# RESPONSES OF INTERTIDAL MACROALGAE AND ASSOCIATED FAUNA TO INTERACTIVE PROCESSES ACTING OVER MULTIPLE SPATIAL SCALES

A Thesis submitted in the fulfilment of the requirements for the degree of

Masters in Marine Biology

at

Rhodes University

By

Bruce Petrus Mostert

July 2010

## Abstract

The decrease of biological diversity from low latitudes near the equator towards high latitudes is one of the most fundamental patterns noted in ecology. These trends have been the subject of numerous terrestrial and marine studies and have caused the proposal of several explanatory hypotheses. No single hypothesis has adequately accounted for these observed trends. Furthermore, large-scale patterns are frequently modified by processes acting at meso- to smallscales. It is imperative to understand the interaction of these processes to elucidate the mechanisms controlling the structure of intertidal assemblages.

The main aim of this thesis was to test the influence of multiple processes at a range of spatial scales on biogenic engineers. Biogenic engineers, such as macroalgae, have been reported to be strongly influenced by processes such as grazing, biogeography and upwelling and subsequent effects are expected to be linked to their associated assemblages. I used infaunal assemblages associated with macroalgae as a model system to understand the interactive effects of meso-scale upwelling in conjunction with large-scale factors (regional and biogeographic). Three species of macroalgae, *Hypnea spicifera, Champia lumbricalis* and *Bifurcaria brassicaeformis*, inhabiting different but overlapping home ranges were used in this study. Smaller scale, physical attributes and the associated fauna of these algal species were compared.

The effects of meso- to large-scale physical gradients on marine organisms have been investigated in many instances and resultant gradients in physical variables observed. This study was undertaken to investigate morphological trends exhibited by *Hypnea spicifera* and *Champia* 

*lumbricalis* to compare possible similarities between coastlines and to determine if inferred meso- to large-scale processes influence physical trends in a similar manner despite the coastlines being affected by different hydrodynamic processes. The macroalgae were located in two distinctly different upwelling regimes, Hypnea spicifera on the east and south coasts and Champia lumbricalis on the west coast. Upwelling (delivery of nutrients and primary production) was not found to be an important factor in determining the physical characteristics of macroalgae but there were clear patterns linked to latitude. Mean percentage cover of Hypnea spicifera was positively correlated with distance along the east and south coasts. Mean mass and mean surface area of *H. spicifera* were, however, negatively correlated with distance from Port St Johns. Mean frond length showed a negative trend but this relationship was not statistically significant. On the west coast, there was a significant increase in mean frond length from north to south for *Champia lumbricalis*. Mean surface area and mean mass of *C. lumbricalis* exhibited non-significant negative trends from north to south while there was a non-significant positive trend for mean percentage cover. Following the "Productivity Hypothesis", these patterns from north to south along the coastlines of South Africa could have important implications for biodiversity associated with these algae.

Many previous studies have focussed on the effects of upwelling on species (i.e. effects of nutrients and temperature) but have failed to separate this effect from large scale effects such as biogeography and latitudinal gradients. I tested the influence meso-scale upwelling, large-scale biogeographic processes and latitudinal gradients with two different species of macroalgae one on the east and south coasts of South Africa and the other on the west coast. *Hypnea spicifera* inhabits the east and south coasts of South Africa spanning two biogeographic provinces and is generally affected by relatively weak upwelling, whereas *Champia lumbricalis* inhabits the west coast spanning one biogeographic province which is subjected to intense persistent upwelling

year round. Within the east and west coast biogeographic provinces there are, however, regions with both upwelling and non-upwelling.

On the east and south coasts, entire assemblages differed significantly among the three Regions (St Lucia, Port Alfred and Knysna, while assemblages between upwelling/non-upwelling areas were not different. Assemblages on the different shores differed significantly from each other. There were no significant effects of region or upwelling for the number of individuals of Crustacea or Polychaeta, while Mollusca showed a significant effect of region. The number of individuals of other taxa showed a significant interaction of region and upwelling. Region had a significant effect on number of species of molluscs and other taxa, while there was no effect for either region or upwelling for the Crustacea or Polychaeta. In general different factors were shown to be important (region and shore) while upwelling was rarely important.

On the west coast assemblages associated with *C. lumbricalis* were not influenced by region or upwelling but there were significant differences between shores. Region, upwelling ad shore did not affect number of individuals. There was a significant interaction of region and upwelling for the number of species of crustaceans, while numbers of species of Mollusca, Polychaeta and other taxa showed no effects.

In general, regional factors strongly influenced most organisms, while upwelling played a minor role. Hypotheses about differences between upwelling and non-upwelling regions in terms of species abundances and composition due to the input of cold nutrient rich water were not supported. A link between the effects of larger-scale biogeographic factors and their influence on habitat forming taxa and the resultant effects on associated infauna would be a likely explanation for the patterns observed in this study.

Diversity of assemblages is known to be influenced by the structural complexity of a habitat, increasing complexity increases the amount of available niches therefore potentially increasing the number of species found within that habitat. Three species of macroalgae, *Hypnea spicifera*, *Champia lumbricalis* and *Bifurcaria brassicaeformis* were selected on the basis of being structurally similar and having their distributional ranges overlap in order to elucidate the effects of structure and macroalgal species on associated assemblages. *Hypnea spicifera* is different in terms of surface area and biomass from *Champia lumbricalis* and *Bifurcaria brassicaeformis*. Assemblages of species found on the three rhodophytes showed both shore and the species of alga had significant effects on composition. Only numbers of individuals of molluscs were affected by the species of alga. Crustacea and Polychaeta showed an interaction of the species of alga with shore. In the case of this study, it is likely that the three species of macroalgae mitigate biological stressors such as predation and physical stressors such as wave exposure and desiccation.

In general, meso-scale upwelling is suggested to be marginalised when considering the structuring of assemblages associated with macroalgae, while large scale biogeography has more of an influence. Within shores, assemblages were also strongly influenced by smaller-scale factors such as differences in the structure and species of alga. This study indicates the importance of investigating patterns across a range of spatial scales to gain a comprehensive understanding of factors influencing intertidal organisms.

### Acknowledgements

There are many people I would like to express my gratitude to. Firstly I would like to thank my supervisor, Professor Christopher McQuaid for all his assistance. Thanks for your patience and guidance over the past few years. I would not have reached this point without your help, for which I am extremely grateful.

I would also like to express my eternal gratitude to my co-supervisor Doctor Victoria Cole. Thanks for the countless hours and thousands of kilometres spent travelling around the coast of South Africa with me. Your company during those trips, through the cold tough sampling sessions to the fun and exploring was truly appreciated. Your guidance through the planning, analysing and writing phases, was again, truly appreciated.

Doctor Rob Anderson; your guidance and sharing your extensive knowledge of the southern African intertidal flora was greatly appreciated. Professor Johann Lutjeharms; your guidance and sharing extensive knowledge of oceanographic processes of influencing the South African coastline was greatly appreciated.

Tamsyn Livingstone and KZN Wildlife; I am grateful for your hospitality and help in sample collection on the east coast. Evie Weiters, Adam Ludford, Linda Johnson and Alistair Becker thank you for your help in collecting data. Lillian Jacob and Mpho Mdlongwa your help in the lab was greatly appreciated. Linda Johnson your help in the construction of the maps for my thesis was greatly appreciated.

To all my family for your support and encouragement through my university career, especially my Mom, Dad, Sister and Gran, thanks for being interested and enthusiastic about my studies. I only wish that you had been able to join me on some of my trips, I know you all would've thoroughly enjoyed them.

Lastly I'd like to thank my girlfriend Amy for her interest, enthusiasm, patience and support during this process, you are truly appreciated.

## Table of Contents

Abstract	ii	
Acknowledgements	vi	
List of Tables	X	
Table of Figures	xiii	
Chapter 1		
General Introduction	1	
1.1 Influences of biogeography on marine organisms:	2	
1.2 Importance of coastal upwelling:	3	
1.3 Marine organisms as habitats:	5	
1.4 Elucidation of factors affecting epifauna associated with macro-algae:	7	
Chapter 2		
Large Scale Patterns of Hypnea Spicifera and Champia lumbricalis Distribution	10	
2.1 Introduction:	10	
2.2 Methods:	14	
2.2 Results:	18	
2.3 Discussion:	20	
Chapter 3		
Large- to Meso-scale Patterns in Variation in Faunal Assemblages Associated with Macroa	ılgae	
	26	
3.1 Introduction:	.26	
3.2 Methods:	31	
3.2.1 Study sites:	31	
3.2.2 Collection and processing of samples:	36	
3.2.3 Data analysis:	37	
3.3 Results	38	
3.4 Discussion:	47	
Chapter 4		
Comparison of Different Species of Structurally Similar Macroalgae	52	

4.1 Introduction:	52
4.2 Methods:	55
4.3 Results:	58
4.4 Discussion:	65
Chapter 5	
General Discussion	69
5.1 The role of biogenic habitats:	
5.2 Biogeographic patterns:	
5.3 Integration of factors acting at different spatial scales:	74
References	75
Appendix	106

### List of Tables

Appendix C: List of identified infaunal species associated with *Hypnea spicifera* along the east and south coasts and *Champia lumbricalis* along the west coast......108

## Table of Figures

- Figure 3.3: nMDS plot of assemblages living on *H. spicifera* on the east and south coasts of South Africa (upwelling; St Lucia ♦, Port Alfred ■ Knysna ▲; non-upwelling; St Lucia ◊, Port Alfred □, Knysna Δ).
- Figure 4.1: Map indicating the two sampling locations where *H. spicifera, C. lumbricalis* and *B. brassicaeformis* distributions overlapped and were found on the same shore..... 56

## Chapter 1

## **General Introduction**

There is a general tendency in many taxa for species richness to increase from high latitudes at the poles to low latitudes near the Equator (e.g. Rohde 1992, Gaston 1996, 2000, Chown and Gaston 1999). Trends along latitudinal gradients have been the subject of numerous terrestrial (e.g. Wright et al. 1993) and marine studies (Rex et al. 1993, Macpherson and Duarte 1994, Roy et al. 1998, Gray 2001), and several causation hypotheses have been proposed, e.g. the species richness-energy hypothesis, environmental stability hypothesis, species richness-area hypothesis, Rapoport's rule, and the mid domain effect (reviewed in Gaston and Blackburn 2000, Willig et al. 2003). No single hypothesis adequately accounts for all such patterns along latitudinal gradients (Rohde 1992, Gaston and Blackburn 2000, Willig et al. 2003). Macroalgae are unusual in that species richness does not increase from low latitudes to high latitudes (Bolton 1994) Many large scale marine patterns are modified by smaller meso-scale processes (10s to 100s km) such as upwelling (Broitman et al. 2001, Menge et al. 2004, Weiters 2005, Blanchette et al. 2007, Freidenburg et al. 2007) or even smaller scale effects such as wave exposure (McQuaid and Branch 1984, Bustamante et al. 1995a, Bustamante and Branch 1996, Menge 2000). Larger scale patterns may also be influenced by localised processes such as competition, predation and small scale habitat complexity (Dayton 1971, Chapman and Underwood 1994). This interaction between broad and local scale processes highlights the need to understand patterns of distribution and abundance of organisms at a range of spatial scales (see Underwood *et al.* 2000 for review).

#### 1.1 Influences of biogeography on marine organisms:

Biogeography is the study of the geographical distribution of organisms and, although this definition seems relatively simple, it can involve many underlying historical events and processes, including geological and biological evolution, which have profound effects on present biogeographic distribution patterns of species over meso-scales (Brown and Jarman 1978, Myres and Giller 1988, Bustamante and Branch 1996). Patterns in biogeography can be recognised at three different levels (Myres and Giller 1988). Firstly, primary patterns involve species responding to large-scale environmental phenomena (also known as underlying controlling processes) that create non-random spatial distributions. Secondary patterns are formed from a collection of characteristics of a group of species or taxa, such as diversity, richness, endemicity, etc. Tertiary patterns look at the relationships between secondary and abiotic data, such as species-area relationships (Myres and Giller 1988).

Although biogeography is considered important in mapping the distribution of species, the nature of its development makes it highly variable among species, with species occurring over the same area exhibiting different biogeographical patterns and boundaries due to varying physiological and ecological adaptations, and different centres of dispersal for different species (Myres and Giller 1988, Bustamante and Branch 1996). This has been demonstrated over both terrestrial and marine ecosystems (Bustamante and Branch 1996, Crisp *et al.* 1999). It has been suggested that boundaries between the west and south coast provinces in South Africa differ depending on species analysed e.g. Polychaetes (Day 1967), amphipods (Griffiths 1974), opisthobranchs (Gosliner 1987), echinoderms (Thandar 1989) and octocorals (Williams 1992). The elucidation of multispecies biogeographical distribution patterns requires objective and repetitive criteria that is unaffected by the ecology of specific taxa (Bustamante and Branch 1996).

Along with biogeography, a suite of top-down and bottom-up factors affect the intertidal region and contribute to the shaping of intertidal communities (Menge 2000). Bottom up factors include physical aspects of the shore such as wave exposure (McQuaid 1981, McQuaid and Branch 1985, Field and Griffiths 1991, Emanuel *et al.* 1992) and sheltering effects, such as the location of the shore in relationship to bays (Bustamante and Branch 1996). Nutrient gradients over meso-scale distances (Carter and D'Aubrey 1988, Carter and Schleyer 1988, Lutjeharms *et al.* 2000a) also affect assemblages on intertidal rocky shores (Bustamante *et al.* 1995b, Menge 2000, Weiters 2005, Aquilino *et al.* 2009).

#### 1.2 Importance of coastal upwelling:

Nearshore oceanographic processes have been observed to be important in influencing intertidal marine organisms in the intertidal region (Menge *et al.* 1997a, Menge 2000). There are five major geostrophic gyres worldwide, two of which are located in the Northern hemisphere and three in the Southern Hemisphere, all of which have distinct geostrophic currents within them (Garrison 1993). The currents are classified by their position within gyres as Western Boundary Currents, Eastern Boundary currents or transverse currents (Garrison 1993).

Slow moving, cold Eastern Boundary Currents such as the Canary, Benguela, California and Humbolt currents are considered to be biologically productive (Small and Menzies 1981, Huyer 1983, Ware 1992, Patti *et al.* 2008), however there is no agreement as to which local factors (wind mixing, light availability, continental shelf size and shape, local strong currents, temperature, characteristics of the water brought to the surface by upwelling, dominant winds, el Niño oscillation and/or input from major rivers) are responsible for this high productivity in each of these areas (Carr and Kearns 2003, Hardman-Mountford *et al.* 2003, Thomas *et al.* 2004, Ribeiro *et al.* 2005, Patti *et al.* 2008). In the Benguela current, offshore Eckman transport, due to

strong and persistent coastal wind stress injects cold, nutrient-rich water into the euphotic zone, driving primary and secondary production (Small and Menzies 1981, Huyer 1983, Weiters 2005).

Western Boundary currents are generally considered to be oligotrophic, such as the Gulf Stream (Garrison 1993, Paerl *et al.* 1997, Devred *et al.* 2007), the Agulhas Current (Condie 1995, Lutjeharms *et al.* 1989, 2000a, Lutjeharms 2006, 2007), the East Australian Current (Richardson and Poloczanskac 2009) and the Brazilian Current (Fleoter *et al.* 2001, Godoy *et al.* 2002), but upwelling due to oceanographic processes induced by variation in shelf topography is typical in these currents worldwide (Condie 1995). Specifically, widening of the continental shelf along the path of the current can induce persistent upwelling centres and this phenomenon has been noted in the Gulf Stream (Hsueh and O'Brien 1971, Blanton *et al.* 1981), the Kuroshio Current (Nagata 1970, Lutjeharms *et al.* 1993), the East Madagascar Current (Lutjeharms and Machu 2000) and the East Australian Current (McClean-Padman and Padman 1991, Tranter *et al.* 1986) and has also been described by Gill and Schumann (1979), Lutjeharms *et al.* (1989, 2000a, b) and Lutjeharms (2006, 2007) for the Agulhas current.

These meso-scale oceanographic processes can strongly influence patterns of abundance, distribution and biomass of many species of marine intertidal organisms (Menge *et al.* 1997a, Menge 2000, Weiters 2005, Freidenburg 2007) and create striking patterns over such spatial scales (Broitman and Kinlan 2006). Previous studies have attempted to link oceanographic processes with nearshore larval transport and subsequent settlement patterns. Upwelling is thought to transport larvae offshore during times of upwelling events (Parrish *et al.* 1981, Yoshioka 1982, Gaines and Roughgarden 1985, Roughgarden *et al.* 1988) limiting recruitment to

relaxation of prevailing winds and consequent downwelling (Yoshioka 1982, Gaines and Roughgarden 1985, Roughgarden *et al.* 1988, Farrel 1991). In subsequent studies Morgan *et al.* (2009a, b), however, suggested that recruitment is not limited by infrequent relaxation processes but rather by as yet unidentified mechanisms acting within upwelling, and further supports this theory with larval behavioural studies (Morgan *et al.* 2009b, c, Morgan and Fisher 2010).

#### 1.3 Marine organisms as habitats:

Habitat can be defined as "The living place of an organism or community, characterised by its physical or biotic properties" (Andrewartha and Birch 1954, Allaby 1998. Pp. 192). This does, however, not only include abiotic physical structures on the landscape but also structures created by organisms that form secondary habitats for other organisms and this has been referred to as "physical ecosystem engineering" (Jones et al. 1997). Jones et al. (1994) originally defined ecosystem engineers as "organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials" (Jones et al. 1994. Pp. 373). Subsequently this has focused many ecological studies on ecological engineers (e.g. Castilla et al. 2004, McCabe and Gotelli 2003, Jouquet et al. 2006). Ecosystem engineers can be divided into two categories: autogenic and allogenic (Jones et al. 1994, Jones et al. 1997). Allogenic engineers transform the physical state of resources by their actions, making them available for use by other organisms, whereas autogenic engineers alter the environment by incorporating themselves in the engineered environment (Jones et al. 1994, 1997). Biogenic habitats are mostly formed by autogenic ecosystem engineers (Wright et al. 2006) and this phenomenon follows on into the marine ecosystem where biogenic habitats are mostly formed by autogenic engineers (e.g. Seed 1996, Bologna and Heck 1999, Gutiérrez et al. 2003, Burnaford 2004, Prado and Castilla 2006, Borthagaray and Carranza 2007, Cole 2009, Cole and McQuaid in press).

Examples of important habitats formed by autogenic engineers include rainforests (Connell 1978), coral reefs (Connell 1978, Anderson 1992), mangroves (Ellison *et al.* 1999), and submerged macrophytes in freshwater systems (Carpenter and Lodge 1986). Structural complexity created by these habitat-forming organisms is known to be an important factor, often influencing the abundance and diversity of associated taxa (Fletcher and Underwood 1987, Hacker and Steneck 1990, Huston 1994, Beck 1998, Attrill *et al.* 2000). Increasing structural complexity within a habitat increases the available niches present for utilisation by species, and thus often has effects on the number and diversity of species found within the habitat (MacArthur and MacArthur 1961, Gilinski 1984, Dean and Connell 1987c, Attrill *et al.* 2000, Crooks 2002).

The importance of habitat-forming species in the facilitation of diversity of smaller taxa has been highlighted by Bruno *et al.* (2003). Comparisons between bare areas and those that have biogenic habitats have consistently shown that biogenic habitats contain more taxa and a higher diversity. For example, bare soft sediment compared with mussel beds (Ragnarsson and Rafaelli 1999, Commito *et al.* 2005), in benthic habitats, (Diaz *et al.* 2004) and bare rock compared with mussel beds in marine and fresh water habitats (Botts *et al.* 1996, Spooner and Vaughn 2006, Borthagaray and Carranza 2007). Biogenic habitats such as turf-forming coralline algae (Kelaher 2003a) and canopy-forming *Ascophyllum nodosum* (Bertness *et al.* 1999) are known to provide physical structure that in turn provides protection from potential physical stresses such as

desiccation. Quantification of what resources are being made available and the role played by autogenic engineers is an important step in ecological studies involving ecosystem engineers.

#### 1.4 Elucidation of factors affecting epifauna associated with macro-algae:

Macroalgae have been identified as important ecosystem engineers on rocky shores (e.g. Thompson *et al.* 1996, Kelaher *et al.* 2001, Kelaher 2002, 2003a, b, Kelaher *et al.* 2007). The three macroalgal species considered in this study; *Bifurcaria brassicaeformis* (Phaeophyta), *Champia lumbricalis* and *Hypnea spicifera* (Rhodophyta) were deemed to have similar shape, size and sized holdfasts thus potentially providing similar amounts and quality of habitat for associated organisms. *H. spicifera* occurs from north of Richards Bay on the east coast of South Africa, to the west coast as far as Angola, while *C. lumbricalis* is abundant from south Angola to Cape Agulhas on the south coast (Stegenga *et al.* 1997)(Fig 2.1). *B. brassicaeformis* has a much more limited distribution occurring from Cape Columbine on the west coast to Cape Agulhas on the south (Stegenga *et al.* 1997).

