this group reflected the Indo-Pacific distribution pattern. The endemic and "non-endemic" component was pronounced for polychaetes, with these two biogeographic affinities representing 49 % of the species in these groups. Again, this was reflected in the overall distribution pattern. The biogeographic affinity pattern for amphipods reflected the endemic component throughout

the coastline. In addition to this, a large component of cosmopolitan amphipods occurred throughout the study area.

The number of Indo-Pacific species in each unit along the coastline began to decrease markedly at Baia De Maputo (unit 43) for opisthobranchs, octocorals and brachyurans and then again at Durban (unit 38) for bivalves, octocorals, opisthobranchs, brachyurans and prosobranch gastropods. The number of Indo-Pacific species for each of these groups represented the second largest component, biogeographically. The southernmost limit for the majority of Indo-Pacific species appeared to be Cape Point, although they began decreasing in numbers in a stepwise fashion before this point.

The trend for tropical species followed a similar pattern, with a sharp decrease at Baia De Maputo (unit 42) for echinoderms (less so for polychaetes and ascidians) and again at Durban (unit 38) for ascidians, echinoderms and bivalves. The overall pattern for tropical species for all the groups showed a gradual decrease, with the majority of tropical species reaching no further than Cape Point.

Species that were not endemic to southern Africa, but had a patchy distribution within the defined boarders (NE), seemed to follow the same distribution patterns shown by endemic species. This was true for all the groups with a strong representation of range-restricted non-endemic species (opisthobranchs, bivalves, polychaetes and to a lesser degree brachyurans and echinoderms).

The patterns described above reflect changes in distribution along the southern African coast for all the groups except amphipods; this group had a strong endemic (39 %) and
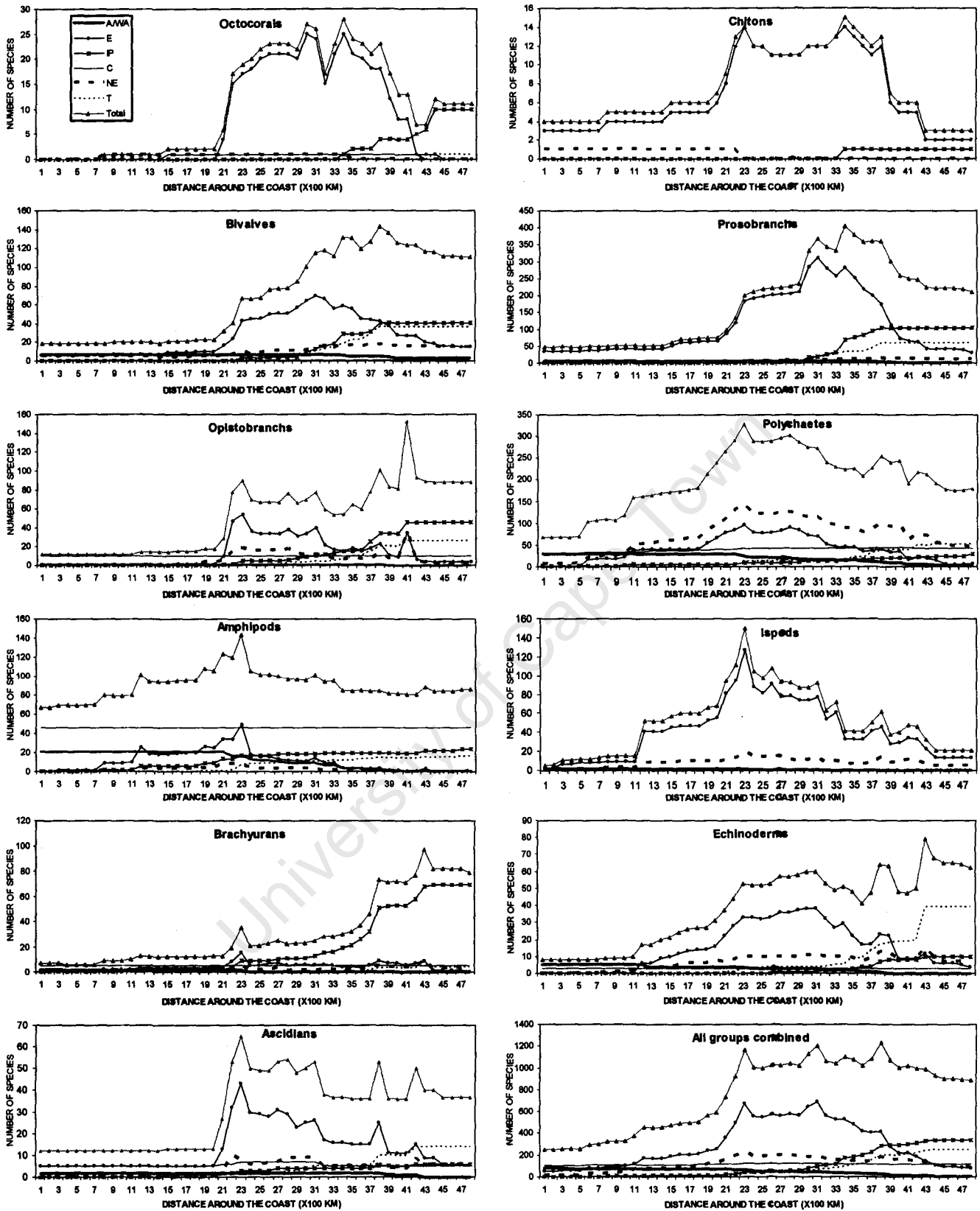
Figure 2.6: Dominant biogeographic affinities of marine invertebrate species along the southern African coastline. A/WA - Atlantic or west African, E - Endemic, IP - Indo Pacific, C - Cosmopolitan, NE- Non-endemic, T-Tropical.

cosmopolitan component (23 %), which dominated the distribution patterns (Table 2.2). For this group the Indo-Pacific and tropical components gradually decreased, with no sudden loss of species and only reached the limit of the distribution in any real way at Cape Point. The pattern evident for all the groups combined reflected those found for polychaetes and prosobranch gastropods, as these two groups were the most abundant.

Figure 2.7 shows biogeographic affinity (as a cumulative percent) of all the faunal groups combined. As expected, endemic species formed the largest component of species in the centre of the study area and thined out towards the boundaries. The percent contribution of endemics was skewed to the west relative to the east coast. Indo-Pacific species composition gradually tapered off from east to west, while tropical species ended sharply at Cape Point. The cosmopolitan component was greatest on the west coast, where more than 40 % of the species composition had a worldwide distribution (dominated by amphipods). The Atlantic West African component was greatest in the west coast, dropping markedly at unit 5, Lüderitz and Cape Point.
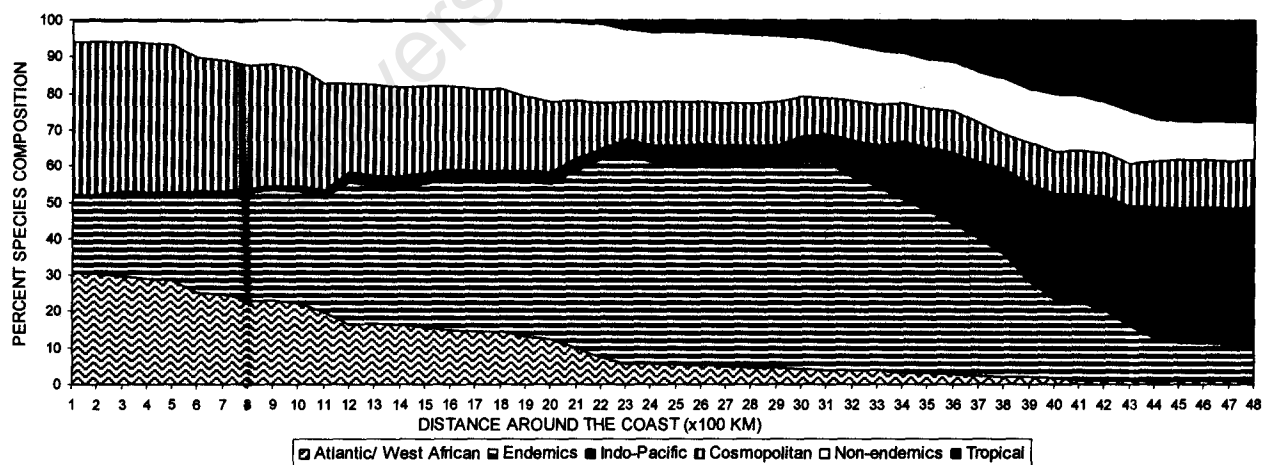

Figure 2.7: Dominant biogeographic affinities of all marine invertebrate species combined along the southern African coastline expressed as cumulative percent contribution.

DISCUSSION

Areal species richness

Globally, southern Africa is recognized as a region of high taxonomic diversity, as well as endemism, for both terrestrial and marine ecosystems (Driver *et al.* 2005). This biodiversity "hotspot" spans tropical, sub-tropical and temperate oceans, with two contrasting currents flowing along opposite shores of the continent. Biogeographic studies documenting species richness and biogeographic patterns of marine biota (Turpie *et al.* 2000) and invertebrates in particular (Barnard 1950, Day 1967a, b, Griffiths 1976, Clark and Courtman-Stock 1976, Kensley 1978, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992, Gibbons *et al.* 1995, Gibbons and Hutchings 1996, Acuña and Griffiths 2002, Primo and Vázquez 2004) have been, and continue to be, a priority.

Species richness for southern African invertebrates, as documented here, followed patterns previously found (Awad *et al.* 2002); with peaks in richness corresponding to biogeographical breaks in the regions formerly examined (unit 15 – unit 42). Biogeographical breaks are often areas of increased richness, as two different bioregions overlap, resulting in species from both zones occurring in the same geographical location, thus elevating diversity (Emmanuel *et al.* 1992, Gibbons *et al.* 1999, Bolton and Stegenga 2002). There are also many range-restricted species that only occur at these ecotones, as shown by Awad *et al.* (2002).

The new study area showed similar results (units 1-14 and units 43-48), with peaks in richness along the west coast corresponding to biogeographical breaks (for some groups). Beta diversity, or change in species composition around Lüderitz, a documented

biogeographical break (Emanuel *et al.* 1992), showed a loss or gain of 46 species at unit 11, and 90 at unit 12. The elevated diversity in units 42 and 43 is likely a reflection of the presence of large bay habitats in these units; generally, sheltered sections of the coastline have been shown to be more diverse than unsheltered regions (Bustamante and Branch 1996)

The sudden increase in polychaete richness at unit 6 reveals the limit of the endemic species distribution for this group (Figure 2.6). Successful fertilization and larval development for some polychaetes is limited to a narrow salinity and temperature range (Ushakova and Sarantchova 2004). Unit 6 comprises both the Groen River mouth and Torra Bay. Both may act as abiotic factors limiting distribution of endemics here. Sampling intensity of polychaetes is high (Gibbons *et al.* 1995), ruling out sampling artefact as a cause for the change in richness in this region (Awad *et al.* 2002).

Not many notable changes in patterns appeared to result from the extension of Indo-Pacific, tropical and cosmopolitan species distribution, as well as the addition of the new sections of coastline. The increase in the number of endemics in each group was a consequence of the larger area of endemism defined for this study, and the fact that species that were previously classified as non-endemic, as they occurred in both South Africa and the neighbouring countries, were reclassified as endemics, under the broader definition used. As a result endemicity for invertebrates more than doubled. At 24 %, Awad *et al.* (2002) referred to the endemicity as artificially high. The new figure of 54% is staggering, but nonetheless comparable to, for example, southern Australian decapod and echinoderm endemicity (56 % endemic), (O' Hara and Poore 2000).

Studies leading to a better understanding of biodiversity, endemism, and environmental factors affecting these patterns, provide vital information, most importantly for the selection and management of conservation areas around South and southern Africa (Siegfried and Hockey 1985, Hockey and Branch 1994, Turpie *et al.* 2000, Awad *et al.* 2002, Roberts *et al.* 2003). Despite continued efforts, our knowledge remains, for the most part incomplete within the southern African region (Gibbons *et al.* 1999) and is dismal further north along the African coastline (Griffiths 2005, Bolton *et al.* 2007). As a result the high levels of endemism found for marine invertebrate species may in fact be an inflated misrepresentation, with species thought to be endemic, actually only representing the southern-most end of their distribution along the African coastline.

