A COMPARISON BETWEEN MACROFAUNAL COMMUNITIES ON MIXED SHORES AND ROCKY AND SANDY SHORES IN FALSE BAY

by

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Declaration:

The contents of this thesis are the results of research carried out under the supervision of Professors A. C. Brown and G. M. Branch in the Zoology Department and Marine Biology Research Institute of the University of Cape Town. The data and ideas presented in this thesis are largely my own, although various colleagues and my supervisors made valuable comments on preliminary drafts.

This work has not been submitted for a degree at any other university or academic institution.

Cameron Ewart Smith

For:

Justine, Hamish, Mum & Dad

TABLE OF CONTENTS

ABSTRACT

The community structures of three shore types namely: "mixed shores" (those where rocky and sandy-shore habitats are intermixed), pure rocky shores and pure sandy beaches in False Bay, South Africa are compared in this study. Four habitats were identified - pure rock (unaffected by sand), mixed rock (rock affected by sand), mixed sand (sand between emergent rocks) and pure sand (beaches with no emergent rock) - representing a gradation from pure rock to pure sandy beaches. The specific aims of this study were to: (1) Sample quantitatively and describe macrofaunal communities on mixed shores in False Bay; (2) make direct comparisons among both the four types of habitats and three types of shores; and (3) test the hypothesis that sand inundation increases diversity at both habitat (α-diversity) and shore (β-diversity) level. The biological communities of mixed shores are described in terms of species composition, trophic organisation and zonation. Mixed-shore zonation patterns are different from those previously described for pure rocky shores in the region. The ability of *Choromytilus meridionalis* and inability of patellid limpets and various algae, to withstand sand inundation are largely responsible for these differences. In particular *Patella cochlear* and, thus, the cochlear zone as a whole, tend to be absent from mixed shores. The highly variable and fragmented nature of mixed shores further complicated the description of zonation patterns. Communities on all four habitats were clearly separable using multivariate techniques. Furthermore, patterns in dominance and diversity suggested that the impacts of sand inundation on mixed rock were severe. Diversity was compared at two levels: firstly, between each habitat type (α-diversity) and secondly between whole shore types (β-diversity). On both mixed rock and mixed shores as a whole diversity was lower than on adjacent pure rocky shores. There was no difference in diversity between mixed sand and pure sand habitats but the inclusion of mixed rock species resulted in greater diversity on mixed shores than sandy beaches. These results are discussed in terms of the intermediate disturbance hypothesis and hypotheses that suggest that there is an increase in diversity with increased habitat heterogeneity. In particular it is suggested that the presence of a disturbance resistant, relatively dominant, competitor – *Choromytilus meridionalis* - results in the lower diversity observed on mixed rock and mixed shores in this study.

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CHAPTER ONE: INTRODUCTION

Over the last three decades there has been a shift of emphasis in ecological studies from those focusing on individual populations to those on entire communities (Strong *et al.* 1984, Giller 1984, Diamond & Case 1986, Southwood 1987). A major problem with this shift, however, has been the definition of "community" with many authors misusing the term and others regarding it as "usefully imprecise" (Kikkawa & Anderson 1986). Whittaker (1975) has defined the term "community" as a combination of plant, animal and bacterial populations, interacting with one another within an environment, thus forming a distinct living system with its own composition, structure, environmental relations, development and functioning. According to this definition therefore, community ecology includes the study of all the populations within a specific habitat, the interactions within and among species making up these populations and the effects that the physical environment has on these species and their interactions.

Communities are most easily characterised by the composition and abundance of their constituent species. These proceed along a dynamic hierarchy of time-related phases, until a species-poor climax community (Huston & Smith 1987) is reached, which exists at equilibrium until it is disturbed. If disturbed during this sequential development, or at equilibrium, the process is set back and proceeds once again towards equilibrium. This is termed succession. Succession was first popularised in terrestrial systems, with the first record being a description of "orderly development" of Irish bog vegetation (King 1685, as cited by Golley 1977). Succession has subsequently been recognised in terrestrial, freshwater and marine ecosystems, and is one of the corner-stone theories of ecology today (Golley 1977, Connell 1978, Connell & Slater 1977, Turner 1983, Sousa 1984a, Huston & Smith 1987, Lake 1990, Farrell 1991, Benedetti-Cecchi & Cinelli 1996, Navarrete 1996). There is still debate, however, about whether communities always return to the same equilibrium point after perturbation, or whether they reach a different species composition. In addition there has been some criticism of the idea that communities ever reach equilibrium. Connell & Sousa (1983) have proposed that the evidence for stability or persistence in communities has not yet been demonstrated sufficiently. Peterson (1984) contests, however, that under appropriate scales of observation, communities can be thought of as relatively stable (i.e. at equilibrium).

Both biological and physical factors affect succession and the final community composition or structure (Hairston *et al.* 1960, Dayton 1971 & 1984, Connell & Slater 1977, Dethier 1984, Kikkawa & Anderson 1986, Menge & Sutherand 1987, Menge & Olsen 1990, Farrell 1991, Benedetti-Cecchi & Cinelli 1996). Physical factors tend to have an overriding effect on communities; i.e. they set absolute limits. Species unable to tolerate prevailing conditions are unable to survive in given habitats and are thus absent. This influences gross distribution patterns. For example, physiological stresses such as desiccation prevent all but a few highly adapted species from successfully inhabiting the high-shore zone on rocky shores (Newell 1979). Forest communities and subtidal reef communities are both affected by light availability amongst other factors. Biological factors such as competition, predation and larval availability tend to refine these gross patterns further, and can influence the eventual outcomes of the succession process.

Disturbances have been well studied in terrestrial plant communities (Huston & Smith 1987), freshwater systems (Resh *et al.* 1988, Power *et al.* 1988) and marine systems (see below). Typically, disturbances remove the occupants of a specific habitat and thus free resources for other individuals, either of the same species or a different species. Therefore those individuals that are able to re-colonise the habitat most rapidly are able to utilise the available resources. Alternately the individuals that are able to survive the disturbance are released from competing for the limiting resource. In sessile marine benthic communities and tropical forest communities, free space is often the critical limiting resource (Connell 1978, Sousa 1984a, Pickett & White 1985, Roughgarden 1986). Disturbances remove dominant competitors and thus allow rapid re-colonisation, often by competitively inferior species. As the community develops over time these early colonisers are then sequentially replaced by superior competitors. If disturbances are sufficiently infrequent the community returns towards a species-poor climax community that is relatively stable.

The intensity and frequency of disturbances are important in maintaining patterns of diversity in communities (Connell 1978, Abugov 1982, Miller 1982, Pickett & White 1985, Petraitis *et al.* 1989). At an intermediate stage after a major disturbance or with continued smaller "intermediate intensity" disturbances, it is hypothesised that diversity will be at a maximum (Fig 1.1) (Connell 1978, Abugov 1982, Miller 1982). Under these conditions the community contains a mixture of both rapidly re-colonising, usually competitively inferior species, and slower re-colonisers, which are usually competitively superior species. Before the competitive dominants monopolise the limited resource in question (usually primary space in intertidal systems), diversity is thus at a maximum. Continued low intensity or spatially disjunct disturbances lead to increased patchiness within a community. Discrete patches are set-back at different times to an earlier phase of the succession hierarchy and therefore contain different species compositions. Diversity is therefore increased due to the increased spatial heterogeneity of the community.

Marine intertidal rocky shores are subject to a wide range of disturbances. Logs (Dayton 1971), ice scour (Whethey 1985, McCook & Chapman 1991 & 1993), sand (Taylor & Littler 1982, McQuaid & Dower 1990), trampling (Brosnan & Crumrine 1994), desiccation or thermal stress (Connell 1961, Sutherland 1970, Branch 1975, Underwood 1980, Tsuchiya 1983), predation (Menge 1976, Paine & Levin 1981, Paine *et al.* 1985), boulder bashing (Sousa 1979a&b), harvesting (Lasiak & Field 1995) and storm damage (Whitman 1987) cause mortality in intertidal systems. Communities affected by these disturbances, however, do not act in a uniform manner. Some comply with the intermediate disturbance hypothesis, while others show patterns of decreased diversity following disturbance. This can largely be attributed to the nature, i.e. frequency and intensity, of the disturbance (Petraitis *et al.* 1989).

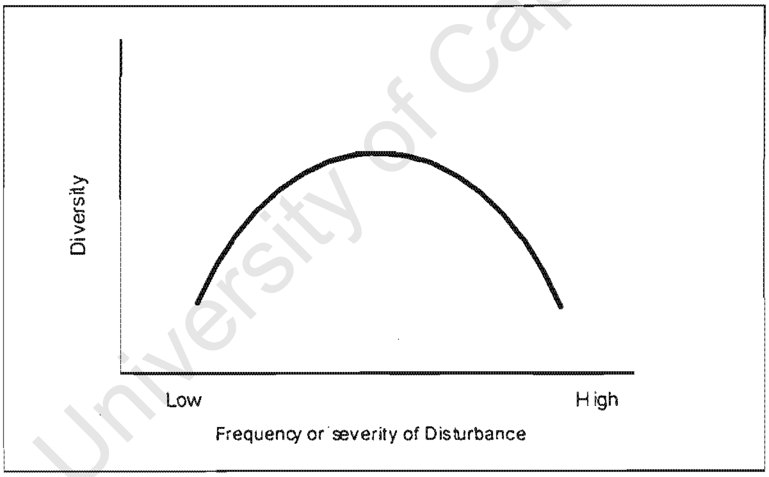

Figure 1.1. A schematic representation of the intermediate disturbance hypothesis (after Connell 1978)

The effects of sand inundation and scouring have received some attention in the literature. However, few papers have dealt with the effects on entire communities (Daly & Mathieson 1977, Taylor & Littler 1982, Littler *et al.* 1983, Dower 1989, McQuaid & Dower

1990). Sand influences intertidal communities in two principle ways. Sand can be deposited onto shores in large amounts, smothering the organisms that are unable to avoid it. This is particularly devastating for sessile communities and, if it persists for a sufficient length of time, can cause high mortality amongst species that are not able to tolerate inundation (Marshall & McQuaid 1989, Branch *et al.* 1990, Engeldow & Bolton 1994, Trowbridge 1996). Sand also has a scouring effect under conditions of strong wave action when it is suspended in the water column. This abrasive effect can interfere with growth, movement, filter feeding and respiration, while increasing weathering of shells or of the epithelia of intertidal algae (Emerson & Zedler 1978, Devinny & Volse 1978, Stewart 1983, D'Antonio 1986, Engeldow & Bolton 1994, Webb & Korrubel 1994).

Intertidal rocky and sandy shores have been well studied along the entire South African coastline (see Branch & Griffiths 1988, Brown & McLachlan 1990 and Field & Griffiths 1991). However, very few studies have focused on shores of mixed sand and rock ("mixed shores" as defined by Bally *et al.* 1984), because rocky-shore and sandy-beach ecologists consider these shores atypical of their particular habitats of interest. This has resulted in these mixed shores being largely neglected, even though they constitute approximately 31% of South Africa's coastline (Underhill & Cooper, 1982 in Bally *et al.*, 1984). Bally *et al.* (1984) define mixed shores as shores of either rock or sand that have the extraneous material (either sand or rock) present in sufficient quantities to exert an ecological influence on the communities inhabiting those shores. These workers go further and define eight categories or types of shores, six of which may be regarded as mixed shores (Fig 1.2). The particular categories of shores studied in this thesis are shaded in Fig. 1.2. For the purposes of this study, I examined mixed-shore communities at two levels: firstly I compared specific habitats within shore types. Secondly, I compared whole shore types. In particular I am concerned with four habitats, namely:

rocky components on mixed shores, i.e. "mixed rock" (MR), sandy components of mixed shores, i.e. "mixed sand" (MS), pure rocky shores, i.e. "pure rock" (R) and pure sandy beaches, i.e. "pure sand" (S). Further, I defined three shore types namely: pure rocky shores, pure sandy beaches and mixed shores, which encompassed both mixed sand and mixed rock habitats.

	1	2	3	4	5	6	7	8
		MIXED SHORES						
HWS	PURE SAND	SAND with isolated ROCKS	SAND with Many ROCKS	SAND	ROCK	ROCK with extensive SAND	ROCK With patches of SAND	PURE ROCK
LWS				ROCK	SAND			

Figure 1.2. The range of shore types defined by Bally *et al.* (1984). These depend on the abundance of sand and rock. HWS = high water spring, LWS = Low water spring. The shaded categories indicate those studied in this thesis.

In South Africa, Bally *et al.* (1984), Dower (1989), McQuaid & Dower (1990), Brown *et al.* (1991) have all investigated mixed shores and have shown that they do not respond to sand inundation in a uniform way around the coast of South Africa. On the species-rich East Coast, sand inundation has been demonstrated to increase species richness on mixed shores when compared to shores not affected by sand (McQuaid & Dower 1990). It was proposed that this was largely due to increased patchiness and habitat heterogeneity caused by sand inundation. By contrast, Brown et al. (1991) have demonstrated that in False Bay, Cape Peninsula, species richness is lower on mixed shores. Their study was only qualitative however, and a more quantitative approach is still required in order to improve our understanding of the dynamics of mixed shores in this region.

The aim of this study was to quantitatively sample the biological communities on three mixed shores and compare them with adjacent pure rocky and pure sandy shores within

False Bay. These data were then used in order to make direct comparisons among the community structures on these shores. Sampling concentrated on the biota occurring on these shores, as the physical natures of mixed shores, rocky shores and sandy beaches have previously been described (Bally *et al.* 1984, Brown *et al.* 1991, McQuaid 1980, Griffiths & Branch 1991, Bally 1981). Furthermore, no attempt was made to quantify the area occupied by each habitat, as the primary concern of this project was with biological communities within each of the identified habitat types, not their relative importance. However, equal sampling effort was directed at each habitat in order to allow for valid comparisons amongst habitats and whole shore types. The specific objectives this thesis were:

1. To describe patterns of community structure on mixed shores in False Bay in terms of community composition, trophic organisation and vertical zonation (Chapter 3).
2. To make direct comparisons between specific habitats on mixed shores (namely, mixed rock and mixed sand), and their adjacent pure habitat types (namely, pure rock and pure sand)(Chapter 4).
3. To make direct comparisons among three shore types namely mixed shores (encompassing both mixed rock and mixed sand habitats), pure rocky shores and pure sandy beaches (Chapter 4).
4. To test the hypothesis that sand inundation in False Bay increases diversity on mixed shores (Chapter 5).

CHAPTER TWO: METHODS

2.1 Study sites

Three shores, namely Muizenberg Corner (MC), Dido Valley (DV) and Smitswinkel Bay (SB) were chosen for this study (Plates 1-3). These sites are all situated within False Bay, along the eastern side of the Cape Peninsula, South Africa (Fig. 2.1). The three sites were chosen to represent typical mixed shores (according to the definitions provided in chapter 1).

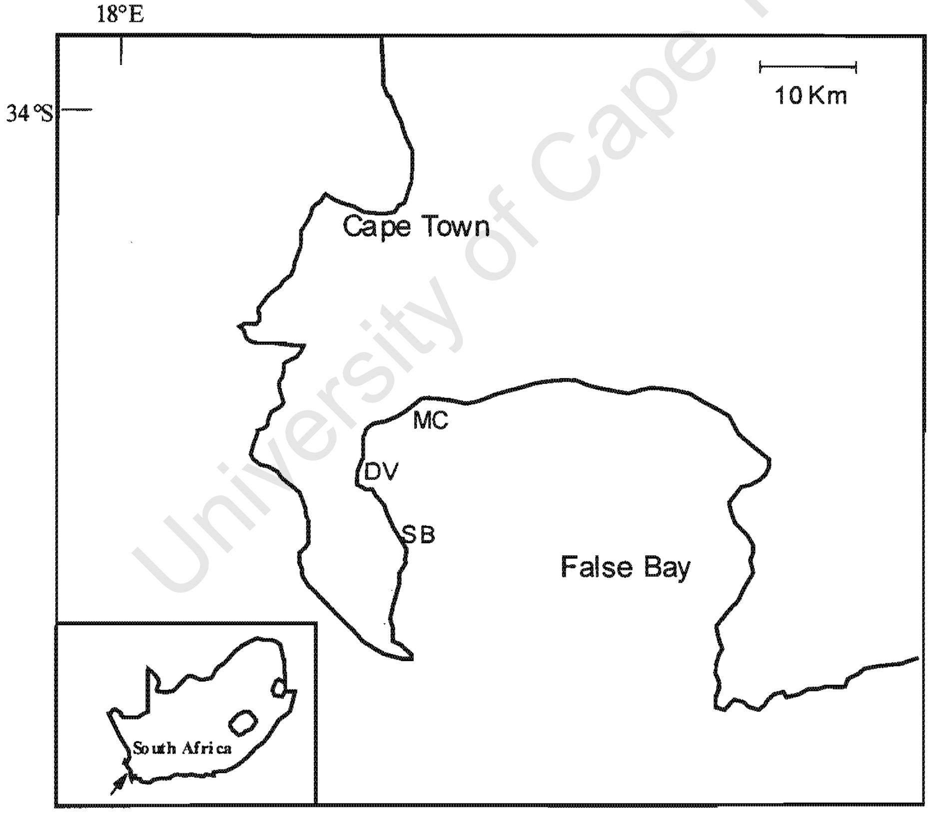

Figure 2.1. Map of the Cape Peninsula showing the location of study sites, MC = Muizenberg Corner, DV = Dido Valley and SB = Smitswinkel Bay.