Meso-scale variations in nutrients (Carter and D'Aubrey 1988) and primary production of phytoplankton have been observed and studied in many instances (e.g. Carter and Schleyer 1988, Lutjeharms *et al.* 2000a). The effects of these variations have been the subject of many studies involving algal assemblages, composition and abundance within the rocky intertidal region (Bustamante *et al.* 1995b, Weiters 2005, Freidenberg *et al.* 2007, Aquilino *et al.* 2009) and rocky shore taxa (Harris *et al.* 1998, Menge *et al.* 1999, Menge 2000, Phillips 2005, Blanchette *et al.* 2007). Meso-scale variations in primary productivity along coastlines can be attributed to upwelling processes and the accompanying changes in physical and chemical dynamics

associated with the water column (Lutjeharms et al. 2000a, Lutjeharms 2007). Studies in the past have examined the effects of these upwelling events on intertidal organisms over meso-scale distances (e.g. Dayton et al. 1999, Menge 2000, Broitman et al. 2001, Menge et al. 2004, Weiters 2005, Blanchette et al. 2007, Freidenburg et al. 2007) but this has not been done across large scales over which biogeographic or latitudinal effects may be encountered. Consequently, it is difficult to generalise the effects of upwelling in a biogeographic context. Biogeography has been shown to have strong effects on intertidal organisms in southern Africa (Emanuel et al. 1992, Bustamante and Branch 1996). The southern African coast was originally classified into three biogeographical provinces (Stephenson 1939, 1944, 1948). Later work by Emanuel et al. (1992) and subsequent work by Bustamante and Branch (1996), however, proposed four main biogeographical provinces: (1) the subtropical Natal province, (2) the warm temperate Agulhas province, (3) the cool temperate Namagua province, and (4) the cool temperate Namib province. Although four biogeographic provinces have been proposed for most fauna around the southern African coastline, Bolton (1986) suggested that the marine algae are governed by two provinces, a warm temperate province with west and south coast components and a subtropical province on the east coast. Further work by Bolton et al. (2004) indicates that the change from tropical to temperate flora occurs around St Lucia, however they consider the Natal province to be composed of a mixture of tropical and temperate flora forming a large overlap region. Along both the east and west coasts, two upwelling and two non-upwelling areas separated by mesoscales were selected. Upwelling along the east and south coasts occurred in two biogeographic provinces; the subtropical Natal province and the warm temperate Agulhas while the upwelling areas along the west coast were both incorporated in the cool temperate Namaqua province (Emanuel et al. 1992, Bustamante and Branch 1996).

The effects of large-scale (biogeography), meso-scale (upwelling), and small-scale (physical/structural attributes of the macroalgae) factors on epifaunal assemblages associated with *H. spicifera* and *C. lumbricalis* around the coast of South Africa are investigated.

In Chapter 2, large scale patterns are investigated in terms of their influences on two habitatforming species (*H. spicifera* and *C. lumbricalis*). This addresses whether these different species of algae are influenced by similar processes affecting their size, biomass and cover over broad latitudinal scales (covering most of their range). In Chapter 3, biogeographical factors and mesoscale upwelling are investigated with the same two species of algae to determined whether such processes influence (directly or indirectly) the associated fauna. In Chapter 4, smaller scale factors are investigated using *H. spicifera* and *C. lumbricalis* and another structurally similar species, *B. brassicaeformis*. The role of structure on associated fauna was studied. The broader implications of this hierarchy of ecological factors are discussed in Chapter 5.

## Chapter 2

## Large Scale Patterns of *Hypnea Spicifera* and *Champia lumbricalis* Distribution

#### 2.1 Introduction:

The increase of biological diversity from high latitudes towards the equator is one of the most fundamental patterns noted in ecology (Brown and Lomolino 1998, Gaston 1996, Rosenzweig 1995, Willig 2001, Willig et al. 2003). This trend is possibly one of the oldest patterns noted in ecological history, and was first described by von Humboldt in the early 1800s (Hawkins 2001). The pattern is consistent for most taxa (e.g. plants, mammals, fish, insects) and covers a variety of habitats, both terrestrial and marine, but not all organisms conform to this trend (e.g Gray 2001). The identification of a single mechanism that explains latitudinal gradients in species richness has been elusive and a multifactor approach is more commonly employed (see Willig et al. 2003 for review). The search for a mechanism to explain latitudinal trends started in the 1950's (Dobzhansky 1950, Hutchinson 1959) and the first review of possible factors accounting for latitudinal gradient in species richness was compiled by Pianka (1966). Over 30 explanatory hypotheses have since emerged in an attempt to explain this long standing important trend. Some are, however, too specific to account for the ubiquitous nature of the gradient, others could not produce the gradient and are considered to involve circular logic and are thus deemed implausible. A great number are tightly linked due to the use of similar explaining mechanisms and of these, six are deemed to hold the most promise for explaining our understanding of species richness and latitudinal gradient relationships (reviewed in Willig et al. 2003).

The most promising hypotheses explaining trends in biological diversity trends include the following. The Geographic Area Hypothesis; the tropics are comprised of a greater surface area and are thus able to support more species, this, in conjunction with higher productivity, produces higher species diversity at lower latitudes (Terborgh, 1973, Rosenzweig 1995). The Ambient Energy Hypothesis; organisms' physical responses to temperature form the basis of this hypothesis (Willig *et al.* 2003), high latitude environments are less hospitable than those at low latitude (Kaufman 1998, Willig et al. 2003) and thus more costly adaptations are required for survival leading to lower species richness (Brown 1988, Willig et al. 2003). The Rapoport-Rescue Hypothesis proposes that the distributional ranges of species are inversely related to latitude (Rapoport 1975, Rabinovich and Rapoport 1975, Stevens 1989, Willig et al. 2003). High latitudes have large seasonal variation and species living here have broad physiological tolerances, this broad tolerance leads to not only persistence at a specific locale but leads to a large home range while the opposite occurs at low latitudes leading to continual dispersal and persistence of species into unfavourable habitats (Willig et al. 2003). The Evolutionary Speed Hypothesis; due to high temperatures at low latitudes evolutionary speed is increased, leading to high temperature induced speciation rates (Rohde 1992). Latitudinal gradients in temperature thus lead to greater species numbers in low latitudes compared with high latitudes where speciation rates are slower due to fewer temperature induced mutations, slowed selection pressure and slower generation times (Rohde 1992). The Geometric Constraints Hypothesis; the effect of environmental gradients on biota along a latitudinal gradient are overlooked (Willig et al. 2003) and the gradients observed are due to random placement of species within a specific bound area which is defined by a physical or physiological border (e.g. continental coastlines, salinity gradients) (Colwell and Hurtt 1994). The Productivity Hypothesis; annual input of solar radiation is inversely correlated to latitude and relates to energy availability, productivity and biomass (Robinson 1966, reviewed in Willig et al. 2003). In general productivity (measured by actual evapotranspiration) is correlated to species richness but does not encompass all species (e.g. Currie 1991). This hypothesis fails to provide a mechanism whereby species richness increases and is limited by the available energy as opposed to a simple increase in population density with energy increase (Currie 1991, reviewed in Willig *et al.* 2003). A step towards testing this hypothesis requires there to be a latitudinal trend in biomass or habitat-creating taxa.

Variation in abundances of species and diversity is known to occur across large scales along coastlines worldwide (e.g. Australia, Underwood and Chapman 1998; Canada, Archambault and Bourget, 1996; Europe, Jenkins *et al.* 2005, Cole and Chapman, 2007; Japan, Nakaoka *et al.* 2006; South Africa, Bustamante and Branch 1996, Xavier *et al.* 2007; South America, Rivadeneira *et al.* 2002, Kelaher *et al.* 2007; USA, Foster 1990, Blanchette *et al.* 2006, Sagarin and Gaines 2006). Large-scale processes are generally thought to influence the pattern and number of species across large areas and this has prompted studies that investigate the role these processes play in biological variation (Underwood and Chapman 1998).

The effects of meso- to large-scale physical gradients on marine organisms have been investigated in many instances (e.g. upwelling, Menge *et al.* 2004, Weiters 2005, Xavier *et al.* 2007; temperature, Crisp 1964, Broitman *et al.* 2001). Offshore Ekman transport found in winddriven upwelling systems, and subsequent relaxation of this process, has been identified as an important oceanographic process influencing temporal and spatial variation in recruitment rates (Gaines and Roughgarden 1985, Roughgarden *et al.* 1988, Farrell *et al.* 1991, Alexander and Roughgarden 1996). It has been suggested that variation in propagule supply, due to differing strengths of offshore Eckman transport, accounts for the differences in the broad patterns present in community structure between the coasts of northern California and Oregon (Connolly and Roughgarden 1998, 1999a, b). Patterns in functional groupings over continental scales have also been suggested to vary due to environmental gradients associated with factors that vary with latitude, such as solar radiation (Gaines and Lubchenco 1982, Brown and Lomolino 1998).

At smaller spatial scales biological interactions are also known to influence the assemblage composition and species distribution on the rocky intertidal shore (Broitman *et al.* 2001). Top-down effects of predators, such as seastars and whelks, can have effects on dominant sessile functional groups, hence altering rocky shore assemblages (Paine 1974, Menge 1976, Castilla and Duran 1985, Paine *et al.* 1985, Castella and Paine 1987, Navarrete 1996, Navarrete and Menge 1996). Algal competitive interactions have often been demonstrated by experimental manipulations, the results showing that encrusting algal forms are out- competed by corticated algae and kelp functional groups, which then become the dominant space occupiers (e.g. erect fleshy algae over encrusting calcified algae, reviews in Lubchenco and Gaines 1981, Santelices 1990, Steneck and Dethier 1994). Under high herbivory pressure, competitive hierarchies can be altered (Lubchenco and Gaines 1981, Sousa *et al.* 1981, Branch and Moreno 1994). For example, corticoid algae or kelps are replaced by crustose algae as the dominant space occupier under high grazing pressure (Branch and Moreno 1994).

All of these afore-mentioned processes can affect the distribution and abundance of species at different scales along the coast. Although this study does not look into the processes that control the distributional abundance patterns or physical attributes of *Hypnea spicifera* along the east and south coasts and *Champia lumbricalis* along the west coast, these trends can be related back to, or inferred from, well-known and described physical and biological processes that occur along these two coastlines. This study was undertaken to investigate physical trends exhibited by

both species of algae to compare possible similarities between coastlines and to see if inferred meso- to large-scale processes influence physical trends in a similar manner despite the coastlines being affected by different hydrodynamic processes.

#### 2.2 Methods:

*Hypnea spicifera* and *Champia lumbricalis* are both rhodophyte macro-algae commonly found on wave-exposed rocks in the Lower Balanoid Zone (Stegenga *et al.* 1997). *Hypnea spicifera*, although classed within the Rhodophyta, is typically green in colour with the purplish base giving the only hint of the red pigments that are diagnostic of the red algae. Branching from the rhizomes are stiff green axes, which give rise to green spikes (Fig 2.1a) (Stegenga *et al.* 1997). *Hypnea spicifera* occurs from the northern Natal Province, south through the Warm Agulhas Province around the Cape of Good Hope into the Namaqua province, before moving north into the Namib province (Issac and Hewitt 1953, Stegenga *et al.* 1997). *C. lumbricalis* has branching rhizomes that give rise to reddish-brown segmented septae that bear bundles of branches (Fig 2.1b). *C. lumbricalis* occurs from Cape Agulhas, up the West Coast through the Namaqua province, to the southern border of the Namib Province (Stegenga *et al.* 1997). Despite previous studies documenting the broad distribution of these algae, they were not present at all sites investigated for this study. For the purposes of this study, *H. spicifera* and *C. lumbricalis* were therefore sampled in the central part of their distributions during June and July 2009.

Moving westwards from Port St Johns on the east and south coasts of South Africa, 1150 km of coast was sampled, all sites were out of bays on the open coast. Six samples of *H. spicifera* were randomly selected and collected from each of eight shores from Kidd's Beach (north) to Vermont (south) (Fig 2.2). The mass (entire holdfast and associated fronds on an individual plant

were scraped from the rock and weighed), surface area of the alga and the maximum length of six fronds from each plant were measured and recorded. The surface area of each plant was calculated as described by Johnson and Scheibling (1987). The weight of a 5x5 cm piece of water proof paper measured and recorded. The paper was then dipped in oil (Johnson & Johnson Baby  $OiI^{TM}$ ) and left to drip dry for approximately 30 seconds so a monomolecular layer of oil coated both sides of the paper. The paper was then reweighed and the weight of the oil coating the 5x5 cm (surface area of 50 cm<sup>2</sup>, two sides of a 25 cm<sup>2</sup> piece of paper) paper was recorded. The weight of a macroalgal sample was measured and recorded. The macrolalgal sample was then dipped in oil and allowed to drain until it was deemed to have a monomolecular layer of oil coating it (2 -5 minutes) and reweighed. From the weight of the oil coating the macroalga the surface area was calculated as per the following equation.

In addition to measurements of mass, surface area and length, the cover of algae was estimated within the central range of the distribution of *H. spicifera* distribution. Five randomly placed quadrats (0.5 m x 0.5 m) were sampled on each shore from Port St Johns (north) to Plettenberg Bay (south), encompassing the main distribution of *H. spicifera*, to measure point intersects of area covered by *H. spicifera* (Fig 2.2). The relationships among distance from Port St Johns, mean plant surface area, mean frond-length, mean mass and mean percentage cover of *H. spicifera* were determined. Correlation coefficients (Pearson's r) between distance and each of these variables were calculated.

Sampling of *C. lumbricalis* was conducted along a 656 km stretch of coastline from Groenrivier on the west coast to Vermont on the south coast (Fig 2.2). All sites were out of bays, on the open coast, and were considered to have similar exposure to waves. Six samples of *C. lumbricalis* were collected at 10 sites from Groenrivier to Vermont and from these samples surface area of the alga was measured and recorded. Ten samples of *C. lumbricalis* were collected from the 8 sites from Groenrivier to Bloubergstrand and the mean mass and mean length of 6 fronds were calculated. Twenty haphazardly-placed quadrats (0.5 m x 0.5 m) were sampled at each of these sites (Onrus and Vermont were, however, not included as they fall outside the Namqua province). In each quadrat, percentage cover of the alga was estimated from 100 evenly spaced points. The relationships between distance from Hondeklipbaai, a randomly selected point north of Groenrivier, mean plant surface area, mean frond-length, mean mass and mean percentage cover of *C. lumbricalis* were determined. Correlation coefficients (Pearson's *r*) between distance and each of these variables were calculated.



Figure 2.1: Typical *H. spicifera* (a) and *C. lumbricalis* (b) plants found in the rocky shore intertidal region

(a)

(b)



Figure 2.2: Map indicating *H. spicifera* sampling sites along the east and south coasts, starting at Port St Johns in the north and moving south to Vermont. *C. lumbricalis* was sampled along the west coast starting at Groenrivier in the north and moving south to Bloubergstrand.

#### 2.2 Results:

On the east and south coasts, mean percentage cover of *H. spicifera* was significantly positively correlated with distance from Port St Johns (r = 0.85, d.f. = 3, P < 0.05) (Appendix A). Mean mass (r = -0.77, d.f. = 4, P < 0.01) and mean surface area (r = -0.77, d.f. = 4, P < 0.01) decreased significantly in a south west direction from Port St Johns to Vermont (Appendix A). Mean frond length decreased moving southwest from Port St Johns towards Vermont, but the relationship was not significant (r = -0.03, d.f. = 4, P > 0.05) (Appendix A).

There was an increase in mean percentage cover of *C. lumbricalis* from north to south, moving from Hondeklipbaai to Onrus, but this was, however, not significant (r = 0.36, d.f. = 18, P > 0.05) (Appendix B). Mean surface area (r = -0.21, d.f. = 8, P > 0.05) and mean mass (r = -0.38, d.f. = 8, P > 0.05) of *C. lumbricalis* showed a decrease from north to south (Appendix B). Although these results, were not significant, there was a significant increase in the mean length of *C. lumbricalis* fronds, from north to south (r = 0.74 d.f. = 8, P < 0.01) (Appendix B).

Table 2.1: Correlation analysis of relationships between mean distance south from the most northerly site and mean percentage cover, mean surface area, mean mass and mean frond length of *H. spicifera* (a) and *C. lumbricalis* (b). For this table: \* P < 0.05, \*\* P < 0.01.

	(a) H. spicifera		(b) <b>(</b>	(b) C. lumbricalis	
	d.f.	Pearson's r	d.f.	Pearson's r	
Mean percentage cover	3	* 0.85	18	0.36	
Mean surface area	4	**- 0.77	4	- 0.21	
Mean mass	4	**- 0.77	8	- 0.38	
Mean frond length	4	- 0.03	8	** 0.74	

#### 2.3 Discussion:

This study showed only one significant trend with respect to the physical variables of C. lumbricalis moving south from Hondeklipbaai to Onrus. Along the 660 kilometers from Hondeklipbaai to Vermont where C. lumbricalis was sampled, mean frond length increased significantly from north to south. Bustamante et al. (1995a) showed that primary production in epilithic micro-algae was correlated with nutrient availability and when macro-algae were considered, functional forms of macro-algae changed from foliose algae on the west coast to coralline algae on the east coast, however macro-algal standing stocks did no correlate with the productivity gradient, with equally high standing stocks on the east and west coasts and low standing stocks on the south coast. On the South African coast, it has been suggested that wave exposure has an effect on autotrophs, filter feeders, grazers and invertebrate predators (McQuaid and Branch 1985, Branch and Griffiths 1988, Gibbons 1988, Field and Griffiths 1991, Bustamante and Branch 1996), although it is acknowledged that higher biomass on the west coast is due to nutrient input from upwelling (Brown 1992, Pitcher et al. 1992, Bustamante and Branch 1996). The increase in frond lengths from north to south on the west coast does not agree with previous work on the effects of upwelling on algae as the more frequent and intense upwelling in the northern part of the Namaqua province (Brown 1992, Bustamante et al. 1995b) would suggest greater frond lengths, due to greater growth rates (Nielson and Navarrete 2004, Weiters 2005). Annual input of solar radiation is considered to be higher at low latitudes and relates to energy availability, productivity and biomass (Robinson 1966). These two well studied and plausible phenomena fail to create more than one substantial trend when looking at physical attributes of macroalgae over a large scale. The west coast is subjected to low SST due to the nature of the Benguela current and its associated upwelling (Brown 1992, Bustamente et al. 1995b). It is well know that temperature has a regulating effect on metabolism and that low temperatures slow growth rates. This effect would provide a plausible explanation whereby the

low sea surface temperature cancels out the solar energy input at low latitudes. I propose another mechanism whereby the grazing influences the frond length of *C. lumbricalis*, producing the north to south trend despite the high input of nutrients in the northern part of the Namaqua province.

Grazing has a substantial effect on macro-algae, as seen in the Aleutian Islands of Alaska where sea urchins regulated kelp abundance (Estes and Palmisano 1974, Estes and Duggins 1995) and noted on South African shores by Bustamante et al. (1995a) where the limpets, Scutellastra argenvillei and Cymbula granatina (both formally Patela) feed primarily on kelp. A high diversity of limpets is found on the South African rocky shore (Branch 1971, 1975) and Scuellastra argenvillei and Cymbula granatina are noted as two of the most important grazers on the west coast due to their high densities and large size and besides feeding on kelp, they are known to be generalist grazers (Eekhout et al. 1992). These limpets are found in their highest concentrations in the Namaqua province and numbers decrease southwards (Eekhout et al. 1992). Grazing by these and other limpets could be responsible for the increase in frond length of C. lumbricalis seen from north to south. The mean percentage cover also increased slightly along the 470 kilometres of coast from Hondeklipbaai to Bloubergstrand, and again upwelling had no effect on the percentage cover of C. lumbricalis along the latitudinal gradient from north to south. Broitman et al. (2001) noted that there was higher cover of corticoid algae at sites affected by upwelling on the coast of central Chile, however the slight trend of increasing cover in a southwards direction could be due to top down effects of grazing as previously mentioned

Mean mass and mean surface area of *C. lumbricalis* both showed a negative correlation from Hondeklipbaai to Vermont. The mean mass increased from Strandfontein to Bloubergstrand but then decreased at Vermont and Onrus. Intense upwelling located at Groenrivier and Cape Columbine (Nelson and Hutchings 1983, Jury 1985, Shannon 1985, DeMarcq *et al.* 2003) did not have an effect on either the mean mass or mean surface area. The mean surface area of *C. lumbricalis* showed a slight negative correlation with distance from north to south with no distinct peaks or troughs coinciding with upwelling or non-upwelling sites. Bustamante and Branch (1996) found that wave exposure had a controlling effect on biomass of species associated with rocky shores around South Africa, and given that *C. lumbricalis* was sampled from shores of similar orientation to swell out of bays no trend was expected. Upwelling centres at Groenrivier and Cape Columbine had no effect on *C. lumbricalis* in terms of mass and surface area but generally stronger upwelling is considered to occur in the northern part of the Namaqua province providing more nutrients for primary production. Additional nutrients would allow algae in the north to obtain greater biomass and surface area compared to areas further south where upwelling is not as strong or persistent (Brown 1992, Bustamente *et al.* 1995b).