While this may be the case, with some Indo-Pacific and tropical species being mis-classified as endemic, it is not likely the norm. The inferred high levels of endemism apparent in southern Africa (Turpie *et al.* 2000, Awad *et al.* 2002, Procheş and Marshall 2002, Primo and Vázquez 2004) have been attributed to both its geographical isolation and the effects of the current system (Procheş and Marshall 2002, Primo and Vázquez 2004). The Atlantic and Indian Oceans straddle the southern African coastline, while the Southern Ocean presents a distinct boundary south of the tip of Africa. The cooler temperatures and flow direction of the Benguela Current on the Atlantic west coast, and the Southern Ocean's cool temperatures, south of the coastline, inhibit dispersal twofold. The southward-flowing Agulhas Current inhibits range expansion northwards on the east coast, while carrying Indo-Pacific species southwards. Furthermore the insular nature of the marine provinces precludes dispersal at various points along the coastline (Emanuel *et al.* 1992), leading to the conclusion that the high levels of endemism indicated may be real.

Species richness decreased towards the northern borders of the study region for all the groups investigated. Again the lack of taxonomic studies north of South Africa, resulting in insufficient data to determine patterns, may explain these results. It is also possible that species diversity does decline northwards along these sections of the coastline. Studies documenting diversity along the Namibian coastline are few, but a number of biological collections have recorded invertebrate and seaweed species diversity as low, in keeping with the Benguela system (Sakko 1998). Species richness may only begin to increase as the sub-tropical waters of Angola are reached. Molluscs, for example, shows increased numbers in Angola versus Namibia (Sakko 1998). Very few tropical species found in Angola are able to survive the colder Namibian environment.

Species richness shows a similar decline along the east coast for some assemblages (Procheş and Marshall 2002), while other taxa show an increase in richness (Turpie *et al*.2000). The extensive (2700 km) and highly diverse Mozambique coastline (Griffiths 2005) may in fact show a clear increase in richness towards lower latitudes. The resulting systematic addition of new tropical species could progressively increase species richness towards the equatorial zones further north of our borders, corroborating the "universal" pattern of high diversity at low latitudes (Stevens 1989). This is an eventuality that only further investigation can elucidate.

Latitudinal species richness

The worldwide trend in species diversity for terrestrial and marine species shows a latitudinal decrease in species richness away from the equator for many taxa (Barbour *et al*. 1987, Stevens 1989, Cox and Moore 1993, Witman *et al*. 2004). For marine fauna in

the northern hemisphere, there is evidence for a decrease in species richness towards the poles for fish, foraminifera, and molluscs (including both gastropods and bivalves) (Fischer 1960, Roy *et al.* 1996, 1998). This pattern is true for foraminifera (Buzas *et al.* 2007) but opposite or asymmetrical for molluscs, polychaetes and demosponges in the southern hemisphere (Astorga *et al.* 2003, Valdovinos *et al.* 2003); with no pattern evident for sub-tidal polychaetes and nematodes (Gobin and Warwick 2006). A global investigation revealed a latitudinal decrease in richness in both hemispheres on a regional and local scale (Witman 2004). On smaller scales gradients in species richness are less clear (Okuda *et al.* 2009). Latitudinal diversity, measured as species richness for southern African species shows a marked tendency to increase in diversity towards the higher latitudes (Hockey and Branch 1994).

Individual taxa investigated, showed slightly different trends for the two coastlines. The tendency for richness to increase with latitude for prosobranch gastropods, polychaetes, isopods, amphipods and to some degree bivalves, is clear along both coasts. This is consistent with patterns found for southern hemisphere molluscs, polychaetes and sponges by Astorga *et al.* (2003) and Valdovinos *et al.* (2003), but contrary to results found for crabs and northern and southern hemisphere molluscs (Astorga *et al.* 2003, Fortes and Absalão 2004). Octocorals, chitons, opisthobranchs, brachyurans, echinoderms and ascidians all show an increase in diversity with latitude for the west coast, but for the east coast, very little change occurs until 27 °S, where opisthobranch richness spikes and all the other groups dip. Diversity continues to decrease until 32 °S and then increases again for all the groups. Polychaete diversity in this study showed a marked increase with latitude, along both coastlines. This is comparable to Chilean benthic polychaete diversity, which showed an increase towards southern latitudes (Hernández *et al.* 2005). The pattern

for the entire invertebrate assemblage combined shows species richness increases with increased latitude along the west coast but there is no real change along the east coast (Figure 2.5). Notably, current knowledge on distribution patterns of species increases towards higher latitudes along the southern African coastline as well.

Patterns in diversity have been related to, among other factors, range size, temperature tolerance, geometric constraints (mid-domain effect), competition levels, productivity, extinction rates, habitat diversity and biogeographic zone size (see Table 2.3 for complete list and description) (Zacharias and Roff 2001, for a synthesis see Willig *et al.* 2003, Fortes and Absalão 2004). In an attempt to consider the causal mechanism underlying the patterns found here, a discussion of a few select few mechanisms follows. The paucity of data collected in the correct format, prohibits proper empirical analysis of each hypothesis, and in this case restricts the discussion to a more superficial level, but nonetheless allows for a better understanding of the patterns found.

Table 2.3: Hypothesis for causal mechanisms underlying marine diversity patterns (Adapted from Zacharias and Roff 2001)

Causal Mechanism	Hypothesis (H)	Explanation
Area	Area H	Species increase with area
Competition	Numerous H	
Disturbance	Intermediate H	Diversity is greatest between disturbances
Heterogeneity	Structural complexity H	Diversity increases with increased habitat complexity
History	Historical explanation	Past events explain diversity
Latitude	Latitudinal diversity	Diversity decreases with increasing latitude
Isolation	Island biogeography	Islands foster the evolution of new species with greater species richness
Predation	Keystone H	Certain keystone species have greater influence than is suggested by their abundance or biomass
Productivity	Productivity – diversity	Diversity initially increases with productivity then declines.
	Species - energy	Increases in productivity results in mores species with lower vulnerability to extinction
Stability / time	Stability time H	Stable environments foster an increase in diversity over time
Succession	Succession H	Diversity is lowest initially and at climax stage
Synthesis	Synthesis of all possible causes	Synthesis

The productivity diversity hypothesis states that diversity increases initially with productivity, followed by a decline (Rex 1981). Branch and Hockey (1994) found that rocky shore species richness did not correlate to latitude, but was inversely proportional to productivity along the coast, while zooplankton in contrast shows no correlation with productivity (Gibbons and Hutchings 1996). The west coast, with its nutrient-rich upwelled waters, supports a far greater biomass of fewer species, compared to the species-rich, nutrient-poor south and east coasts. Species diversity expressed both per latitude and per 100 km unit along the coastline was markedly lower along the west coast compared to the east coast for all groups examined (Figure 2.3 and Figure 2.4). Ergo no correlation exists between productivity, measured as primary production and species richness along this coastline.

The increased productivity along the west coast is linked to upwelling events; these events are associated with increased variability in temperature, as well as periods of reduced oxygen circulation afterward (Sakko 1998). A stable environment is thought to promote an increase in diversity over time (Zacharias and Roff 2001), while a decrease in physical stress results in decrease in range size and increase in diversity (Brown *et al.* 1996). South and east coast environments, compared to the west coast, experience less high wave energy (Branch and Griffiths 1988), and have fewer upwelling cells that radically affect the water parameters, possibly reflecting a more stable environment with a corresponding increased richness compared to the west coast. A similar correlation between zooplankton diversity and environmental stability has been found (Gibbons and Hutchings 1996). Thus, while productivity is thought to increase diversity, the increased stress placed on west coast organisms may effectively decrease species richness.

The area hypothesis postulates that an increase in available area results in an increase in species diversity (Rosenzweig 1995). Valdovinos *et al.* (2003) ascribed mollusc diversity increases to increased refuge areas, geographical isolation due to diverging current systems, as well as increased shelf area. Available shelf area along the east coast increases around Port Elizabeth, coinciding with an increase in species richness. A possible explanation for this peak in richness could be related to increased coastline length from 100 to 200 km for this band of latitude. The peak is, however, evident at Port Elizabeth in the areal species richness results as well (Figure 2.3) and by implication is a true increase in richness for the region. The Agulhas Bank, south of the tip of Africa, represents the region where the shelf size is greatest and the two major oceanic currents bathing the coastlines converge. Species richness reaches its apex in this region. The diversity peak along the coast at Durban may also be due to the widening of the continental shelf. However, the shelf on the west coast is far wider than the east coast and diversity there is very low.

On large scales, temperature, through its constraining effect on metabolism, is considered the most important abiotic determinant of marine community composition (Zacharias and Roff 2001). Diversity for brachyurans showed a tendency to increase with latitude along the west coast and decrease with increased latitude along the east coast. South American crabs show a similar decrease in diversity with increased latitude along both the east and west coastlines, with patterns linked to sea surface temperature changes (Astorga *et al.* 2003), at smaller scales this pattern was not evident. Available area and temperature as a determinant of range size are considered in Chapter 4.

High species richness along the east coast can be attributed to Indo-Pacific species that are carried southward further than would be expected. In an attempt to explain latitudinal gradients in species richness worldwide, a number of variables effecting distribution have been proposed to effect species richness, none correlate well. However, energy input (measured as temperature or potential evapotranspiration), is thought to correlate best (Rohde 1999, Astorga *et al.* 2003) for a number of groups. Sea surface temperatures around southern Africa (Figure 2.8) decreases gradually along the coast, from the north-west coast to the south west coast, where a minimum for summer and winter occurs at unit 15. Thereafter temperatures show a general increasing trend to unit 40, mirroring the areal species richness pattern. Sea surface temperature correlation has been found for Australian echinoderms and decapods; however richness for these groups correlated with latitude as well (O'Hara and Poore 2000).

Eurytolerance of species has been linked to richness in the tropics (Stevens 1989); species with lower tolerance to changes in temperature are thought to have smaller ranges. These species are, however as equally able to disperse as species with large ranges, they are thus able to distribute to adjacent areas where adults can survive but environmental conditions prevent them from reproducing. They none-the-less inflate species richness. Based on this theory, species richness peaks should correlate to areas of low variability in temperature (negative correlation). Despite the cool upwelled waters, resulting in sudden water temperature changes along the west coast, variability seems greater along the south coast, where richness is greater (Figure 2.8). This trend is opposite to Stevens (1989) explanation for species richness i.e. in this study species richness was highest at regions of high variability. Thus seasonal variation may explain increased richness patterns, instead of the postulated decrease. While the temperature

data used were collected offshore and may not adequately reflect the inshore environment, they certainly reflect temperature trends and proper statistical analysis of this question is required (see Chapter 4). In addition to seasonal variation, local and regional patterns in climate variability swiftly change large scale patterns in species diversity over longer terms (Fisher *et al.* 2008).