Plate 1. Muizenberg Corner mixed shore (note extensive mussel cover)

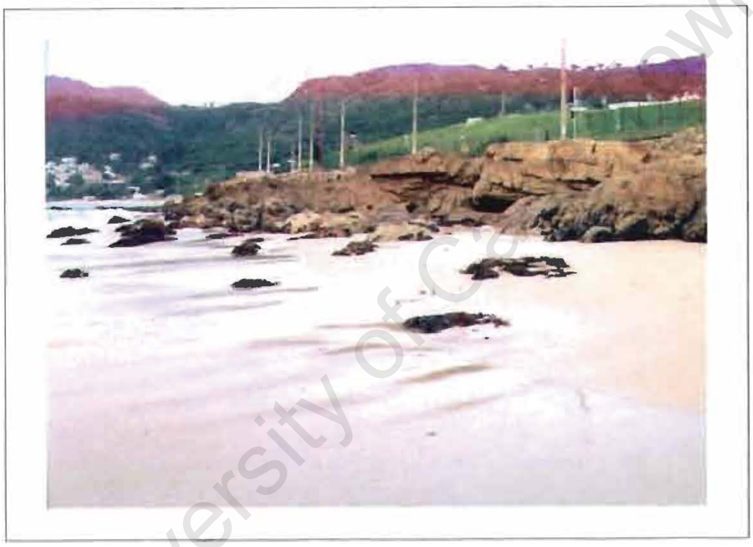

Plate 2. Dido Valley mixed shore

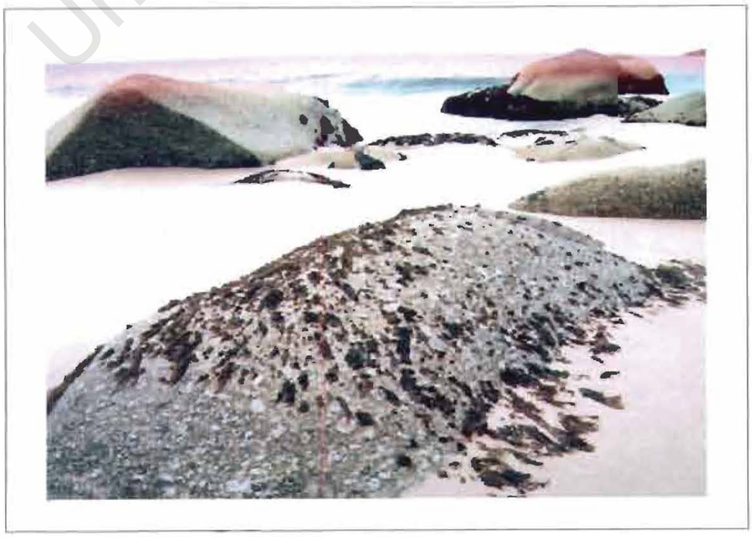

Plate 3. Smitswinkel Bay mixed shore

On Muizenberg Corner samples were taken from the mixed-shore directly below the railway station. Pure sand and pure rock samples were taken approximately 100 m from the interface with the mixed shore. Samples were taken from the mixed shore to the south (i.e. Simonstown side) of Dido Valley beach (beneath the Lower North Battery). Pure sand samples were taken from the beach north of the railway workers hut and pure rock samples were taken on the rocky shore approximately 100 m North of the beach. Mixed shore samples were taken on the southern side of Smitswinkel Bay, pure sand (North of the mixed shore) and pure rock (South of the mixed shore) were sampled approximately 50 m from the mixed rock interface. The rock type at both Muizenberg corner and Dido Valley is predominantly sandstone while granite dominates the rocky component at Smitswinkel Bay.

2.2 Description of the physical parameters influencing the study sites

The western Cape experiences a Mediterranean climate. Summer is typically hot, dry and windy, while winter is relatively cold and wet. False Bay is influenced by a strong seasonal wind pattern. In winter (May to September) the prevailing winds blow off-shore from the North West, while in summer (September to March) the prevailing winds blow onshore, from the South East. Consequently, sand tends to be deposited on-shore during the summer and removed during winter, although this can vary unpredictably (pers. obs.). During spring (September to October) and autumn (March to April) winds tend to be more varied, which leads to more frequent movements of sand off- and on-shore.

The water temperature within False Bay also shows a marked seasonal trend. During summer the water is strongly influenced by filaments of warm water that break away from the Agulhas current in the region of the Agulhas retroflection and head north up the West coast. These push warm water into the Bay and temperatures can vary between 12-19°C. In winter the offshore winds cause upwelling along the western coastline of False Bay and the water temperature is cooler, usually between 10-14°C.

All three shores were classified as intermediate in exposure (as per Bustamante 1994, Bustamante & Branch 1996a) based on previous knowledge of the shores and the presence of kelp subtidally and a high biomass of mussels on the shores.

2.3 Sampling Procedure

Mixed rock habitats (MR) were sampled in September 1995 during spring low tides. Three transects were surveyed from MLWS (mean low water spring) to the high-shore splash zone. Samples consisting of 30 x 30 cm quadrats were scraped clean of all organisms at 2-m intervals up shore. Where mussels covered 100% of the substratum, 10 x 10 cm quadrats were used.

Rocky (R), sandy (S), and mixed sand (MS) substrates were sampled in September 1998 during spring low tides. For each, three transects were surveyed, consisting of one 30 x 30 cm (scraped) quadrat in each of four zones namely LLOW, LOW, MID and HIGH. Where comparable samples did not exist on the MR sampled previously (e.g. where 10 x 10 cm quadrats had been taken in mussel beds) these zones were re-sampled with 30 x 30 cm quadrats.

On R and MR all organisms within the quadrats were collected and the rocks were scraped in order to collect encrusting organisms. This did, however, lead to certain species, particularly encrusting coralline algae, being under-represented in this study.

Sand and mixed sand samples were also taken using 30 x 30 cm quadrats, and were excavated using a conventional garden spade to a depth of 20 cm or until rock was struck. The sand was placed in 1mm-sieve bags and agitated in the surf until only the large sand fraction and macrofauna remained. These were then placed in a bottle and returned to the laboratory.

All specimens were fixed in 4% formalin for at least three weeks, before being rinsed in fresh water and transferred to 1-% phenoxotol (monoethylene glycol) for storage. Samples were then washed in fresh water to remove excess phenoxotol and sorted to species (guides used included Day 1967 & 1974, Griffiths 1976, Kensley 1978, Branch & Branch 1981, Branch *et al.* 1994). Species were counted and the blotted wet mass was obtained. The samples were then dried in an oven to constant mass at 60°C, and re-weighed to give dry mass. In the case of molluscs, biomass estimates included the mass of the shell.

Physical parameters recorded for each quadrat during the study include: height above the nearest sand, a description of sand cover, orientation (i.e. sea facing or non-sea facing) and height above MLWS.

Sediment samples were taken to a depth of 5 cm from the driftline, mid-shore and low-shore. In the laboratory, sand was dried and passed through a series of sieves to obtain mean grain size, sorting and skewness (see Brown & McLachlan 1990 for a complete description of analytical methods).

2.4 Data Analysis

A matrix of variables (= quadrats) and cases (= species or physical variables) was constructed from these data. This matrix formed the basis of all multivariate techniques and data analyses. All analyses were based on biomass data rather than abundance data because of the difficulties associated with recording accurate numbers for plants, particularly algae and colonial organisms.

2.4.1 Statistical procedures

Parametric statistics were calculated following the methods described in Zar (1984). When assumptions of normality and homoscedacity were not met even after transformation of data, non-parametric procedures were used as described by Sokal & Rohlf (1981). Both parametric and non-parametric statistics were calculated using the computer program STATISTICA (StatSoft Inc., Tulsa, USA. 1996). Details of specific statistical tests undertaken are provided in the methods sections of the following chapters. Shannon's diversity and Pielou's evenness index were calculated using PRIMER v3.1a (Plymouth Routines in Multivariate Ecological Research; Carr 1994).

Two univariate measures of community structure, namely Shannon's diversity (H') and Pielou's evenness index (J') were calculated in this study. These were used in chapter three and chapter five to describe diversity of the macrofauna sampled. Shannon's diversity index (H') was calculated according to equation 2.1. Shannon's index records maximum diversity when all individuals belong to different species. Pielou's evenness index (J') was calculated according to equation 2.2. Evenness is a measure of the 'evenness' of distribution of individuals into species of a community. When individuals are distributed among species in equal proportions, evenness is greatest.

$$H' = -\sum_{i=1}^{k} p_i \log p_i$$ .... *Equation 2.1*

$$J' = \frac{H'}{H'_{\max}}$$ .... *Equation 2.2*

Where:

p_i = The fraction of a sample of individuals belonging to species *i*

k = Number of species in either a 'sample' or 'population'

$H'_{\max} = \log \mathrm{k}$

Washington (1984)

2.4.2 Multivariate statistical procedures

Multivariate analyses were conducted following the strategy (Fig. 2.2) of Field *et al.* (1982) using the computer package PRIMER v3.1a (Plymouth Routines in Multivariate Ecological Research; Carr 1994). This strategy is briefly described below.

Raw data in the form of biomass per square metre were first root-root transformed or transformed to presence/absence (Equation 2.3 see Field, *et al.* 1982, Clarke 1993) before similarity indices were calculated.

$$Y_{ij} = \sqrt{\sqrt{X_{ij}}}$$ .... *Equation 2.3*

Where Y_{ij} is the transformed data from the i^{th} row of the j^{th} sample. Root-root transformation reduces the weighting of large or abundant species and is similar to a logarithmic transformation. An advantage of this transformation is that if used with the

Bray-Curtis measure of similarity (as in this study), the calculated coefficient of similarity is invariant to scale change, i.e. it does not matter whether scores are expressed in units of cm^{-2} or m^{-2}. Presence/absence transformation lends equal weight to rare and common species and, thus, is biased towards rare species.

After transformation, data were subjected to an analysis of similarity, which summarises the overall similarity between pairs of samples. The most popular similarity index used by marine scientists is the Bray-Curtis measure of similarity (Equation 2.4 Clarke 1993). This measure is preferable to other similar similarity indices, as it is not affected by joint absences. It does, however, tend to give more weight to abundant species (Field *et al.* 1982).

$$\delta_{jk} = \frac{\sum_{i=1}^{s} \left| Y_{ij} - Y_{ik} \right|}{\sum_{i=1}^{s} \left(Y_{ij} + Y_{ik} \right)} \quad \text{.. } \textit{Equation 2.4}$$

The similarity measure is used to compare each sample to each other sample, and can be summarised in the form of a dendrogram or ordination. Dendrograms were derived from a group-average sorting, which joins two groups of samples together at the average level of similarity between all samples in a given group and all samples in another. This procedure produces distinct, easily identifiable groups. Unfortunately, however, using dendrograms alone has a few problems (see Field *et al.* 1982) and it is thus advisable to combine it with another graphic representation (such as ordination) in order to aid interpretation.

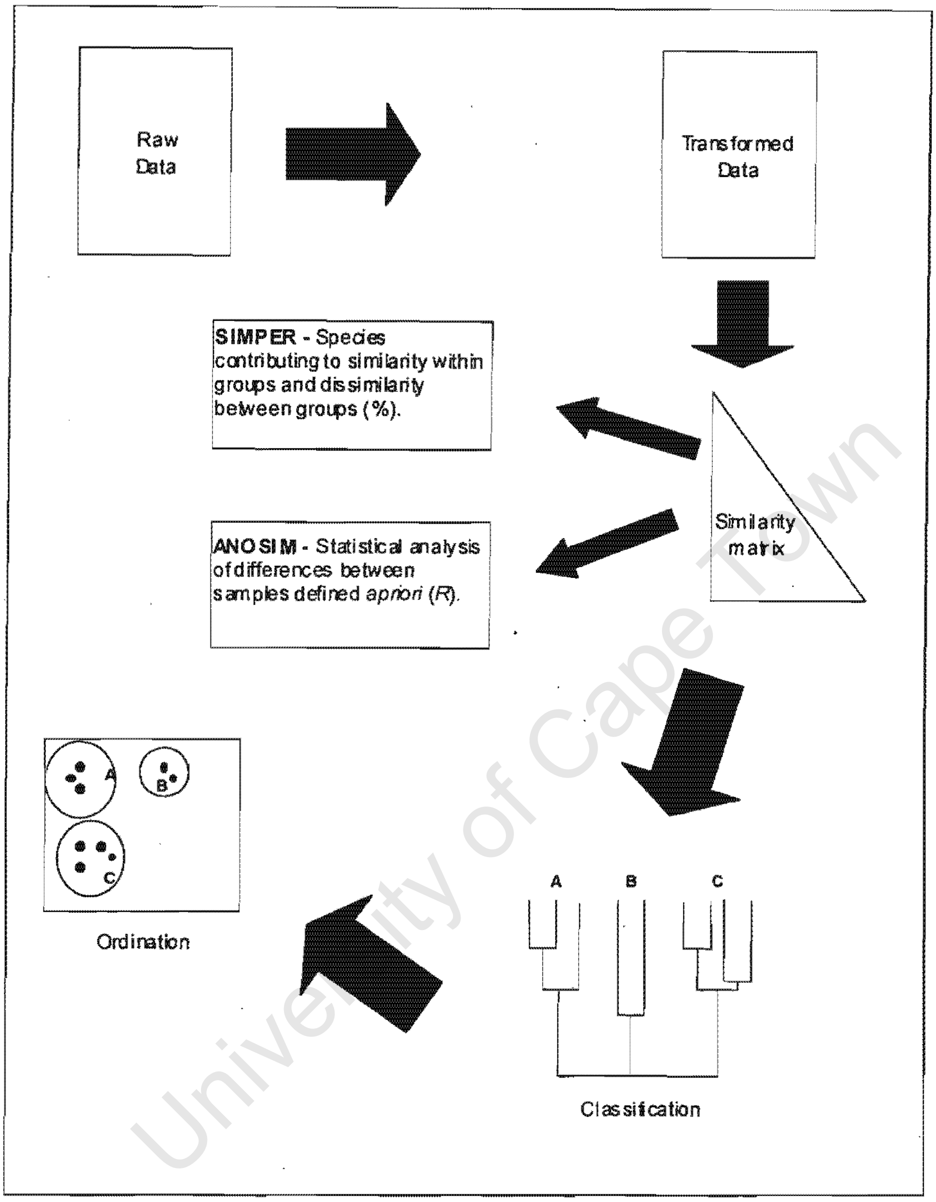

Figure 2.2. Schematic representation of the steps in a generic multivariate analysis of community data (after Field *et al.* 1982 with suggested modifications by Clarke & Warwick 1994).

Numerous ordination procedures are available, but Field *et al.* (1982) prefer the Multi-dimensional scaling (MDS) approach. Simply, MDS produces an ordination of samples in a specified number of dimensions. Samples are plotted in Euclidean space (in 2 or higher dimensions) according to the dissimilarity (a measure of distance) calculated between each sample. These distances are then minimised to give the "best-fit", calculated by regressing interpoint distances on the corresponding dissimilarities. The goodness-of-fit is expressed as a stress value for each plot.