Percentage cover of *H. spicifera* increased from north to south, while individual plants showed a decrease in mass and surface area along this same gradient. The low mean percentage cover of *H. spicifera* at Port St Johns could be due to high temperatures experienced at these locations on the east coast of South Africa causing desiccation and die back, as the mean temperatures decreases further west less desiccation occurs allowing more *H. spicifera* in the intertidal region (e.g. Hodgson 1984, Hawkins and Hartnoll, 1985, Norton 1985, Nelson *et al.* 2010). Emanuel *et al.* (1992) and Bustamante and Branch (1996) describe two provinces, the subtropical Natal province on the east coast and the warm temperate Agulhas province on the south coast, which have different rocky shore fauna and flora, while Vermont and Onrus are located in the western
overlap region (Bolton and Anderson 1990, Jackelman *et al.* 1991, Stegenga *et al.* 1997) and this could account for the differences in cover along this stretch of coast line.

Mean mass and mean surface area both showed a significant negative trend moving southwest from Port St Johns to Vermont, this distribution of *H. spicifera* transverses the Natal province to the Agulhas province (Emanuel *et al.* 1992, Bustamante and Branch 1996), implying that mean mass and mean surface area decreases from the former to the latter. Bustamante *et al.* (1995a) found that average macroalgal standing stocks were significantly lower on the south coast (Port Alfred to De Hoop) than the north coast (Umdoni to Nqabara), while results from Bustamante and Branch (1996) have, however, found that in terms of fauna and flora biomass patterns, there was no difference between the Natal and Agulhas provinces. Neither study specifically considered *H. spicifera* and this trend may not hold true for this particular species. Mean frond length had a slight negative trend from Port St Johns to Vermont, although frond lengths at Vermont and Onrus were longer than those from other sites. The frond lengths are likely to be controlled by top down effects such as herbivores, including the gastropod *Haliotis midae* (Wood and Buxton 1996) and fish (Burger 1990, van der Elst 1990) grazing on the macro-algae or bottom up effects such as inputs from wind driven upwelling common on some of the coast within these two biogeographic regions (Lutjeharms and Machu 2000, Lutjeharms 2007).

Underwood and Chapman (1998) found that trends are not always apparent over one specific sampling episode but may only become apparent during specific seasons. It would thus be useful repeat this study several times during different seasons to either support the observed patterns, such as the increase of frond length of *C. lumbricalis* from north to south, the increase of the mean percentage cover of *H. spicifera* from north to south and the decrease of mass and surface

area of *H. spicifera* from north to south, or to determine if there are other patterns that may not be apparent in the present study. The complex ecological processes which may contribute to the composition, distribution and abundance of species within the intertidal region also need to be further investigated. These effects have the ability to influence organisms on the rocky shore such as macro-algae and mussels (e.g. Harley *et al.* 2006, Menge *et al.* 2008) which in turn provide habitat for macro-fauna (e.g. Borthagaray and Carranza 2007, Cole *et al.* 2007) showing that overall many processes must be taken into account when considering the composition and abundance of species within the intertidal region.

Mean mass and surface area are closely related parameters and thus similar correlations were expected. A decrease in mean mass and surface area noted from north to south on the east and south coasts concurs with results from Bustamante et al. (1995a) who found lower algal standing stocks in the Agulhas province than in the Natal province. The results presented by Bustamante et al. (1995a), however contradict the gradients of primary production seen around the South African coast and they suggest that standing stocks of macroalgae are in fact a poor indicator of primary production and these stocks only represent a fraction of the potential algal stocks (Littler and Littler 1980, Hay 1981, Bosman et al. 1987). An investigation into the cause of high standing stocks of macroalgae in the Natal province in view of the low primary production expected here would be useful in understanding the South African coastline more thoroughly. On the west coast C. lumbricalis showed no trends for mean mass, surface area or cover but a positive trend in frond length moving from north to south. The study on the west coast only covered the Namaqua province, and results from the macroalgal correlations conform to the biogeographic boundaries of this province with no significant changes in mass surface area or cover, indicating that processes in addition to transitions between biogeographical provinces must influence frond lengths. Following the productivity hypothesis (Robinson 1966, reviewed in Willig *et al.* 2003), these trends in physical attributes of habitat forming macro-algae from north to south along the coastlines of South Africa could have important implications for biodiversity associated with these algae (investigated in Chapters 3 and 4).

## Chapter 3

# Large to Meso-scale Patterns in Variation in Faunal Assemblages Associated with Macroalgae

## 3.1 Introduction:

Biogeography is the study of the geographical distribution of organisms and often involves many underlying historical events and processes, including geological and biological evolution which have profound effects on current biogeographic distribution patterns of species over meso-scales (Myres and Giller 1988, Bustamente and Branch 1996). Biogeography is, however, not the only factor influencing the intertidal region, as a suite of top down and bottom up factors contribute to the shaping of assemblages (Menge 2000). Along with other bottom up effects such as wave exposure (McQuaid and Branch 1985, Field and Griffiths 1991, Bustamante and Branch 1996), gradients in nutrients and primary productivity have been shown to vary over meso-scale distances (Carter and D'Aubrey 1988, Carter and Schleyer 1988, Lutjeharms *et al.* 2000a, b), and to have effects on species assemblages associated with the intertidal region (Bustamente *et al.* 1995a, b, Menge 2000, Weiters 2005, Aquilino *et al.* 2009). These meso-scale variations in nutrients and primary productivity can in many cases be attributed to upwelling, which influences the physical and chemical dynamics associated with the water column (Lutjeharms *et al.* 2000a, b, Lutjeharms 2007). Upwelling injects cold nutrient rich water into the euphotic zone in the intertidal region, increasing primary production (Lutjeharms *et al.* 2000a).

Southern Africa is bordered by two distinctly different surface boundary currents; the Agulhas Current, along the east and south coasts (Stramma and Lutjeharms 1997, Lutjeharms 2007) and

the Benguela Current, along the west coast (Shannon and Nelson 1996, Shillington 1998, DeMarcq *et al.* 2003). These currents have similar oceanography to many others found in the world's oceans, and of particular interest to this study is meso-scale upwelling that is associated with these currents.

Oceanographic processes due to the variation in topography of the continental shelf along coastlines are commonplace worldwide. Upwelling induction by widening of the continental shelf along the path of a current is typical in all Western Boundary Currents (Condie 1995) and has been noted in the Gulf Stream (Hsueh and O'Brien 1971, Blanton *et al.* 1981), the Kuroshio (Nagata 1970, Lutjeharms *et al.* 1993), the East Madagascar Current (Lutjeharms and Machu 2000) and the East Australian Current (McClean-Padman and Padman 1991, Tranter *et al.* 1986) and described by Gill and Schumann (1979) and Lutjeharms *et al.* (2000a, 2007) for the Agulhas current.

On the east coast of South Africa, the Agulhas current is generally considered to be an oligotrophic water body, but persistent upwelling has been identified at locations where the width of the continental shelf increases (Condie 1995, Lutjeharms *et al.* 1989, 2000b, Lutjeharms 2006, 2007). This upwelling occurs at the northern end of the Natal Bight where the shelf width increases between Durban and Richards Bay producing an upwelling cell that lasts year round (Lutjeharms *et al.* 1989, 2000a, b, Lutjeharms 2006, 2007). The continental shelf is also wider from East London to Port Elizabeth, resulting in similar upwelling (Lutjeharms and Roberts 1988, Lutjeharms *et al.* 2000a, Lutjeharms 2006, 2007). Wind-driven upwelling also occurs on the shoreward edge of the Agulhas Current along the south coast and is particularly prominent at

head-lands during periods of strong and persistent westerly winds (Schumann *et al.* 1982, Lutjeharms *et al.* 2000a, Lutjeharms, 2006, 2007).

The west coast is dominated by the Benguela current. Offshore Eckman transport, due to strong, persistent coastal wind stress results in upwelling of cold nutrient-rich sub-surface water, and means the Benguela is considered to be similar to other biologically productive Eastern Boundary Currents such as the Humbolt and Canary upwelling regions (Small and Menzies 1981, Huyer 1983, Ware 1992, Patti *et al.* 2008). The combined effect of the large-scale circulation patterns and the local factors within Eastern Boundary Current systems accounts for the high level of primary production (Carr and Kearns 2003, Patti *et al.* 2008). There is an abundance of hydrodynamic features within the Benguela current that are defined by complex physical and chemical dynamics operating over meso-scale distances (Weiters 2005). Wind-driven upwelling associated with eastern boundary currents injects cold, nutrient-rich water into the euphotic zone, driving primary and secondary production (Small and Menzies 1981, Huyer 1983, Weiters 2005).

Over the past 65 years many studies have dealt with and described the geographical distribution of the flora and fauna found in the southern Africa intertidal and littoral region (e.g. Stephenson 1936, 1939, 1944, 1948, Stephenson *et al.* 1940, Brown and Jarman 1978, Branch and Branch 1981, Field and Griffiths 1991, Emanuel *et al.* 1992, Bustamante and Branch 1996). Generally, three biogeographic provinces have been proposed for southern Africa: (1) the cold-temperate West Coast, (2) the warm-temperate South Coast, and (3) the subtropical East Coast (Stephenson and Stephenson 1972). More rigorous studies by Emanuel *et al.* 1992 describe these same regions, renaming them and including a fourth: (1) the subtropical Natal province, (2) the warm

temperate Agulhas province, (3) the cool temperate Namaqua province, and (4) the cool temperate Namib province. Experimental evidence (Bustamante ad Branch 1996) supports these proposed provinces except for the Namib as no data were collected from this region.

Previous studies have independently suggested upwelling and biogeography as affecting species distribution and composition in the intertidal region. Upwelling affects the species distribution in a multitude of ways. Most recently larval transport and settlement patterns linked with nearshore oceanographic processes associated with upwelling have come under debate. Initially oceanographic processes were thought to move larvae offshore during upwelling (Parrish et al. 1981, Yoshioka 1982, Gaines and Roughgarden 1985, Roughgarden et al. 1988, Connolly and Roughgarden 1998) and settlement was perceived to only occur when prevailing winds relaxed and subsequent downwelling occurred (Yoshioka 1982, Gaines and Roughgarden 1985, Roughgarden et al. 1988, Farrel 1991). Morgan et al. (2009a) contradicted this theory whilst studying offshore transport of 45 species of Crustacea in a strong persistent upwelling region, indicating that movement on and offshore were determined by larval migrations within the water column. This theory was further supported by a study of crab postlarvae during upwelling which illustrated that offshore transport was no more prevalent during a year of strong upwelling, and suggested further investigation into this phenomenon (Morgan et al. 2009b). Subsequently the recruitment of eight invertebrate taxa were investigated in a region of strong persistent upwelling and only mussels were deemed to recruit during periods of downwelling, while other processes were suggested as causal mechanisms for larval delivery (Morgan et al. 2009c). Larval retention of 19 Crustacea taxa in nearshore waters during strong persistent upwelling was again observed by Morgan and Fisher (2010) and larval migrations were deemed to be the causal mechanism. It must be noted, however, that all these studies were conducted at one site and concentrate heavily on Crustacea largely ignoring the recruitment of other taxa. I suggest that replication with sites

and taxa be taken into account before this can be a widely accepted phenomena especially in the light that upwelling regions are considered to be a recruitment limited area (Morgan *et al.* 2009a).

Intertidal flora is thought to be directly influenced by upwelling which typically injects cold nutrient rich water into the intertidal region (Small and Menzies 1981, Huyer 1983, Weiters 2005). The increase in nutrients in the intertidal region classically leads to an increase in growth rate and maximum length of intertidal macroalgae, as demonstrated for the turf forming algae, *Gelidium chilense* by Weiters (2005) and the red algae, *Mazzaella laminarioides* (Nielsen and Navarrete 2004) along the coast of Chile. Similar results were obtained by Broitman and Kinlan (2006) who found that spatial structure of primary producer biomass was linked with upwelling. Upwelling was noted to affect biomass of algae by Bosman *et al.* (1987) and morphological form of the kelp *Egregia menziesii* (Blanchette *et al.* 2002), upwelling also influenced niche realisation within a kelp forest during a nutrient rich La Niña event in the Californian upwelling region (Dayton *et al.* 1999). Upwelling is also observed to cause changes in abundances of specific taxa of macroalgae, for example Broitman *et al.* (2001) describe and increase in kelp in the low intertidal region and corticoid algae in the mid-intertidal in upwelling regions in South Africa.

Fauna also demonstrate patterns in relation to upwelling, mussels have shown faster growth rates at upwelling centres and it is postulated that this is due to greater food supply from increased intertidal phytoplankton and/or input from nearshore kelp beds, maximum size was also suggested to be influenced by upwelling (Xavier *et al.* 2007). This phenomenon is also prevalent

for other intertidal filter feeding invertebrates (Menge 1992, Menge *et al.* 1994, 2004, Dahlhoff and Menge 1996, Sanford and Menge 2001). Menge *et al.* (2003) suggest that upwelling has effects on entire ecosystems found within the intertidal region and in particular population dynamics and species interactions were affected. Blanchette *et al.* (2009) compare the biological and trophic structure three of the most prevalent global upwelling systems and conclude that although limited trends may be present in regions affected by similar oceanographic processes, overall biological and ecological functioning are likely to be context dependant. Recent work (Cole and McQuaid in press), however, questions the effect of upwelling on assemblages associated with two biogenic engineers, *Perna perna* and *Mytlilus galloprovincialis*, over large scales suggesting that effects of upwelling may be overwhelmed by biogeographic differences.

This study, investigating the well-known hydrodynamic patterns associated with the coast line of South Africa and in particular the warm, oligotrophic, fast-flowing Agulhas current and the cold, nutrient-rich, Benguela Current, and upwelling associated with these currents, aims to determine the influences of upwelling and biogeographic region on the composition of infaunal assemblages associated with two species of macroalgae, *Hypnea spicifera* (east and south coasts) and *Champia lumbricalis* (west coast).

#### 3.2 Methods:

#### 3.2.1 Study sites:

Rocky shores in South Africa are exposed to relatively weak, localised upwelling along the east and south coasts (Lutjeharms 2000a, b, 2007), while more persistent and intense upwelling occurs along the west coast (Nelson and Hutchings 1983, Weiters 2005). All study sites were on wave exposed shores, out of bays. To test the effects of upwelling and biogeography, upwelling and non-upwelling areas were sampled in each of the provinces, two sites were chosen from each of the five identified upwelling cells (Fig 3.1 a, b, c), distance between sites ranged between 5 to 30 km depending on accessibility. Two corresponding non-upwelling sites, separated by distances of 80 - 100 km from upwelling cells were chosen.

All upwelling and non-upwelling regions were determined using an AVHRR (Advanced Very High Resolution Radiometer) snapshot of sea surface temperatures for the east and south coasts for 3 days in May 2008 (Fig 3.1 a) and literature on the oceanography of the chosen regions. On the east coast a kinetically-driven upwelling cell occurs between Richard's Bay and Cape St Lucia (32°E; 29°S) where the continental shelf widens downstream of St Lucia (Gill and Schumann 1979, Lutjeharms 2006). Upwelling is speculated to occur anywhere from 30 % (Pearce 1977) to 78 % percent of the time (Lutjeharms 2006). The non-upwelling area was selected south of this upwelling cell (Chaka's Rock, Ballito) (Fig 3.2).



(b)

(a)



(c)

33



Figure 3.1: Three day composite Sea Surface Temperature maps of the South African coastline indicating the St Lucia and Port Alfred upwelling cells on the east and south coasts (composite data starts 27-05-2008) (a), the Port Alfred and Robberg Upwelling cells on the south coast (composite data starts 20-05-2008) (b) and the Cape Columbine and Groenrivier upwelling cells on the west coast (composite data starts 30-12-2007) (c). All maps are three day composite Sea Surface Temperature data sets available at <a href="http://www.rsmarine.org.za">www.rsmarine.org.za</a>.

Along the South Coast, upwelling is restricted to prominent headlands or capes (Schumann *et al.* 1982, Groschen and Schumann 1990) where the coastline topography, combined with summer easterly winds results in the formation of comparatively short-lived upwelling cells (Schumann

and Martin 1991, Lutjeharms 2006). On the South Coast, a relatively strong upwelling cell occurs at Port Alfred and Kenton  $(33^{\circ}\text{E}; 26^{\circ}\text{S})$  (Fig 3.1a, b) and the corresponding non upwelling area; Kidds Beach and Kaysers Beach  $(33^{\circ}\text{E}; 27^{\circ}\text{S})$ , occurs north of Port Alfred (Fig 3.2). Upwelling areas on the south coast were at the headlands; Brenton-on-Sea and Robberg  $(34^{\circ}\text{E}; 23^{\circ}\text{S})$  (Fig 3.1b) and corresponding non-upwelling areas were situated at Glentana and Dana Bay  $(34^{\circ}\text{E}; 22^{\circ}\text{S})$  (Fig 3.2).

The Southwest Cape is characterised by a complex coastline with many capes and bays with mountains running perpendicular the shore in some cases (Jury 1985). The relatively narrow continental shelf (30-40 km), combined with the shear wind stresses caused by this topography results in a localised upwelling centre associated with Cape Columbine ( $32^{\circ}E$ ;  $17^{\circ}S$ ) (Jury 1985, Shannon 1985) (Fig 3.1c, 3.2). The corresponding non upwelling area was located north of the Cape Peninsula (Bloubergstrand, Melkbosstrand) (Fig 3.2). The Namaqualand coastline ( $28^{\circ}S - 31^{\circ}S$ ) is relatively uniform, lacking major capes or bays, and the wind-stress remains constant throughout the year, producing a persistent upwelling cell where cold water is present throughout most seasons (Shannon 1985, DeMarcq *et al.* 2003). Two shores at Groenrivier ( $30^{\circ}E$ ;  $17^{\circ}S$ ) were selected as the upwelling area (Fig 3.1c) while Doringbaai and Strandfontein ( $31^{\circ}E$ ;  $14^{\circ}S$ ) were selected as the corresponding non-upwelling areas (Fig 3.2).



Figure 3.2: Map of South Africa indicating upwelling and non-upwelling sampling sites located in the Natal and Agulhas Provinces where *H. Spicifera* was collected along the east and south coasts and upwelling and non-upwelling sampling sites in the Namaqua Provinces along the west coast where *C. lumbricalis* was collected.

## 3.2.2 Collection and processing of samples:

Six samples of each species of rhodophyte macroalga, *Hypnea spicifera* on the east and south coasts, and *Champia lumbricalis* on the west coast, were collected from the two sites situated within each upwelling and non-upwelling areas. *H. spicifera* is distributed along the east coast from north of Richards bay to the west coast as far as Angola, this alga however was not abundant on the west coast and a second species, *C. lumbricalis* was chosen. *C. lumbricalis* is of similar size and structure to *H. spicifera* and is abundant from Cape Agulhas on the south coast to Angola. An entire plant was considered to include fronds and spreading holdfast, in situations

where holdfasts coalesced, the holdfast was split at a midpoint between the two plants. The collection method consisted of placing a pre-labeled plastic bag over a haphazardly selected macroalga plant during low tide, the holdfast was then scraped from the rock with a metal scraper and the plastic bag was sealed. Macroalga plants were separated by 10 centimetres to 20 metres. 70% ethanol was used to preserve the samples until they were processed.

In the laboratory, the macroalgal samples were carefully washed and cleaned of all associated epifauna, which were collected using a 0.5 mm sieve and preserved in 70 % ethanol. The lengths of six of the longest fronds from each sample of macroalga were then measured. The surface area of each plant was calculated as described by Johnson and Scheibling (1987) and the methodology in Chapter 2, Pp. 15. Epifauna were identified to species level where possible using a dissecting microscope and standard identification keys (Griffiths 1976, Kensley 1978, Killburn and Rippey 1982, Branch *et al.* 2007).

#### 3.2.3 Data analysis:

Densities of epifauna were standardised to 1cm<sup>2</sup> of macroalgae. Number of species was, however, expressed per plant. To test hypotheses about species composition and abundances, PRIMER6 (Clarke and Gorley 2006) was used to create non Multi-Dimensional Scaling (nMDS) ordination plots, based on Bray-Curtis similarity matrices (Bray and Curtis 1957), that were used to visualise differences in assemblages. These data were analysed using Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson *et al.* 2005). For each group of taxa, three factors were considered. The first level consisted of three randomly selected regions (St Lucia, Port Alfred and Knysna on the east/south coasts) and two randomly selected regions on the west coast (Cape Columbine and Groenrivier), upwelling or non-upwelling was

orthogonal to region. Nested within each upwelling and non upwelling cell were two shores, where six replicates of macroalgae were sampled. Pair-wise *post hoc* tests were done when there was a significant effect of region and/or upwelling or the interaction between region and upwelling.