Higher levels of spatial beta diversity have been indicated as a possible cause of high species richness and endemicity at lower latitudes (Koleff *et al.* 2003). Trends in this study show the reverse, with richness peaking at higher rather than lower latitudes. Awad *et al.* (2002) found that beta diversity was greatest at the biogeographical breaks, i.e. species richness peaks manifested as a function of beta diversity.
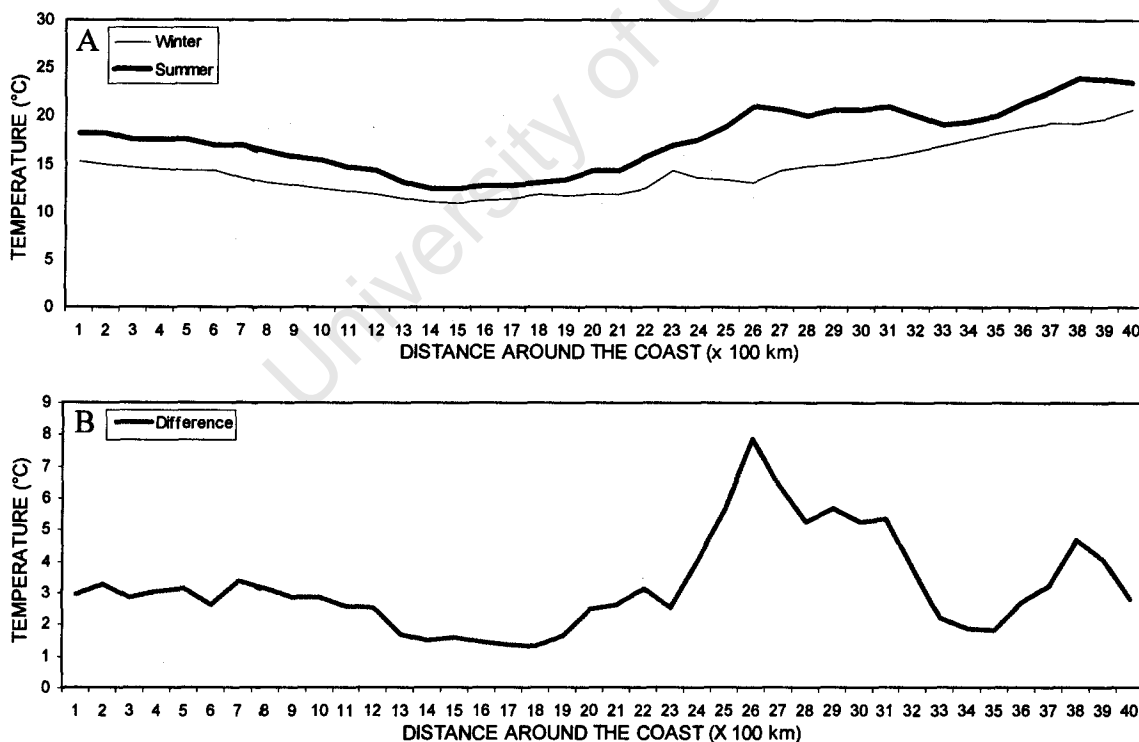
Figure 2.8: A Mean summer and winter sea surface temperatures along the southern African coastline (modified from Donn, 1990), the x- axis is expressed in terms of units 1 –40 along the coastline. B The difference between mean summer and winter sea surface temperatures along the southern African coastline.

Biogeography

The subtropical extraction effect caused by the decrease in water temperature along the east coast of southern Africa results in the stepwise loss of Indo-Pacific and tropical species along this coastline, and a resulting stepwise loss in species richness for some groups (Gibbons *et al.* 1995, Turpie *et al.* 2000). In this study invertebrate richness, however, increases as endemic species replace the warmer water fauna.

Endemic and Indo-Pacific species dominated the coastline, the former representing the greatest proportion (53 %) of species found. The majority of endemics were found in the centre of the study area and decreased towards the edges, as would be expected (Figure 2.3, Figure 2.6 and Figure 2.7), as found by Awad *et al.* (2002). The distribution patterns of the endemic species mirror the overall species richness distribution pattern for invertebrates (Figure 2.4 and Figure 2.6). Indo-Pacific species comprise 17 % of the biota, increasing in numbers, as well as percent composition, to the north-east.

A number of Indo-Pacific species extended as far south as Cape Point, due to the southward flowing Agulhas Current. The changes in environmental factors associated with different biogeographic provinces resulted in the stepwise loss of warm water species (Indo-Pacific and tropical). There appears to be three "boundaries", at Maputo (unit 43), Durban (unit 38) and finally Cape Point (unit 22), each acting as a cut-off point for warm water species, resulting in a steady decrease in number of species lost along the coastline. The tropical species follow similar trends, with species unable to cross Baia De Maputo region, the biogeographic break at Durban and finally reaching their limit at unit 22. The change in number of species is sharpest at Durban, where mean monthly temperature drop below 20 °C, a value used to define tropical regions (Bolton and

Anderson 1997). The Atlantic species on the west coast show smaller, but similar cut off points at Toscanini (unit 5) and biogeographic breaks at Lüderitz (unit 11 –12) and Cape Point (unit 22).

Atlantic, west coast and cosmopolitan species featured most prominently along the west coast. Atlantic species initially represented 30 % of the biota, but decreased steadily along the entire coastline. Cosmopolitans dominated (42 % down to 32 % composition) the first 1000 km along the west coast and thereafter endemics became the major contributor to faunal assemblages. Mean annual sea temperatures along the southern African coastline vary from 18-24 °C in summer and 15- 20 °C in winter. Water temperatures decrease with increase in latitude along both coastlines, with the west coast temperatures a number of degrees colder at similar latitudes. Polar and temperate invertebrates and fish species have larger thermal tolerance windows than their tropical counterparts (Pörtner 2002). The gradual decrease of the Atlantic and west coast species continues throughout the study area, with this group penetrating the warmer waters of the south and north coast, possibly indicating the wider thermal tolerance of this "temperate" component of the biota. Tropical species, with theoretically lower thermal tolerance limits, reached their distribution end-point sharply at unit 22. Indo-Pacific's, comprising the greatest number of species and possibly a wider variety of thermal tolerance levels, penetrated the cooler water to a greater extent.

Distribution patterns of endemic species and species that are not endemic, but have restricted distribution were very similar. A strong correlation (Pearson r correlation $p < 0.05$) exists between richness patterns for these two groups (Correlation: $r = .87592$). The pattern was especially clear for polychaetes and isopods, two very different groups with

varied life history characteristics. It is not clear from the limited scope of this study if there is a common causal mechanism for this pattern. It may relate to a perfect suite of environmental conditions for the component species, with environmental barriers preventing further distribution of both. Alternatively, it may reflect the non-endemic individual's ability to survive and be fecund in a large variety of environments with limited ability to disperse across biogeographic boundaries. Non-endemic peaks occur in False Bay, Durban Bay and Port Elizabeth; all protected and highly sampled regions. These peaks may thus be a reflection of the higher sampling effort in these regions, or most feasibly a lack of sampling elsewhere, specifically throughout the African continent (Griffiths 2005). Thirty percent of the non-endemic species that fell in this category were only found in one (20 %) or two (10 %) units (100-200 km) along the coastline. It is possible that factors effecting endemic species distribution are acting on non-endemic patchy species as well.

The poor state of taxonomy worldwide, in Africa and locally, results in the perpetuation of the lack of knowledge of species origin and distribution. Species misidentification and subsequent categorization results in erroneous distribution patterns being analyzed and examined. Cosmopolitan or "non-endemic" species may include cryptogenic, introduced species, or misidentified species that resemble European species. While the status of marine invertebrate species has been examined for the South African coast the improvement of taxonomic knowledge and more complete exploration of the African coastline may result in species being re-classified as introduced cryptogenic species, previously un-recognized endemics, as cosmopolitan species.

CONCLUSION

➢ The main conclusions from this chapter are as follows:

➢ Species richness along the coastline increases with increased latitude.

➢ The overall pattern is stepped, showing changes at major geographical boundaries.

➢ The diversity pattern found here may be related to sea surface temperature, environmental variability, life history characteristic and ability to cross biogeographic breaks.

➢ Range-restricted species appear to be more common in regions of high diversity, at higher latitudes.

CHAPTER 3

RANGE SIZE, RANGE ENDPOINTS AND RANGE RESTRICTION

INTRODUCTION

A coastline's varying hydrographical features, in particular change in temperature, salinity, turbidity and nutrient concentration (Barange *et al.* 1992, Gibbons *et al.* 1995, Macpherson 2003), are key factors that affect the distribution of species. Upwelling fronts and wind advection, for example, can act as range delimitations that affect species dispersal ability, by acting as boundaries separating bodies of water (Barange *et al.* 1992, Dingle 1995, Alexander and Roughgarden 1996).

The majority of South African marine invertebrate species (60 %) have pelagic stages in their life cycles (Day 1974), which allows for passive dispersal. However, dispersal processes are thought to be controlled to a large degree by physical factors, which may trap or advect larvae away from appropriate settling substratum (Gaines and Bertness 1992, McQuaid and Phillips 2000).

In order to contextualise diversity we must first complete the task of examining the physical environment occupied. The oceanographic features of southern Africa present an ideal setting for comparative biogeographical studies. The west coast is affected by the northward-flowing, cold (8 - 14 °C) Benguela system, while the warm (up to 27 °C) southward-flowing Agulhas Current affects the east coast (Ekman 1953, Branch and Branch 1981, Field and Griffiths 1991).

The Benguela Current is bounded in the north by the Angola Current and in the south by the Agulhas retroflection area. This system is characterised by wind-driven upwelling and has established upwelling cells at Cape Frio, North of Cape Cross, Luderitz, Hondeklip

Bay, Cape Columbine and the Cape Peninsula. Each cell varies in temperature, strength and regularity (Verheye *et al.* 1992). These upwelling cells, which are also felt inshore, bring cold, nutrient-rich waters to the surface, which supports a large biomass of primary and secondary consumers (Bustamante *et al.* 1995). In addition to upwelling in the northern Benguela, there is a periodic intrusion of warm equatorial water into this region, reaching as far south as 25 °S. This water body replaces the cold, upwelled water and has adverse effects on recruitment (Mann 1992). These "Benguela Niño's" also often coincide with eruptions of hydrogen sulphide from mud layers, which affect the entire water column and reduce oxygen in the coastal zone (Chapman and Shannon 1985).

In contrast, the fast-flowing Agulhas Current is nutrient poor, with the exception of cold upwelling areas. The Agulhas washes down the east coast with shelf-driven upwelling occurring inshore all year round between Durban and Richards Bay (Lutjeharms *et al.* 1989). The cold, nutrient-rich upwelled water flows from the central water depths onto the shelf, influencing the water characteristics of the entire Natal Bight (Lutjeharms *et al.*, 1999). An additional upwelling cell is located between Mbashe and the eastern edge of Algoa Bay, with its core at Port Alfred. The coldest inshore waters are at Port Alfred and Port Elizabeth (Lutjeharms *et al.* 2000). The Current remains close to the shoreline until it reaches East London, where it separates from the coast as the continental shelf broadens.

Biogeographic studies in southern Africa have focused on species richness (Awad *et al.* 2002), biogeographic zones and how the oceanographic features affect these zones, including both qualitative and quantitative studies (Ekman 1953, Stephenson and Stephenson 1972, Emanuel *et al.* 1992, Bustamante and Branch 1996). Distribution patterns for a number of invertebrate species have been determined (Kensley 1978,

Barnard 1950, Day 1967a, b, Griffiths 1974, Clark and Courtman-Stock 1976, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992, Primo and Vázquez 2004) and applied to the selection of possible reserves (Turpie *et al.* 2000, Awad *et al.* 2002, Bolton and Stegenga 2002). Thus far no detailed study of range sizes, range size frequency or distribution of range-restricted species has been done.

There are vast variations in range size distribution for the marine species of southern Africa. Range-restricted species, such as the endangered, pulmonate limpet *Siphonaria compressa*, occupy a limited section of a single habitat type at only two sites along the coastline (Angel *et al.* 2006). The mollusc *Janthina prolongata*, by contrast, is found along the entire southern African coastline, as well as in Australia, China, the Red Sea and numerous other localities (OBIS 2006).

Mean geographic range size of species differs between taxa, functional or trophic groups, as well as along spatial scales: longitudinally, latitudinally and with continent size (Gaston 1996). There are numerous studies examining range-size frequency distribution of species which consider continental, global and regional scale patterns (Tokeshi 1992, Arita 2005, and refs therein) as well as artefacts and mechanisms governing them (for a review see McGeoch and Gaston 2002). Taxonomic assemblage range-size-frequencies have been found, in most cases, to be strongly right-skewed on linear scales; i.e. the majority of species have very small range sizes (Brown *et al.* 1996, Gaston 1996, Gaston *et al.* 2005). Log transformation of the data results in both normal (Gaston 1996, 1998) and left-skewed results (Brown *et al.* 1996, Blackburn and Gaston 1996), with no clear ecologically driven pattern emerging. There are, nevertheless, some cases where linear scale distributions are bi-modal or hollow, particularly at finer scales (Blackburn *et al.* 1997, Tokeshi 1992). At

regional scales, patterns in range-size frequency distributions have been linked to species-area relationships, beta diversity, and patterns in the scaling of beta-diversity (Arita 2005). Until a clear pattern emerges which provides a general description of the shape of species-range size frequency distributions, the theoretical understanding thereof will remain elusive (Willig *et al.* 2003). Understanding species biogeography depends on a better understanding of range size frequency distributions, and the underlying cause of the patterns.