The species responsible for the groups identified using classification and ordination can be examined using the SIMPER program (PRIMER v3.1a). This calculates the contribution of individual species to the overall calculated measure of similarity. Such "species level" data are lost through classification and ordination procedures (Clarke 1993). The species contributing principally to the dissimilarity between any two samples *j* & *k* can be investigated by measuring the Bray-Curtis dissimilarity between the samples (Clarke 1993):

$$\delta_{jk} = \sum_{i=1}^{s} \delta_{jk}(i) \quad \text{...} \; \textit{Equation 2.5}$$

Where

$$\delta_{jk}(i) = \frac{100\left|Y_{ij} - Y_{ik}\right|}{\sum_{i=1}^{s}\left(Y_{ij} + Y_{ik}\right)} \quad \text{.................................} \textit{Equation 2.6}$$

Clarke (1993)

δ_{jk} (eqn 2.5) is the dissimilarity between samples *j* & *k* for *S* species, where $\delta_{jk}(i)$ (eqn 2.6) is the contribution of the i^{th} species to δ_{jk}. From this, one can then average the dissimilarity between all sample pairs within the groups in question ($\bar{\delta}_{jk}$) and similarly by averaging over each $\delta_{jk}(i)$ one can calculate the average contribution of the i^{th} species to this overall dissimilarity between the groups $\bar{\delta}_i$. Species can then be arranged according to decreasing mean contribution to the dissimilarity ($\bar{\delta}_i$) between groups.

Although many of the above-mentioned techniques identify differences in the community composition among samples, they do not indicate whether these differences are statistically significant. Statistical differences among groups of samples that have been identified *a-priori* can be calculated using an Analysis of Similarity (ANOSIM) procedure (Clark2 1993, PRIMER v3.1a). Three ANOSIM designs are possible, namely: a one-way, two-way nested and two-way crossed design as per the terminology of analysis of variance (Fig. 2.3 & 2.4) (see Clark 1993).

ANOSIM calculates a correlation coefficient R based on the average rank similarities within groups ($\bar{r}_W$) and between different groups ($\bar{r}_B$) (Clarke 1993)(eqn 2.7).

$$R = (\bar{r}_B - \bar{r}_W)/(M/2) \quad \text{.................................} \textit{Equation 2.7}$$

Where $M = n(n-1)/2$ and n is the total number of samples under consideration.

(Clarke & Warwick 1994)

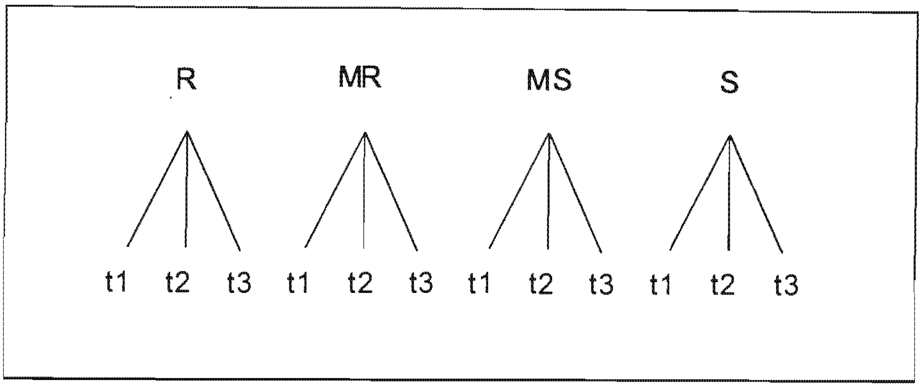

Figure 2.3. Organisation of samples for a One Way statistical comparison among habitats, where R = pure rock, MR = mixed rock, MS = mixed sand, S = pure sand and t1-t3 are individual transects sampled on each habitat type

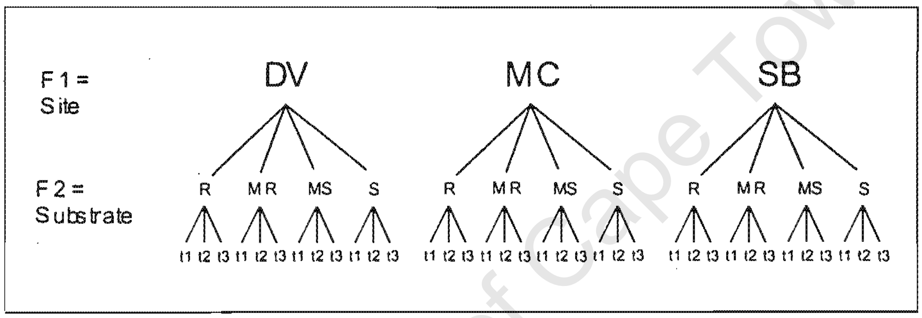

Figure 2.4. Organisation of the Two-Way Crossed design for statistical testing, where R = pure rock, MR = mixed rock, MS = mixed sand and S = pure sand and t1-t3 are individual transects sampled on each habitat type.

R can never technically lie outside the range (-1,1) and $R = 1$ only if all replicates within sites are more similar to each other than any replicates between sites. *R* is approximately zero if the null hypothesis (H_o = no difference between groups) is true i.e. that similarities between and within sites are the same on average. Statistical differences of *R* from zero can then be tested using a permutation test. This produces a theoretical distribution of possible *R* values from the samples in question by randomly re-labelling samples and calculating the associated distribution of *R* values from these relabelled sets. In general there are $(kn)!/(n!)^k k!$ distinct ways of permuting the lables for n

replicates in each of k groups. The true value of R can then be compared to the resulting spread of R values from the permutations, which is the range of R expected if H_0 is true. If H_0 is true there will be little effect on average of this random re-labelling and the calculated R will be greater than the true R more often than if H_0 is false. The significance of this can then be assessed using equation 2.8.

$$p = 100\,(t+1)/(T+1) \qquad \textit{Equation 2.8}$$

Where T = the number of permutations or re-labellings and t = the number of permutations that result in an R greater than the true R.

(Clarke & Warwick 1994)

CHAPTER THREE: FAUNA AND FLORA OF MIXED SHORES IN FALSE BAY (WESTERN CAPE) WITH PARTICULAR REFERENCE TO ZONATION PATTERNS ON ROCKY SUBSTRATES

3.1 Introduction

The effects of sand on the biological communities living on rocky shores have been described in terms of both single-species responses (Marshall & McQuaid 1989, Kendrick 1991, de Rooij *et al.* 1995, Brown & Trueman 1996a) and whole-community responses (Seapy & Littler 1982, Taylor & Littler 1982, Littler *et al.* 1983, Dower 1989, McQuaid & Dower 1990, Brown *et al.* 1991). The effects that rocky outcrops in the midst of sandy beaches have on biological communities have also been noted (Brown *et al.* 1991). However, few studies (Bally *et al.* 1984, Dower 1989, Brown *et al.* 1991) have looked at the functioning of mixed shores as a unique ecosystem. In South Africa some work has been done on mixed shores (Dower 1989, McQuaid & Dower 1990, Brown *et al.* 1991, Zitha 1994, Brown & Trueman 1996a & b), although this is relatively sparse when compared to the wealth of publications on pure rocky shores and pure sandy beaches (Branch & Griffiths 1988, Brown & McLachlan 1990, Field & Griffiths 1991 and references therein).

In particular, zonation patterns, i.e. the distribution of animals and plants up the shore, of intertidal rocky shore and sandy beach communities have been well-documented (Lewis 1955, Stephenson & Stephenson 1972, Branch & Branch 1981, Barnes & Hughes 1982, Brown & McLachlan 1990, Little & Kitching 1996). These relatively uniform patterns in zonation exist primarily in response to the dynamic, yet relatively uniform, physical environmental gradient in which intertidal organisms live. Once or twice daily, depending on geographical location, they are exposed to air at low tide, which has a marked influence on the biota capable of surviving on this land-sea boundary (Newell 1979).

Early workers assumed that physical variables such as temperature, desiccation etc. were of overriding importance in determining intertidal zonation patterns (e.g. Broekhuysen 1940, Wolcott 1973 as cited by Branch & Branch 1981). Many authors have questioned this however, and biological interactions have been shown to play an equally important role (Branch & Branch 1981). A combination of abiotic and biotic factors probably best explains most observed intertidal zonation patterns on rocky shores (Bustamante 1994, Bustamante & Branch 1996a, Bustamante *et al.* 1997). Typically upper limits of zones tend to be set by physiological tolerances to environmental stresses, while lower limits tend to be set by biological interactions, such as competition and predation (Griffiths & Branch 1991).

Another framework to describe zonation patterns has been proposed by Barnes & Hughes (1982). They suggest that the factors affecting zonation patterns can be viewed on two different levels, i.e. ultimate and proximate factors. Ultimate factors such as competition for resources or the restricted potential of any species to perform optimally under differing environmental conditions leads to the general phenomenon of zonation or change along an environmental gradient. This gradient may be any kind of transition, be it marine-terrestrial, depth on a coral reef, or altitude on a mountainside *et cetera.* Proximate factors which in turn have three major subdivisions, i.e. physiological, behavioural and ecological, act in limiting the specific zones in question occupied by different species. In all species, physiological tolerances differ and are limited. This prevents them from occurring outside their own window of acceptable environmental conditions. Behavioural patterns can also affect zonation because a species can actively choose to settle in or migrate to a suitable zone. Finally, ecological interactions such as predation can affect the structure of intertidal communities where vulnerable prey species can be removed from an otherwise suitable zone.

The zonation patterns of South Africa's intertidal systems have been described previously. Isaac (1937) produced a description of the algal zonation along the northern, central and southern regions of the West Coast. The general patterns of zonation along the entire coast were then described by Stephenson (1939 & 1943), in a system that is still in use today. Several authors (Bokenham & Neugebauer 1938, Bright 1938, Eyre 1939, McQuaid 1980, Branch & Branch 1981, McQuaid *et al.* 1985) have described the zonation patterns on rocky shores of the South Western Cape.

Rocky shores in the South Western Cape can be split into four zones (see Branch & Branch 1981, Griffiths & Branch 1991). A subtidal algal fringe usually dominates the low shore. Above this, the limpet *Patella cochlear* and a limited suite of algal species dominate the cochlear zone. The next zone or middle region of the intertidal region is the Balanoid zone and is characterised by species such as the barnacle *Chthamalus dentatus*, limpet *Patella granularis* and winkle *Oxystele* sp.. This zone can be split further into a lower balanoid (consisting of barnacles and many seaweeds) and upper balanoid (consisting of mainly barnacles), although some species can be found across the entire zone. The zone furthest from the sea is the Littorina zone and is dominated by the small gastropod *Nodilittorina africana knysnaensis.*

The effects of sand inundation and scouring on the zonation of rocky shores have not been well studied. Seapy & Littler (1982) and Trowbridge (1996) have demonstrated some small-scale changes in zonation of algae on rocky shores influenced by sand inundation and siltation. Zonation on mixed shore has been described on the East Coast of South Africa by Dower (1989). However, there has been no similar work on shores of this nature on the Cape Peninsula.

This chapter will describe the fauna and flora found on mixed shores and discusses the general zonation patterns found on rocky substrata of these shores in False Bay.

3.2 Methods

Samples for this study were collected from three sites: Dido Valley, Smitswinkel Bay and Muizenberg Corner (see Fig. 2.1). A full description of the methodology for sample collection is given in Chapter 2.

The mean number of species per quadrat on both rocky and sandy substrates was compared between shores using a Kruskal-Wallis ANOVA. This test was chosen as variances were found to be heteroscedastic (Bartlett's test for homogeneity of variances) and data severely violated the assumption of normality required for a parametric ANOVA (Zar 1984).

Species were classified according to both their trophic category and phylogeny (see Appendix 1; information obtained from McQuaid 1980, Dower 1989, Nel pers. comm., Griffiths pers. comm.). The number of species in each category was then obtained. Species numbers in both the phylogenetic and trophic groups were analysed using 5x3 and 7x3 contingency tables respectively. In order to simplify the data in the analysis between shores, some groups were combined. Thus for the analysis of trophic groups detritivores, scavengers and omnivores were combined into one group. For the taxonomic analysis, bryozoans, cnidarians, echinoderms, flatworms, nermerteans, nematodes and insects were grouped into one "other" category.

Zonation

Biomass and total species number (from all three shores combined) were regressed against height above MLWS (Mean Low Water Spring). Shannon's index for diversity (Equation 2.1) and Pielou's evenness index (Equation 2.2) were also regressed against height above MLWS.

Multivariate analyses of community structure were performed according to the strategy outlined in chapter 2.

3.3 Results

From the three study sites, a total of 110 species was recorded, 92 in mixed rock samples and 21 in mixed sand samples with 3 species occurring in both sand and rocky samples (see Appendix 1 for a complete species list showing trophic grouping, taxonomic classification and presence at each site). Total species richness varied among sites. Dido Valley (39 species) had fewer species than Smitswinkel Bay (63 species) and Muizenberg Corner (81 species). The mean number of species per sample on the mixed-rock components at each site varied significantly among sites (Fig. 3.1A), with Muizenberg Corner ($\bar{x}$ = 12.81) having the highest number of species followed by Smitswinkel Bay ($\bar{x}$ = 6.05) and Dido Valley ($\bar{x}$ = 4.32; Kruskal-Wallis ANOVA, H =

24.34, n = 82, $p<0.001$). Mean species number per quadrat also varied significantly among samples from the mixed-sand at each site (Fig. 3.1B; Kruskal-Wallis ANOVA, H = 14.17, n = 36, $p<0.001$). Smitswinkel Bay had relatively few species ($\bar{x}$ = 0.5) while Muizenberg Corner and Dido Valley had a significantly greater number of species per quadrat ($\bar{x}$ =3.75). The mean biomass.m^{-2} on rocky substrates also differed between Muizenberg Corner ($\bar{x}$ = 5642 g.m^{-2}) and the two other sites Smitswinkel Bay ($\bar{x}$ = 772 g.m^{-2}) and Dido Valley ($\bar{x}$ = 1326 g.m^{-2}) which did not differ from each other (*ANOVA F* =11.46, df = 2,78, $p<0.0001$; Students Newmen-Keuls $p<0.0001$). There was no difference in the mean biomass in mixed sandy substrates on Smitswinkel Bay ($\bar{x}$ = 6.5 g.m^{-2}), Dido Valley ($\bar{x}$ = 1.5 g.m^{-2}) and Muizenberg Corner ($\bar{x}$ = 6.2 g.m^{-2} *ANOVA F* = 2.54, df = 2.78, $p>0.05$).

The total number of species differed among trophic groups, with the detritivores having the greatest species richness. Primary producers, herbivores, filter feeders, scavengers and carnivores had fewer species, while the other category had the least species of all groups (Fig. 3.2; χ^2 = 13.33, df = 6, $p<0.05$). However, there was no significant difference in the number of species in each trophic group among sites (Fig. 3.2; χ^2 = 19.87, df = 12, $p>0.05$).

Biomass at all sites was dominated by filter feeders, principally the Mediterranean mussel (*Mytilus galloprovincialis*) and black mussel (*Choromytilus meridionalis*) (Fig. 3.3). For clarity the cumulative percentage of biomass of filter feeders and a 'non-filter feeder' category are presented (Fig. 3.3). The 'non-filter feeder' category is the total for all other trophic groups combined. The cumulative percentage contribution to the biomass of the 'non-filter feeder' category is presented separately in Figure 3.4.

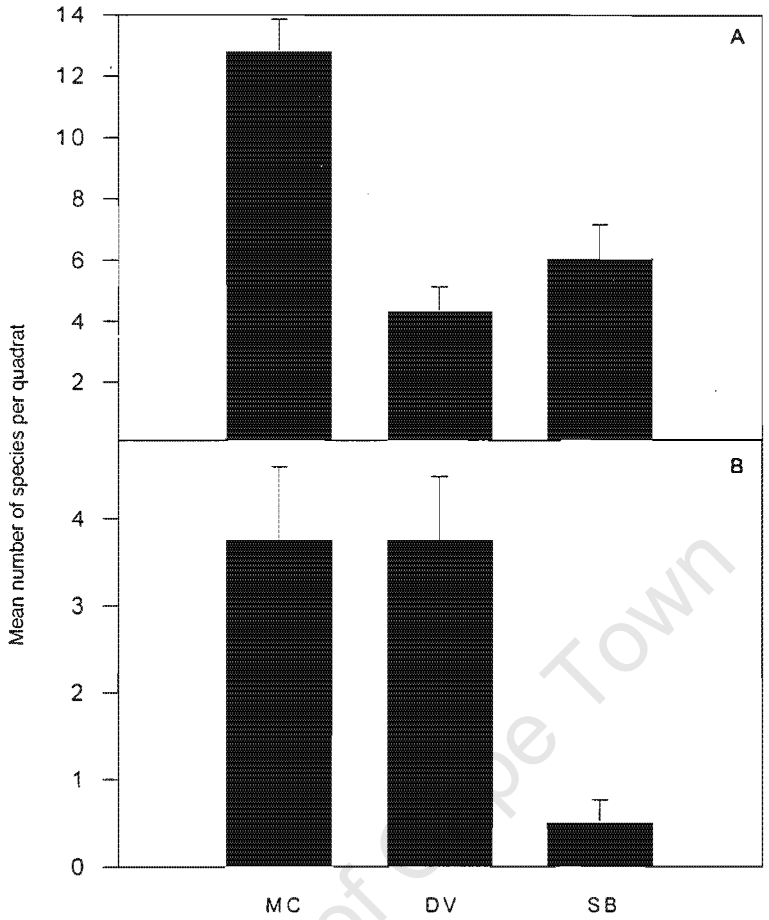

Figure 3.1. Mean number of species per quadrat on (A) mixed rock and (B) mixed sand habitats. Error bars are standard error. MC = Muizenberg Corner, DV = Dido Valley and SB = Smitswinkel Bay.