Analysis of Variance (ANOVA), using GMAV5 (Underwood *et al.* 2002), was used to analyse univariate data of number of species and number of individuals in four taxonomic groups: crustaceans, molluscs, polychaetes and other taxa. The same experimental design was used as for the multi-variate analysis. Where interactions were not significant (P > 0.25), interaction terms were pooled with the factor Shore for a more powerful test of the main effects (region and upwelling) (Underwood 1997). When sources of variation were significant, Student-Newman-Keuls (SNK) *post hoc* tests were used to determine the direction of differences.

### 3.3 Results:

nMDS plots indicated the three regions on the east and south coasts were relatively distinct from each other. There was, however a slight overlap between Port Alfred and Knysna and points from each of these regions did not plot further away from those within Port Alfred or Knysna (Fig 3.2). Although St Lucia and Port Alfred were similar, points representing samples from these regions did not overlap. Between the points there was however, no distinct difference in distance between points from the same region and points from either St Lucia or Port Alfred regions. Knysna and St Lucia were distinctly different in distance from each other with points within each region being closer to one another than points between Knysna and St Lucia. PERMANOVA showed that assemblages among the three Regions differed significantly ( $F_{2, 60} = 5.38$ , P = 0.001), while assemblages between upwelling/non-upwelling areas were not different ( $F_{1, 60} = 0.29$ , P = 0.89). Assemblages on the different shores differed significantly from each other ( $F_{6, 60} = 5.49$ , P = 0.001).

On the east and south coasts, the number of individuals per unit of surface area of *H. spicifera* showed no significant effects of region or upwelling for Crustacea or Polychaeta. Analysis of the number of individuals of molluscs showed a significant effect of region ( $F_{2, 8} = 8.44$ , P = 0.01) (Table 1), but SNK tests could not differentiate among the three regions. There was a significant interaction of region and upwelling ( $F_{2, 60} = 7.03$ , P = 0.027) for the number of individuals of other taxa (Table 1), SNK *post hoc* tests showed that for non-upwelling the number of individuals in St Lucia and Port Alfred were equal but less than for Knysna, but again the *post hoc* tests could not differentiate between upwelling and non-upwelling areas. For both St Lucia and Port Alfred, the number of individuals found in upwelling areas was equal to non-upwelling areas (Table 3.1).

In general, region had an effect on the number of species found on *Hypnea spicifera* while upwelling had no effect. Groups of taxa showing a significant effect of region included the molluscs ( $F_{2,8} = 11.57$ , P < 0.01). St Lucia had fewer species of molluscs than both Port Alfred and Knysna (Table 3.1). Other taxa also showed a significant effect of Region ( $F_{2,8} = 7.16$ , P =0.02), with St Lucia and Port Alfred having fewer numbers of species than Knysna (Table 3.1). There was no effect of either region or upwelling for the Crustacea ( $F_{2,8} = 3.21$ , P = 0.09;  $F_{1,8} =$ 0.47, P = 0.51) or the Polychaeta ( $F_{2,8} = 4.38$ , P = 0.052;  $F_{1,8} = 1.45$ , P = 0.26) (Table 3.1). nMDs plots indicated the two regions on the west coast overlapped with there being no distinct differences in distance between Columbine and Groenrivier. There was, however, a distinct grouping in the Columbine region that did not overlap with and was separated from Groenrivier (Fig 3.3). PERMANOVA showed that assemblages on *C. lumbricalis* were not influenced by region or upwelling but there were significant differences between shores ( $F_{4, 40} = 4.26$ , P = 0.001). Furthermore region and upwelling did not affect number of individuals.

Analysis of the number of individuals found on *C. lumbricalis* on the west coast showed no effect of the main factors tested: region and upwelling. There was a significant interaction of region and upwelling for the number of species of crustaceans ( $F_{4, 1} = 7.87$ , P = 0.05). At Cape Columbine, the number of species found at the upwelling area was equal to that from the non-upwelling area, while at Groenrivier species richness for upwelling areas was greater than for non-upwelling areas. There was no effect of upwelling as a main factor at Cape Columbine or Groenrivier (Table 3.2).



Figure 3.3: nMDS plot of assemblages living on *H. spicifera* on the east and south coasts of South Africa (upwelling; St Lucia  $\blacklozenge$ , Port Alfred  $\blacksquare$  Knysna  $\blacktriangle$ ; non-upwelling; St Lucia  $\diamondsuit$ , Port Alfred  $\Box$ , Knysna  $\bigtriangleup$ ).



Figure 3.4: nMDS plot of assemblages associated with *Champia lumbricalis* on the west coast of South Africa (Groenrivier non-upwelling  $\diamond$ , Columbine non-upwelling  $\Delta$ , Columbine upwelling  $\blacklozenge$ , Groenrivier upwelling  $\blacktriangle$ ).

Table 3.1: Analysis of variance of (a) the number of individuals per surface area of *H. spicifera* and (b) number of species per plant of *H. spicifera* (n = 6), for Crustacea, Mollusca, Polychaeta and other taxa. The factor "Region" was random (3 levels), "Upwelling" was fixed and orthogonal (2 levels) and "Shore" was random and nested in Upwelling (2 levels). Homogeneity of variance was tested with Cochran's C test. Student-Newman-Keuls (SNK) *post hoc* tests were done for significant results to determine directions of difference. For this and the following tables: \* P < 0.05, \*\* P < 0.01, SL = St Lucia, PA = Port Alfred, K = Knysna.

Crustacea		(a) Number of individuals Cochran's $C = 0.65 **$		(b) Number of species Cochran's $C = 0.14$	
Source	d.f.	M.S.	S F	M.S.	F
			_		
Region = Re	2	1.18	1.62	161	3.21
Upwelling = Up	1	0.39	0.53	23	0.47
Shore (Re x Up)	6	<sup>x</sup> 0.76		<sup>x</sup> 63	
Re x Up	2	<sup>x</sup> 0.63		<sup>x</sup> 12	
Residual	60	0.04		4	
Total	71				
Pooled	8	0.72	15.01	50	11.54
Mollusca		Cochran's $C = 0.2$	9 *	Cochran's <i>C</i> = <b>0.28</b> *	
Region = Re	2	0.10	8.44**	57	11.57**
Upwelling = Up	1	0.00	0.010	0	0.0000
Shore (Re x Up)	6	<sup>x</sup> 0.01		<sup>x</sup> 6	
Re x Up	2	<sup>x</sup> 0.00		<sup>x</sup> 3	
Residual	60	0.00		2	
Total	71				
Pooled	8	0.01	5.45	5	2.47
		SL < K = PA			

Other taxa		Cochran's $C = 0.69$	**	Cochran's <i>C</i> = <b>0.36</b> **	
Region = Re	2	0.03	3.8100	158746	7.16
Upwelling = Up	1	0.01	0.2700	2532	0.11
Shore (Re x Up)	6	0.01	3.58**	<sup>x</sup> 25468	
Re x Up	2	0.05	7.03**	<sup>x</sup> 12333	
Residual	60	0.00		6218	
Total	71				
Pooled	8			22184	3.57
SNK		SL: Non-Up= Up		L = PA < K	
		PA: Non-Up = Up			
		K: Non	-Up > Up		
Polychaeta		Cochran's $C = 0.24$		Cochran's $C = 0.20$	
Region = Re	2	0.0011	3.67	17	4.38
Upwelling = Up	1	0.0002	0.67	6	1.45
Shore (Re x Up)	6	<sup>x</sup> 0.0004		<sup>x</sup> 5	
Re x Up	2	<sup>x</sup> 0.0002		<sup>x</sup> 1	
Residual	60	0.0001		3	
Total	71				
Pooled	8	0.0003	3.00	4	1.39

<sup>x</sup> Denotes *post-hoc* pooling, P > 0.25. New *F*-values are given for those tested against the pooled term.

2.18

Table 3.2: Analysis of variance of (a) the number of individuals per surface area of *C. lumbricalis* and (b) number of species per plant of *C. lumbricalis* (n = 6), for Crustacea, Mollusca, Polychaeta and grouped other taxa. The factor "Region" was random (2 levels), "Upwelling" was fixed and orthogonal (2 levels) and "Shore" was random and nested in Upwelling (2 levels). Homogeneity of variance tested with Cochrans C test. Student-Newman-Keuls (SNK) *post hoc* tests were done for significant results to determine directions of difference. For this and the following tables: \* P < 0.05, \*\* P < 0.01, CB = Columbine, GR = Groenrivier.

		(a) Number of individuals		(b) Number of sp	pecies
Crustacea		Cochran's $C =$	0.59 **	Cochran's $C = 0.29$	
Source	d.f.	M.S.	F	M.S.	F
Region = Re	1	0.02	0.78	1	0.210
Upwelling = Up	1	0.00	0.01	18	0.450
Shore (Re x Up)	4	<sup>x</sup> 0.03		5	1.420
Re x Up	1	<sup>x</sup> 0.00		39	7.87*
Residual	40	0.01		3	
Total	47				
Pooled	5	0.02	1.6032		
SNK				Up (Re):	B: Up = Non-Up
					GR: Up > Non-Up
				Re (Up):	Up: $CB = GR$
					Non Up: CB = GR
Mollusca		Cochran's <i>C</i> = <b>0.59</b> **		Cochran's $C = 0$	.24
Region = Re	1	0.12	0.12	0.52	0.12
Upwelling = Up	1	1.74	1.77	0.19	0.02
Shore (Re x Up)	4	<sup>x</sup> 1.14		4.40	2.02
Re x Up	1	<sup>x</sup> 0.36		11.02	2.51

Residual

Total

Pooled

40

47

5

0.17

0.98

5.84

Other taxa		Cochran's $C = 0$	.97 **	Cochran's <i>C</i> = <b>0.9564</b> **	
Region = Re	1	0.06	1.59	6.75	1.47
Upwelling = Up	1	0.04	0.90	3.00	0.65
Shore (Re x Up)	4	<sup>x</sup> 0.04		<sup>x</sup> 4.04	
Re x Up	1	<sup>x</sup> 0.05		<sup>x</sup> 6.75	
Residual	40	0.02		1.07	
Total	47				
Pooled	5	0.04	2.2601	4.58	4.26
Polychaeta		Cochran's $C = 0$	.75 **	Cochran's <i>C</i> = <b>0.90</b> *	
Polychaeta Region = Re	1	Cochran's $C = 0$ 0.04	4.31	Cochran's <i>C</i> = <b>0.90</b> * 9.19	2.46
Polychaeta Region = Re Upwelling = Up	1	Cochran's $C = 0$ 0.04 0.00	4.31 0.08	Cochran's <i>C</i> = <b>0.90</b> * 9.19 0.19	2.46 0.01
Polychaeta Region = Re Upwelling = Up Shore (Re x Up)	1 1 4	Cochran's $C = 0$ 0.04 0.00 <sup>x</sup> 0.01	4.31 0.08	Cochran's <i>C</i> = <b>0.90</b> * 9.19 0.19 3.73	2.46 0.01 1.65
Polychaeta Region = Re Upwelling = Up Shore (Re x Up) Re x Up	1 1 4 1	Cochran's $C = 0$ 0.04 0.00 <sup>x</sup> 0.01 <sup>x</sup> 0.00	4.31 0.08	Cochran's <i>C</i> = <b>0.90</b> * 9.19 0.19 3.73 20.02	2.46 0.01 1.65 5.37
Polychaeta Region = Re Upwelling = Up Shore (Re x Up) Re x Up Residual	1 1 4 1 40	Cochran's $C = 0$ 0.04 0.00 <sup>x</sup> 0.01 <sup>x</sup> 0.00 0.00	4.31 0.08	Cochran's <i>C</i> = <b>0.90</b> * 9.19 0.19 3.73 20.02 2.25	2.46 0.01 1.65 5.37
Polychaeta Region = Re Upwelling = Up Shore (Re x Up) Re x Up Residual Total	1 1 4 1 40 47	Cochran's $C = 0$ 0.04 0.00 <sup>x</sup> 0.01 <sup>x</sup> 0.00 0.00	4.31 0.08	Cochran's <i>C</i> = <b>0.90</b> * 9.19 0.19 3.73 20.02 2.25	2.46 0.01 1.65 5.37

<sup>x</sup> Denotes *post-hoc* pooling, P > 0.25. New *F*-values are given for those tested against the pooled term.

## Table 3.2 continued

## 3.4 Discussion:

Analysis of the entire assemblage associated with *Hypnea spicifera* on the east and south coasts shows that the three regions; St Lucia, Port Alfred and Knysna, were significantly different from each other. The difference between the Knysna and Port Alfred regions was weakly supported by visualisation, while other analyses strongly support the differences in assemblages among all three regions. This separation between the St Lucia region and Port Alfred/Knysna Regions is supported by biogeographical studies by Emanuel *et al.* (1992) and Branch and Bustamante (1996), which place St Lucia in the Natal province and Port Alfred and Knysna in the Agulhas province. This study suggests that there is, however, a difference in assemblages associated with *H. spicifera* between the two regions in the Agulhas province, Port Alfred and Knysna. Underlying large scale processes such as historical events or differences in average sea temperatures (Levin 1992) between these two regions could explain the differences in assemblages even though both are within the Agulhas province.

Entire assemblages associated with *H. spicifera* in upwelling areas did not differ significantly from assemblages found in non-upwelling areas for any of the analyses. These results do not concur with previous studies (Bustamante *et al.* 1995a, Menge *et al.* 1997a, b, Menge *et al.* 2003) which suggest that assemblage composition is affected by upwelling. Previous studies, have however only considered one upwelling and one non-upwelling area often in the same biogeographic province. The present study suggests that over a large-scale, biogeography has an overriding effect on assemblage composition. This phenomenon is demonstrated by Cole and McQuaid (in press) showing that fauna associated two biogenic ecosystem engineers were not influenced by nutrient input associated with upwelling but rather large scale effects of region.

The entire assemblages on the east and south coast shores produced conflicting results. Initially, visualisation of results using MDS suggested there was no distinct difference in the assemblages between shores, however this result was not strongly supported. Further statistical analysis showed that shore did have an effect on assemblages. Oceanographic processes acting over meso-scale distances (10 to 100 km) often affect marine assemblages (Menge 1992, Menge *et al.* 1994, Bustamante *et al.* 1995b, Bustamente and Branch 1996, Menge *et al.* 1997a, Broitman *et al.* 2001). The shores sampled during this study were separated by meso-scale distances and the coastline sampled is not uniformly affected by oceanographic processes, this would explain the variation between assemblages associated with *H. spicifera* on different shores. Biogeography which acts over hundreds of kilometres (e.g. Gaines and Lubchenco 1982, Bustamante and Branch 1996, Brown and Lomolino 1998, Broitman *et al.* 2001) would have also had an effect on the composition of assemblages associated with *H. spicifera* as shores from different regions were separated by hundreds of kilometres.

When considering individual groups of taxa associated with *H. spicifera*, one striking result was that for both the number of species and number of individuals of Mollusca, region had a significant effect. Both variables conformed to the division of the Natal and Agulhas provinces (Emanuel *et al.* 1992, Bustamante and Branch 1996). Only the number of individuals of grouped other taxa associated with *H. spicifera* showed a significant result for shore and an interaction between upwelling and region. The number of species for individual groups of taxa; Polychaeta, Crustacea and grouped taxa showed no effect for shore, upwelling, region or interaction between any of these factors. Emanuel *et al.* (1992) and Bustamante and Branch (1996) independently found that species composition varies between the Natal and Agulhas provinces, these results may not necessarily indicate that numbers of taxa vary between these two provinces.

Analysis of entire assemblages associated with *Champia lumbricalis* between the Groenrivier and Columbine regions showed that there were no significant differences in composition. This result is to be expected as both these regions occur in the same biogeographic province; Namaqua, (Emanuel *et al.* 1992, Bustamante and Branch 1996) and therefore composition of species assemblages associated with *C. lumbricalis* is expected to be similar. These results do not concur with previous studies (Bustamante *et al.* 1995a, Menge *et al.* 1997a, b, Menge *et al.* 2003) which suggest that assemblage composition is affected by upwelling. Upwelling did not have a significant effect on assemblages associated with *C. lumbricalis*. Previous studies have shown communities in the intertidal region are affected by upwelling (e.g. Bustamante *et al.* 1995a, Menge *et al.* 1997a, b, Menge *et al.* 2003), this study, however contradicts these previous findings. The west coast sampling sites were all encompassed by the Namaqua biogeographic region (Emanuel *et al.* 1992), thus it is not surprising that sites did not exhibit differences in assemblages of species. Data from Bustamante and Branch (1996) also suggests that this is the case. However their data only covers up to Paternoster so does not fully support the Namaqua region proposed by Emanuel *et al.* (1992).

Inconsistent results were seen when the effect of shore on assemblages associated with *C. lumbricalis* were tested. Visualisation suggested that there was no effect of shore, while further statistical analysis suggested there was a significant effect. Rocky shore assemblages are affected by oceanographic processes such as upwelling that act over meso-scale distances (Menge 1992, Menge *et al.* 1994, Bustamante *et al.* 1995, Bustamente and Branch 1996, Menge *et al.* 1997a, Broitman *et al.* 2001), and given that the shores were separated by 10-100s of kilometres these processes would affect the assemblages associated with *C. lumbricalis*.

In general, numbers of species and individuals on the west coast were unaffected by region, upwelling and shore. The west coast study area falls within the Namaqua province as defined by Emanuel *et al.* (1992) and Bustamante and Branch (1996), suggesting that large scale biogeography has more of an effect than small or meso-scale processes such as within shore variability or upwelling. The interaction of region and upwelling affected the number of species of crustaceans. Intense upwelling associated with topographical features within specific areas of the Benguela current (Demarq *et al.* 2003), would create conditions that would affect some species (Bustamante *et al.* 1995b, Connolly and Roughgarden 1998, Dayton *et al.* 1999, Menge 2000, Broitman *et al.* 2001, Menge *et al.* 2004, Weiters 2005, Blanchette *et al.* 2006, Freidenburg *et al.* 2007) and this coupled with oceanographic processes that act over meso-scales (Menge 1992, Menge *et al.* 1994, Bustamante *et al.* 1995, Bustamente and Branch 1996, Menge *et al.* 1997a, Broitman *et al.* 2001), would have created the differences seen in the Crustacea associated with *C. lumbricalis.* 

Upwelling, biogeography and smaller scale differences between shores are deemed important in determining the species composition and abundance of intertidal assemblages (e.g. Emanuel *et al.* 1992, Bustamante and Branch 1996, Underwood and Chapman 1996, Weiters 2005, Morgan *et al.* 2009a, b, c, Morgan and Fisher 2010). When all three were, however considered in the same study, biogeography was seen to have an overriding effect over the other processes. Meso-scale upwelling did not appear to influence the infaunal assemblages associated with the two biogenic ecosystem engineers. Larger-scale biogeographic factors (e.g. temperature and solar radiation) are therefore suggested to play a more important role in structuring intertidal ecosystems. Chapter 2 demonstrated the effects of large-scale biogeographic factors on the habitat forming ecosystem engineers. A link between the effects of larger-scale biogeographic

factors and their influence on habitat forming taxa and the resultant effects on associated infauna would be a more likely explanation for the observations.

## Chapter 4

# Comparison of Different Species of Structurally Similar Macroalgae

## 4.1 Introduction:

A variety of microhabitats occur on intertidal rocky shores. These microhabitats are formed by a multitude of physical features, such as rock crevices, pits and rock pools (Emerson and Faller-Fritsch 1976, Raffaelli and Hughes 1978, Garrity and Levings 1984, Moran 1985, Underwood and Chapman 1989, McCoy and Bell 1991, Underwood and Chapman 1992, Chapman 1992, Beck 1998), and biological features such as algal turf and structures produced by sessile organisms (Underwood 1976, Underwood and Jernakoff 1984, Daleo et al. 2006, Borthagaray and Carranza 2007, Pinn et al. 2008). When considering physical features, Underwood and Chapman (1989, 1992) found that pits and crevices in the rock-surface affected the population structure, changes in temporal densities and rates of dispersal of littorinid snails. Emerson and Faller-Fritsch (1976) found a suite of different mechanisms involving topography that affected littorinid populations. Erlandsson et al. (2005) found that topography (rock depressions, slope and aspect) had strong effects on two intertidal organisms, Perna perna and Octomeris angulosa and an intertidal alga Gelidium pristoides. Biological features such as mussel beds have been found to greatly increase species diversity compared with bare soft sediment (Ragnarsson and Rafaelli 1999, Commito et al. 2005) or rock where mussel beds are scarce or absent (Borthagaray and Carranza 2007).

The development of an understanding of habitat structure and its effects on populations and assemblages has met with little success (Dean and Connell 1987b, McCoy and Bell 1991, Beck 1998) as there has been little consistency between definition and measurement of structure within or among habitats (McCoy and Bell 1991, Beck 1998). At least three major elements have been identified in relation to habitat: complexity, heterogeneity and scale (McCoy and Bell 1991, Beck 1998, 2000). This study focuses on the structural complexity of habitats; this is represented by abundance and variation in structural components, biomass and surface area (McCoy and Bell 1991, Beck 1998). Structural complexity is known to be an important factor that directly influences the diversity of communities associated with habitats (Fletcher and Underwood 1987, Hacker and Steneck 1990, Huston 1994, Beck 1998, Attrill et al. 2000). Increasing complexity increases the amount of available niches therefore potentially increasing the number of species found within that habitat (MacArthur and MacArthur 1961, Gilinski 1984, Dean and Connell 1987c, Attrill et al. 2000, Crooks 2002, Borthagaray and Carranza 2007). Increasing complexity also has the ability to influence abundance of organisms within a habitat (Underwood and Chapman 1989, 1992). For example increasing algal complexity has been known to have effects on infaunal diversity and abundance (Hacker and Steneck 1990, Gee and Warwick 1994, Hull 1997, Bologna and Heck 1999, Burnaford 2004, Cole 2009).