Southern Africa, with its high levels of endemism (Chapter 2), both terrestrially and in the marine environment, offers a unique setting to examine range-size-frequencies. Although interpretation and comparison between regions is difficult (Gaston 1994, 1996), primarily because reliable taxonomic data are only available for 11 degrees of latitude, out of the possible 70 degrees of latitude, for the whole of Africa. Nonetheless, the current investigation may shed light on the southern African faunal assemblage patterns and the forces that drive them.

To clarify the processes driving species distribution and limitation, I examined range end-point distribution and endemicity peaks along the coastlines, in addition to range size frequencies. Small-ranged species have always been prioritised, or at the very least are considered, when conservationists examine regions for reserve selection (Turpie *et al.* 2000, Awad *et al.* 2002). It is intuitive that species occupying a limited region along the coastline require careful conservation consideration, in particular because small range species are at greater risk of extinction (Rode and Lieberman 2004).

including salinity, productivity and temperature, which in turn affect the distribution of species by acting as environmental borders (Barange *et al.* 1992, Emmanuel *et al.* 1992, Awad *et al.* 2002, Zacherl *et al.* 2003). As a result range endpoints or borders of species, while occurring throughout the coastline, show peaks at biogeographic breaks (Day 1967 a, Gaylord and Gaines 2000, Awad *et al.* 2002)
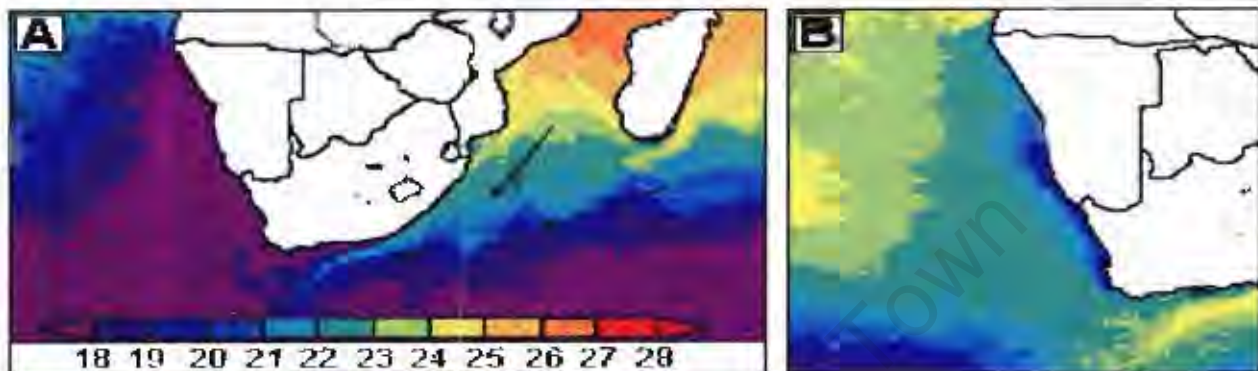

Figure 3.1. Sea surface temperatures showing the warm Agulhas Current (A) and the cold Benguela Current and upwelling region (B). Modified from http://daac.gsfc.nasa.gov/oceancolor/tutorials/module2.shtml

A perfect example illustrating these changes is the convergence of the cool Benguela and warm Agulhas Current round the southern tip of Africa. This biogeographical crossroads is the meeting point of two water bodies with distinct features, most importantly varying water temperatures (Figure 3.1). The steep gradient in water temperature change, apparent at the point of convergence of the two currents, poses physiological challenges that limit distribution of species at these junctions.

Zoogeographical provinces are identified through the examination of distribution of organisms within a region. Peaks in range end-points at the determined biogeographic boundaries, in addition to community analysis within these zones, clarify the boundaries of zoogeographical provinces (Engel and Summers 1999). Additionally, it has been surmised

that peaks in range endpoints, regions of peaked endemism and more specifically restricted endemic species, all coincide at biogeographical crossroads.

In this chapter the following questions are addressed.

- ➢ What are the range size frequency distributions of the various marine taxa?
- ➢ What are the distribution patterns of range-restricted endemics, and how do biogeographic breaks affect these?
- ➢ Where do range endpoints peak?

METHODS

Range size data

Range size could be measured either as the area of occupancy (in 100 km coastline units) or latitudinal range (in degrees). Internationally, comparative biogeographers use latitudinal range size to investigate patterns. Of the 4800 km of coastline that were examined during this study, 700 km fall within the same latitudinal band. Thus in order to examine range size frequencies, range restriction and regions of restriction, areal range size was the more appropriate measure. This enabled clarification of patterns within latitudinal bands.

The study region was divided into 48, 100 km units, and range size was calculated as the number of 100 km units occupied by each species. Biogeographic affinities were used to extrapolate worldwide area of occupancy, or range size of widely distributed species. This was measured using a map wheel on a 1:35 000 000 scale map of the world. Thus, a

species occupying 10 units along the coastline was calculated to have a 1000 km area of occupancy. The values determined using this method, depend on the scale of the map utilised, resulting in a rough approximation of the actual area occupied.

Range-restricted species distribution

Range sizes that are less than 4 ° latitude have been defined as small (Gaston 1997). For the purpose of this study I defined range-restricted species as species with an extent of occurrence less than 500 km (1-5 °), dividing them into five categories from 100-500 km long ranges along the southern African coastline. Distributions of the restricted species were determined and plotted for each group.

Range end point distribution

This study divided the coastline into 48, 100 km units. A species occupying units 5, 6, 7 and 8 was said to have a range that started at unit 5 and ended at unit 8. Thus range start and endpoints refer to the western and eastern most point of a species range along the coastline. Beta diversity establishes the rate of change of species composition along a gradient, or in this case a coastline, without referring to species assemblages. In order to establish how species assemblages changed along the coastline, specifically at biogeographic borders, I investigated range endpoints for each group. Endpoint distribution was plotted to highlight points of change, or boundaries, between species assemblages.

Range size frequency distribution

Studies investigating range size frequencies examine area of occupancy for the species involved, in this case the number of kilometres occupied by species along the coastline. The data being examined are presence / absence records for invertebrates found along the shoreline of southern Africa. Species distribution was assumed to be continuous between two known regions of occupancy; furthermore it was assumed that appropriate habitat was available in each unit of occupancy. In other words, extent of occurrence was assumed to be area of occupancy as well.

The data were collected from various literature sources (Barnard 1950, Day 1967a, b, Griffiths 1974, Clark and Courtman-Stock 1976, Kensley 1978, Kilburn and Ripey 1982, Gosliner 1987, Thander 1989, Williams 1992). The sources date from 1967 – 1992, as a result, current updated range sizes may differ, as distribution patterns of the examined species may have changed over the last 20 years. Additionally, sampling methods varied vastly between studies.

The data collected were plotted as range size frequency distributions for each group investigated. Results were presented as the number of species found for each range size and since results were not normal, the equivalent graphs for log transformed data were included. This also facilitated comparison with previous literature, as many studies follow the same methodology, due to the skewed nature of the results. The shapes of the range size frequency distributions were examined.

RESULTS

Range-restricted species distribution

Figure 3.3 showed that the largest peaks of range-restricted endemic species for all the groups combined, occurred at False Bay (unit 23), followed by Port Elizabeth (unit 31), Durban (unit 38), St Lucia (unit 41), Baia De Maputo (unit 43) and lastly around East London (units 33-34) (See Figure 2.2 for map showing the units along the coastline). The number of range-restricted endemic species decreased from south to north along the south and east coast; this mirrored the decrease in number of endemics and number of species found in each unit (Figure 2.3). The slight peak of restricted endemics at Lüderitz can be attributed to amphipods and polychaetes, which both have more west coast species than any of the other groups (around 60 species at Luderitz). It should be noted that the results for all the groups combined were biased by the more abundant groups.

When considering the different faunal groups, two clear patterns emerged (Figure 3.3). Bivalves and prosobranch gastropods had the largest peak at unit 31, while the majority of the other groups show a considerable peak around unit 23 (Cape Point). Centred on the Cape Point region there are more than 80 endemic species restricted to only one unit and an additional 111, restricted to two units. Port Elizabeth (unit 31) has 36 and 63 endemics species restricted to one and two units respectively. Figure 3.2 shows similar peaks for the range-restricted species that are non-endemic: Cape Point (97 species, unit 23), Port Elizabeth (38 species: unit 31), Durban (42 species: unit 38) and St Lucia (66 species, unit 41), thus making these regions of peak endemism.
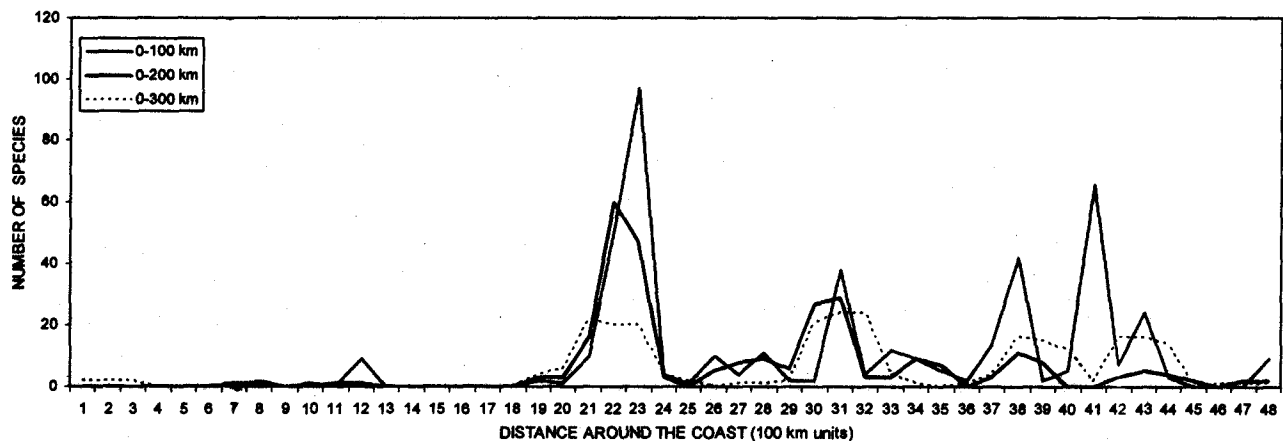
Figure 3.2: Distribution patterns of non-endemic range-restricted species that are restricted to 1-3 units (100 – 300 km) along the southern African coastline but have a scattered distribution elsewhere in the world.

Range end point distribution

Limits of distribution for various biogeographic affinities are reflected as peaks in distribution endpoints. Ends of distribution points for all the groups combined (Figure 3.4) show discernable peaks, predictably, at or around all the biogeographic breaks (units 22/23, 34 and 38) as well as at Port Elizabeth (unit 31) and the region south of Maputo (unit 41 - 43). An additional number of small peaks occurred at Lüderitz (unit 12), Stilbaai (unit 26), and Knysna (unit 28), as well as at the eastern and western most limits of the study area.