Taxonomic groups differed in their total number of species, with molluscs having the greatest species richness. Algae, crustaceans, polychaetes had fewer species while the 'other' category contained the least species (Fig. 3.5; $\chi^2 = 18.18$, df = 4, $p < 0.01$). No differences in the number of species per taxonomic group were found among individual sites (Fig. 3.5; $\chi^2 = 10.71$, df = 8, $p > 0.1$).

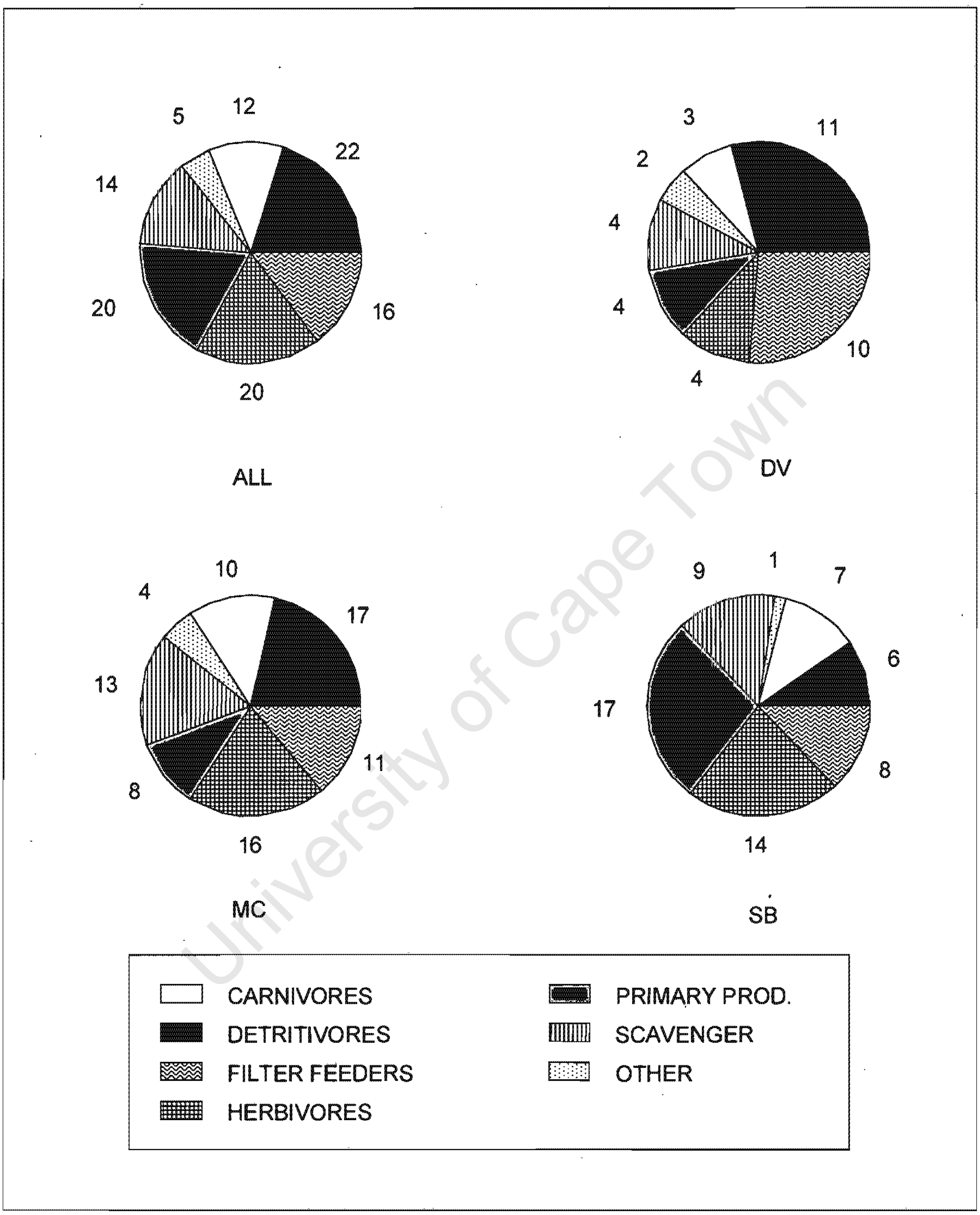

Figure 3.2. The number of species in each trophic group on all shores combined (ALL) and at each site DV = Dido Valley, MC = Muizenberg Corner and SB = Smitswinkel Bay

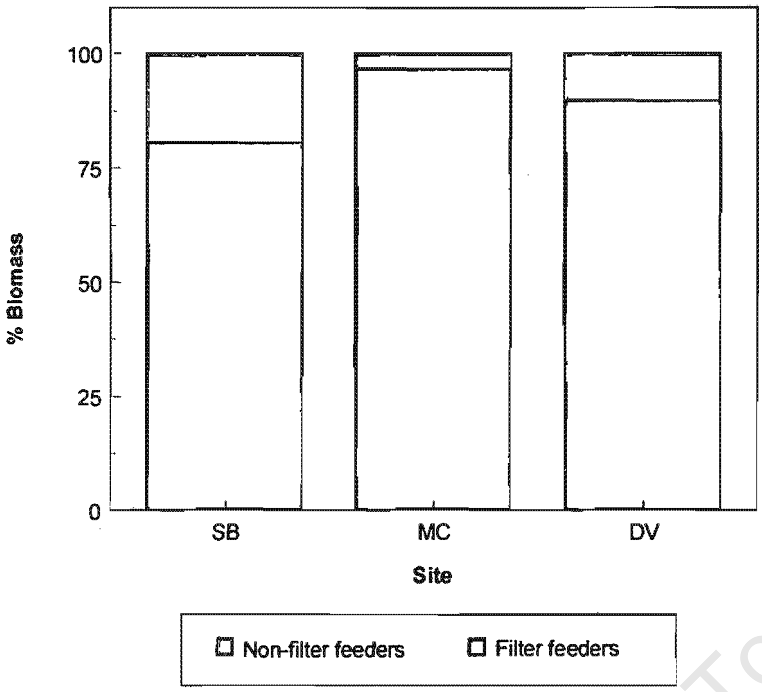

Figure 3.3. The percentage contribution of filter feeders (blue) and non-filter feeders (green) to total biomass.

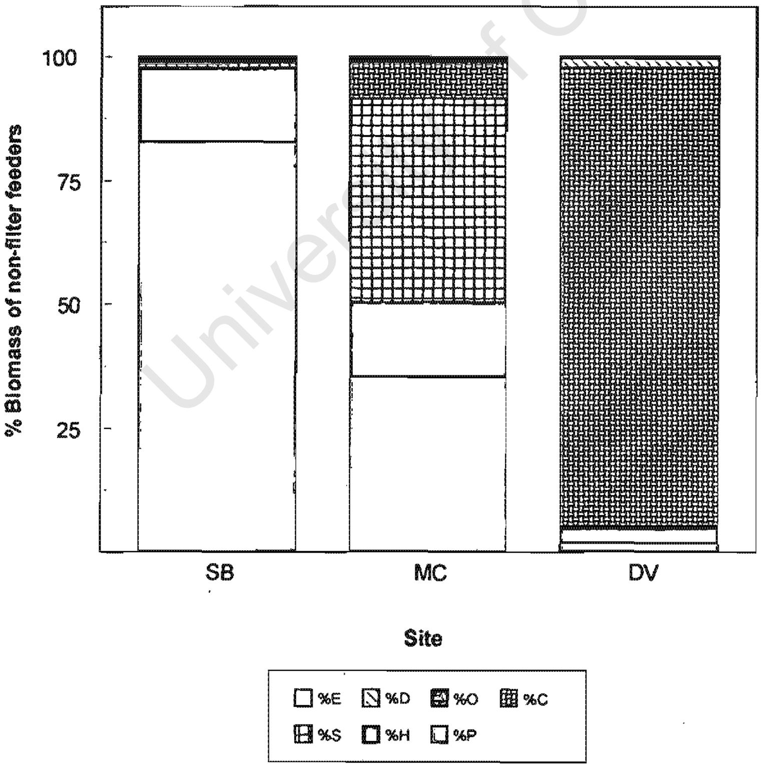

Figure 3.4. The breakdown of the percentage contribution to biomass of the non-filter feeders (from Fig. 3.3) for each shore. E = other, D = detritivores, O = omnivores, C = carnivores, S= scavengers, H= herbivores, P = primary producers.

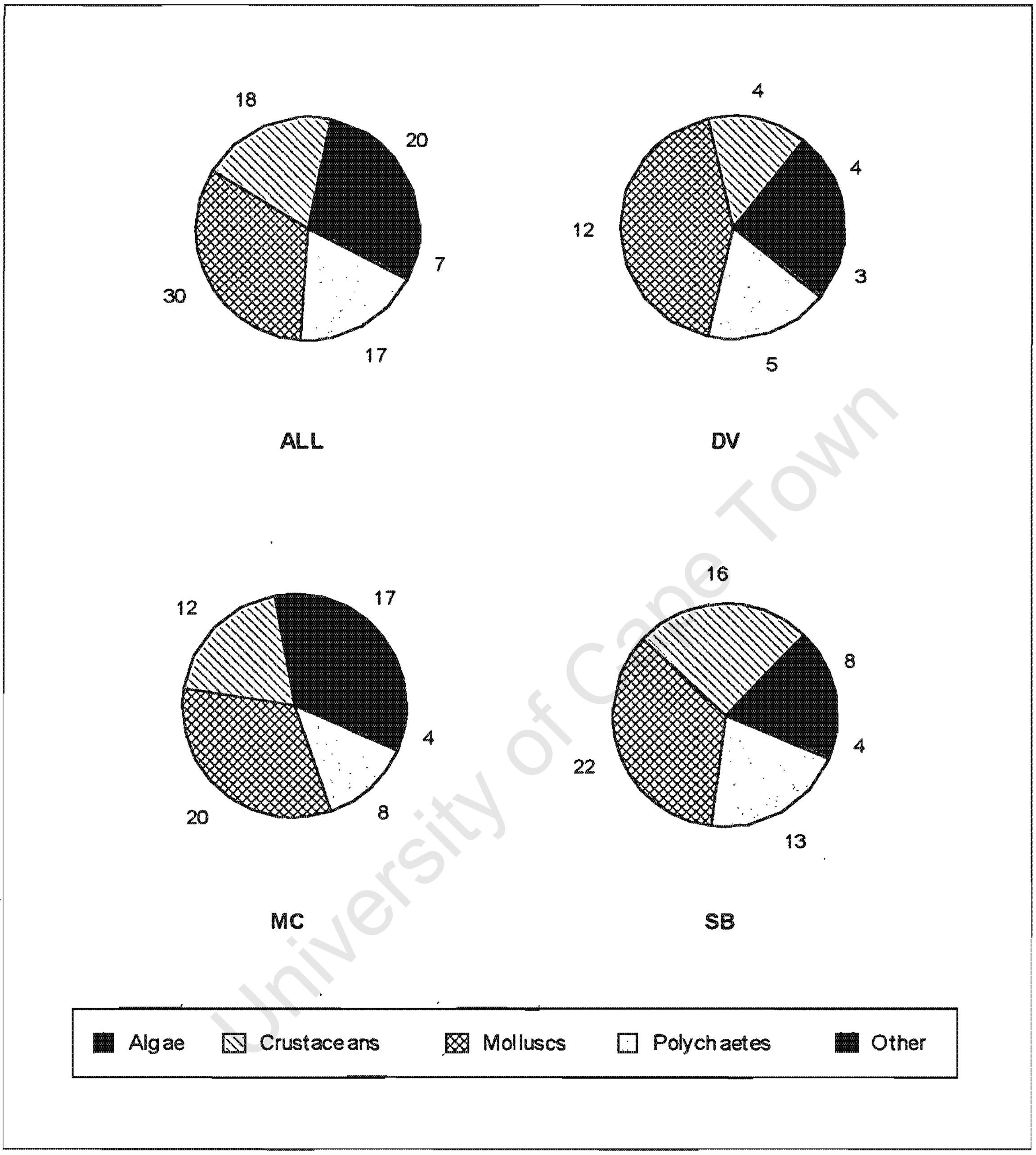

Figure 3.5. The number of species in each taxonomic group on all shores combined (ALL) and at each site DV = Dido Valley, MC = Muizenberg Corner and SB = Smitswinkel Bay

Molluscs dominated the total biomass at all sites (Fig. 3.6). For simplicity, molluscs (Fig. 3.6) and 'non-molluscs' (Fig. 3.7) are presented separately. After the molluscs, the next most important component of biomass varied between shores. On Dido Valley the Cnidaria, represented almost entirely by a single species *Bunodactis reynaudi*, were the next most important component constituting some 96% of the biomass of the 'non-molluscs'. On Smitswinkel Bay, algae made up approximately 98% of the 'non-molluscs', while on Muizenberg Corner the 'non-molluscs' group was made up of algae 74% and Crustacea 23%.

Zonation on hard substrata

Biomass (Fig. 3.8) and species richness (Fig. 3.9) both decreased with height above MLWS (r^2 = 0.529, df = 1,73 $p<0.0001$ & r^2 = 0.629, df = 1,73 $p<0.0001$ respectively). However, Shannon's index of diversity and Pielou's evenness index did not vary significantly with height above MLWS (r^2 = 0.0103 df = 1,61 $p>0.4$ & r^2 = 0.0529 df = 1,61 $p>0.06$ respectively).

Feeding guild distribution

Filter feeders dominated the low shore of all sites (Figs 3.10-3.12) but decreased with height above MLWS. Other important contributors to biomass on the low shore differed among sites with little consistency in the various groups. However, the biomass of all groups decreased with height above MWLS with few exceptions (on Dido Valley herbivore, and on Smitswinkel Bay carnivore biomass increased up the shore). On the high shore two groups, the primary producers or herbivores dominated biomass (Figs 3.10-3.12).

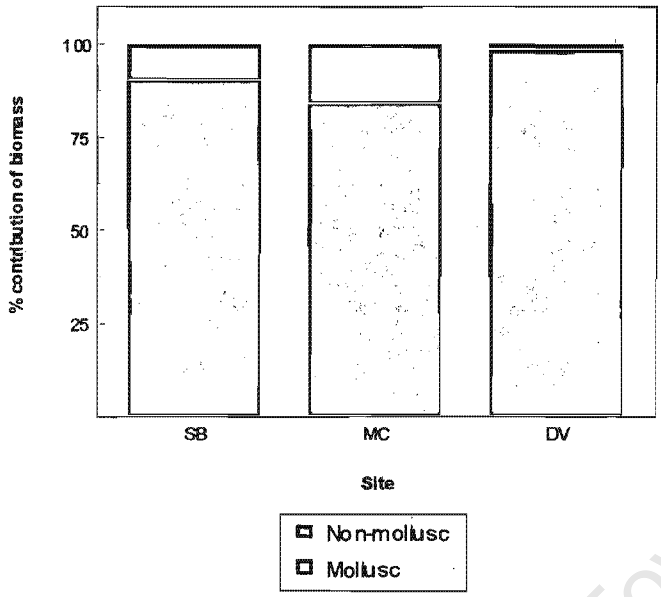

Figure 3.6. The percentage contribution of molluscs to the total biomass.