The creation, physical alteration or maintenance of habitats by organisms is termed ecosystem engineering (Jones *et al.* 1994, 1997). Organisms that form such habitats by the direct or indirect control of the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials are termed ecosystem engineers (Jones *et al.* 1994, 1997). All ecosystems are influenced by ecosystem engineers due to direct or indirect influences on biotic and abiotic resources that are utilised by other organisms (Jones *et al.* 1994, 1997).

Ecological engineering can have negative or positive effects on species richness and abundances on small scales but, overall, the net effect on larger scales is generally positive, with greater species richness due to increased habitat diversity and availability of different niches (Jones *et al.* 1994, 1997). Ecosystem engineers can be divided into two different categories. Allogenic engineers indirectly alter biotic and abiotic materials from one physical state to another, and autogenic engineers directly transform the environment by incorporating themselves into the altered environment (Jones *et al.* 1994, 1997). Initially the provision of living space by an autogenic engineer was not seen as ecosystem engineering (Jones *et al.* 1994). Jones *et al.* (1997), did, however, include change in structure and shape of the engineer in their definition of autogenic engineering as this created living space and use of the engineer was not deemed to be simply a trophic link.

Jones *et al.* (1994, 1997) previously identified six factors that will affect the impact that ecosystem engineer have on any given environment. These factors include: life span of the engineer; population density; local and regional spatial distribution; the amount of time present at a site; the type of engineer, formation rate and impact of the engineering and its persistence; the number and type of resources that are altered, how they are altered and the effect this has on other species dependent on these resources. This study focuses on the engineering produced by different species of the same type of engineers (i.e. different species of intertidal macroalgae), and the habitats they produce.

Three different species of algae, with overlapping distributions were compared. *Hypnea spicifera* occurs from north of Richards Bay on the east coast to the West Coast of South Africa as far as

Angola (Stegenga *et al.* 1997), while *Champia lumbricalis* is abundant along the West Coast stretching from Angola to east of The Cape Peninsula as far as Cape Agulhas (Stegenga *et al.* 1997). *Bifurcaria brassicaeformis*, in contrast has a more limited distribution and occurs from Cape Columbine on the west coast to the southern most tip of Africa, Cape Agulhas (Stegenga *et al.* 1997). *H spicifera* and *C. lumbricalis* have similar frond structure and branching, while *B. brassicaeformis* has more robust fronds with less branching. Thus, given the similarity of the structures of the three algae, I hypothesised that faunal assemblages associated with the three seaweeds would be similar.

### 4.2 Methods:

The study was carried out within the region where the three species overlap to avoid confounding due to biogeographic effects. Study sites were where all three macroalgae, *H. spicifera*, *C. lumbricalis* and *B. brassicaeformis*, co-occurred on the same shore. Such sites were, however, rare as these macroalgae were sparsely distributed in this overlapping distribution range, and during this study only two sites were found to have all three present; Vermont,  $(34^{\circ}\text{E}; 1^{\circ}\text{S})$  and Onrus  $(34^{\circ}\text{E}; 10^{\circ}\text{S})$ (Map Fig 4.1).



Figure 4.1: Figure 0.1 Map indicating the two sampling locations where *H. spicifera*, *C. lumbricalis* and *B. brassicaeformis* distributions overlapped and were found on the same shore.

Six samples of each macroalga, including holdfasts, were collected from each of the two sites, Vermont and Onrus. The collection method consisted of placing a pre-labelled plastic bag over a haphazardly selected macroalga. The holdfast was scraped from the rock with a metal scraper and the plastic bag was then sealed. 70 % ethanol was used to preserve the samples until they were processed.

In the laboratory, macroalgal samples were washed, and the epifauna collected using a 0.5 mm sieve and preserved in 70 % ethanol. The lengths of six of the longest fronds from each sample of macroalga were then measured. The surface area of each macroalgal sample was calculated

following Johnson and Scheibling (1987) and procedures described in Chapter 2, Pp. 15. The weight of a monomolecular layer of oil (Johnson & Johnson Baby Oil <sup>TM</sup>) coating a known surface area was used to create an equation whereby the weight of the oil coating a 1 cm<sup>2</sup> surface area was know. Each macroalgal sample was weighed and then dipped in Johnson & Johnson Baby Oil <sup>TM</sup> and re-weighed, the weight of the oil coating each sample was then converted into surface area. The epifauna were identified to species level using a dissecting microscope.

All epifauna data except for entire assemblage data were expressed per square centimetre of macroalga before statistical analyses were done. PRIMER6 (Clarke and Gorley 2006) was used to create Bray-Curtis similarity matrices (Bray and Curtis 1957) for species composition and abundance, and from this matrix, non Multi-Dimensional Scaling (nMDS) ordination plots were used to visualise differences in assemblages between the two different shores and three different macroalgae sampled on each shore.

Untransformed multi-variate data were analysed using Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2005). For each broad taxon (Crustacea, Polychaeta, Mollusca and Other taxa), two levels were considered in the analysis: shore (Vermont and Onrus), and orthogonal to shore, three different macroalgae (*H. spicifera, C. lumbricalis* and *B. brassicaeformis*), with six replicates of each macroalga from each shore. Multi-variate pair-wise *post hoc* tests were done when there was a significant effect of the type of macroalgae or an interaction between shore and macroalga.

Analysis of Variance (ANOVA), using GMAV5 (Underwood *et al.* 2002), analysed univariate data of number of species and number of individuals of crustaceans, molluscs, polychaetes, other taxa and surface area of macroalgae. In the analysis, two factors of the experiment were considered using the same experimental design as for the multi-variate analysis. Where interactions were not significant (P > 0.25, Underwood 1997), interaction terms were pooled with the Residual for a stronger test of the main effect of interest (macroalgae). In cases where variances were heterogeneous (Cochran's test), there were no suitable transformations to create homogeneous variances and as large designs such as this are robust to violation of this assumption (Underwood 1997), the analysis was performed on non-transformed data. When sources of variation were significant, Student-Newman-Keuls (SNK) *post hoc* tests were done to determine the direction of differences.

#### 4.3 Results:

nMDS plots were used to visualise differences in the assemblages associated with the three different macroalgae on the two shores (Figure 4.2). There were no distinct groupings, assemblages from all three macroalgae produced points that were interspersed with each other. The two shores also did not show distinct groupings. Despite, there being no visual differences and stress values being quite high (above 1.7 sensu Clarke 1993, indicating that the visual representation is not very reliable) the assemblages of species found on the three Rhodophyta showed both shore ( $F_{1, 30} = 2.91$ , P = 0.003) and algae ( $F_{2, 30} = 3.69$ , P = 0.021) had significant effects on the assemblages associated with the algae. Consistent with the nMDS plots, *post hoc* tests could not differentiate among the assemblages associated with the three macroalgae (Table 4.1).
Univariate analysis showed the surface area ( $F_{2, 30} = 3.78$ , P = 0.03) and biomass ( $F_{2, 32} = 3.71$ , P = 0.04) of the three macroalgae showed significant effects. SNK tests indicated *H. spicifera* had less surface area than *B. brassicaeformis* and *C. lumbricalis* in both cases (Table 4.2). Univariate analyses of the number of individuals on the three different macroalgae showed no distinct patterns (Table 4.3). The numbers of polychaetes differed significantly between shores ( $F_{1, 30} = 5.95$ , P = 0.02), and the numbers of individuals of molluscs were affected by the species of alga ( $F_{1, 32} = 8.18$ , P = 0.001). SNK tests indicated that the number of individuals associated with *B. brassicaeformis* and *C. lumbricalis* were similar, but there were fewer than associated with *H. spicifera* (Table 4.2).

Univariate analyses showed that for both molluscs and other taxa, neither shore nor alga had an effect on the number of species present (Table 4.2). Significant results were, however, obtained for the interaction of algae and shore for the other two taxa considered: Crustacea ( $F_{1, 30} = 5.43$ , P = 0.0097) and Polychaeta ( $F_{1, 30} = 4.31$ , P = 0.023) (Table 4.2). The SNK *post hoc* tests indicated that the number of crustacean species at Vermont had similar numbers associated with *B. brassicaeformis* and *C. lumbricalis*, but less than those found on *H. spicifera*. SNK *post hoc* tests could not differentiate among the numbers of species found associated with the three different macroalgae at Onrus (Table 4.2). The number of species of polychaetes found at *spicifera*. SNK *post hoc* tests could not differentiate among the number of *c. lumbricalis* were equal but less than *H. spicifera*. SNK *post hoc* tests found at Vermont associated with *B. brassicaeformis* and *C. lumbricalis* and *C. lumbricalis* and *C. lumbricalis* and *C. lumbricalis* found at Vermont associated with *B. brassicaeformis* and *C. lumbricalis* and *C. lumbricalis* were equal but less than *H. spicifera*. SNK *post hoc* tests could not differentiate among the number of species found at Vermont associated with *B. brassicaeformis* and *C. lumbricalis* were equal but less than *H. spicifera*. SNK *post hoc* tests could not differentiate among the numbers of species found on three different macroalgae at Onrus (Table 4.2).



Figure 4.2: nMDS plot of assemblages living on three different species of macroalgae, *B. brassicaeformis* (Vermont  $\diamond$ , Onrus  $\blacklozenge$ ), *C. lumbricalis* (Vermont  $\Delta$ , Onrus  $\blacktriangle$ ) and *H. spicifera* (Vermont  $\Box$ , Onrus  $\blacksquare$ ) on the South Coast of South Africa.

Table 4.1: PERMANOVA table of assemblages associated with *H. spicifera, C. lumbricalis* and *B. brassicaeformis*, standardised according to surface area. The factor "Shore" was random (2 levels), "Algae" was fixed and orthogonal (2 levels). For this and the following tables: \* P < 0.05, \*\* P < 0.01.

Source	d.f.	M.S.	F			
Shore = Sh	1	4436	2.91**			
Algae = $A$	2	8523	3.69 *			
Sh x A	2	2309	1.51			
Residual	30	1524				
Total	35					
SNK	H. spicifera < C. lumbricalis = B. brassicaeformis					
	Onrus = Vermont					

Table 4.2: ANOVA tables comparing (a) the surface area of *H. spicifera, C. lumbricalis* and *B. brassicaeformis*. The *brassicaeformis*, and (b) the biomass of *H. spicifera, C. lumbricalis* and *B. brassicaeformis*. The factor "Shore" was random (2 levels), "Algae" was fixed and orthogonal (2 levels). Variances were heterogeneous (Cochran's test), but there were no suitable transformations to create homogeneous variances. Student-Newman-Keuls (SNK) *post hoc* tests were done for significant sources of variation to determine directions of difference. *Hyp* = *H. spicifera, Ch* = *C. lumbricalis, Bi* = *B. brassicaeformis*.

		(a) Surface area Cochran's $C = 0.77$ , $P < 0.01$		(b) Biomass Cochran's $C = 0.77, P < 0.01$	
Source	d.f.	M.S.	F	M.S.	F
Shore $=$ Sh	1	151	0.00	1	0.00
Algae = $A$	2	1131703	3.78*	2	<b>3.7</b> 1*
Sh x A	2	385816	1.29	<sup>x</sup> 2	
Residual	30	299638		<sup>x</sup> 30	
Total	35			35	
Pooled				32	
SNK		Hyp <	Bi = Ch	Нур	< Bi = Ch

<sup>x</sup> Denotes *post-hoc* pooling, P > 0.25. *F*-values are given for those tested against the pooled term.

Table 4.3: ANOVA tables comparing (a) the number of individuals per surface area of *H. spicifera, C. lumbricalis* and *B. brassicaeformis,* and (b) the number of species per plant of *H. spicifera, C. lumbricalis* and *B. brassicaeformis.* For Crustacea, Mollusca, Polychaeta and other taxa. The factor "Shore" was random (2 levels), "Algae" was fixed and orthogonal (2 levels). Variances were heterogeneous (Cochran's test), but there were no suitable transformations to create homogeneous variances. Student-Newman-Keuls (SNK) *post hoc* tests were done for significant sources of variation to determine directions of difference. *Hyp = H. spicifera, Ch = C. lumbricalis, Bi = B. brassicaeformis,* V = Vermont, O = Onrus.

		(a) Number of Individuals		(b) Number of Species	
Crustacea		Cochran's $C =$	0.42, <i>P</i> > 0.05	Cochran's $C =$	<b>0.85</b> , <i>P</i> < 0.01
Source	d.f.	M.S.	F	M.S.	F
Shore = Sh	1	0.0463	2.48	0.0007	4.05
Algae = $A$	2	0.0378	2.02	0.0016	1.76
Sh x A	2	<sup>x</sup> 0.0052		0.0009	5.43**
Residual	30	<sup>x</sup> 0.0196		0.0002	
Total	35				
Pooled	32	0.0187			
SNK				V: Bi = Ch < Hyp	
				O: Hyp = Ch = Bi	

Mollusca		Cochran's $C =$	<b>0.84</b> , <i>P</i> < 0.01	Cochran's $C$	= <b>0.97</b> , <i>P</i> < 0.01
Shore = Sh	1	0.0136	1.35	0.0004	1.90
Algae = A	2	0.0826	8.18**	0.0012	1.91
Sh x A	2	<sup>x</sup> 0.0081		0.0006	2.67
Residual	30	<sup>x</sup> 0.0102		0.0002	
Total	35				
Pooled	32	0.0101			
SNK	Bi = Hyp < Ch				
Other taxa		Cochran's $C =$	<b>0.73,</b> <i>P</i> < 0.01	Cochran's C =	= <b>0.83</b> , <i>P</i> < 0.01
Shore = Sh	1	0.0017	2.21	0.0001	1.62
Algae = A	2	0.0012	0.52	0.0002	1.47
Sh x A	2	0.0022	2.81	<sup>x</sup> 0.0001	2.58
Residual	30	0.0008		<sup>x</sup> 0.0000	
Total	35				
Pooled	32			1.8038	
Polychaeta		Cochran's $C =$	0.39, <i>P</i> >0.05	Cochran's C =	= <b>0.96</b> , <i>P</i> < 0.01
Shore $=$ Sh	1	0.0096	5.95*	0.0005	2.04
Algae = A	2	0.0034	0.82	0.0008	0.78
Sh x A	2	0.0042	2.58	0.0011	4.31*
Residual	30	0.0016		0.0002	
Total	35				
SNK				V : <i>Bi</i> =	= Ch < Hyp
				O: Hy	p = Ch = Bi

Table 4.3 continued

<sup>x</sup> Denotes *post-hoc* pooling, P > 0.25. *F*-values are given for those tested against the pooled term.

#### 4.4 Discussion:

The use of the rhodophyte as a natural 'sampling package' (*sensu* Kitching *et al.* 2001, Anderson *et al.* 2005) removes the need for an arbitrary decision on size and shape of the sample unit (Bellehumeur *et al.* 1997), this assumes the size of the hold fast and fronds of the three macroalgae were of similar size and shape, due to plants being exposed to similar conditions within the same shore, thus providing similar structural habitat for organisms (Anderson *et al.* 2005). Small-scale patchiness can be produced among macroalgal plants by spatial arrangement, variation in density, spatial arrangement and diversity of neighbouring macroalgae (Theil and Vásquez 2000), and disparity in the physical condition of the macroalgae (Cole and Sims 1999). The use of alga as a sampling package may therefore not be consistent within a shore. Furthermore, different species of algae may also sample different amounts of habitat. As such, the surface area and biomass of *H. spicifera* differed significantly from those of *C. lumbricalis* and *B. brassicaeformis*, suggesting that *H. spicifera* has different structural complexity or is a different size from the other two macroalgae.

The number of individuals of polychaetes were affected by shore while and the number of individuals of molluscs were affected by the species of macroalgae. Abundances of intertidal organisms associated with biogenic habitats have been shown to vary in a number of studies, both between habitats on the same shore and between different shores. For example Kelaher *et al.* (2001) considered the effects of several environmental variables (e.g. epiphytes, length and density of fronds) and spatial sampling scale on the abundance of infaunal assemblages associated with coralline algal turfs, abundances of gastropods were shown to vary among the four shores and habitats depending on different environmental variables. Kelaher (2003) further consider the effect of frond lengths on gastropod abundances, showing that coralline turfs with

short fronds support higher gastropod abundances. Vásquez *et al.* (2009) found that abundances of amphipods differed among different species of macroalgae in Mediterranean shallow water habitats. Leite *et al.* (2007) investigated the effect of structural variation and its effects on amphipods and conclude that differences are due to algal size and morphological complexity. Cole and Chapman (2007) investigated spatial variation of polychaetes associated with biogenic reefs and found evidence of variation between over both 5-10s metres and 10s kilometres in Wales and Portugal and variations at a higher taxonomic resolution. Small scale microhabitats within the algae may have been different enough to produce variation in the numbers of individual molluscs among the different algal species. This points towards small-scale variation and processes being important in the structuring of assemblages (Archambault and Bourget 1996, Underwood and Chapman 1996, Anderson *et al.* 2005). Other mechanisms such as behavioural aggregation (Chapman 1998), settlement cues (LeTourneux and Bourget 1988) offer possible explanations for the observed differences.

When grouping all taxa together, both species of macroalgae, and shore had an effect on the infaunal assemblages associated with them. Although it was not possible to distinguish how the assemblages differed at these scales as post-hoc tests gave inconsistent results, the overall differences in numbers of individuals and species across all taxa found associated with macroalgae and on different shores may have produced this significant effect. Studies such as that of Hull (1997) have shown that the species of alga has effects on species richness, diversity and abundance of ostracods, although the species of algae were markedly different in terms of structural complexity. Bates (2009) surveyed an impressive number of species of macroalgae in search of taxonomic relatedness between macroalgae and infaunal assemblages, finding that assemblages differed as much on the same species as with species from another kingdom. Bates (2009) also concluded that a quarter of the functional groups of macroalgae had different taxon

richness. Seed and O'Connor (1981), and Taylor and Cole (1994) also describe variations in associated infaunal assemblages in terms of composition richness and abundance. *C. lumbricalis* and *B. brassicaeformis* were relatively similar in terms of biomass and surface area, however *H. spicifera* was different, showing that in terms of entire assemblages, species of algae has an effect regardless of how structurally similar the algae are. Macroalgae biogenic habitats provide protective structures guarding from physical factors such as temperature change, ultraviolet radiation, desiccation, hydrodynamic stresses (Bates 2009) and biological factors such as predation (Martin-Smith 1993, Norderhaug *et al.* 2005).

Sampling scale would affect assemblages and would be a likely explanation for the differences in entire assemblages between species of algae and shore observed in this study. Underwood and Chapman (1996) and Anderson *et al.* (2005) found that assemblages are likely to vary on a scale of a few centimetres to meters within the same shore and that shores separated by a hundreds of meters are also likely to exhibit variation in assemblages. This is supported by several authors (e.g. Chapman *et al.* 1995, Archambault and Bourget 1996, Blanchard and Bourget 1999, Anderson *et al.* 2005).

Algae may act as a refuge by eliminating food value, predation, competition and physical disruption in laboratory experiments (Hacker and Steneck 1990). Studies by Attrill *et al.* (2000) concluded that there was no evidence that structural complexity influenced the composition of associated macroinvertebrates but rather biomass and therefore increasing surface area of seagrass affected the composition of the associated faunal community. This has been observed in other instances in both terrestrial and marine habitats (e.g. Rey 1981, Russo 1987, Koukouras *et al.* 1992, MacDonald and Johnson 1995, Kelaher 2003a ,b, Leite *et al.* 2007), while other authors

(e.g. Crisp & Mwaiseje, 1989, Chemello and Milazzo, 2002) suggest that architecture does play a part in epifaunal diversity and abundance. In the case of this study the three species of algae could provide similar amounts of protection from predation, shelter from other physical factors such as wave exposure and desiccation (e.g. Dommasnes 1968, Gibbons 1988, Downes *et al.* 2000, Monteiro *et al.* 2002). With a difference among *H. spicifera* and *C. lumbricalis, B. brassicaeformis* in terms of biomass and surface area and no significant differences in univariate analysis of the number of species and individuals per taxa, with the exception of Mollusca, it can be concluded that the macrofauna associated with *H. spicifera, C. lumbricalis* and *B. brassicaeformis* use the algae as habitat despite differences or similarities in surface area and biomass.