Individual groups mirrored the results for all the groups combined (Figure 3.4), with peaks apparent at biogeographic breaks. The greatest peaks in the number of species that reach their western-most (octocorals, ascidians, chitons, amphipods, isopods, polychaetes, and bivalves) and eastern most (amphipods and isopods) limit of distribution occurred at units 22 and 23. Ascidians and chitons had their largest peaks in eastern-most point of
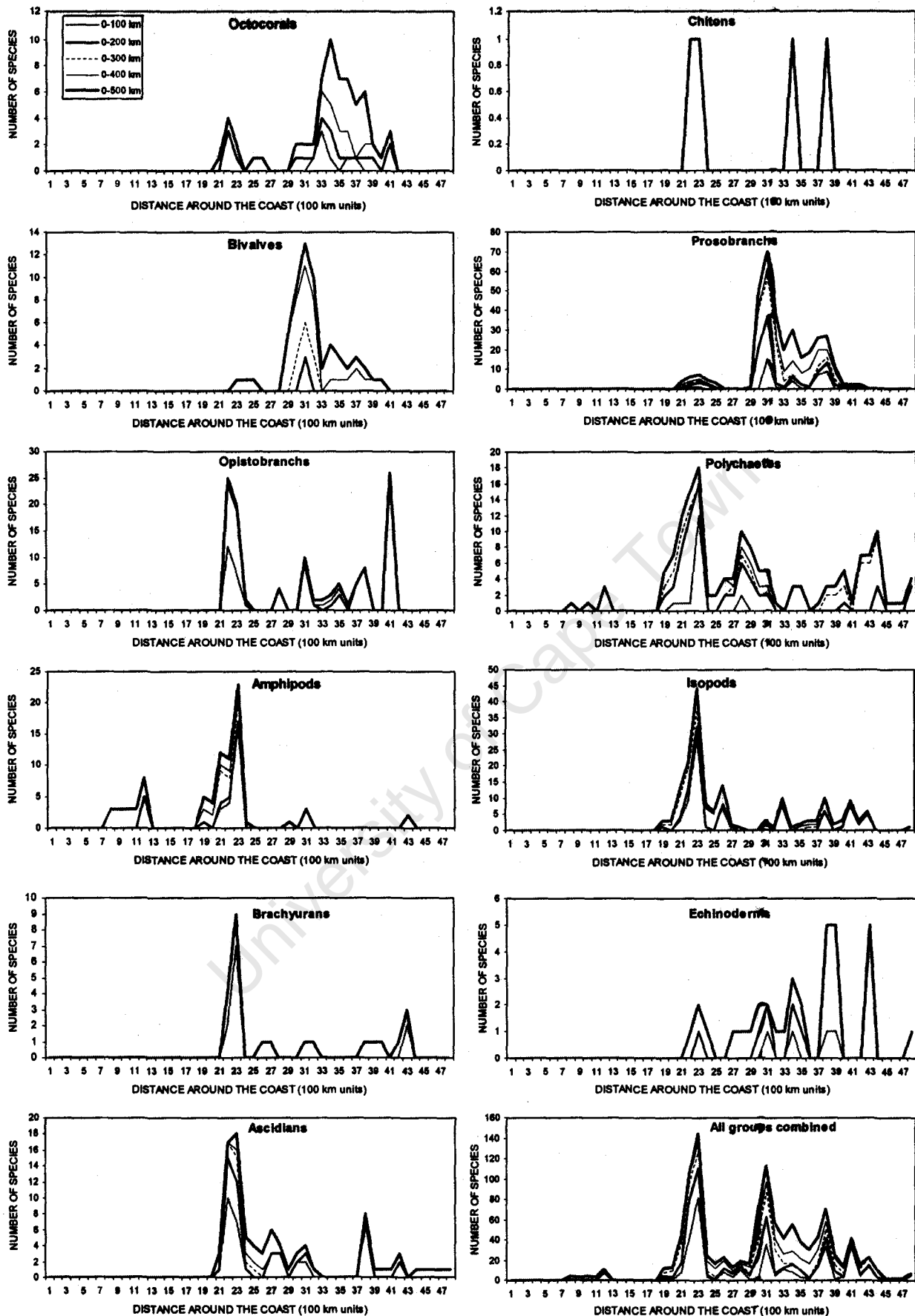
Figure 3.3: Distribution patterns of endemic species that are restricted to 1 – 5 units along the southern African coastline (1 unit = 100 km).

distribution at unit 38, while echinoderms peaked at unit 39 and prosobranch gastropods at unit 34. Opisthobranchs, brachyurans and echinoderms peaked at unit 43. All the groups had varying sized peaks at or around unit 31 (Port Elizabeth). For prosobranch gastropods and bivalves these peaks reflect a central point of endemicity (Figure 2.3).

In most cases the peaks in western-most and eastern-most limit of distribution occurred at the same unit along the coastline. The most notable exception was units 30 - 31 (Figure 3.4) for all the groups combined. Prosobranch, octocorals, chitins, bivalves, polychaetes and echinoderms all had slightly disjunctive start and endpoints contributing to this pattern. Bivalve start and endpoints differed at almost all major peak regions. Echinoderms and prosobranchs peaks were different around unit 38, while polychaetes differed at unit 42.

Table 3.1 expresses the results as the percentage of species reaching their western and easter-most limit of distribution, at each unit. The number is expressed as a percent of the total number of species found in the study area and as a percent of species found in that unit that reach their distribution limit. Cape Point had the greatest effect on the distribution of species, limiting distribution of 13 % of species westwards, mostly endemics (Figure 2.5) and 7 % eastwards, predominantly Atlantic species (Figure 2.6). Almost 50 % of species in this unit reach their distribution limit here. The biogeographic break at Durban (unit 38) limits 14 % of all species (7 % southwards and 6 % northwards). This change reflects an increase in the number of tropical and Indo-Pacific species and a decrease in endemic species. The Port Elizabeth (unit 31) and Maputo (unit 41 - 43) peaks affect 10 % (7 % east and 3 % westwards) and 6 % of species respectively (3 % east and westwards). These peaks reflect decreases in endemics and increases in the tropical and Indo-Pacific components of invertebrates (Figure 2.6).

Table 3.1: The percentage of species that reach their western-most and eastern-most limit of distribution at various points along the southern African coastline, listed in decreasing order of importance. Only units with more than 5 % of endpoints are shown.

Unit along coast	Percent of all species reaching their western distribution limit	Percent of all species reaching their eastern distribution limit	Percent of all species reaching their distribution limit (Total)	Percent of species in this unit reaching their distribution limit
23	13	7	20	47
38	7	6	14	30
22	8	4	12	34
31	3	7	10	23
34	5	3	8	19
37	5	2	7	17
41	3	3	6	17
21	5	1	6	23
48	1	6	6	18
30	5	1	6	14
43	3	3	6	15
42	2	3	6	15
33	2	3	5	13

Range size-frequency distribution

Figure 3.5 shows the range size distribution of marine invertebrate species found along the southern African coast. Figure 3.6 shows the same results logged to the base 10. The solid bars indicate endemic species, while the open bars indicate non-endemic species. On the linear scale (Figure 3.5), three patterns emerge for invertebrates along the coast. Ascidians and isopods are strongly right skewed, i.e. the majority of species have small ranges, while bivalves, prosobranchs and to a smaller extent brachyurans, are slightly left skewed (i.e. most have large ranges). A more even distribution of the data is evident after log transformation for prosobranch and bivalves, while brachyurans become more right skewed (Figure 3.6). Ascidian and isopod log transformed data remains right skewed, but not as pronounced. All the other groups show bi-modal results, with large numbers of
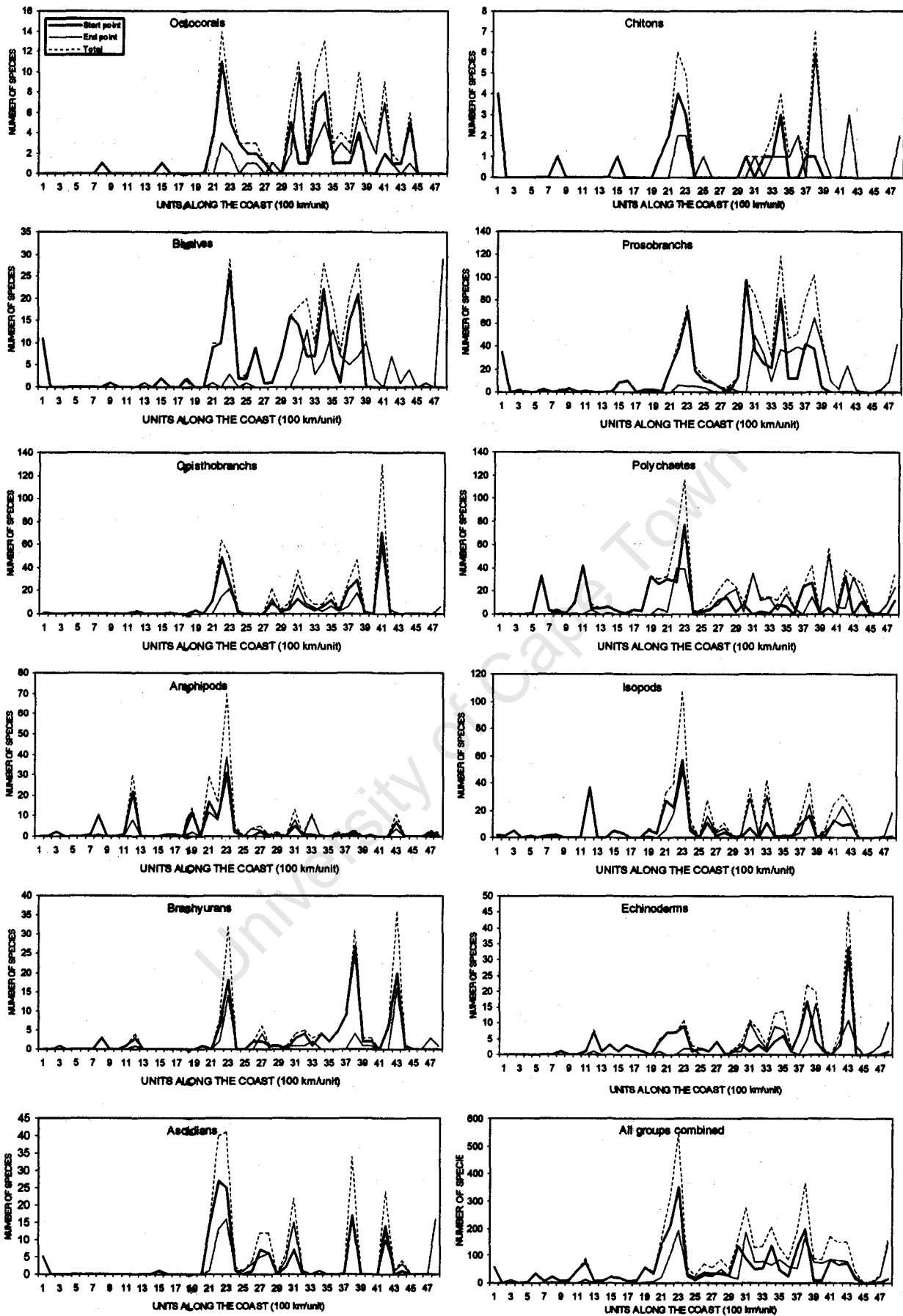
Figure 3.4: Patterns of western and eastern most endpoints of distribution for invertebrate groups.

species with very small ranges, and with very large ranges. Chitons have an even assortment of range sizes. The frequency distribution of range sizes for the whole group combined was also bi-modal. Log transformation of these groups produced bi-modal results (Figure 3.6).