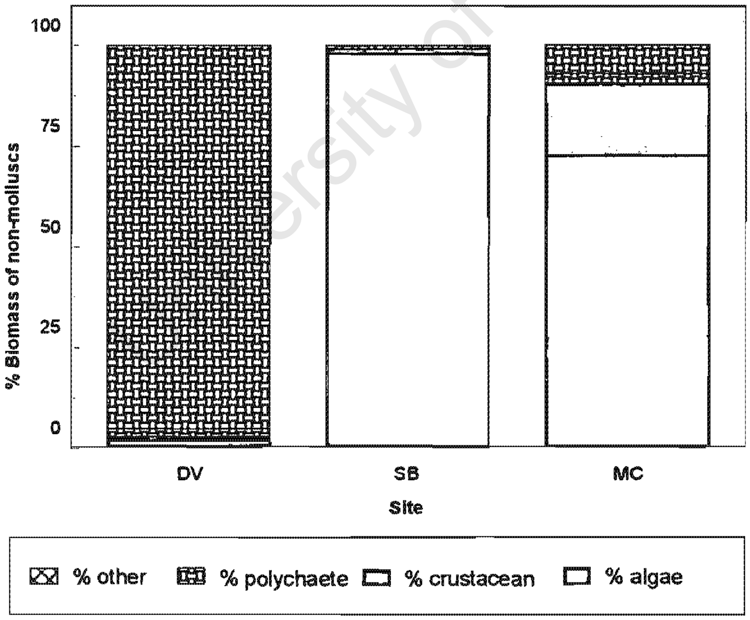

Figure 3.7. The percentage contribution of individual phylogenetic classes to the non-molluscan category (from Fig. 3.6).

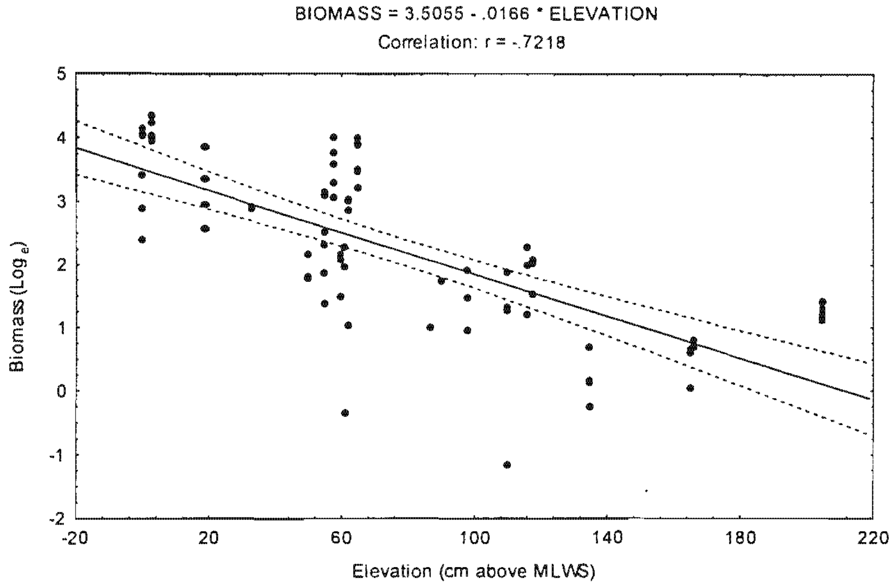

Figure 3.8. Regression of biomass (g.m^{-2}) against height above MLWS. Broken lines are 95% confidence limits for the regression line.

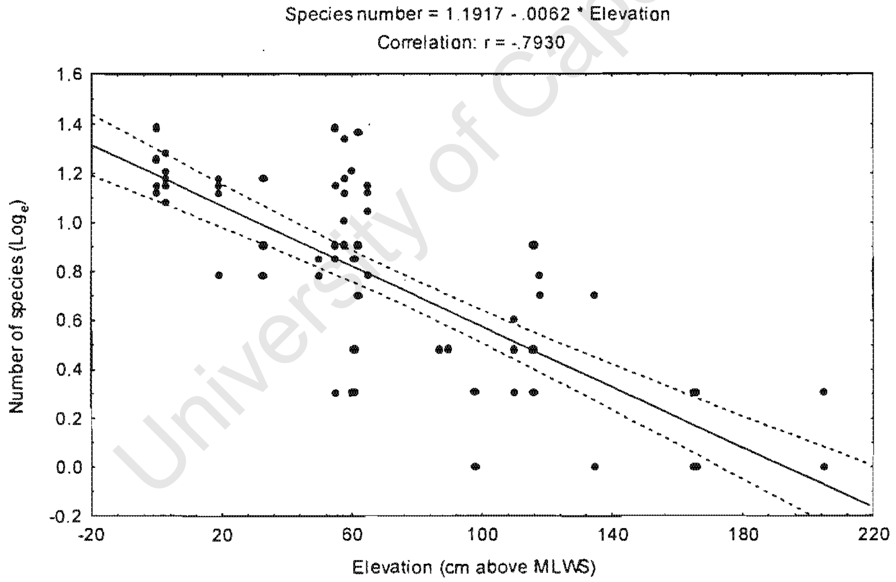

Figure 3.9. Regression of species number against height above MLWS. Broken lines are 95% confidence limits for the regression line.

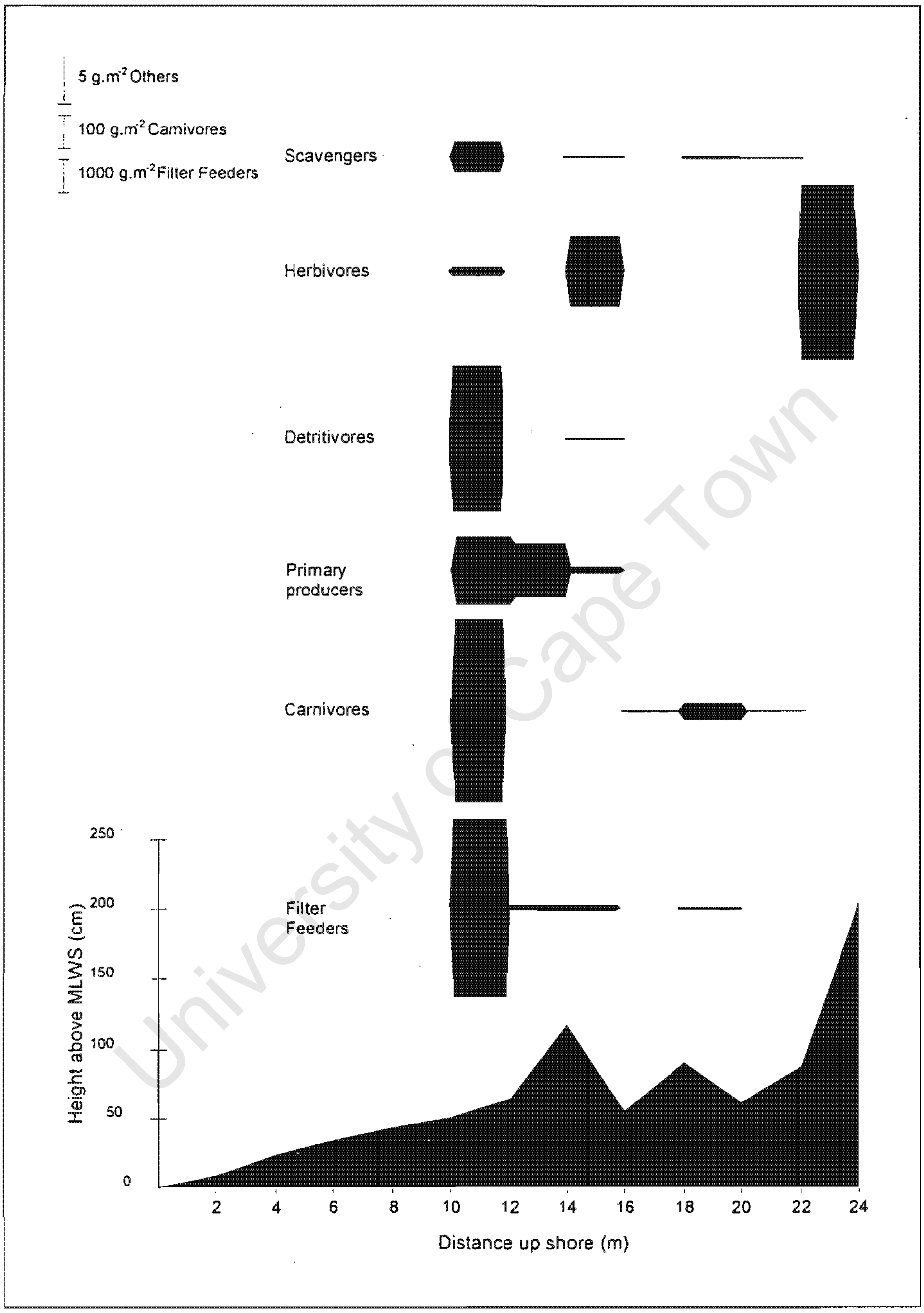

Figure 3.10. Kite diagram showing vertical distribution of biomass within each trophic group at Dido Valley.

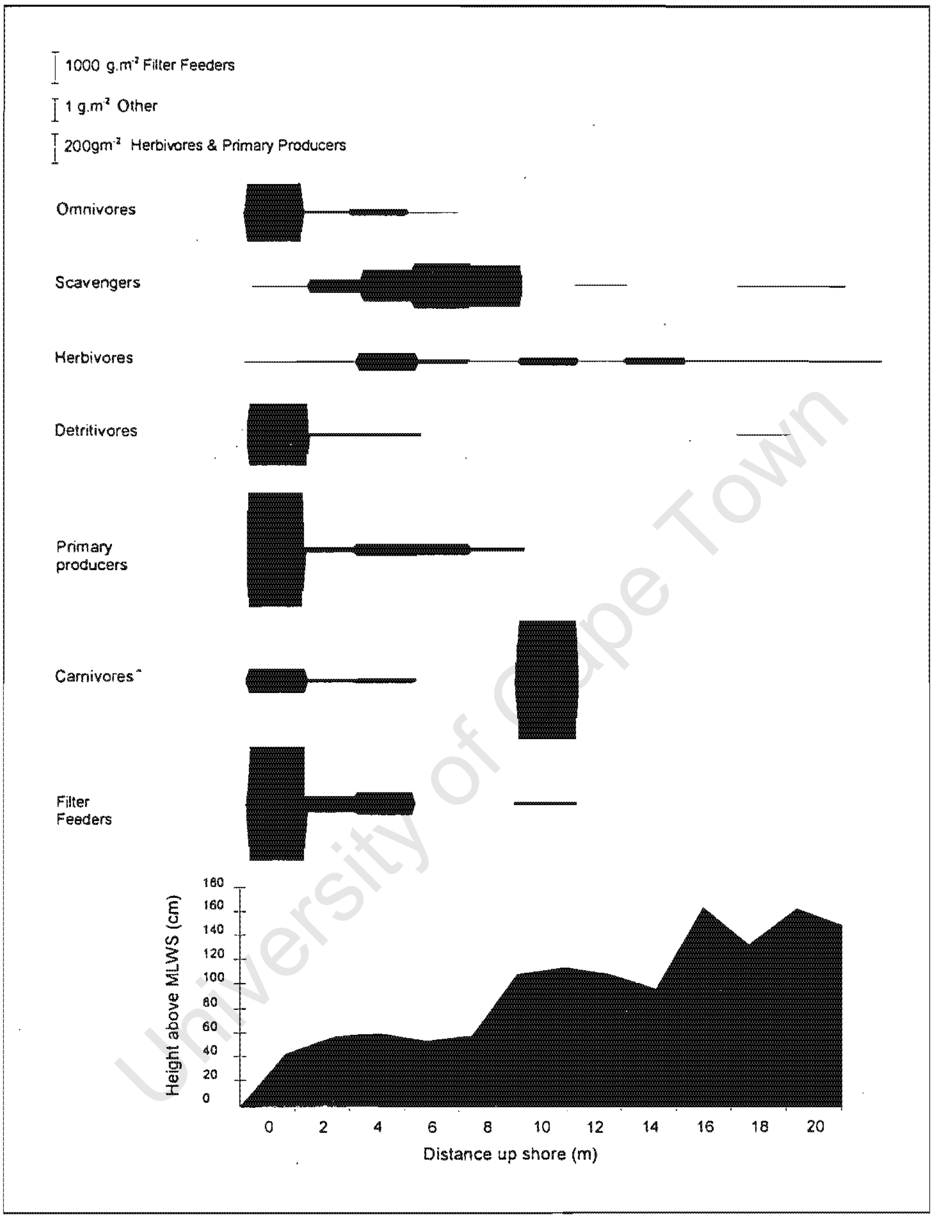

Figure 3.11. Kite diagram showing vertical distribution of biomass within each trophic group at Smitswinkel Bay.

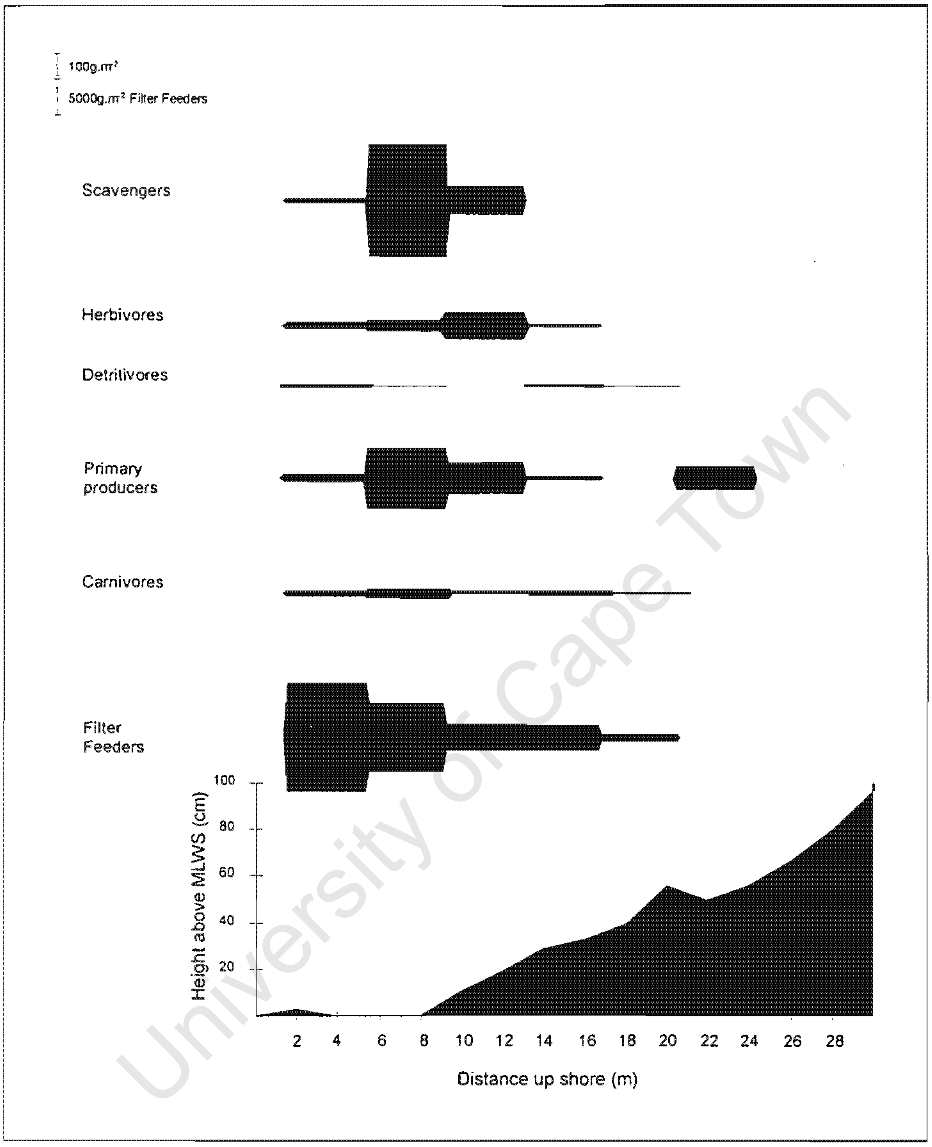

Figure 3.12. Kite diagram showing vertical distribution of biomass within each trophic group at Muizenberg Corner.

Patterns of zonation in community structure

The Bray-Curtis similarity index for all 81 samples showed certain gross groupings at a low similarity level (Fig. 3.13A). However, these patterns were not evident on the 2D plot of the results from multi-dimensional scaling (Fig. 3.13B). Furthermore the stress level of 0.23 associated with this plot is considered unacceptable (Clarke, 1993). When cluster analysis and multidimensional scaling were done on each shore separately however, patterns of distribution became more evident. Bray-Curtis similarity indices calculated for the three shores separately showed three or more distinct groups of samples on each shore (Figs 3.14-3.16A). These groupings were also clearly separated by the 2D MDS plots of these analyses (Figs 3.14-3.16B), and tend to cluster low-, mid- and high-shore samples.