# Chapter 5

# General Discussion

The Southern African coastline stretches over two biogeographic provinces on the east and south coasts (Natal and Agulhas) and two on the west coast (Namib and Namaqua) (Emanuel et al. 1992). Each coastline is affected by two distinct boundary currents, the Benguela on the west coast and the Agulhas on the east coast, each with their own suite of hydrodynamic processes that are shared by other eastern and western boundary currents worldwide (e.g. Nagata 1970, Hsueh and O'Brien 1971, Gill and Schumann 1979, Blanton et al. 1981, Small and Menzies 1981, Huyer 1983, Tranter et al. 1986, McClean-Padman and Padman 1991, Ware 1992, Lutjeharms et al. 1993, Lutjeharms and Machu 2000, Lutjeharms et al. 2000a, b, 2007, Patti et al. 2008). This system provided an ideal opportunity to investigate how intertidal organisms are affected by large scale effects on two adjacent coasts that are influenced by distinctly different oceanographic environments (Chapter 2). The hydrodynamic processes observed along these two coastlines operate, however, act over meso-scale distances, and of particular interest to this study was the influence the meso-scale process of upwelling (as described by Lutjeharms et al. 2000a, b, 2007 for the east coast and Ware 1992 and Patti et al. 2008 for the west coast)(Chapter 3). Upwelling has been described as being extremely important in affecting single species and structuring intertidal assemblages (e.g. Huyer 1983, Roughgarden et al. 1988, Connolly and Roughgarden 1998, Blanchette et al. 2002, Menge et al. 2003, Xavier et al. 2007, Blanchette et al. 2009, Morgan et al. 2009a, b, c, Morgan and Fisher 2010). Species forming biogenic habitats can be strongly influenced by upwelling (e.g. Small and Menzies 1981, Huyer 1983, Weiters 2005, Xavier *et al.* 2007). Biogenic habitats are an important part of intertidal systems as they support a substantial biodiversity (e.g. Fielding et al. 1994, Seed and Suchanek 1992, Porras et *al.* 1996, Kelaher *et al.* 2001). It was therefore important to consider if biogenic habitats of similar sizes support similar species assemblages so that general conclusions could be drawn (Chapter 4).

#### 5.1 The role of biogenic habitats:

Habitats play an integral part in the distribution of organisms, yet they are threatened by habitat destruction and therefore it is important to clarify the role played by habitats if the consequences of habitat loss and modification are to be fully understood (Fahrig and Merriam 1994). Heterogeneity in phytal habitats has been recognised to affect both the density and abundance of infaunal species (e.g. Hicks 1980, 1986, Gee and Warwick 1994, Jarvis and Seed 1996). Variations in size, shape and texture of algal species are suggested as the basic components contributing to the complexity of the habitat (Gee and Warwick 1994). Associated infauna densities have been related to the complexity of the algal structure as habitable space varies with complexity (e.g. Hicks 1985, Hacker and Steneck 1990, Beck 1998, Beck 2000, Attrill et al. 2000) as does protection from biological factors (e.g. predation and competition) (Coull and Wells 1983, Russo 1987) and physical factors (e.g. wave action and desiccation) (Whatley and Wall 1975, Seed 1996, Thompson et al. 1996). Plant size (Gunnill 1982, Kelaher et al. 2001, Kelaher 2003a) and plant physiology (Hagerman 1966) also affect associated infaunal assemblages. A large amount of work has been done on correlations between physical characteristics and densities of associated infauna (e.g. Edgar 1983a, b, Dean and Connell 1987a, b, c, Hacker and Steneck 1990).

Different biogenic engineer species are suggested to host different infaunal assemblages (e.g. Bruno and Bertness 2001), indicating that the loss of one habitat forming species may alter entire

intertidal assemblages. This has important implications for generalisations made about assemblages associated with biogenic habitats. Similarly sized and structured biogenic habitats provided by different species may not always host similar assemblages due to a multitude of external factors as discussed in Chapter 4. The assessment of infaunal assemblages associated with biogenic habitats within shores must therefore take into account each different species of biogenic engineer to provide an accurate survey.

When the physical variables of the three algae were analysed, H. spicifera differed from C. lumbricalis and B. brassicaeformis suggesting that H. spicifera had a potentially different structure compared with the other two macroalgae. Following the theories proposed in the biodiversity ecosystem functioning debate (Ehrlich and Ehrlich 1981, Lawton and Brown 1993, Vitousek and Hooper 1993, Naeem et al. 1995) loss of a structurally different habitat, such as H. spicifera, may lead to changes to intertidal ecosystems. Kuhn (1962) initially expressed that ecosystem functioning is in part governed by biodiversity. Abiotic (physical and chemical) and biotic (e.g. parasitism, predation, facilitation and competition) factors create patterns in the distribution and abundance of species (Naeem 2002). Abiotic factors were deemed to set largescale patterns while biotic factors work over smaller scales modifying large-scale patterns (e.g. McQuaid and Branch 1984, Diamond and Case 1986, Kikkawa and Anderson 1986, Gee and Giller 1987, Weiher et al. 1998). Ecosystems respond to declining biodiversity in four possible ways, hypotheses summarising these responses include the Redundant Species hypothesis which suggests that minimum diversity facilitates ecosystem functioning, and that remaining species are, however, otherwise superfluous (Lawton and Brown 1993). Due to the habitat-forming nature and high biodiversity associated with the macroalgae in this study (Appendix C), it is unlikely that these species are redundant to ecosystem functioning. The Rivet hypothesis proposes that all species play a unique integral role in ecosystem functioning (Ehrlich and Ehrlich 1981). The Idiosyncratic Response hypothesis suggests that as diversity changes ecosystems processes change, the change, however, is unpredictable (Naeem *et al.* 1995). A Null hypothesis is also proposed where ecosystem functioning is unaffected by changes in biodiversity (Vitousek and Hooper 1993). It is unlikely that loss of the species of macroalgae to intertidal ecosystems would not lead to any changes in ecosystem functioning or associated biodiversity. It may, however, be possible that loss of intertidal macroalgae may lead to dramatic changes to the ecosystem (sensu the rivet hypothesis) or unpredictable and idiosyncratic responses. An understanding of the biodiversity associated with these macroalgae and the role that they play in providing habitat, as investigated in this study, make it easier to predict ecosystem responses to biodiversity plays an important role in structuring ecosystems which in turn influence the biogeochemical processes (Schulze and Mooney 1993, Hulot *et al.* 2000) making up the biodiversity ecosystem functioning theory. Consequently, the identity of the macroalgae in this study is important such that loss of habitat-forming taxa with high associated diversity would lead to extensive ecosystem responses.

#### 5.2 Biogeographic patterns:

The size, shape and structure of biogeographic ranges are of great interest, as these features are affected by environmental factors and ecological processes (Brown *et al.* 1996). As a result the boundaries of these ranges are changeable over space and time (Brown *et al.* 1996). Distributions of organisms within biogeographic regions are due to a multitude of underlying historical events and processes (Myres and Giller 1988, Brown *et al.* 1996). Current processes also play an integral role in the makeup of biogeographic regions, for example nutrient gradients in oceans (Carter and D'Aubrey 1988, Carter and Scheyer 1988, Lutjeharms *et al.* 2000a). The area

sampled on the west coast is encompassed by one biogeographic region for both flora and fauna (Bolton *et al.* 1986, Emanuel *et al.* 1992, Bustamante and Branch 1996, Bolton and Anderson 1997, Stegenga *et al.* 1997). Flora and fauna on the east and south coasts adhered to different biogeographic provinces. The subtropical Natal and warm temperate Agulhas provinces are proposed for fauna (Emanuel *et al.* 1992, Bustamante and Branch 1996), while a single warm temperate province is proposed for the flora (Bolton *et al.* 1986, Bolton and Anderson 1997, Stegenga *et al.* 1997). The Western Overlap encompasses the area where species found in the subtropical Natal province and the Namaqua province overlap between the Cape Peninsula and Cape Agulhas (Jackelman *et al.* 1991, Bolton and Anderson 1997, Stegenga *et al.* 1997). Fauna in this study conformed to the two biogeographic provinces on the east and south coasts (Chapter 3). Macroalgae did not vary among the sites sampled, complying with the single proposed province, large scale trends were, however, observed from low latitudes to high latitudes (Chapter 2).

The boundaries for biogeographic provinces can be considerably altered by climatic variables (Brown *et al.* 1996, Rutherford *et al.* 2000, Erasmus *et al.* 2002), changing climatic variables as seen with current climate change often shifts positions of these boundaries (Brown *et al.* 1996 Rutherford *et al.* 2000, Erasmus *et al.* 2002). The shifting of biogeographic boundaries in relation to climate change has profound effects on habitat forming biogenic species (e.g. Berke *et al.* 2010), altering their home ranges and affecting their latitudinal limits. This in turn will have effects on associated infaunal assemblages greatly changing the biodiversity and composition of intertidal assemblages.

### 5.3 Integration of factors acting at different spatial scales:

Scale has an important effect when considering intertidal assemblages as oceanographic processes act over different scales from small scale factors of centimetres to metres (Underwood and Chapman 1996) to meso-scale factors, 10s km to 100s km (Carter and Scheyer 1988, Lutjeharms *et al.* 2000a, b). These processes all contribute to forming large-scale patterns (1000s km) (Brown *et al.* 1996). The meso-scale process upwelling has previously been considered to be highly important in the structuring of intertidal assemblages (e.g. Huyer 1983, Roughgarden *et al.* 1988, Connolly and Roughgarden 1998, Blanchette *et al.* 2002, Menge *et al.* 2003, Weiters 2005, Xavier *et al.* 2007, Blanchette *et al.* 2009, Morgan *et al.* 2009a, b, c, Morgan and Fisher 2010). This study however points to meso-scale upwelling being marginalised in the large-scale structuring of assemblages, while large scale biogeography has more of an influence in this respect. Small-scale variations within shores and variation between shores indicated that processes acting over these scales play an important role in structuring these assemblages. This study indicates that a comprehensive understanding of intertidal bioveristy requires the integration of multiple factors from a range of spatial scales.

# References

Alexander SE and Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: a coupled benthic-oceanic model. *Ecological Monographs*. 66:259-275.

Allaby M (1998) A dictionary of ecology. New York Oxford University Press, UK. Pp. 192.

- Anderson MJ, Connell SD, Gillander BM, Saunders JE and Landers TJ (2005) Relationships between taxonomic resolution and spatial scales of multivariate variation. *Journal of Animal Ecology*. 74:636-646.
- Anderson RA (1992) Diversity of eukaryotic algae. Biodiversity and Conservation. 1:267-292.
- Andrewartha HG and Birch LC (1954) The Distribution and Abundance of Animals. The University of Chicago Press, Chicago, IL.
- Aquilino KM, Bracken ME, Faubel MN and Stachowicz JJ (2009) Local-scale nutrient regeneration facilitates seaweed growth on wave-exposed rocky shores in an upwelling system. *American Society of Limnology and Oceanography*. 54(1):309-317.
- Archambault P and Bourget E (1996) Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Marine Ecology Progress Series*. 136:111-121.
- Attrill MJ, Strong JA and Rowden AA (2000) Are macroinvertebrate communities influenced by seagrass structural complexity. *Ecography*. 23(1):114-121.
- Bates CR (2009) Host taxonomic relatedness and functional-group affiliation as predictors of seaweed-invertebrate epifaunal associations. *Marine Ecology Progress Series*. 387:125-136.
- Beck MW (1998) Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. *Marine Ecology Progress Series*.

169:165 -178.

- Beck MW (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*. 249:29-49.
- Bellehumeur C, Legendre P and Marcotte D (1997) Variance and spatial scales in tropical rain forest: changing the size of sampling units. *Plant Ecology*. 130:89–98.
- Berke SK, Mahon AR, Lima LP, Halanych KM, Wethey DS and Woodin SA (2010) Range shifts and species diversity in marine ecosystem engineers: patterns and predictions for European sedimentary habitats. *Global Ecology and Biogeography*.19(2):223-232.
- Bertness MD, Leonard GH, Levine JM, Schmidt PR and Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology*. 80(8):2711-2726.
- Blanchard D and Bourget E (1999) Scales of coastal heterogeneity: influence on intertidal community structure. *Marine Ecology Progress Series*. 179:163-173.
- Blanchette CA, Broitman BR and Gaines SD (2006) Intertidal community structure and nearshore oceanography around Santa Cruz Island, California, USA. *Marine Biology*. 149:689-701.
- Blanchette CA, Helmuth B and Gaines SD (2007) Spatial patterns of growth in the mussel, *Mytilus californianus* across major oceanographic and biogeographic boundary at Point Conception, Califoria, USA. *Journal of Experimental Marine Biology and Ecology*. 340:126-148.
- Blanchette CA, Miner BG and Gaines SD (2002) Geographic variability in form, size and survival of *Egregia menziesii* around Point Conception, California. *Marine Ecology Progress Series*. 239:69-82.

Blanchette CA, Wieters EA, Broitman BR, Kinlan BP and Schiel DR (2009) Trophic structure

and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. *Progress in Oceanography*. 83:107-116.

- Blanton JO, Atkinson LP, Pietrafesa LJ and Lee TN (1981) The intrusion of Gulf Stream water across the continental shelf due to topographically-induced upwelling. *Deep-Sea Research*. 28:393-405.
- Bologna PA and Heck KL (1999) Macrofaunal associations with seagrass epiphytes Relative importance of trophic and structural characteristics. *Journal of Experimental Marine Biology and Ecology*. 242:21-39.
- Bolton JJ (1986) Marine phytogeography of the Benguela upwelling region on the west coast of southern Africa: a temperature dependent approach. *Botanica Marina*. 29 (3):251-256.
- Bolton JJ 1994 Global seaweed diversity patterns and anomalies. *Botanica Marina*. 36:241-246.
- Bolton JJ and Anderson RJ (1990) Correlation between intertidal seaweed community composition and seawater temperature patterns on a geographical scale. *Botanica Marina*. 33: 447-457.
- Bolton JJ and Anderson RJ (1997) Marine vegetation. In: Vegetation of Southern Africa. Cowling RM, Richardson DM and Pierce SM (Eds). Cambridge University Press. Pp. 248-375.
- Bolton JJ, Leliaert F, De Clerck O, Anderson RJ, Stegenga H, Engledow HE and Coppejans E (2004) Where is the western limit of the tropical Indian Ocean seaweed flora? An analysis of intertidal seaweed biogeography on the east coast of South Africa. *Marine Biology*. 144:51-59.
- Borthagaray IA and Carranza A (2007) Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. *Acta Oecologia*. 31:243-250.

- Bosman AL, Hockey PA and Siegfried WR (1987) The Influence of Coastal Upwelling on the Functional Structure of Rocky Intertidal Communities. *Oecologia*. 72(2):226-232.
- Botts PS, Patterson, BA and Schloesser DW (1996) Zebra Mussel Effects on Benthic Invertebrates: Physical or Biotic? *Journal of the North American Benthological Society*. 15(2):179-184.
- Branch GM (1971) The ecology of *Patella Linnaeus* from the Cape Peninsula, South Africa. I. Zonation movements and feeding. *Zoologica Africana*. 6:1-38.
- Branch GM (1975) Intraspecific competition in *Patella cochlear* Born. *Journal of Animal Ecology*. 44:263-81.
- Branch GM and Branch M (1981) The living shores of South Africa. C. Struik, Cape Town, South Africa.
- Branch GM and Griffiths C (1988) The Bengula ecosystem part V. The coastal zone. Oceanography and Marine Biology Annual Review. 26:395-486.
- Branch GM and Moreno CA (1994) Intertidal and subtidal grazers. In: Rocky shores: exploitation in Chile and South Africa. Sigfried WR (Ed.). Springer-Verlag, Berlin. Pp. 75-100.
- Branch GM, Griffiths CL, Branch ML and Beckley LE (2007) Two Oceans: A guide to the marine life of southern Africa. Struik Publishers South Africa. Pp. 360.
- Bray JR and Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*. 27:325-49.
- Broitman BR, Navarrete SA, Smith F and Gaines SD (2001) Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series*. 224:21-34.
- Broitman BR and Kinlan BP (2006) Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. *Marine Ecology Progress Series*. 327:15-25.

Brown AC and Jarman NG (1978) Coastal marine habitats. In: Biogeography and Ecology of

Southern Africa. Werger MJA (Ed.). The Hague: W. Junk. Pp. 1241-1277.

Brown JH and Lomolino MV (1998) Biogeography, second edition, Sunderland, MA: Sinauer.

- Brown JH, Stevens GC and Kaufman DM (1996) The Geographic Range: Size, Shape, Boundaries and internal Structure. *Ecology*. 27:597-623.
- Brown JS (1988) Patch use as an indicator of habitat preference, predation risk and competition. *Behavioural Ecology and Sociobiology*. 22:37-47.
- Brown PC (1992) Spatial and seasonal variation in Chlorophyll distribution in the upper 30m of the photic zone in the southern Benguela/Agulhas ecosystem. *South African Journal of Marine Science*. 12:515-525.
- Bruno JF and Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Marine Community Ecology. Bertness MD, Gaines SD and Hay ME (Eds.). Sinauer, Sunderland. Pp. 201–218.
- Bruno JF, Stachowicz JJ and Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecology and Evolution*. 18(3):119-125.
- Burger LF (1990) The distribution patterns and community structure of the Tsitsikarma rocky littoral Ichthyofauna. MSc thesis Rhodes University.
- Burnaford JL (2004) Habitat modification and refuge from sub-lethal stress drive a marine plant-herbivore association. *Ecology*. 85(10):2837-2849.
- Bustamante RH and Branch GM (1996) Large scale patterns and trophic structure of southern African rocky shores: The roles of geographic variation and wave exposure. *Journal of Biogeography*. 23(3):339-351.
- Bustamante RH, Branch GM and Eekhout S (1995a) Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology*. 76:2314-2329.
- Bustamante RH, Branch GM, Eekhout S, Robertson B, Zoutendyk P, Schleyer M, Dye A, Hanekom N, Keats D, Jurd M and McQuaid CD (1995b) Gradients of intertidal primary

productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia*. 102:189-201.

- Carpenter ST and Lodge DM (1986) Effects of submersed macrophytes on ecosystem processes. *Aquatic Biology*. 26:341-370.
- Carr ME and Kearns EJ (2003) Production regimes in four Eastern Boundary Current systems. Deep-Sea Research II. 50:3199-3221.
- Carter RA and d'Aubrey J (1988) Inorganic nutrients in Natal continental shelf waters. In: Coastal Ocean Studies of Natal, South Africa, Lecture Notes on Coastal and Estuarine Studies. Schumann EH (Ed.). Springer, Berlin. 26:131-151.
- Carter RA and Schleyer MH (1988) Plankton distributions in Natal coastal waters. In: Coastal Ocean Studies of Natal, South Africa. Lecture Notes on Coastal and Estuarine Studies. Schumann EH (Ed.). Springer, Berlin. Pp. 26:152-177.
- Castilla JC and Duran LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos*. 45:391-399.
- Castilla JC and RT Paine (1987) Predation and community organization on Eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural*. 60:131-151.
- Castilla JC, Lagos NA and Cerda M (2004) Marine ecosystem engineering by the alien ascidian
   *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology Progress Series*.
   268:119-130.
- Chapman MG (1992) Living at the fringe of intertidal society. PhD Thesis University of Sydney, Australia. Pp. 223
- Chapman MG (1998) Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. *Marine Ecology Progress Series*. 162:71-8.

- Chapman MG and Underwood AJ (1994) Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology*, 179:145-169.
- Chapman MG, Underwood AJ and Skilleter GA (1995) Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *Journal of Experimental Marine Biology and Ecology*. 189:103-122.
- Chemello R and Milazzo M (2002) Effect of algal architecture on associated fauna: some evidence from phytal molluscs. *Marine Biology*. 140:981-990.
- Chown SL and Gaston KJ (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology and Evolution*. 15(8):311-315.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology. 18:117-143.

Clarke KR and Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

- Cole RG and Syms C (1999) Using spatial pattern analysis to distinguish causes of mortality: an example from kelp in north-eastern New Zealand. *Journal of Ecology*. 87:963-972.
- Cole VJ (2009) Densities of polychaetes in habitat fragments depend on the surrounding matrix but not the complexity of the remaining fragment. *Austral Ecology*. 34:469-477.
- Cole VJ, Chapman MG and Underwood AJ (2007) Landscapes and life-histories influence colonisation of polychaetes to intertidal biogenic habitats. *Journal of Experimental Marine Biology and Ecology*. 348:191-199.
- Cole VJ and McQuaid CD (in press) Bioengineers and their associated fauna respond differently to the effect of biogeography and upwelling. Ecology.
- Colwell RK and Hurtt GC (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist*. 144:570-595.

Commito JA, Celano EA, Celico HJ, Como S and Johnson CP (2005) Mussels matter:

Postlarval dispersal dynamics altered by a spatially complex ecosystem engineer. Journal of Experimental Marine Biology Ecology. 316:133-147.

Condie SA (1995) Interaction between western boundary currents and shelf waters: a mechanism for coastal upwelling. *Journal of Geophysical Research*. 100:22811-24818.

Connell JH (1978) Diversity in tropical rainforests and coral reefs. Science. 199:1302-1310.