Thirty percent of species had range sizes smaller than 500 km and 52 % smaller than 1500 km. Twenty-eight percent of species have range sizes that are larger than an estimated 4900 km, while 20 % of species range sizes are bigger than 5300 km. Endemics species clearly dominate the left side of the spectrum with small-ranged species being dominant. Comparatively few species that are non-endemic have small ranges. The Indo-Pacific and tropical components of the biota are responsible for the disproportionately high number of large-ranged species. An interesting observation was that nearly 10 % of endemic species had fairly large ranges extending for more than 2500 km along the coastline. It is possible that these species are in fact more wide spread and their full distribution has not yet been charted.
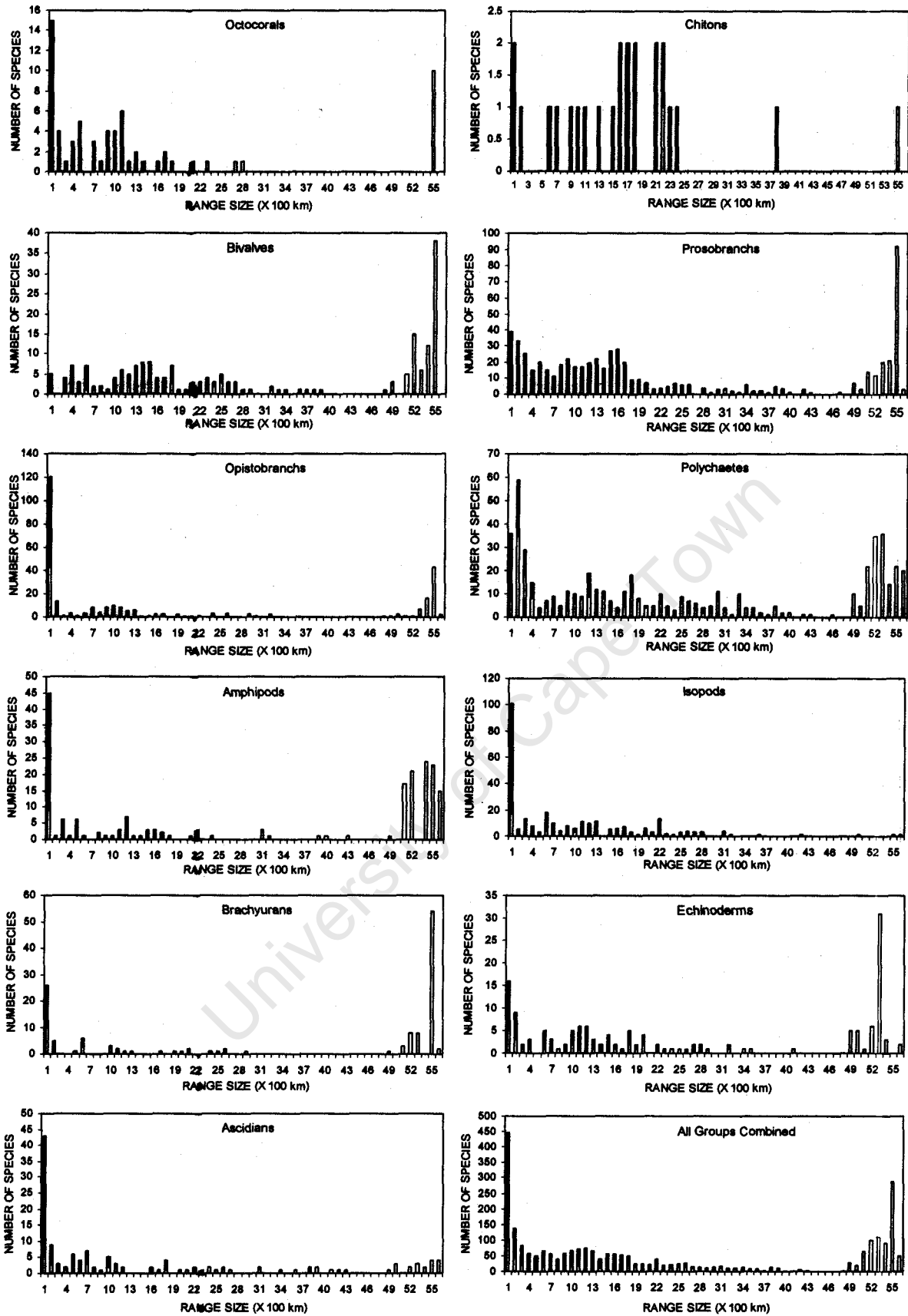
Figure 3.5: Range size frequency distribution of geographical range sizes for southern African marine invertebrate species. Solid bars represent endemics and open bars represent non-endemic species.

Figure 3.6: Log transformed range size frequency distributions of geographical range sizes for southern African marine invertebrate species. Solid bars represent endemics and open bars represent non-endemic species.
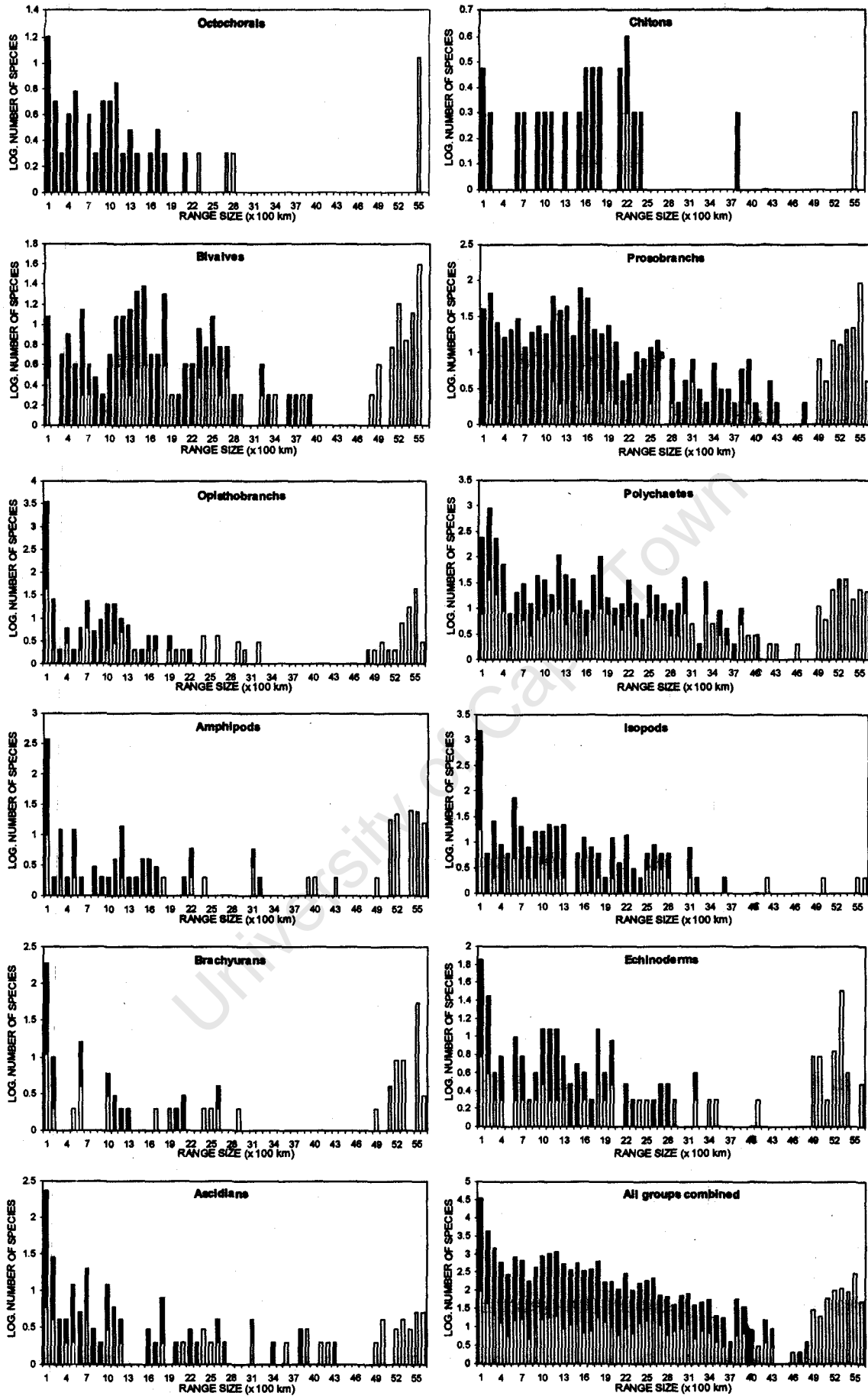
DISCUSSION

Range-restricted species distribution

A species is defined as endemic to an area if it occurs there and nowhere else (Gaston and Spicer 2002). The IUCN categories and criteria for endangered species include a category establishing extent of occurrence and area of occupancy. Species with a small extent of occurrence and reduced areas of occupancy, within that extent of occurrence, are considered critically endangered. Thus in order to adequately conserve biological diversity and specifically endangered species, it is imperative that we identify "hotspots" of range-restricted species.

Species with restricted ranges and/ or low abundances have been found to make up a sizeable proportion of the total number of species for a given area (Ellingsen et al. 2007). Additionally, regions of elevated endemism and diversity are often analogous, with a clear positive correlation between these two population measures (Stevens 1989, Santelices and Marquet 1998). This pattern has previously been found for southern African marine species as well (Emanuel et al. 1992, Turpie et al. 2000, Acuña and Griffiths 2002). Moreover, peaks in richness and restricted endemics are frequently observed at biogeographic breaks (Emanuel et al. 1992, Engle and Summers 1999, Turpie et al. 2000, Acuña and Griffiths 2002) constituting an additional means of confirming the existence and location of the break (Engle and Summers 1999). The majority of the groups investigated here had their largest peak of restricted species at unit 23 (Cape Point). The Cape Point region represents the clearest biogeographic break along the coast, with consensus among authors regarding its existence and location (Stephenson 1972, Emanuel et al. 1992, Bolton and Anderson 1997).

Other regions with large peaks of range-restricted endemics included False Bay, Durban and East London. Each of these is a known biogeographic crossroads for invertebrate assemblages (Emanuel *et al.* 1992). St Lucia, Baia De Maputo and Port Elizabeth all had peaks of restricted species. St Lucia is a marine protected area, where diversity and abundance is greater than the adjacent section of coastline. There are two possible reasons for this: firstly it is a reserve and has been far more extensively sampled than adjacent regions and secondly it is the southernmost tip of the true coral reefs. Intertidal investigations have shown this region is biogeographic division between the Subtropical Natal and Tropical Indo-West Pacific provinces, creating an overlap zone (Bolton *et al* 2004, Sink *et al* 2005).

A number of species in my data were recorded from a single location or cell only, as a result, the high frequency of 100 km range sizes could be an artifact of rarity and infrequent recordings. While, such species may reflect low abundance and narrow distribution (O'Hara and Poore 2000), present data may simply reflect the only location at which this particular habitat or species has been sampled (i.e. may be the only published record of what is in reality a much more widespread species). To some degree, peaks in restricted species correspond to regions where there are universities with marine departments; as a result, these regions would be better sampled than elsewhere, and peaks in rarity may be exaggerated.

Bivalve and prosobranch endemicity patterns differed from the other groups in that their largest peak of endemism was at unit 31 (Port Elizabeth), a pattern also found for coastal fish and attributed to a higher diversity of inshore habitats (Turpie *et al.* 2000). For both these groups endemism peaked here and then dropped off towards the borders (Awad *et*

al. 2002 and Figure 2.3). The Agulhas Current flows southwards, following the continental shelf down the east coast of South Africa. At 25 °E, around Port Elizabeth, there is a significant bi-annual leakage or complete retroflection of the Current (Lutjeharms and van Ballegooyen 1988). In addition to habitat diversity it could be inferred that this upstream retroflection, in some way inhibits distribution of these groups, resulting in the peak of restricted species. Cold inshore upwelled waters at Port Elizabeth (Lutjeharms *et al.* 2000), may further limit distribution.

The magnitude of the range-restricted species peaks decreased from Cape Point to the borders of the study area, as did species richness and endemicity (Awad *et al.* 2002 and Figure 2.3). Small geographic ranges have been linked to high diversity regions (Stevens 1989, Santelices and Marquet 1998). In an attempt to explain the link between high diversity (species richness) and small range size in the tropics, Stevens (1989) introduced the concept of the "Rescue Effect". This is a process whereby species with very small ranges spread into adjacent areas, but are unable to reproduce in these areas because the population is not well adapted to the local conditions. The species richness is maintained by a continuous supply of new migrants or "accidental species".

Peaks in species restricted to 100 - 500 km coincide with peaks in diversity along the coastline (Figure 2.3), leading one to consider the possibility of the Rescue Effect inflating regional diversity at these "peak" areas. These regions also coincide with biogeographical zone borders; consequently there are peaks in range endpoints (Figure 3.4), a common phenomenon (Gaston 1997, Engel and Summer 1999).