Samples from Dido Valley separated into three groups at 25% similarity (Figs 3.14 A & B). Group 1 was characterised by the presence of *Mytilus galloprovincialis* (48.7%), *Choromytilus meridionalis* (25.9%), *Syllis spongicola* (6.8%) *and Exosphaeroma truncatitelson* (6.1%), where the numbers in brackets are the contribution to the similarity of the group re-scaled as a percentage. Group 2 was characterised primarily by the following species: *C. meridionalis* (60%), *Bunodactis reynaudi* (24.2%) and *E. truncatitelson* (8.4%). Group 3 contained only three species: *Nodilittorina africana knysnaensis* (63%), *B. reynaudi* (17.3%) and *C. meridionalis* (14.1%). The contributions of individual species to the dissimilarity between these three groups are presented in Table 3.1.

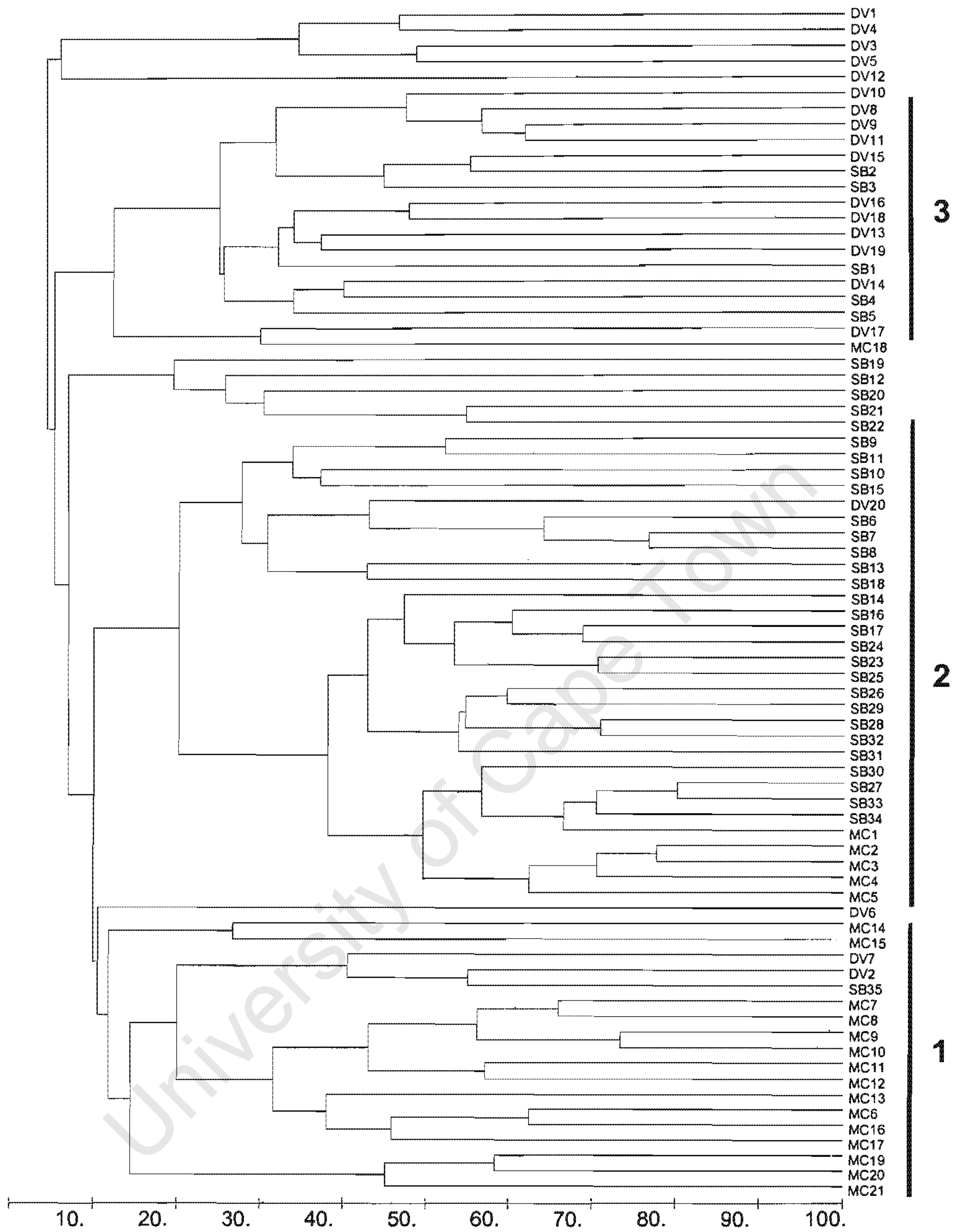

Figure 3.13A. Dendrogram of all quadrats sampled on mixed rock. Samples are identified for example DV1: DV refers to site (i.e. DV = Dido Valley, SB = Smitswinkel Bay and MC = Muizenberg Corner), 1 refers to quadrat number where 1 is the lowest sample. Three rough groupings are evident **1**, **2** and **3** (but see Fig. 3.13B)

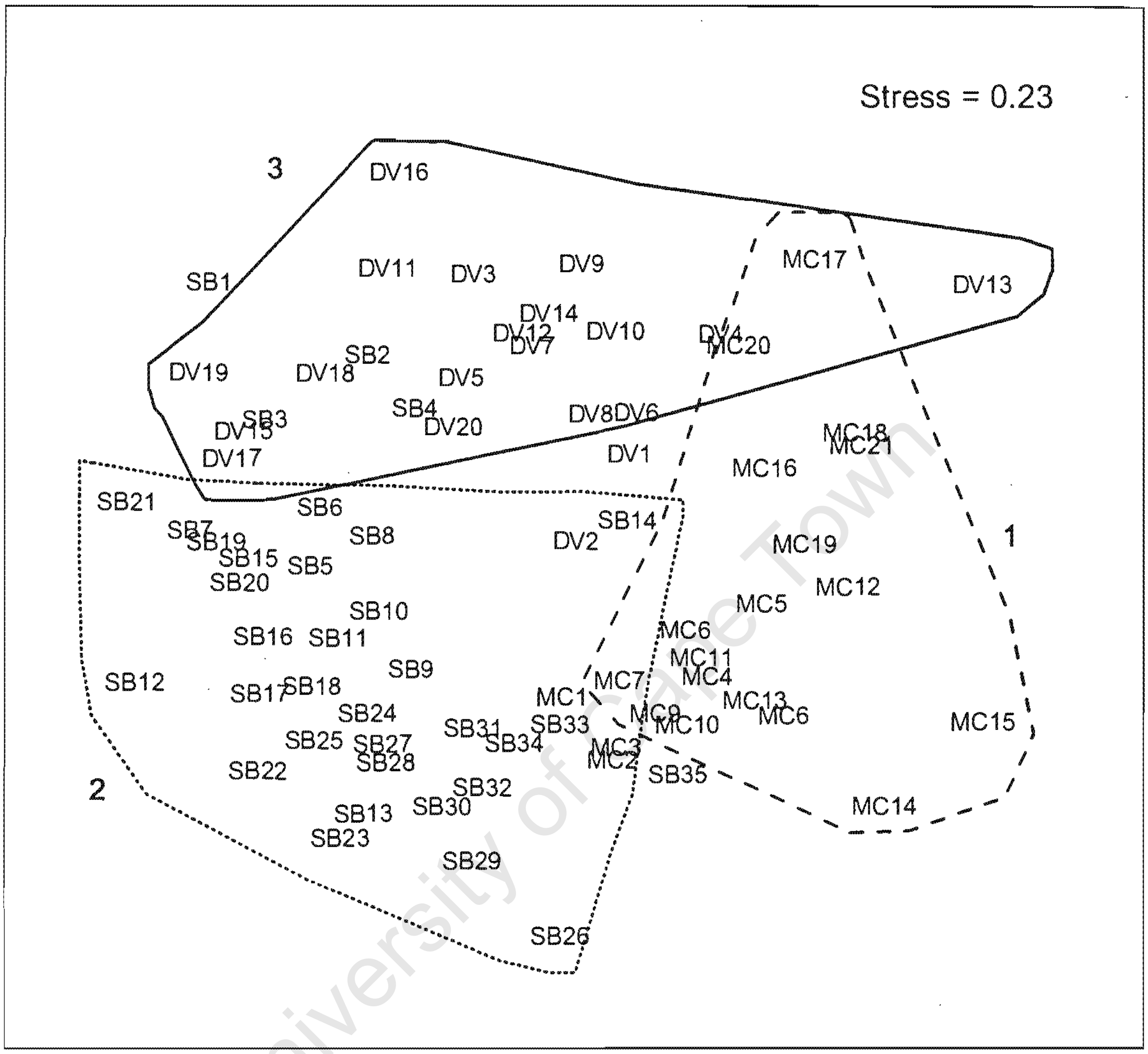

Figure 3.13B. MDS plot of all mixed rock quadrats. Three rough groups are identifies **1**, **2** and **3** (See Fig. 3.13A.)

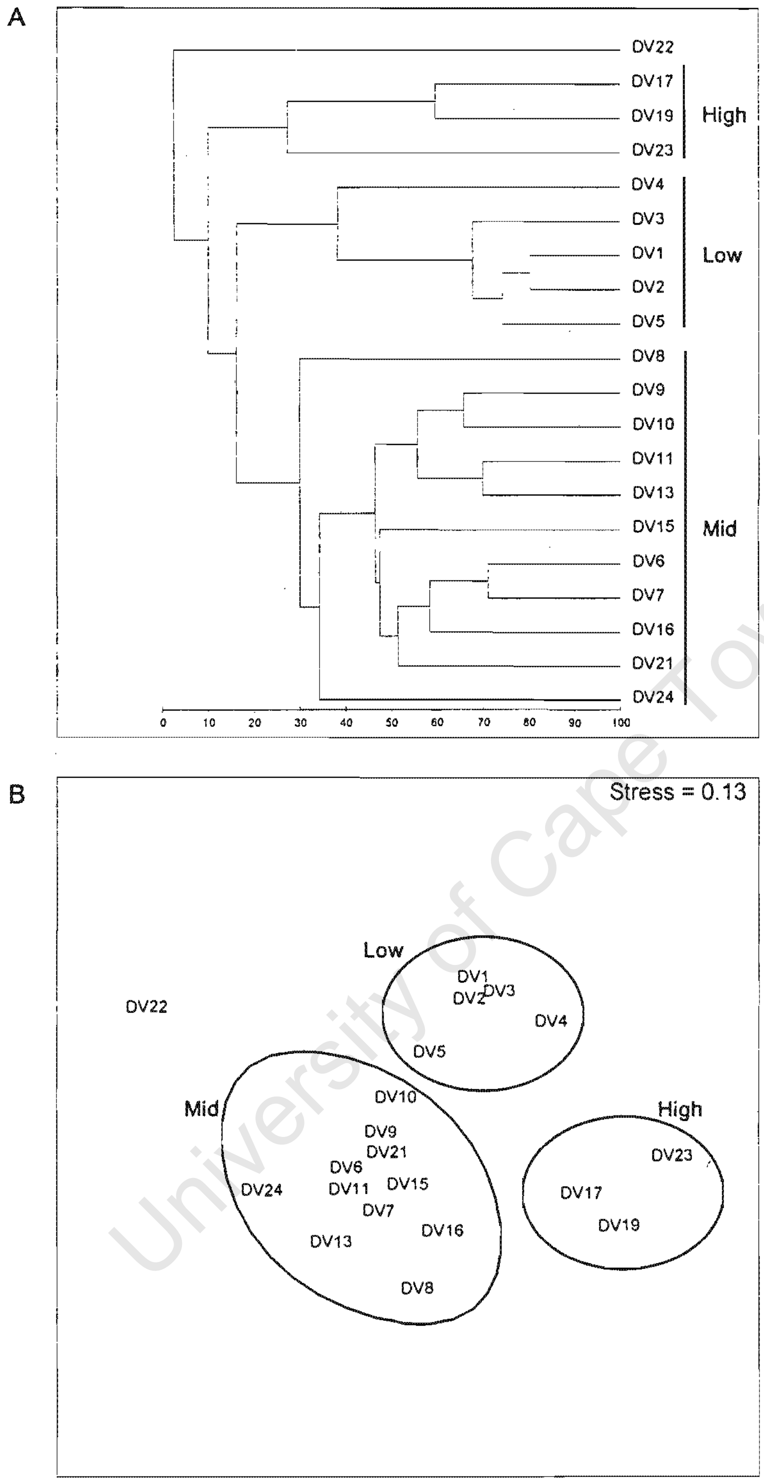

Figure 3.14. Dendrogram (A) and 2-D MDS plot (B) of mixed rock quadrats from Dido Valley with clusters delineated at approximately 25% similarity.

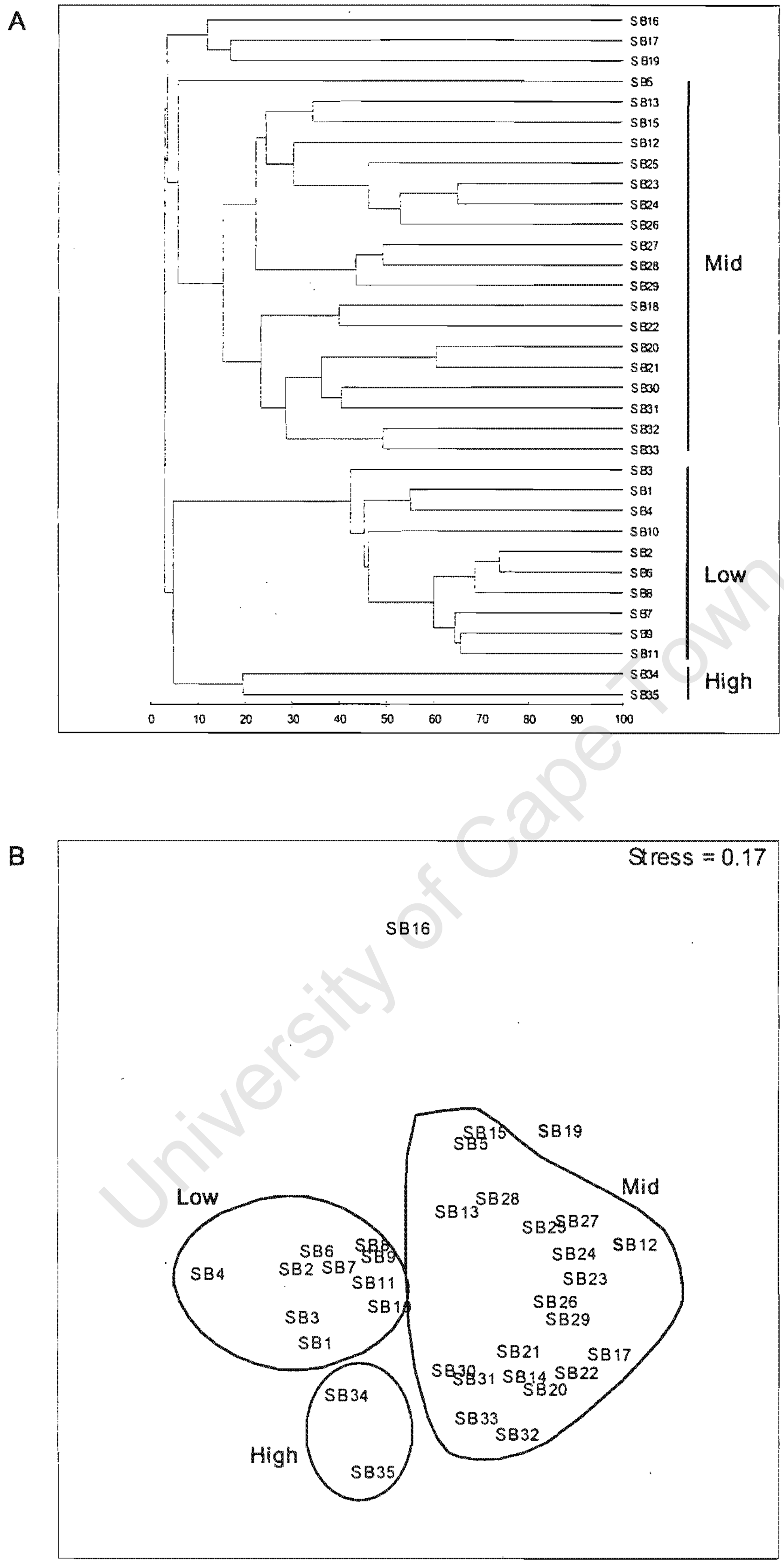

Figure 3.15. Dendrogram (A) and 2-D MDS plot (B) of mixed rock quadrats from Smitswinkel Bay with cluster delineated at approximately 15% similarity.