- Connolly SR and Roughgarden J (1998) A Latitudinal Gradient in Northeast Pacifc Intertidal Community Structure: Evidence for an Oceanographically Based Synthesis of Marine Community Theory. *The American Naturalist.* 151(4):311-326.
- Connolly SR and Roughgarden J (1999a) Increased recruitment of northeast Pacific barnacles during the 1997 El Niño. *Limnology and Oceanography*. 44:466-469.
- Connolly SR and Roughgarden J (1999b) Theory of marine communities: competition, predation, and recruitment dependent interaction strength. *Ecological Monographs*. 69:277-296.
- Coull BC and Wells JBJ (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology*. 64:1599-1609.
- Crisp DJ (1964) Mortalities in marine life in North Wales during the winter of 1962-63. In: The effects of the severe winter of 1962-63 on marine life in Britain. Crisp DJ (Ed.). *Journal* of Animal Ecology. 33:190-197.
- Crisp DJ and B Mwaiseje (1989) Diversity in intertidal communities with special reference to the *Corallina officinalis* community. *Scientia Marina*. 53(2–3):365–372.
- Crisp MD, West JG and Linder HP (1999) Biogeography of the terrestrial flora. In: *Flora of Australia, Introduction*. AE Orchard and HS Thompson (Eds.). Second edition. CSIRO, Melbourne. 1:321-367
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions. The role of ecosystem engineers. *Oikos*. 97:153-166

- Currie DJ (1991) Energy and large-scale patterns of animal and plant species richness. American Naturalist. 137:27-49.
- Dahlhoff EP and Menge BA (1996) Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Marine Ecology Progress Series*. 144:97-107.
- Daleo P, Escapa M, Alberti J and Iribarne O (2006) Negative effects of an autogenic ecosystem engineer: Interactions between coralline turf and an ephemeral green alga. *Marine Ecology Progress Series*. 315:67-73.
- Day JH (1967). A monograph of the Polychaeta of Southern Africa. Part 1 Errantia and Part 2 Sedentaria. British Museum of Natural History Publication.
- Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*. 41:351-389.
- Dayton PK, Tegner MJ, Edwards PB and Riser KL (1999) Temporal and spatial scales of kelp demography: The role of oceanographic climate. *Ecological Monographs*. 69(2):219-250.
- Dean RL and Connell JH (1987a) Marine invertebrates in an algal succession. I. Variations in abundance and diversity with succession. *Journal of Experimental Marine Biology and Ecology*. 109:195-215.
- Dean RL and Connell JH (1987b) Marine invertebrates in an algal succession. II. Tests of hypotheses to explain changes in diversity with succession. *Journal of Experimental Marine Biology and Ecology*. 109:217-247.
- Dean RL and Connell JH (1987c) Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity and diversity. *Journal of Experimental Marine Biology and Ecology*. 109:249-273.

- Demarcq H, Barlow RG and Shillington FA (2003) Climatology and variability of sea surface temperature and surface chlorophyll in the Benguela and Agulhas ecosystems as observed by satellite imagery. *African Journal of Marine Science*. 25:363-372.
- Devred E, Sathyendranath S and Platt T (2007) Delineation of ecological provinces using ocean colour radiometry. *Marine Ecology Progress Series*. 346:1-13.
- Diamond J and Case TJ (1986) Community Ecology. New York. Harper and Row.
- Diaz RJ, Solan M and Valente RM (2004) A review of approaches for classifying benthic habitats and evaluating habitat quality. *Journal of Environmental Management*. 73:165-181.
- Dobzhansky T (1950) Mendelian populations and their evolution. *The American Naturalist*. 84:401-418.
- Dommasnes A (1968) Variations in the meiofana of *Corallina officinalas* L. In Western Norway. *Sarsia*. 34:117-124.
- Downes BJ, Lake PS, Schrieber ESG and Glaister A (2000) Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia*. 123(4)569-581.
- Edgar GJ (1983a) The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. *Journal of Experimental Marine Biology and Ecology*. 70: 129-157.
- Edgar GJ (1983b) The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. *Journal of Experimental Marine Biology and Ecology*. 70:159-179.
- Eekhout S, Raubenheimer CM, Branch M, Bosman AL and Bergh MO (1992) A holistic approach to the exploitation of intertidal stocks: Limpets as a case study. *South African Journal Of Marine Science*. 12:1017-1029.

- Ehrlich PR and Ehrlich AH (1981) Extinction. The causes and consequences of the disappearance of species. New York. Random House.
- Ellison AM, Farnsworth EJ and Merkt RE (1999) Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography*. 8(2):95-115.

Elst R van der (1990) A guide to the common sea fishes of southern Africa. Struik, Cape Town.

- Emanuel BP, Bustamante RH, Branch GM, Eekhout S and Odendaal FJ (1992) A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal Of Marine Science*. 12:341-354.
- Emerson RH and Faller-Fritsch RJ (1976) An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. *Journal of Experimetal Marine Biology and Ecology*. 23:285-297.
- Erasmus BFN, Van Jaarsveld AS, Chown SL, Kshatriya M and Wessels KDJ (2002)
  Vulnerability of South African animal taxa to climate change. *Global Change Biology*.
  8: 679-693.
- Erlandsson J, McQuaid CD and Kostylev VE (2005) Contrasting spatial heterogeneity of sessile organisms within mussel (*Perna perna* L.) beds in relation to topographic variability. *Journal of Experimental Marine Biology and Ecology*. 314:79-97.
- Estes JA and Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*. 65:75-100.
- Estes JA and Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. *Science*. 185:1058-1060.
- Fahrig L and Merriam G (1994) Conservation of fragmented populations. *Conservation Biology*. 8:50-59.

Farrell TM (1991) Models and mechanisms of succession: an example from a rocky intertidal

community. Ecological Monographs. 61:95-113.

- Field JG and Griffiths CL (1991) Littoral and sublittoral ecosystems of southern Africa. In: Ecosystems of the World: Intertidal and littoral ecosystems. Mathieson AC and Nienhuis A (Eds.). Elsevier Science Publisher, Amsterdam. Pp.323-346.
- Fielding PJ, Weerts KA and Forbes AT (1994) Macroinvertebrate communities associated with intertidal and subtidal beds of *Pyura stolonifera* (Heller) (Tunicata: Ascidiacea) on the Natal coast. *South African Journal of Zoology*. 29:46-53.
- Fletcher WJ and Underwood AJ (1987) Interspecific competition among subtidal limpets effects of substratum heterogeneity. *Ecology*. 68:387-400.
- Floeter SR, Guimaraes RZ, Rocha LA, Ferreira CE, Rangle A and Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography*. 10(4):423-431.
- Foster MS (1990) Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia*. 192:21-34.
- Freidenburg TL, Menge BA, Halpin PM, Webster M and Sutton-Grier A (2007) Cross-scale variation in top-down and bottom-up control of algal abundance. *Journal of Experimental Marine Biology and Ecology*. 347:8-29.
- Gaines SD and Lubchenco J (1982) A unified approach to marine plant-herbivore interactions.II. Biogeography. *Annual Review of Ecology and Systematics*. 13:111-138.
- Gaines SD and Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences, USA*. 82:3707-3711.
- Garrison T (1993) Oceanography: An Invitation to marine science. Dodson K, Horne N, Aborgast M, Eisenmen R and Lee J (Eds.). Wadsworth USA. Pp. 184-209.

Garrity SD and Levings SC (1984) Aggregation in a tropical neritid. Veliger. 27:1-6.

- Gaston KJ (1996) Biodiversity-latitudinal gradients. *Progress in Physical Geography*. 20:466-476.
- Gaston KJ and Blackburn TM (2000) Pattern and Process in Macroecology. Blackwell Science, Oxford.
- Gee JM and Warwick M (1994) Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Marine Ecology Progress Series*. 103:141-150.
- Gee JRH and Giller PS (1987) Organization of communities past and present. London: Blackwell Scientific Publications.
- Gibbons MJ (1988). The Impact of Wave Exposure on the Meiofauna of Gelidium pristoides (Turner) Kuetzing (Gelidiales: Rhodophyta). Estuarine, Coastal and Shelf Science. 27:581-593.
- Gilinski E (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology*. 65:455-468.
- Gill AE and Schumann EH (1979) Topographically induced changes in the structure of an intertidal coastal jet application to the Agulhas Current. *American Meteorological Society*. 9:975-991.
- Godoy EA, Almeida TC and Zalmon IR (2002) Fish assemblages and environmental variables on an artificial reef north of Rio de Janeiro, Brazil. *Journal of Marine Science*. 59:138-143.
- Goschen WS and Schumann EH (1990) Upwelling and the occurrence of cold water aroundCape Recife, Algoa Bay, South Africa. South African Journal of Marine Science. 16:57-67.
- Gosliner T (1987) Biogeography of the opisthobranch gastropod fauna of southern Africa. *American Malacological Bulletin.* 5:243-258.

Gray JS (2001) Marine diversity: the paradigms in patterns of species richness examined.

Scientia Marina. 65:41-56.

- Griffiths CL (1974) The gammaridean and caprellid Amphipoda of southern Africa. Ph. D. Dissertation, University of Cape Town, South Africa.
- Griffiths CL (1976) Guide to the benthic marine amphipods of southern Africa. Cape Town. Trustees of the South African Museum. Pp.1-106.
- Gunnill FC (1982) Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetiafastigiata*. *Marine Biology*. 69:263-280.
- Gutierrez JL, Jones CG, Strayer DL and Iribarne O (2003) Molluscs as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos*. 101:79-90.
- Hacker SD and Steneck RS (1990) Habitat Architecture and the abundance and body-sizedependant habitat selection of a phytal amphipod. *Ecological Society of America* 71(6):2269-2285.
- Hagerman L (1966) The macro- and meiofauna associated with *Fucus serratus* L. With some ecological remarks. *Ophelia*. 3:1-43.
- Hardman-Mountford NJ, Richarson AJ, Agenbag JJ, Hagen E, Nykjaer L, Shillington FA and Villacastin C (2003) Ocean climate of the South East Atlantic observed from satellite data and wind models. *Progress in Oceanography*. 59:181-221.
- Harley CDG (2006) Effects of physical ecosystem engineering and herbivory on intertidal community structure. *Marine Ecology Progress Series*. 317:29-39.
- Harris JM, Branch GM, Elliott BL, Currie B, Dye AH, McQuaid CD, Tomalin BJ and Velasquez C (1998) Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *South African Journal Of Zoology*. 33(1):1-11.

Hawkins BA (2001) Ecology's oldest pattern? Trends in Ecology and Evolution. 16(8):470.

Hawkins SJ and Hartnoll RG (1985) Factors determining the upper limits of intertidal canopy-

forming algae. Marine Ecology Progress Series. 20(32):265-271.

- Hay ME (1981) The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology*. 62:739-750.
- Hicks GRF (1980) Structure of phytal harpcticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of experimental Marine Biology and Ecology*. 44:157-192.
- Hicks GRF (1985) Meiofauna associated with rockyshore algae. In: Ecology of Rocky Coasts. Moore PG and Seed R (Eds.). London, Hodder Stoughton.
- Hicks GRF (1986) Meiofauna associated with rocky shore algae. In: The ecology of rocky coasts: essays presented to J. R. Lewis. Moore PG and Seed R. (Eds.) Columbia University Press, New York, New York, USA. Pp. 36-56.
- Hodgson LM (1984) Desiccation tolerance of *Gracilaria tikvahiae* (Rhodophyta). *Journal of Phycology*. 20:444-446.
- Hsueh Y and O'Brien JJ (1971) Steady coastal upwelling induced by an along-shore current. Journal of Physical Oceanography. 1:180-186.
- Hull SL (1997) Seasonal changes in diversity and abundance of ostracods on four species of intertidal algae with differing structural complexity. *Marine Ecology Progress Series*. 161:71-82.
- Hulot FD, Lacroix G, Lescher-Moutoué F and Loreau M (2000) Functional diversity governs ecosystem response to nutrient enrichment. *Nature*. 405:340-344.
- Huston MA (1994). Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.
- Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *The American Naturalist*. 93:145-59.

Huyer A (1983) Coastal upwelling in the California Current system. Progress in

Oceanography. 12:259-284.

- Issac WE and Hewitt F (1953) The morphology, geographical distribution and ecology of *Hypnea spicifera* (Suhr.) Harv. *Journal of South African Botany*. 19(3):73-84.
- Jackelman JJ, Stegenga and Bolton JJ (1991) The marine benthic flora of the Cape Hangklip area and its phytogeographical affinities. *South African Journal of Botany*. 57: 295-304.
- Jarvis SC and Seed R (1996) The meiofauna of *Ascophyllum nodosum* (L.) Le Jolis: characterisation of the assemblages associated with two common epiphytes. *Journal of Experimental Marine Biology and Ecology*. 199:249-267.
- Jenkins SR, Coleman RA, della Santina P, Hawkins SJ, Burrows MT and Hartnoll RG (2005) Regional scale differences in the determination of grazing effects in the rocky intertidal. *Marine Ecology Progress Series*. 287:77-86.
- John DM and Pople W (1973) The fish grazing of rocky shore algae in the gulf of guinea. Journal of Experimental Marine Biology and Ecology. 11:81-90.
- Johnson SC and Scheibling RE (1987) Structure and dynamics of epifaunal assemblages on intertidal macroalgae Ascophyllum nodosum and Fucus vesiculosus in Nova Scotia, Canada. Marine Ecology Progress Series 37:209-227.
- Jones CG, Lawton JH and Shachak M (1994). Organisms as ecosystem engineers. *Oikos*. 69(3):373-386.
- Jones CG, Lawton JH and Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*. 78(7):1946-1957.
- Jouquet P, Dauber J, Lagerlo J, Lavelle P and Lepage M (2006) Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology*. 32:153-164.
- Jury MR (1985) Case studies of alongshore variations in wind-driven upwelling in the Southern Benguela Region. In: *South African ocean colour and upwelling experiment*. Shannon

LV (Ed). Galvin and Sales (Pty), Cape Town. Pp. 29-46.

- Kaufman DM (1998) The structure of mammalian faunas in the New World: from continents to communities. PhD thesis. University of New Mexico, Albuquerque. Pp. 130.
- Kelaher BP (2002) Influence of physical characteristics of coralline turf on associated macrofaunal assemblages. *Marine Ecology Progress Series*. 232:141-148.
- Kelaher BP (2003a) Effects of frond length on diverse gastropod assemblages in coralline turf. Journal of the Marine Biological Association of the United Kingdom. 83:159-163.
- Kelaher BP (2003b) Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf. *Oecologia*. 135:431-441
- Kelaher BP, Chapman MG and Underwood AJ (2001) Spatial patterns of diverse macrofaunal assemblages in coralline turf and their associations with environmental variables. *Journal of the Marine Biological Association of the United Kingdom.* 81:917-30.
- Kelaher BP, Underwood AJ and Chapman MG (2003) Experimental transplantations of coralline algal turf to demonstrate causes of differences in macrofauna at different tidal heights. *Journal of Experimental Marine Biology and Ecology*. 282:23-41.
- Kelaher BP, Castilla JC, Prado L, York P, Schwindt E and Bortolus A (2007) Spatial variation in molluscan assemblages from coralline turfs of Argentinean Patagonia. *Journal of Molluscan Studies*. 73:139-146.
- Kensley BF (1978) Guide to the marine isopods of southern Africa. Rustica Press Ltd, Wynberg, Cape Town. Pp. 173.
- Kikkawa J and Anderson DJ (1986) Community ecology. London. Blackwell.
- Kilburn R and Rippey E (1982) Sea shells of southern Africa. Cadell E-M (Ed.). Macmillan South Africa Ltd, Johannesburg. Pp. 249.
- Kitching RL, Daiqin L and Stork NE (2001) Assessing biodiversity 'sampling packages': how similar are arthropod assemblages in different tropical rainforests? *Biodiversity and*

Conservation. 10:793–813.

- Koukouras A (1992) Relationship of sponge macrofauna with the morphology of their hosts in the north Aegean Sea. *Int. Rev. Gesam. Hydrobiol.* 77: 609-619.
- Kuhn TS (1962) The structure of scientific revolutions. University of Chicago Press, Chicago, Illinois, USA.
- Lawton JH and Brown VK (1993) Redundancy in ecosystems. In Biodiversity and ecosystem function. Schulze ED and Mooney HA (Eds.). New York: Springer Verlag. Pp. 255-270.
- Leite FPP, Tanaka MO and Gebara RS (2007) Structural variation in the brown alga Sargassum cymosum and its effects on associated amphipod assemblages. Brazilian Journal of Biology. 67(2): 215-221.
- LeTourneux F and Bourget E (1988) Importance of physical and biological settlement cues used at different spatial scales by the larvae of Semibalanus balanoides. *Marine Biology*. 97:57–66.
- Levin SA (1992) The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology*. 73(6):1943-1967.
- Littler MM Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgal functional form groups model. *The American Naturalist*. 116:25-44.
- Lubchenco J Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Reviews of Ecology and Systematics*. 12:405-437.
- Lutjeharms JRE (2006) The Agulhas current. Springer-Verlag Berlin Heidelberg. Chapter 1, Pp. 1-16. Chapter 4, Pp. 91 -113, Chapter 5. Pp. 121-150.
- Lutjeharms JRE (2007) Three decades of research on the greater Agulhas Current. Ocean Science. 3:129-147.

Lutjeharms JRE and Roberts HR (1988) The Natal Pulse; an extreme transient on the Agulhas

Current. Journal of Physical Oceanography. 93:631-645.

- Lutjeharms JRE, Gründlingh ML and Carter RA (1989) Topographically induced upwelling in the Natal Bight. *South African Journal of Science*. 85:310-316.
- Lutjeharms JRE, Liu C-T, Chuan W-S and Shyu C-Z (1993) On some similarities between the oceanic circulations of Southern Africa and of Taiwan. *South African Journal of Science*. 89:367-371.
- Lutjeharms JRE and Machu E (2000) Upwelling inshore of the East Madagascar Current. Deep-Sea Research I. 47:2405-2411
- Lutjeharms JRE, Cooper J and Roberts M (2000a). Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research*. 20:737-761.
- Lutjeharms JRE, Valentine HR and Ballegooyen VR (2000b) The hydrography and water masses of the Natal Bight, South Africa. *Continental Shelf Research*. 20:1907-1939.
- MacArthur RH and MacArthur JW (1961) On Bird species diversity. Ecology. 42:594-598
- MacDonald DW and Johnson PJ (1995) The relationship between bird distribution and the botanical and structural characteristics of hedges. *Journal of Applied Ecology*. 32 492-505.
- Macpherson E and Duarte CM (1994) Patterns in species richness, size, and latitudinal range of East Atlantic fishes. *Ecography*. 17:242-248.
- Maggi E, Bertocci I, Vaselli and Benedetti-Cecchi L (2009) Effects of changes in number, identity and abundance of habitat-forming species on assemblages of rocky seashores. *Marine Ecology Progress Series*. 381:39-49.
- Martin-Smith K (1993) Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology*. 174:243–260.

McCabe DJ and Gotelli NJ (2003) Caddisfly diapause aggregations facilitate benthic

invertebrate colonization. Journal of Animal Ecology. 72:1015-1026.

- McClean-Padman J and Padman L (1991) Summer upwelling on the Sydney inner continental shelf: the relative roles of local wind forcing and meso-scale eddy encroachment. *Continental Shelf Research*. 11:321-345.
- McCoy ED and Bell SS (1991) Habitat structure: the evolution and diversification of a complex topic. In: Habitat Structure: The Physical Arrangement of Objects in Space, Bell SS, McCoy ED and Mushinsky HR (Eds.). Chapman and Hall, New York. Pp. 3-27.
- McQuaid CD (1981) The establishment and maintenance of vertical size gradients in populations of *Littorina africana knysnaensis* (Phillipi) on an exposed shore. *Journal of Experimental Marine Biology and Ecology*. 54:77-89.
- McQuaid CD and Branch GM (1984) The influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Marine Ecology Progress Series*. 19:145-151.
- McQuaid CD and Branch GM (1985) Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series*. 22:153-161.
- Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs*. 46:355-393.
- Menge BA (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecological Society of America*, 73(3), 755-765.
- Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology Ecology*. 250:257-289.
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA and Yamada SB (1994). The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological*
Monographs. 64(3):250-286.

- Menge BA, Daley BA, Wheeler PA and Strub PT (1997a) Rocky intertidal oceanography: An association between community structure and nearshore phytoplankton concentration. *Limnology and Oceanography*. 42(1):57-66.
- Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E and Strub PT (1997b) Benthicpelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proceedings of the National Academy of Sciences, USA*. 94(26):14530-14535.
- Menge BA, Daley BA, Lubchenco J, Sanford E, Dahlhoff E, Halpin PM, Hudson G and Burnaford JJ (1999) Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs*. 69:297-330.
- Menge BA, Lubchenco J, Bracken ME, Chan F, Foley MM, Freidenburg TL, Gaines SD, Hudson G, Krenz C, Leslie H, Menge DNL, Russel R and Webster MS (2003) Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences, USA*. 100(21):12229-12234.
- Menge BA, Blanchette C, Raimondi P, Freidenburg TL, Gaines SD, Lubchenco J, Lohse D, Hudson G, Foley M and Pamplin J (2004) Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs*. 74(4):663-684.
- Menge BA, Francis C and Lubchenco J (2008). Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecology letters*. 11:151-162.
- Monteiro SM, Chapman MG and Underwood AJ (2002) Patches of the ascidian *Pyura* stolonifera (Heller, 1878): structure of habitat and associated intertidal assemblages. Journal of Experimental Marine Biology and Ecology. 270(2):171-189.
- Moran MJ (1985) Distribution and dispersion of the predatory intertidal gastropod Morula marginalba Blanville. Marine Ecology Progress Series. 22:41-52.