An a-priori investigation showed that peaks in range-restricted species and species richness peaks correlate significantly (Statistica: Pearsons correlation r ≈ 0.903, P > 0.05) (Table 3.2) for invertebrate distribution. All the groups investigated separately showed varying strength of positive correlations (Table 3.2). This correlation between restricted species richness and species richness is remarkable, but as with any correlation-based conclusion, the connection may be caused by any co-varying factor, in particular variable hydrographical conditions.

Table 3.2: Correlation values comparing species richness and range-restricted diversity along the coastline: Pearson's correlation r, P > 0.05.

Group name	Pearson's-r correlation value
All groups restricted	0.643
Amphipods	0.716
Ascidians	0.648
Bivalves	0.424
Brachyurans	0.166
Chitons	0.487
Echinoderms	0.546
Isopods	0.668
Octocorals	0.644
Opisthobranchs	0.514
Polychaetes	0.645
Prosobranchs	0.678

Gaston (1997) explained this correlation using the transition zone theory. A transition zone or ecotone is where species of both adjacent biogeographic zones are found living together in an overlap area (Bolton and Anderson 1997), which thus harbours increased diversity (Traut 2005). Species that are not found in either zone may also be restricted to the narrow region defined by the overlap of the two biogeographic zones, thus inflating the species richness peaks, resulting in what is known as the edge effect. The peak of endemic species at regions of peak diversity may be as a result of species restricted to the ecotone. The Cape Point, Durban and East London peaks coincided with recognised biogeographic breaks, where species richness has been shown to peak (Awad *et al.* 2002, Figure 2.3). Similar peaks in endemicity have been found for fish (Turpie *et al.* 2000).

The inflated diversity at regions of overlap, or ecotones, may also be related to speciation. Biogeographic barriers are postulated to facilitate allopatric speciation, resulting in high levels of narrow endemism, possibly at or around the biogeographic breaks (Myers 1997). Large-ranged species are more likely to have their ranges bisected by a biogeographic break along the coastline (Chown and Gaston 2000), resulting in two separate groups residing in adjacent regions.

The biogeographic zones along the east and south coast, with the predominantly southward-flowing current system, vary in length from 500 - 1000 km. An Indo-Pacific species, for example, with a large range penetrating right down to unit 38, my first biogeographic break, may be limited at this break by varying hydrological features of the coastline. The barrier may act as a "knife-like" delimitation of distribution, thus limiting species range expansion and facilitating vicariant speciation. Alternatively some species may be able to cross the "barrier" to form viable reproductive populations, colonising a new niche at the peripheral region of the species geographic range (peripatric speciation).

The dominance of large-ranged species along this largely temperate coastline may furthermore be linked to the breadth of fundamental tolerance capacity. Marine species with large geographical ranges have been shown to have a greater tolerance or capacity to survive change in the physical environment. (Gaston and Spicer 2001). Thus, environmental variability within a species range habitat is predictive of large geographical ranges for marine algae and gastropods (Harley *et al.* 2003). The west coast is exposed to high wave energy (Branch and Griffiths 1988, Emanuel *et al.* 1992), which results in a greater degree of physio-geographic heterogeneity (Emanuel *et al.* 1992) within the ranges of west coast species. Consequentially, the constituent species of the west coast may be

large-sized, large-ranged species utilising a greater variability of niches, possibly explaining the greater number of cosmopolitan species along this coastline (Figure 2.6).

Furthermore, there exists a positive relationship between interspecific species abundance and range size (Gaston *et al.* 1997), although the underlying mechanisms of this relationship are poorly understood. The greater biomass and lower diversity along the west coast (Bustamante and Branch 1996), points towards a plausible relationship between local abundance and range size, assuming that the greater biomass reflects greater abundance, and is not an artefact of animal size only.

In addition to endemic restricted species, I investigated distribution of non-endemic range-restricted species along the coastline (Figure 3.2). The peaks of range-restricted species are still concentrated at the biogeographic breaks, with some differences that are highlighted here. The number of species restricted to 100 km at False Bay (unit 23) increased by 14, whereas at St Lucia (unit 41) and Maputo (unit 43) they increased by 30 and 10 respectively. The latter species increases may represent the northern-most point of distribution for these animals. Alternatively their global distribution may be highly variable and patchy and they are indeed "range-restricted" to this region. The inclusion of all restricted species did not change the patterns found.

Factors acting on endemic restricted species are acting on all restricted species in a similar fashion. Additionally, endemicity patterns may be real and not an artefact of insufficient sampling, as the coastline is limiting. Since endemics and non-endemic restricted species are limited to the same regions along the coastline, possibly by similar mechanisms, endemic species may in fact be widespread with patchy distribution and

again insufficient taxonomic knowledge is limiting my ability to make any conclusive generalisations.

Range endpoints distribution

Range endpoint peaks (Figure 3.4) occur along the southern African coastline at areas where there are major oceanographic changes, principally upwelling regions. The largest peak in endpoints at False Bay (unit 23) represents more than 13 % of all species along the coastline that are prevented from distribution westward, while 7 % are prevented from eastwards distribution (Table 3.1). The adjacent Cape Point area (unit 22) has an upwelling cell. A total of 77 % of range endpoints occur at upwelling cells along the coastline, which by and large, coincide with biogeographical breaks.

Geographical ranges of species are limited by specific abiotic or biotic limiting conditions in ecological gradients that prevent further distribution along the edge of the animal's range. These factors are often species or taxon specific (for a review see Brown *et al.* 1996). The general trend is that abiotic or physical factors set limits at higher latitudes and biotic factors limit species distributions at lower latitudes. The ubiquitous nature of the ocean furthermore ensures that any marine boundaries are dynamic and may change periodically.

The bulk of marine invertebrate species practice external fertilisation and as a result have free-swimming larval stages able to move, in some cases across ocean realms (McQuaid and Phillips 2000), resulting in extreme heterogeneity in dispersal scale among species. Scale in turn depends on taxonomic group, as well as functional group examined (Kinlan

and Gaines 2003). Dispersal of species may be limited by temperature changes or changes in oceanographic features, including those associated with biogeographic breaks, upwelling cells, deep oceanic regions, brackish water, coves or inlets, as well as river inlet systems (Hansen 1978, Vermeij 1987, Alexander and Roughgarden 1996, Gaylord and Gaines 2000, Oyarzun *et al.* 2002, Sink 2001, Pörtner 2002, Macpherson 2003). In addition to these features, dispersed larvae are further reliant on shoreward transport to ensure they are brought back into contact with appropriate habitat (Pineda 1991).

The biogeographical breaks along the southern African coastline reflect changes in the marine environment from cool temperate to warm temperate to subtropical (Emanuel *et al.* 1992). In addition to these changes, upwelling cells are found around Toscanini (unit 5), Lüderitz (unit 12), Port Nolloth (unit 16), Lamberts Bay (unit 19), Cape Point (unit 22), Port Elizabeth (unit 31) and the Durban to Richards Bay region (units 38-40). The continual changes in physical, chemical and biological environmental conditions result in an unpredictable, variable marine habitat (Sakko 1998) that delimits species distribution. These upwelling–induced boundaries seem to act in both directions, preventing distribution westwards as well as eastwards (Figure 3.4) most notably on the south and east coastlines (units 22 - 48). Upwelling zones are recognised barriers for dispersal (Macpherson 2003) in both directions, acting differentially on different life history characteristics of species (Gaylord and Gaines 2000). However, the Lüderitz upwelling cell (unit 12) along the west coast, despite being one of the most intense in the world, only limits the distribution of 20 % of the species found in this unit, lending less credibility to my argument.

Agulhas Current upwelling cells occur between Durban and Richards Bay, as well as at East London to Port Elizabeth (Lutjeharms *et al.* 2000) where the shelf width increases. Thermal tolerance for species around these temperatures is considerably wider (Pörtner 2002) and thus temperature may have a lesser effect on limiting distribution at these biogeographic breaks. These areas nonetheless do act as dispersal barriers as range endpoints peak here. In addition to upwelling, the Agulhas Current retroflection may limit southward movement of species spawned into the current further north off Port Elizabeth (Lutjeharms and van Ballegooyen 1988).

Range size frequency distribution

Range sizes of marine invertebrate species in southern Africa vary from a single record in one, 100 km (endemics) stretch, to a number of records in an area covering many thousands of kilometres (cosmopolitan species). More than 30 % of species examined in this study had ranges smaller than 500 km long (24 % of these being endemics). Species with ranges greater than 4900 km make up 28 % of the biota. The remaining 40 % have ranges in between. The large component of biota with large ranges in the size frequency distribution patterns can be attributed to the large tropical and Indo-Pacific component of the fauna, while the small range size peaks reflect numerous endemics.

A general pattern of range size frequency distribution for species was documented for the first time by Willis (1922) and has been found for many organisms by subsequent authors (Brown *et al.* 1996, Ellingsen *et al.* 2007). When the range size frequency distribution area is plotted on a linear axis the shape of the distribution is highly right skewed, i.e. most species have very small to medium sized ranges, while a few species have very large

ranges. Range size frequency distribution patterns for benthic marine organisms, including cephalopods, stomatopods and decapods do not show a single overall pattern (Macpherson 2003).

Species level heritability is the degree to which closely related species share the same attributes such as range size. A significant species level heritability in geographic range size is evident for Cretaceous gastropods and birds (Hunt *et al.* 2005). Such species level range size similarity may become more similar with time, following speciation (Waldron 2007). As a result, grouping together species of similar heritability is likely to show as many species with similar range sizes.

Overlaying the range size frequency patterns are additional patterns. These can be explained in a number of ways. Species that have evolved along similar lines, such as congeners, are likely to have similar ranges, suggesting that the ecological interactions that limit geographic distribution have acted on similar species in similar ways (Brown *et al.* 1996). Additionally, range size has been linked to animal size, life history characteristics, population size, area and energy (Roy *et al.* 2001, Roy *et al.* 2002, Macpherson 2003, Storch *et al.* 2005).

A number of marine organisms have bipartite life histories, whereby sedentary adults, have free-living planktonic stages, able to traverse the oceanic realm, enabling some degree of range expansion. Range sizes of pelagic taxa, or species with pelagic developmental modes in their life history, are generally larger than those of benthic non-pelagic taxa (Scheltema 1971, Hansen 1978, Scheltema and Williams 1983, Highsmith 1985, Féral 2002, Macpherson 2003, Chapter 4). Thus range size distribution patterns for

species with pelagic stages are likely to be left skewed, while those without would have more small-ranged species (Macpherson 2003).

Opisthobranchs, brachyurans, bivalves, ascidians and octocorals all have pelagic stages in their development (Barnard 1950, Millard 1975, Kilburn and Rippey 1982, Gosliner 1987, Williams 1992). Bivalve and brachyurans do have more larger-ranged species; however ascidians and opisthobranch gastropods do not follow this pattern. Echinoderms, polychaetes and prosobranch gastropods have species with pelagic stages, as well as those without (Day 1967a, b, Clark and Courtman-Stock 1976, Kilburn and Rippey 1982, Thander 1989). This may be evident as the balance between small-ranged (mostly endemics) and larger-ranged (non-endemics) species represented by the bi-modal results (Figure 3.5).

Both amphipods and isopods undergo direct development. Thus no pelagic stage occurs in the development of these organisms (Griffiths 1974, Kensley 1978). Amphipod and isopod range size frequency distribution should by inference be right skewed, with many small-ranged species and few large-ranged species. Isopods do show this pattern, but amphipods have both large and small-ranged species. It should be noted that 83 % of isopods examined were endemic to southern Africa, compared to 39 % of amphipods, implying that the ecological interactions that limit distribution of isopods do not necessarily limit amphipods in the same way.

The relationship between animal size and range size can be positive or negative. However, comprehensive analyses over large range sizes resulted in a positive relationship (Stanley 1986, Brown *et al.* 1996, Gaston and Blackburn 1996 b). Larger-

bodied marine bivalves are better able to expand their geographical ranges (Roy *et al.* 2001, Roy *et al.* 2002) than their smaller counterparts, resulting in larger ranges. On the other hand, theoretical model-based results predict that large and small sized animals would have larger ranges, while species with medium sized bodies would have the largest ranges (Hui and McGeoch 2006).