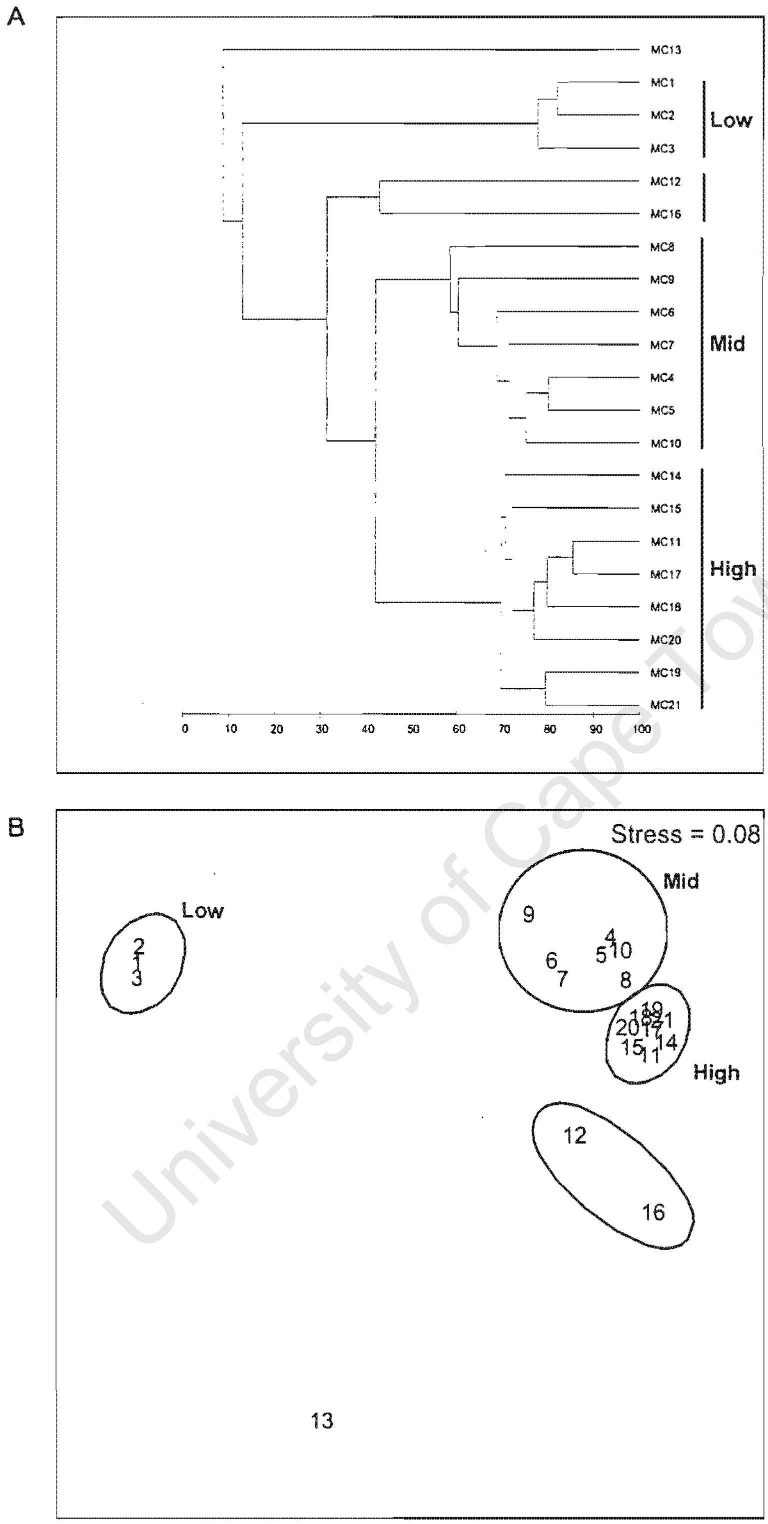

Figure 3.16. Dendrogram (A) and 2-D MDS plot (B) of mixed rock quadrats from Muizenberg Corner with cluster delineated at approximately 40% similarity.

Table 3.1. Breakdown of average dissimilarities between groups one and two, one and three, and two and three respectively from Dido Valley. Species are listed in order of decreasing contribution. δ_i Is the average contribution of the *ith* species to the dissimilarity between groups, δ_i /SD(δ_i) is the ratio between average contribution of the *ith* species (δ_i) and the standard deviation of the δ values for that species [SD(δ_i)] and Cum δ_i % the cumulative contribution to the total dissimilarity, re-scaled as a percentage

Species	δ_i	δ_i **/SD(**δ_i**)**	δ_i **%**	**Cum** δ_i **%**
Group one vs. Group two				
Mytilus galloprovincialis	29.50	2.33	38.23	38.23
Choromytilus meridionalis	9.09	1.23	11.78	50.01
Bunodactis reynaudi	8.52	0.69	11.03	61.05
Exosphaeroma truncatitelson	3.78	1.93	4.90	65.95
Syllis spongicola	3.24	1.96	4.20	70.15
Scoloplos johnstonei	3.06	0.61	3.97	74.12
Group one vs. Group three				
Mytilus galloprovincialis	32.87	2.48	36.56	36.56
Choromytilus meridionalis	14.20	2.06	15.80	52.36
Bunodactis reynaudi	10.42	0.76	11.60	63.96
Exosphaeroma truncatitelson	4.32	1.73	4.80	68.76
Syllis spongicola	4.03	2.51	4.48	73.24
Nodilittorina africana knysnaensis	3.35	0.66	3.72	76.96
Group two vs. Group three				
Choromytilus meridionalis	23.62	1.26	27.20	27.20
Bunodactis reynaudi	16.74	1.02	19.28	46.47
Nodilittorina africana knysnaensis	15.31	0.56	17.63	64.11
Mytilus galloprovincialis	5.27	0.55	6.06	70.17
Polysiphonia corymbifera	4.96	0.60	5.71	75.88
Exosphaeroma truncatitelson	4.95	0.93	5.70	81.58
Siphonaria aspera	4.15	0.30	4.78	86.36

The samples from Smitswinkel Bay also separated into three groups at 5% similarity (Figs 3.15 A & B). Group 1 was dominated by *N. africana knysnaensis*. Group 2 was more diverse and four species, namely *M. galloprovincialis* (32.6%), *C. meridionalis* (24.9%), *E. truncatitelson* (11.5%) *and N. africana knysnaensis* (7.4%) contributed to the similarity between samples. Group 3 also had four species that were responsible for most of the similarity between these samples. These were *Patella granularis* (33.1%), *M. galloprovincialis* (24.8%), *C. meridionalis* (14.2%) and *N. africana knysnaensis* (12.5%). The contributions of the most important species to the dissimilarities between groups of samples from Smitswinkel Bay are presented in Table 3.2.

Table 3.2. Breakdown of average dissimilarities between groups one and two, one and three, and two and three respectively from Smitswinkel Bay. Species are listed in order of decreasing contribution. δ_i Is the average contribution of the *ith* species to the dissimilarity between groups, δ_i /SD(δ_i) is the ratio between average contribution of the *ith* species (δ_i) and the standard deviation of the δ values for that species [SD(δ_i)] and Cum δ_i % the cumulative contribution to the total dissimilarity, re-scaled as a percentage

Species	δ_i	**δ_i /SD(δ_i)**	**δ_i %**	**Cum δ_i %**
Group One vs. Group Two				
Mytilus galloprovincialis	11.47	1.19	13.00	13.00
Nodilittorina africana knysnaensis	8.69	1.23	9.85	22.86
Choromytilus meridionalis	8.65	1.21	9.81	32.67
Porphyra capensis	7.44	0.37	8.44	41.11
Amphiroa ephedraea	5.71	0.56	6.48	47.58
Oxystele variegata	4.19	0.37	4.75	52.34
Group One vs. Group Three				
Nodilittorina africana knysnaensis	14.73	1.30	17.72	17.72
Mytilus galloprovincialis	13.24	0.89	15.94	33.66
Patella granularis	12.98	0.98	15.62	49.28
Choromytilus meridionalis	7.33	1.02	8.82	58.09
Siphonaria aspera	4.70	0.33	5.65	63.75
Unknown Bivalve A	2.84	0.40	3.42	67.17
Group Two vs. Group Three				
Mytilus galloprovincialis	11.07	1.14	13.16	13.16
Choromytilus meridionalis	7.28	1.36	8.65	21.81
Patella granularis	6.22	0.92	7.39	29.20
Nodilittorina africana knysnaensis	5.24	0.65	6.23	35.44
Porphyra capensis	3.83	0.33	4.55	39.99
Amphiroa ephedraea	3.73	0.63	4.43	44.42
Gymnogongrus polycladus	3.14	0.61	3.73	48.15
Jania sp.	2.89	0.36	3.43	51.59

The samples from Muizenberg Corner separated into four groups at 45% similarity, on the cluster diagram and 2D MDS plot (Figs 3.16 A & B). Group 1 contained five species, four of which significantly contributed to the similarity of the group. These species were *Ulva* sp. (51.9%), *E. truncatitelson* (20.3%), *Tricolia capensis* (13.1%) and *Exosphaeroma pallidum* (9.8%). Group 2 also contained four species: *C. meridionalis* (46.1%), *M. galloprovincialis* (24.3%), *T. capensis* (7.9%) and *B. reynaudi* (7.9%), that contributed to similarity. Group 3 had three species that contributed significantly to the similarity of the samples of within the group namely: *C. meridionalis* (47.9%) *T. capensis* (11.2%) and *B. reynaudi* (6.9%). As group 4 only contains two samples the SIMPER program could not calculate percentage contributions to similarity. Table 3.3 contains the contributions that the major species make to the measured dissimilarities between these groups.

to four

Table 3.3. Breakdown of average dissimilarities between groups one a~~nd two, one a~~nd th~~ree, and two and three respectively~~ from Muizenberg Corner. Species are listed in order of decreasing contribution. δ_i Is the average contribution of the *ith* species to the dissimilarity between groups, δ_i /SD(δ_i) is the ratio between average contribution of the *ith* species (δ_i) and the standard deviation of the δ values for that species [SD(δ_i)] and Cum δ_i % the cumulative contribution to the total dissimilarity, re-scaled as a percentage.

Species	δ_i	δ_i **/SD(**δ_i**)**	δ_i **%**	**Cum** δ_i **%**
		Group One vs. Group Two		
Choromytilus meridionalis	25.21	3.99	29.50	29.50
Mytilus galloprovincialis	12.91	6.50	15.10	44.60
Ulva sp.	11.03	2.36	12.90	57.50
Bunodactis reynaudi	5.52	1.62	6.46	63.96
		Group One vs. Group Three		
Choromytilus meridionalis	29.61	12.68	34.22	34.22
Ulva sp.	8.50	6.77	9.83	44.04
Caulacanthus ustulatus	5.05	1.55	5.83	49.88
Bunodactis reynaudi	4.81	4.22	5.55	55.43
		Group One vs. Group Four		
Choromytilus meridionalis	11.84	27.88	12.68	12.68
Gigartina radula	10.23	3.44	10.96	23.65
Burnupena lagenaria	10.20	2.73	10.93	34.57
Ulva sp.	7.88	8.19	8.44	43.02
Burnupena cincta	6.09	0.91	6.52	49.54
Nothogenia erinacea	5.47	0.91	5.86	55.40
		Group Two vs. Group Three		
Choromytilus meridionalis	10.67	2.70	18.48	18.48
Mytilus galloprovincialis	6.16	3.50	10.67	29.15
Caulacanthus ustulatus	3.82	1.53	6.62	35.77
Burnupena catarrhacta	3.27	1.92	5.66	41.43
Tricolia capensis	3.05	2.92	5.29	46.72
Cirolana venusticauda	3.04	2.13	5.27	51.99
		Group Two vs. Group Four		
Gigartina radula	8.23	3.44	11.68	11.68
Burnupena lagenaria	8.20	2.78	11.64	23.32
Mytilus galloprovincialis	6.18	5.97	8.78	32.10
Burnupena cincta	4.91	0.96	6.97	39.07
Nothogenia erinacea	4.37	0.96	6.21	45.28
Acanthochitona garnoti	3.16	1.71	4.49	49.77
Choromytilus meridionalis	3.05	1.17	4.33	54.09
		Group Three vs. Group Four		
Choromytilus meridionalis	9.92	8.21	14.90	14.90
Gigartina radula	6.50	3.49	9.76	24.66
Burnupena lagenaria	5.96	2.29	8.96	33.62
Burnupena cincta	3.89	0.97	5.84	39.46
Nothogenia erinacea	3.44	0.97	5.17	44.63
Acanthochitona garnoti	2.67	1.94	4.01	48.64
Caulacanthus ustulatus	2.64	1.74	3.96	52.60

3.4 Discussion

No uniform pattern of community composition or zonation was observed across the three sites in this study, but rather differences in the number of species, species composition, biomass, trophic structure and zonation were recorded. Community structure is controlled on rocky intertidal shores by a number of physical and biological factors, for example: wave exposure, temperature regime, food availability, substrate stability, predation, competition, larval availability and disturbance (Connell 1961, Paine 1966, Paine & Levin 1981, Underwood & Denley 1984, Dayton 1971, Stephenson & Stephenson 1972, Sousa 1979a, Underwood *et al.* 1983, Dayton 1984, Lubchenco 1986, Menge 1991, Bustamante 1994, Bustamante *et al.* 1995, Bustamante & Branch 1996a & b). These same factors drive patterns in community structure on mixed shores to a large degree as mixed shore communities are dominated (both in species richness and biomass) by the rocky-shore component of the community (Dower 1989, Brown *et al.* 1991).

The relative numbers of species recorded in each of the major intertidal taxonomic groups did not differ among shores. Molluscs consistently had the greatest species richness (all shores combined) with algae, crustaceans and polychaetes having lower species richness (Fig. 3.3). These results differed from those of Dower (1989) on the East Coast who found the highest diversity in the arthropod group, with the Annelida second and the Mollusca third.

The detritivore group was the most diverse functional group in this study, followed by the primary producers, herbivores and filter feeders. This result was different from previous studies on pure rocky shores around the peninsula (McQuaid 1980). McQuaid (1980) found the lowest diversity in the detritivore and omnivore groups and highest in the primary producers, herbivores and carnivores. This difference can be explained however by the inclusion of many sand-dwelling isopods and amphipods found on mixed sand, which tend to be detritivores or scavengers. My result was also different from those of mixed shores on the East Coast (Dower 1989). Dower (1989) found the highest diversity in the carnivore and scavenger groups followed by herbivores, detritivores, primary producers and filter feeders.

Filter feeders dominated the biomass on all shores sampled in this study. This pattern was similar to that found on exposed rocky shores in the region that are not inundated by sand (McQuaid 1980, Griffiths & Branch 1991, Bustamante *et al.* 1995, Bustamante & Branch 1996a)(see chapter 4). The dominance of filter feeders on Dido Valley and Muizenberg Corner was extreme, however, while on Smitswinkel Bay it was more similar to that on exposed rocky shores. Other important groups that contributed to biomass were the primary producers, carnivores and herbivores. The three sites showed different patterns in biomass with the second most important group at Dido Valley being the carnivore group, while Smitswinkel Bay had two other important groups namely primary producers and herbivores, and Muizenberg Corner had three other important groups - carnivores, herbivores and primary producers.

Muizenberg Corner consists of flat rocky ledges and has a very gentle gradient. This resulted in a continual inundation of sand over nearly the entire shore. On this shore *C. meridionalis* and *M. galloprovincialis* dominated biomass. At Dido Valley and Smitswinkel Bay however, the nature of sand inundation and scour differed. Dido Valley consists of a series of ledges that rise above the sand. They are not as influenced by sand inundation as Muizenberg Corner, but rather are exposed to severe sand scouring. On this shore the dominance of mussels is less. The populations of mussels observed on Dido Valley form remnant populations rather than thick beds, as was the case at Muizenberg Corner. At Smitswinkel Bay, where large-scale sand movement was more frequent, the spatial and temporal distribution of inundation events was more irregular. On this shore the dominance of mussels was less marked than on either Dido Valley or Muizenberg Corner.

Two filter-feeding molluscs, *Mytilus galloprovincialis* and *C. meridionalis*, were the most important species by mass. *Choromytilus meridionalis* is able to withstand and actually prefers inundation by sand (Day 1974, Marshall & McQuaid 1993), while *M. galloprovincialis* must be able to withstand sand scouring (pers. obs.). On shores inundated by sand, these species are able to withstand scouring and inundation events better than other primary space occupiers are, which allows these two species to monopolise the primary space available. Further the dominance of these two species explains the dominance of the filter-feeding and molluscan categories.