Morgan SG and Fisher JL (2010) Larval behaviour regulates nearshore retention and offshore

migration in an upwelling shadow and along the open coast. *Marine Ecology Progress* Series. 404:109-126.

- Morgan SG, Fisher JL, Miller SM, McAfee ST and Largier JL (2009a) Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology*. 90(12):3489-3502.
- Morgan SG, Fisher JL, Mace AJ, Akins L, Slaughter AM and Bollens SM (2009b) Cross-shelf distributions and recruitment of crab postlarvae in a region of strong upwelling. *Marine Ecology Progress Series*. 380:173-185.
- Morgan SG, Fisher JL and Mace AJ (2009c) Larval recruitment in a region of strong, persistent upwelling and recruitment limitation. *Marine Ecology Progress Series*. 394:79-99.
- Myres AA and Giller PS (1988) Process, pattern and scale in biogeography. In: Analytical Biogeography: An integrated approach to the study of animal and plant distributions. Myres AA and Giller PS (Eds.). Chapamn and Hall, London. Pp. 3-12.
- Naeem S (2002) Disentangling the impacts of diversity of ecosystem functioning in combinatorial experiments. *Ecology*. 83:2925–2935.
- Naeem S, Thompson LJ, Lawler SP, Lawton JH and Woodfin RM (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions: Biological Sciences*. 347(1321):249-262.
- Nagata Y (1970) Detailed temperature cross section of the cold water belt along the northern edge of the Kuroshio. *Journal of Marine Research*. 28:1-14.
- Nakaoka M, Ito N, Yamamoto T, Okuda T and Noda T (2006) Similarity of rocky intertidal assemblages along the Pacific coast of Japan: effects of spatial scales and geographic distance. *Ecological Research*. 21:425-435.
- Navarrete SA (1996) Variable predation: effects of whelks on a mid-intertidal successional community. *Ecological Monographs*. 66:301-321.

- Navarrete SA and BA Menge (1996) Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs*. 66:409-429.
- Nelson G and Hutchings L (1983) The Benguela Upwelling Area. *Progress in Oceanography*. 12:333-356.
- Nelson TA, Olson J, Imhoff L and Nelson AV (2010) Aerial exposure and desiccation tolerances are correlated to species composition in "green tides" of the Salish Sea (northeastern Pacific). *Botanica Marina*. 53:103-111.
- Nielsen KJ and Navarrete SA (2004) Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecology Letters*. 7:31-41.
- Norderhaug KM, Christie H, Fossa JH and Fredriksen S (2005) Fish-macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. *Journal of the Marine Biological Association of the United Kingdom*. 85:1279-1286.
- Norton TA (1985) The zonation of seaweeds on rocky shores. In: The ecology of rocky coasts, Moore PG and Seed R. (Eds.) Hodder and Stoughton Educational, UK. Pp. 7-21.
- O'Connor NE and Crowe TP (2005) Biodiversity loss and ecosystem functioning: distinguishing between number and identitity of species. *Ecology*. 86(7):1783-1796.
- Paerl HW (1997) Coastal eutrophication and harmful algal blooms: Importance of atmospheric deposition and groundwater as "new" nitrogen and other nutrient sources. *Limnology* and Oceanography. 42(5):1154-1165.
- Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*. 15:93-120.
- Paine RT, Castilla JC and Cancino J (1985) Perturbation and recovery patterns of starfishdominated intertidal assemblages in Chile, New Zealand, and Washington State. *The American Naturalist.* 125:679-691.

Parrish RH, Nelson CS and Bakun A (1981) Transport mechanisms and reproductive success of

fishes in the California. Current Biology and Oceanography 1:175-203.

- Patti B, Guisande C, Vergara R, Riveiro I, Maneiro I, Barreiro A, Bonanna A, Buscaino G, Cuttitta A, Basilone G and Mazzola S (2008) Factors responsible for the differences in satellite-based chlorophyll a concentration between the major global upwelling areas. *Estuaries and Coasts*. 76:775-786.
- Pearce AF (1977) Some features of the upper 500 m of the Agulhas Current. *Journal of Marine Research.* 35:731-753.
- Phillips NE (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. *Marine Ecology Progress Series*. 295:79-85.
- Pianka ER (1966) Latitudinal gradients in species diversity: a Review of concepts. *The American Naturalist.* 100(910):33-46.
- Pinn EH, Thompson RC and Hawkins SJ (2008) Piddocks (Mollusca: *Bivalvia: Pholadidae*) increase topographical complexity and species diversity in the intertidal. *Marine Ecology Progress Series*. 355:173-182.
- Pitcher GC, Brown PC and Mitchell-Innes BA (1992) Spatio-temporal variability of phytoplankton in the southern Benguela upwelling systems. *South African Journal of Marine Scence*. 12:439-456.
- Porras R, Bataller JV, Murgui E and Torregrosa MT (1996) Trophic structure and community composition of polychaete inhabiting some *Sabellaria alveolata* (L) reefs along the Valencia Gulf Coast, Western Mediterranean. *PSZN I: Marine Ecology*. 17:583-602.
- Prado L and Castilla JC (2006) The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: biodiversity, habitat structural complexity and environmental heterogeneity. *Journal of the Marine Biological Association of the United Kingdom*. 86:417-421.

Rabinovich JE and Rapoport EH (1975) Geographical variation in the diversity of Argentine

passerine birds. Journal of Biogeography. 2:141-57.

- Raffaelli DG and Hughes RN (1978) The effects of crevice size and availability on populations of *Littorina rudis* and *Littorina nentoldes*. *Journal of Animal Ecology*. 47:71-83.
- Ragnarsson SA and Raffaelli D (1999) Effects of the mussel Mytilus edulis L. on the invertebrate fauna of sediments. Journal of Experimental Marine Biology Ecology. 241:31-43.
- Rapoport EH (1975) Areografia: Estrategias Geograficas de Especies. Mexico City, DF: Fundo Cult. Econ.
- Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL and Wilson GDF (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature*. 365:636-639.
- Rey JR (1981) Ecological biogeography of arthropods on *Spartina* islands in north-west Florida. *Ecological Monographs*. 51:237-265.
- Ribeiro AC, Peliz A and Santos AMP (2005) A study of the response of chlorophyll-a to a winter upwelling event off Western Iberian using SeaWiFS and in situ data. *Journal of Marine Systems*. 53:87-107.
- Richardson AJ and Poloczanska ES 2009 Australia's Oceans. In: A Marine Climate Change Impacts and Adaptation Report Card for Australia. Pp. 1-6.
- Rivadeneira MM, Fernandez M and Navarrete SA (2002) Latitudinal trends of species diversity in rocky intertidal herbivore assemblages: spatial scale and the relationship between local and regional species richness. *Marine Ecology Progress Series*. 245:123-131.

Robinson N 1966. Solar Radiation. Elsevier New York.

- Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*.65:514–527.
- Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University Press, Cambridge.

- Roughgarden J, Gaines SD and Possingham HP (1988) Recruitment dynamics in complex life cycles. *Science*. 241:1460-1466.
- Roy K, Jablonski D, Valentine JW and Rosenberg G (1998) Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proceedings of the National Academy of Sciences,* USA. 95:3699-3702.
- Russo AR (1987) Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods. *Marine Ecology Progress Series*. 36:101-105.
- Rutherford MC, Powrie LW and Schulze RE (1999) Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Diversity and Distributions*. 5:253-262.
- Sagarin RD and Gaines SD (2006) Recent studies improve understanding of population dynamics across species ranges. *Oikos*. 115:386-388.
- Sanford E and Menge BA (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Marine Ecology Progress Series*. 209:143-157.
- Santelices B (1990) Patterns of organizations of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. *Hydrobiologia*. 192:35-57.
- Schulze ED and HA Mooney (1993) Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.
- Schumann EH, Perrins L-A and Hunter IT (1982) Upwelling along the South Coast of the Cape Province, South Africa. *South African Journal of Science*. 78:238-242.
- Schumann EH and Martin JA (1991) Climatological aspects of the coastal wind field at Cape Town, Port Elizabeth and Durban. *South African Geographical Journal*. 73:48-51.
- Seed R (1996) Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United*

Kingdom. 76:203-210.

- Seed R and O'Connor RJ (1981) Community organization in marine algal epifuanas. *Annual Review of Ecology and Systematics*. 12:49-74.
- Seed R and Suchanek TH (1992) Population and community ecology of *Mytilus*. In: The Mussel Mytilus: Ecology, Physiology, Genetics and Culture. Gosling (Ed.). Elsevier, Amsterdam. Pp. 87–169.
- Shannon LV (1985) The Benguela ecosystem. Part I. Evolution of the Benguela, Physical features and processes. Oceanography and Marine Biology Annual Reviews. 23:105-182.
- Shannon LV and Nelson G (1996) The Benguela: large scale features and processes and system variability. In The South Atlantic: Present and Past Circulation. Wefer G, Berger WH, Siedler G and Webb DJ (Eds). Berlin, Springer: 163–210.
- Shillington FA (1998) Benguela upwelling system off southwestern Africa, coastal segment (16°E). In The Sea. 11. The Global Coastal Ocean; Regional Studies and Synthese.
  Robinson AR and Brink KH (Eds.). New York, Wiley. Pp. 583-604.
- Small LF and Menzies DW (1981) Patterns of primary productivity and biomass in a coastal upwelling region. *Deep-Sea Research*. 28(A):123-149.
- Sousa WP, Schroeter SC and Gaines SD (1981) Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia*. 48:297-307.
- Spooner DE Vaughn CC (2006) Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology*. 51:1016-1024
- Stegenga H, Bolton JJ and Anderson RJ (1997) Seaweeds of the South African West Coast, Hall AV (Ed.), Bolus Herbarium, University of Cape Town. Pp. 198, 335, 370.

Steneck RS and Dethier MN (1994) A functional group approach to the structure of algal-

domlinated communities. Oikos. 69(3):476-498.

- Stephenson TA (1936) The marine ecology of the South African coast, with special reference to the habits of limpets. *Protocols of the Linnean Society of London*. 148:74-79.
- Stephenson TA (1939) The constitution of the intertidal fauna and flora of South Africa, I. Biological Journal of the Linnean Society, London. 40:487-536.
- Stephenson TA (1944) The constitution of the intertidal fauna and flora of South Africa, II. Annals of the Natal Museum. 10:261-358.
- Stephenson TA (1948) The constitution of the intertidal fauna and flora of South Africa, part III. *Annals of the Natal Museum*.11:207-324.
- Stephenson TA, Stephenson A and du Toit CA (1940) The South African intertidal zone and its relation to currents, VIII. Lamberts Bay and the West coast. Annals of the Natal Museum. 9:345-380.
- Stepheson TA and Stephenson A (1972) Life between the tidemarks on rockyshores. San Francisco, Freeman. Pp.425.
- Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*. 133:240-256.
- Stramma L and Lutjeharms JRE (1997) The flow field of the subtropical gyre in the South Indian Ocean. *Journal of Geophysical Research* 102:5513-5530.
- Taylor RB and Cole RG (1994) Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. *Marine Ecology Progress Series*. 115:271-282.
- Terborgh J (1973) On the notion of favourableness in plant ecology. *The American Naturalist*. 107:481-501.
- Thandar AS (1989) Zoogeography of the southern African echinoderm fauna. *South African Journal of Zoolology*. 24(3):11-31.

- Thiel M and Vásquez JA (2000) Are kelp holdfasts islands on the ocean floor? I indication for temporarily closed aggregations of peracarid crustaceans. *Hydrobiologia*. 440:45-54.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham Y, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles LJ, Ortega-Huerta MA, Townsend Peterson A, Phillips O and Williams SE (2004) Extinction risk from climate change. *Nature*. 427:145-148.
- Thompson RC, Wilson BJ, Tobin ML, Hill AS and Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *Science*. 202:73-84.
- Tranter DJ, Carpenter DJ and Leech GS (1986) The coastal enrichment of the East Australian Current eddy field. *Deep-Sea Research*. 33:1703-1728.
- Underwood AJ (1976) Analysis of patterns of dispersion of intertidal prosobranch gastropods in relation to macroalgae and rock pools. *Oecologia* (Berlin). 25:145-154.
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.
- Underwood AJ and Chapman MG (1989) Experimental analysis of the inflyuences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata. Journal of experimental Marine Biology and Ecology*. 134:175-196.
- Underwood AJ and Chapman MG (1992) Experimentson topographic influences on density and dispersion of *Littorina unifasciata* in New South Wales. In: Proceedings of the third international symposium on Littorinid biology. Grahame J, Mill PJ and Reid DG (Eds.).
   The Malacological Society of London. Pp. 169-180.
- Underwood AJ and Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Marine Ecology*. 107:212-224.

Underwood AJ and Chapman MG (1998) A method for analysing spatial scales of variation in

composition assemblages. Oecologia. 117:570-578.

- Underwood AJ and Jernakoff P (1984) The effects of total height, wave exposure, seasonality and rock pools on grazing and the distribution of intertidal macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology*. 75:71-96.
- Underwood AJ, Chapman MG and Connell SD (2000) Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*. 250:97-115.
- Underwood AJ, MG Chapman and Richards SA (2002) GMAV-5 for Windows. An analysis of variance programme. Centre for Research on Ecological Impacts of Coastal Cities. Marine Ecology Laboratories, University of Sydney, Australia.
- Vásquez-Luis M. Guerra-García JM, Sanchez-Jerez P and Bayle-Sempere JT (2009) Caprellid assemblages (Crustacea: Amphipoda) in shallow waters by *Caulerpa racemosa* var. cylindracea from southeastern Spain. *Helgolnd Marine Research*. 63:107-117.
- Vitousek PM and Hooper DU (1993) Biological diversity and terrestrial ecosystem biogeochemistry. In: Biodiversity and ecosystem function. Schulze ED and Mooney HA (Eds.) Springer-Verlag, Berlin, Germany. Pp. 3-14.
- Ware DM (1992) Production characteristics of upwelling systems and the trophodynamic role of hake. In: Benguela Trophic Functioning. Payne AI, Brink KH, Mann KH and Hillborn R (Eds.). South African Journal of Marine Science. 12:501-513.
- Weiher E, Clarke GDP and Keddy PA (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*. 81:309-322.
- Weiters E (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Marine Ecology Progress Series*. 301:43-54.

Whatley RC and Wall DR (1975) The relationship between Ostracoda and algae in littoral and

sublittoral marine environments. In: Biology and palaeobiology of Ostracoda. Swain FM (Ed.). *Bulletin of the American Paleontological Society*. 65:173-203.

- Williams GA (1992) The effects of grazing by *Littorina mariae* on diatom assemblages on natural and artificial surfaces. In: Proceedings of the 3rd international symposium on littorinid biology. Grahame J, Mill PJ, Reid DG (Eds.). The Malacological Society of London, London, Pp. 211-219.
- Willig MR (2001) Commontrends with latitude. In: Encyclopedia of Biodiversity. San Diego: Academic, Levin (Ed). Pp. 701-14.
- Willig MR, Kaufman DM and Stevens RD (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology And Evolution and Systematics*. 34:273-309.
- Wood AD and Buxton CD (1996) Aspects of the biology of the Abalone Haliotis midae (Linne, 1758) on the east coast of South Africa. 1. Feeding biology. South African Journal Of Marine Science. 17:61-68.
- Wright DH, Currie DJ and Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. In: Species diversity in ecological communities. Ricklefs RE and Schluter D (Eds). University of Chicago Press. Pp. 66-74.
- Wright JP and Jones CG (2006) The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience*. 56(3):203-210.
- Xavier BM, Branch GM and Wieters E (2007) Abundance, growth and recruitment of Mytilus galloprovincialis on the west coast of South Africa in relation to upwelling. Marine Ecology Progress Series. 346:189-201.
- Yoshioka PM (1982) Role of planktonic and benthic factors in the population dynamics of the bryozoan, *Membranipora membranacea*. *Ecology*. 63:457-468.



Appendix



length (n = 20) and percentage cover (n = 20) in relation to distance from Hondeklip Bay along the west coast of South Africa, error bars represent standard error. Appendix C: List of identified infaunal species associated with *Hypnea spicifera* along the east and south coasts and *Champia lumbricalis* along the west coast

	Hypnea spicifera	Champia lumbricalis
Crustacea		
Amphipoda	Atylus swammerdamei	Aristias symbiotica
	Caprella danilevski	Atylus swammerdamei
	Caprella longicollis	Caprella danilevski
	Caprella penantsis	Caprella penantsis
	Caprella scaura	Corophium acherusieum
	Corophium acherusicum	Engidotea cobata
	Guernea rhomba	Jassa falcata
	Ischyroceridae parajassa	Laetmatophilus purus
	Jassa falcata	Podocerus inconspicious
	Laetmatophilus purus	Podocerus multispinis
	Parametopa grandimana	Stenothoe adhaerens
	Podocerus multispinis	
	Polycheria atolli	
	Stenothoe adhaerens	
	Stenothoe proboloides rotunda	
	Stenothoe valida	
	Stenothoe gallensis	
Cirripedia	Balanus variegatus	Balanus variegatus
	Chthamalus dentatus	Notomegabalanus algicola
	Octomeris angulosa	
Branchyura	Actaea sp.	Megalope
	Dehaanius quattuordentatus	
	Cyclograpsus punctatus	
	Hymenosoma orbiculare	
	Megalope	
	Plagusia chabrus	
Isopoda	Cirolana venusticauda	Cirolana undulata
	Dynamanella huttoni	Dynamanella huttoni
	Dynamanella ovalis	Dynamenella macrocephala
	Dynamenella macrocephala	Dynamanella ovalis
	Exosphaeroma pallidum	Dynamenella scabricula
	Isocladus tristensis	Exanthura macrura

## Appendix C continued

	Jaeropsis beurosi	Exosphaeroma pallidum
	Mesanthura catenula	Exosphaeroma truncatitelson
	Paridotea fucicola	Guernea rhomba
	Sphaeramene micotylotos	Gnathia africana
	Tanais philetaerus	Idarcturus platysoma
		Jaeropsis beurosi
		Mesanthura catenula
		Paridotea ungulata
		Sphaeramene polytylotus
		Tanais philetaerus
Mollusca	Acanthochiton garnoti	Acanthochiton garnoti
	Anachis kraussi	Aulacomya ater
	Burnupena lagenaria	Burnupena lagenaria
	Cardita variegata	Cymbula occulus
	Dendrofissurella scutella	Eatonina sp.
	Eatonina sp.	Fissurella mutablis
	Fissurella mutablis	Fissurella natalensis
	Fissurella natalensis	Gregariella petagnae
	Gibbula multicolor	Helicon dunkeri
	Helcion concolor	Ischnochiton bergoti
	Helicon dunkeri	Lasea adansoni turtoni
	Ischnochiton textilis	Littorina africana
	Lasea adansoni turtoni	Modiolus auriculatus
	Modiolus auriculatus	Mytilus galloprovincialis
	Mytilus galloprovincialis	Nassarius capensis
	Nassarius capensis	Natica tecta
	Natica tecta	Nucella dubia
	Nucella dubia	Oxystele variegata
	Oxystele tabularis	Scutellastra granularis
	Patella amphanes	Turritella carnifera
	Perna perna	
	Scutellastra granularis	
	Septifer bilocularis	
	Tricolia capensis	
	Turritella carnifera	
Other taxa	Amphipholis squamata	Amphipholis squamata
	Aulactinia reynaudi	Anurida maritima
	Golfingia capensis	Aulactinia reynaudi
	Insect larvae	Golfingia capensis

Appendix C continued

	Mite	Mite
	Nematode	Nematode
	Nemertea	Nemertea
	Ophionereis dubia	Parechinus angulosus
	Parechinus angulosus	Platyhelminth
	Patiriella exigua	Porcellidium sp.
	Pentacta doliolum	
	Platyhelminth	
	Tanystylum brevipes	
Polychaeta	Cirriformia punctata	Exogone clavator
	Exogone clavator	Dodecacaria sp.
	Fabriciinae	Fabriciinae
	Gunnarea capensis	Lepidontus clava
	Lepidonotus durbanensis	Lumbrineris papillifera
	Lumbrineris papillifera	Marphysa posterobranchia
	Marphysa corallina	Myrianida pulchella
	Marphysa posterobranchia	Naineris laevigata
	Myrianida pulchella	Platynereis dumerilii
	Naineris laevigata	Protomystids capensis
	Neanthes willeyi	Pseudonereis variegata
	Phyllodoce castanea	Syllis prolifera
	Platynereis dumerilii	Syllis variegata
	Pseudonereis variegata	
	Streblosoma hesslei	
	Syllis prolifera	
	Syllis variegata	