A brief investigation of average animal size (Table 3.3) for some of the groups analysed offers circumstantial evidence which may explain the patterns I found. Isopods, the animals with the smallest average size, have correspondingly small range sizes, as do most opisthobranch gastropods. However, the latter group has a pelagic developmental stage, which may explain the additional larger ranges for some of the species. Echinoderms had the largest average size and had a slightly left skewed result, but not sufficiently so to be conclusive. Bivalves, with a relatively large average size, had mostly, large -ranged species. I explore animal size in more detail in Chapter 4.

Table 3.3: Mean animals size of invertebrate species, calculated from largest animal found for each species (see Chapter 4).

Group	Mean animal size (mm)
Isopods	13
Opisthobranchs	24
Brachyurans	26
Prosobranchs	41
Bivalves	55
Polychaetes	79
Echinoderms	92

Prosobranchs, the group with the modal range size, are considered to be one of the better-known groups in South Africa (Kilburn and Ripey 1982, Griffiths 2005) and range size patterns for this group (Figure 3.5) shows a broader spread of ranges, with fewer species restricted to less than 100 km, than is pictured for all the groups combined and for a number of the constituent groups. This highlights the possibility that the right skewed

nature of frequency distribution of a number of other groups is a result of insufficient taxonomic knowledge. In particular the high levels of endemism may be misrepresentative of the fauna. A persistent skew result after log transformation, as demonstrated for my data, is typically interpreted as an excess or lack of a particular range size class (Gaston *et al.* 2005), in this case middle sized ranges.

The distortion away from what would be log-normal distribution, a general feature of species range size distribution, has been attributed by Gaston (1998), to three possible problems: Firstly sampling method; with most methods over-estimating the areal occupancy of the constituent species, since species do not necessarily occur continuously in their area of occupancy. A species area of occupancy is the area in which they are found. Secondly the truncated nature of species ranges, which were measured only on the continent, with actual ranges extending beyond being ignored. Lastly, the tendency of anthropogenic activities to result in the fragmentation of areal range size.

The skewness of my data could reflect true patterns, these results, however, may also be attributed to a number of influencing factors, including, the problems highlighted by Gaston (1998). As discussed in the methods section, my data may contain larger than expected range sizes for species because I assumed continuous distribution between two known regions of occupancy. The species may not occur in every intermediate part of the overall range, and may have small pockets of distribution.

The problem of continental extent of occurrence was addressed by extrapolating range size to include worldwide distribution of each species analysed. The resulting data would become largely left skewed (large peaks of species with exceptionally large range sizes),

and may in fact not represent the true distribution, again due to methodology. The possible error incorporated, by assuming extent of occurrence and area of occupancy are equal on a worldwide basis, increases the error by an order of magnitude. Habitat fragmentation, coastal heterogeneity and patchy distribution further complicate results by distorting the range size in favour of larger ranges, despite a lack of continuous habitat. Having said that, the dominance of endemic and Indo-Pacific species along the coastline resulted in a clear bi-modal pattern for the majority of the groups, i.e. there are large numbers of small and large-ranged species. This result is consistent with the bi-modal distribution found on finer scales (Tokeshi 1992). Analytical models have predicted that near the edges of a domain, the range size frequency distribution of ranges will become more uniform, with percentages of rare species mirroring the widespread values, similar to my results (Arita 2005).

Arguably, the most important consideration when examining the results refers again to the worldwide lack of taxonomic knowledge. The data used for this study were limited to taxa for which there was sufficient taxonomic knowledge. For a number of groups that are well known in South Africa, including fish, echinoderms, molluscs, macro algae and decapods, species richness is higher than, or similar to, species richness reported for Europe (Griffiths 2005). However, for poorly known groups, the number of species known for South Africa represents, in some cases, less than 20 % of species known for Europe. This discrepancy has been attributed to lack of research in African seas (Griffiths 2005, Medd 2007).

Due to their extent of occurrence, large-ranged species are more likely to be discovered and described than their smaller-ranged counterparts (Gibbons et al. 2005). Despite this,

endemism is high in southern Africa radiating from the centre of the region under investigation. Regardless of the plethora of possible un-described species in both South Africa and the continent, the number of described species provides sufficient information to investigate patterns, particularly if the results are interpreted with caution.

The bi-modal range size frequencies distribution is exaggerated by the clear absence of middle of the series range sizes. Brown (1984) and Gaston (1998) have shown that increasing the scale of investigation from local, to a regional geographic area, or to continental scales can change the distribution shape from bi-modal to uni-modal. Thus the spatial scale of my investigation would result in a bi-modal or hollow-shaped graph. The departure from log-normal, thus reflects the scale of investigation, which, as I have noted represents mainly local endemics and the large Indo-Pacific component of southern African biota.

Furthermore, the estimate of occupancy distribution shape changes with variable sampling, cover, intensity and over time (McGeoch and Gaston 2002), as well as with trophic level investigated (Hui and McGeoch 2006). Effort, sampling intensity and time of investigation varied for the individual groups examined here, thus the data are not easily comparable. However, the results and the underlying mechanism and patterns evident provide a platform that has generated enough information to stimulate the formation of hypotheses governing causal mechanism of patterns along the southern African coastline. It is possible to speculate that the oceanographic conditions along the southern African coastline preclude average range size species. It appears that biogeographic breaks result in clearly defined cut off points for species distributions, thus limiting maximum range sizes to the maximum size of the biogeographic zone.

Comments on patterns found without adequate consideration of all the co-varying factors results in a fairly superficial discussion. The testing of empirical data against mathematical models has yet to produce positive results, that could culminate in a simple general mathematical description of species-range size distributions (Gaston *et al.* 2005), facilitating a better understanding of patterns found worldwide, as well as locally.

CONCLUSION

The main conclusions from this chapter are as follows:

➢ Peaks in species richness, range-restricted endemics, and range endpoints to a lesser or greater degree are associated with major oceanographic features along the coastline. Biogeographical-breaks and upwelling cell coastal-dynamics may result in the advection or retention of fauna and appear to be vital components affecting species range delimitation.

➢ The overlap of peaks in range endpoints and range-restricted species with existing biogeographic breaks (Emanuel *et al.* 1992), provides a concise re-affirmation of the location of these breaks along the coastline for invertebrates. The additional peaks found at Port Elizabeth need further investigation, and may, in fact reflect a different position for the East London biogeographic break. It is important to note that peaks in richness correspond to positions of Universities with marine department. As a result research efforts in these areas would be greater than elsewhere along the coastline, thus inflating values in these areas.

➢ The contribution of endemic species to species richness is by far greater than any other geographic affinity, particularly towards the centre of the study area (with the

exception of brachyurans and polychaetes), thus understanding factors affecting endemic species richness will contribute greatly to our understanding of southern African invertebrate distribution patterns.

➤ The biogeographic breaks along the coastline are regions of inflated species richness, endemicity, and restricted endemics, as well as possible regions of speciation. These "ecotones" might represent loci of evolution and speciation.

➤ Bi-modal and skew range size frequency distributions evident for most groups can be attributed to the high levels of endemic and Indo-Pacific species, as well as the scale of investigation.

CHAPTER 4

PATTERNS IN RANGE SIZE AND ANIMAL SIZE AMONG SOUTHERN AFRICAN MARINE INVERTEBRATES: THORSON'S RULE, BERGMANN'S RULE OR "RAPOPORT'S EFFECT"

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INTRODUCTION

Worldwide trends show that species richness and diversity increase towards the equator, where both peak (Stevens 1989, Barbour *et al.* 1987, Willig *et al.* 2003). Reasons for this latitudinal gradient in species richness (LGSR) are not well understood, but have been linked to gradients in temperature, stress, productivity, competition, predation, stability (Barbour *et al.* 1989,) and more recently gradients in effective evolutionary time or speciation rates (Rohde 1999, Gaston 2007, Mittelbach *et al.* 2007). There are, however, exceptions that do not follow these general trends (Willig *et al.* 2003).

In addition, a latitudinal gradient in geographical range size exists, whereby species range sizes increase with latitude. This is referred to as Rapoport's Rule (Stevens 1989). When the averages of the north-south length of the geographical ranges of organisms are plotted against latitude, there is a positive correlation; this pattern is linked to a species ability to tolerate changes in climate. Species found in high latitudes are exposed to a wider annual range of temperatures compared to species in lower latitudes. As a result the evolution of eurytolerant species is favoured and these tend to have a larger north–south range size (Stevens 1989).

Rapoport's Rule has been used to explain distributional data from a number of taxa, while some fitted the predicted pattern, others have not, with the pattern instead being attributed to factors such as sampling bias (Colwell and Hurt 1994) and scale (Rohde 1996, Santelices and Marquet 1998). For a review on LGSR and Rapoport's Rule see Gaston *et al.* (1998) and Rohde (1998).

In an attempt to understand gradients in species richness and range sizes, Stevens (1989, 1992) proposed that peaks in species richness were explained by "accidental species" that maintain species richness through the "Rescue Effect". At low latitude, species have small ranges and while they can exist at the margins of their geographical range they are not able to reproduce. Such populations are not well adapted to the local conditions, but are maintained by a continuous supply of new migrants or "accidentals" (i.e. the "Rescue Effect"). As a result the species richness at the margins of these small ranges is artificially inflated (Stevens 1989, 1992). Stevens thus proposes that the latitudinal gradient in species richness appears as a by-product of Rapoport's Rule and the Rescue Effect.

Taylor and Gaines (1999) added an additional component in an attempt to explain reverse gradients in species richness generated by Rapoport's Rule and the Rescue Effect, they suggested that competition plays a role in determining range size at different lattitudes. There is still doubt as to whether Steven's Hypothesis adequately explains the observed trends in latitudinal diversity. However if competition, Rapoport's Rule and the Rescue Effect operate strongly enough, it has been suggested that Steven's Hypothesis for LGSR can be accepted (Taylor and Gaines 1999).

It is important to note that the majority of the groups examined to determine the relationship between range size and latitude have been from high latitudes and the northern hemisphere, with lower latitudes and the southern hemisphere being somewhat neglected (Gaston *et al.* 1998). Rohde (1996) found that the phenomenon is a local one restricted to the Palae- and Nearctic regions above latitudes of 40-50 °N.

Marine invertebrate patterns do not clearly follow the patterns dictated by Rapoport's Rule. Such an example can be seen in the prosobranch gastropods of the eastern Pacific and

western Atlantic Oceans, where along both coasts of the Americas latitudinal diversity patterns are not explained by Rapoport's Rule, species area effect (Steven's Hypothesis), or by recent geological time. However, they did correlate to solar energy input (Roy *et al.* 1998). For eastern Pacific molluscs, latitudinal ranges of species also do not show the trends predicted by Rapoport's Rule, but instead vary with the spatial distribution of major oceanographic barriers (Roy *et al.* 1994).

Rohde (1999) suggested that dispersal ability of many marine invertebrates is likely to be greater at low compared to higher latitudes, which would result in the opposite of Rapoport's Rule. Marine benthic invertebrate species at low latitudes are inclined to produce many small pelagic larvae, compared to high latitude species. This phenomenon has been referred to as Thorson's Rule (Rohde 1999). Thorson's Rule is explained by a number of factors: Species at higher latitudes take longer to develop because of the low temperatures, this exposes their larvae to extended periods of predation and they may not complete their development during brief phytoplankton blooms. Most species are unable to synchronise hatching of larvae with phytoplankton blooms. In harsh cold conditions, non-pelagic larvae benefit more by settling closer to their parent population in known favourable conditions. Small larvae cannot tolerate extreme cold and non-pelagic development may be the result of selection for larger size at the beginning of development. Finally, it is more difficult to precipitate calcium in cold water, which may result in smaller body size for animals with calcareous skeletons. This may in turn elevate levels of viviparity (bearing live young) (Rohde 1999).

Marine parasites show these trends of latitudinal gradients in reproductive strategy (Rohde 1999). The greater dispersal ability of pelagic species at low latitudes would thus result in the opposite of Rapoport's Rule, with larger ranges occurring at lower latitudes. Support