The rarity of primary producers and grazers was particularly noticeable at all sites. Not only were grazing limpets almost totally absent from the primary rock surfaces, but the numbers of smaller limpets found in the infauna of the sand-inundated mussel beds were negligible when compared to the numbers in mussel beds not influenced by sand (see Chapter 4). Possibly the most important species of patellid grazer that was missing was *P. cochlear*. This limpet normally dominates the low-shore 'cochlear zone' on rocky shores, which is so named because of the high densities of this species usually found in this zone (Branch & Branch 1981, Griffiths & Branch 1991). This zone was missing from all three of the mixed shores examined in False Bay. Patellid limpets are intolerant of sand inundation and other physical stresses such as salinity changes, prolonged aerial exposure and changes in temperature, and are often replaced by siphonarid limpets under stressful physical conditions such as those found on mixed shores (see chapter 4; Marshall & McQuaid 1989, Branch *et al.* 1990).

General patterns of zonation on the rocky substrate of mixed shores were not readily comparable to those on pure rocky shores in False Bay. One of the most noticeable features was the proliferation of mussels on all three sites. Both *M galloprovincialis* and *C. meridionalis* were responsible for a large proportion of the similarity within groups. In addition, they were also responsible for the majority of dissimilarities between groups on all shores, with few exceptions (Tables 3.1 - 3.3). The distribution and dominance of these benthic filter feeders was most similar to that described for exposed rocky shores, although all three sites were considered to be of intermediate exposure at the onset of this project. Furthermore, since filter feeders are net importers of 'energy', their dominance means that these mixed shores require a net import of primary production and therefore rely on the nearshore primary production of phytoplankton and algal detritus (McQuaid & Branch 1985, Bustamante *et al.* 1995, Bustamante & Branch 1996b).

On the mixed shores examined, a low-shore zone could be identified which contains predominantly both *C. meridionalis and M. galloprovincialis*. This contrasts with previously identified zonation patterns (e.g. McQuaid 1980) documenting a sublittoral zone dominated by algae. Two potential reasons could explain this "missing zone". Firstly, sand movement is probably most severe in this low-shore zone, where both sand scour and sand burial are probably at their most extreme. This could constantly disrupt algal recruitment, sporeling development and algal survival (Trowbridge 1996). The second factor, which is not entirely independent of the first, is that the black mussel, *C.*

meridionalis, has been shown not only to tolerate sand inundation, but also to prefer areas where it is exposed to sand (Griffiths 1981a & b, Bally *et al.* 1984, Van Erkom Schurink & Griffiths 1990). In the low-shore zone, this species tends to monopolise primary space, because it is not only a dominant competitor, but also tolerant of the prevailing environmental conditions that seem to negatively affect other species. At Muizenberg Corner, *Ulva* sp. dominated the low shore. This is a rapidly recolonising algae and is often the first pioneer species to return to newly created space on intertidal and shallow subtidal reefs (Bokenham & Stephenson 1938, Sousa 1979b, van Zyl & Robertson 1991). It is predicted, however, that *C. meridionalis* will in time out-compete this species and that the area will revert to mussel domination. Above the area dominated by *Ulva* sp. at Muizenberg Corner, the shore reverted to the general pattern of a mussel-dominated low shore.

Immediately above this sublittoral zone on rocky shores there is usually a cochlear zone dominated by *P. cochlear*. Patellid limpets are extremely psammophobic and are unable to tolerate burial even at moderate levels of sand inundation (Marshall & McQuaid 1989). On mixed shores *Patella cochlear* is typically absent from its expected zone and is replaced by a continuation of the lower shore combination of *M. galloprovincialis* and *C. meridionalis.* At all three sites, grazer numbers were found to be relatively low over most of the shore. In addition, *Patella granularis* was scarce in mussel beds, whereas juveniles of this species are an abundant component of the infauna of mussel beds on shores not influenced by sand (C. Velasquez pers. com. & Chapter 4)

The absence of *Patella cochlear* in the cochlear zone on all three mixed shores investigated also leads to the linear pattern of decreasing biomass up shore. This differs from most pure rocky shores in the region, where diversity is high in the algal-dominated sublittoral fringe and then drops in the cochlear zone before increasing again in the lower balanoid zone (McQuaid 1980, McQuaid & Branch 1984, Bustamante *et al.* 1997). This drop in diversity occurs due to the dominance of *Patella cochlear* in this zone.

In conjunction with the absence of *P. cochlear*, the numbers of other grazers were also low and this resulted in a proliferation of early colonising green algae such as *Ulva* sp.. A similar pattern has been recorded by Branch *et al.* (1990) in their work on the West Coast of southern Africa following flooding of the Orange River. The large intrusion of fresh water led to a dilution of nearby coastal waters causing mass moralities of shallow-water and intertidal organisms. The subsequent absence of grazers allowed a proliferation of *Ulva* sp. and other early colonising algal species. Further unpublished work on the effects of black tides (extreme low oxygen events that occur occasionally after proliferation of algal blooms on the West Coast of South Africa)(Branch unpublished data) and the dumping of fine tailings from a Namibian diamond mine (Bustamante *et al.* 1993, Parkins & Branch 1995 & 1997) has yielded similar results. These data demonstrate the important role grazers play in controlling algal abundance and composition on rocky substrates in the region.

The zone furthest away from MLWS, the Littorina zone, was clearly defined on all three shores. In this region there were no noticeable differences between mixed shores and rocky shores. Minimal sand movement or deposition at this level, and consequent absence of burial or scouring at high-shore levels could explain this. Only during extreme storms will the organisms in this region ever be affected by sand, although wind-blown sand may have an impact. Mixed shores are usually in close proximity to open sandy beaches (in fact are often the zone of transition from sandy beach to rocky shore), and wind-blown sand picked up on beaches could blow onto high-shore areas.

One factor that adds to the incongruity in the observed zonation patterns on mixed shores in the present study and those recorded by McQuaid (1980) McQuaid & Branch 1984 and McQuaid *et al.* (1985) is the recent occurrence of the invasive mussel *M. galloprovincialis*. This species was not detected until 1985 (Grant & Cherry 1985) and is thus absent from earlier work. Today however, this species dominates much of the biomass on rocky shores on the West Coast of South Africa (Bustamante 1994, Bustamante & Branch 1996a). As can be seen from tables 3.1 to 3.3 this species plays a major role, in conjunction with *C. meridionalis*, in separating sample groups and thus strongly influences the recorded zonation patterns.

Grazers were scarce on all three mixed shores and only began to appear in significant numbers in the mid-shore zone. This could be compared to a depauperate Balanoid zone on pure rocky shores. However, this zone still contained an abundance of mussels. At Dido Valley and Muizenberg Corner *C. meridionalis* still dominated samples from this 'zone' although it was superseded by *P. granularis* at Smitswinkel Bay.

Mixed shores are extremely heterogeneous with large within-site and between-site differences. Within-site heterogeneity was large even over the small spatial scales that were investigated in this study, and there was also low overall similarity among sites (Figs 3.13A & B). This is indicative of high heterogeneity. Mixed shores can be viewed as far more dynamic and spatially-complex systems than pure rocky shores. Sand movement occurs unpredictably over small spatial and temporal scales. In this they are more similar to sandy beaches, which vary even over tidal cycles. This heterogeneity severely hampers efforts to identify rigid zonation patterns on these shores.

It had been anticipated that when all samples were compared simultaneously, that those from similar shore heights would cluster together. In reality, samples tended to cluster on a within-site basis (Fig. 3.13A,B), not within zones among sites. Only when each site was considered separately (Figs 3.14-3.16) did zonation patterns begin to emerge. High inter-site variability was thus a feature.

The observed patterns of biomass (Fig. 3.8) and diversity (Fig. 3.9) on mixed shores followed the general patterns observed for rocky shores, with biomass and species richness decreasing with height above MLWS. Thus, although increased heterogeneity seems to confuse patterns of biotic zonation it does not greatly influence these basic trends. Intertidal organisms are still predominantly affected by distance from MLWS. These results confirm the findings of Bustamante *et al.* (1997) who found that the high-shore regions of shores exposed to different levels of wave action were more similar than the low-shore regions, which tend to be more effected by the variability in wave climate. In my case, variability in sand inundation applies an additional factor to the conditions creating low-shore heterogeneity (see Chapter 4).

Zonation patterns in a heterogeneous and patchy environment are not easily identifiable. Sand movement on the shores studied in this work seems to influence the distribution of many organisms, and in so doing continually disrupts the patterns of zonation that are expected for these organisms on pure rocky shores. The ability of *C. meridionalis* to survive inundation allows it to survive on the low shore, which is usually occupied by algae on rocky shores not influenced by sand. Furthermore, sand inundation prevents grazers such as *P. cochlear* from occurring in their normal zone while reducing the numbers of other patellids such as *P. granularis* in their respective zones. Thus appreciable differences are noticeable between the zonation on mixed shores and previously described zonation patterns on rocky shores in False Bay. Sand therefore not only influences the composition of the community occurring on mixed shores but also does so in different ways. The levels and frequencies of inundation differed from shore to shore and from zone to zone, and in a patchy manner within zones, and with this variability the dominance of the shores by sand tolerant species (mussels in particular in this study) varied.

These conclusions can, however, be only preliminary because the initial survey of mixed shores was only compared with existing (published) descriptions of zonation patterns on pure rocky shores. In view of the high degree of variability of mixed shores, I thus embarked on a more rigorous comparison of mixed, pure rocky and pure sandy shores. My comparisons for this survey were based on adjacent shores so that the physical regimes of wave action and exposure to air were identical between comparisons. These data form the substance of chapter 4.

CHAPTER FOUR: A COMPARISON OF MACROFAUNAL COMMUNITIES ON FOUR INTERTIDAL HABITATS: MIXED ROCK, PURE ROCK, MIXED SAND AND PURE SAND

4.1 Introduction

Few studies have compared community structure and functioning among pure sandy beaches, sand in-between rocks (mixed sand), rocky areas inundated by sand (mixed rock) and pure rocky shores. In South Africa Bally *et al.* (1984), Dower (1989), McQuaid and Dower (1990) and Brown *et al.* (1991) have all made qualitative comparisons between mixed shores and shores of pure sand or rock. Currently no quantitative studies comparing macrofauna in these habitats using consistent sampling protocols have been undertaken in South Africa.

Chapter 1 introduced mixed shores and outlined the numerous habitats that have been defined (Bally *et al.* 1984). Although mixed shores should be viewed as distinct units, the individual habitats present on them i.e. mixed sand and mixed rock need to be compared with their 'pure' habitat types i.e. pure sandy beach not effected by rocks or pure rocky shore not effected by sand. It is indeed possible to make whole-shore comparisons, i.e. mixed shores vs. sandy beaches or rocky shores. However, details of what happens within habitats on different types of shores can be lost if shores are considered as a whole. In particular differences occurring between sandy substrates on different types of shores could be swamped by the characteristics of rocky substrates because of the dominance of the latter habitats in terms of both species richness and biomass (see chapter 3).

As a consequence, this chapter focuses on the biotic characteristics of each of these habitat types separately (i.e. MR, MS, R & S) and compares them among three shore types; i.e. mixed shores, rocky shores and sandy beaches. Primarily I ask the question whether sandy habitats show similar biotic characteristics whether they are on mixed shores or pure shores, and similarly, if rocky habitats support the same biota on mixed and pure shores.

4.2 Methods

Samples for this study were collected from four zones and on or in four different habitat types (sand, mixed sand, mixed rock and rock) on three shores (Smitswinkel Bay, Muizenberg Corner & Dido Valley). Three transects consisting of one quadrat per zone were collected from each habitat type on each shore (Fig. 4.1). The four zones on rocky substrates were immediately below low water spring (= LLOW), on LWS (= LOW), mid shore (= MID) and high shore (= HIGH). These zones correlated roughly with those identified on mixed shores in Chapter 3. On sandy substrates samples were taken at LWS (LLOW), just below the effluent line (LOW), just above the effluent line (MID) and at the drift line of high-water springs (HIGH). All Samples were obtained using the methodology outlined in Chapter 2.

Univariate analysis

Biomass was divided into functional groups: carnivores, filter feeders, herbivores, primary producers and detritivores. The total biomass and biomass of these groups were analysed individually with 2-way crossed ANOVAs (site * substrate). All biomass data were log-transformed before analysis and normality and homoscedacity checked using graphical methods and Bartlett's test respectively.

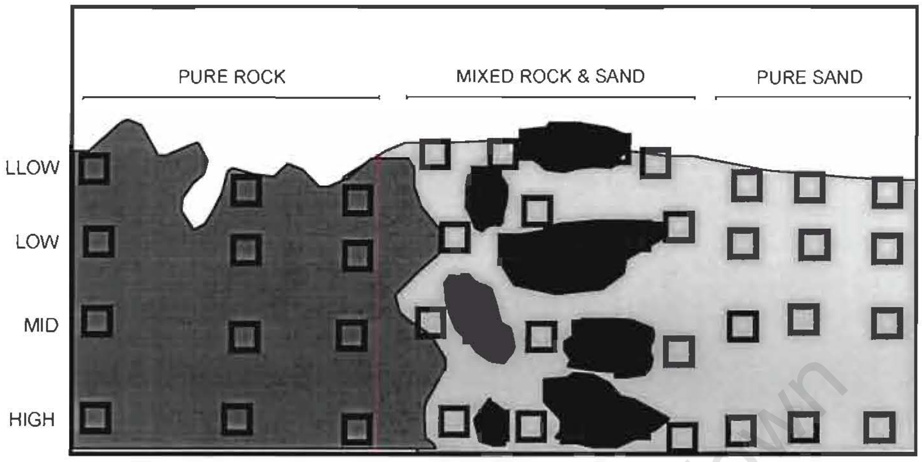

Figure 4.1. Schematic representation of sampling design showing the four zones, (LLOW, LOW, MID and HIGH) in the four habitats (pure rock, mixed rock, mixed sand and pure sand) sampled. The squares represent individual quadrats.

K-dominance curves (Clarke 1990, Lambshead *et al.* 1983) were constructed using biomass per species on a logarithmic scale (Warwick & Clarke 1996). Data were divided into substrate types for the construction of dominance curves. K-dominance curves plot the different species in ranked order against their cumulative percentage biomass. The shape of dominance curves indicates how many species dominate the community, with steep curves indicating that a few species dominate biomass, and shallow curves indicating a more uniform contribution of the species to the total biomass.

The mean sizes of *M. galloprovincialis* in two different habitats were calculated. Approximately 120 mussels from the LOW zone on three shores on mixed rock and pure rocky habitats were measured to the nearest millimetre. Means were compared using a paired *t*-test.

Multivariate analysis

Data from the four quadrats on each transect (i.e. covering the four zones), were combined and the mean dry mass.m^{-2} was calculated for each species. Data were arranged in rectangular matrices where cases = species and samples = sites/substrates. Classification and ordination were performed as per the methods described in Chapters 2 and 3. Two transformations were used on the data: a √√-transformation and a transformation to presence/absence. Statistical differences between the *a-priori* groups i.e. mixed substrate vs. pure substrate were undertaken using a 2-way crossed ANOSIM on the similarity matrix calculated on presence/absence data (Clarke 1993), i.e. site * substrate (2 levels) with 3 replicate transects (Fig. 2.4). The contributions of each species to dissimilarity between groups were calculated with the SIMPER routine (Similarity Percentages Clarke 1993) as per Chapters 2 & 3.

The community composition of each zone was compared between R and MR, and S and MS habitats using a one-way ANOSIM (Fig. 2.3)(see Chapter 2, Clarke 1993). Comparisons were made between habitats (e.g. High on MR vs. High on R etc.), in order to assess differences in the level of similarity in community composition of the different zones on mixed rock and pure rock and similarly mixed sand and pure sand habitats.

All multivariate techniques were undertaken on the computer program PRIMER v3.1a (Plymouth Routines in Multivariate Ecological Research; Carr 1994). All univariate statistics were calculated on the computer program STATISTICA (StatSoft Inc., Tulsa, USA. 1996) following the approach of Zar (1984).

4.3 Results

In total, 144 quadrats were collected from Smitswinkel Bay, Muizenberg Corner and Dido Valley in False Bay. Significant differences were observed in species composition, biomass of functional feeding groups and total biomass among the four habitats sampled.

Species composition differed among all habitats sampled. Four groups corresponding with the four habitat types were recorded after Bray-Curtis similarities were calculated on presence-absence data and plotted in a cluster diagram (Fig. 4.2 A). These groups were also well represented in a 2-D MDS plot (Fig. 4.2 B), with an acceptable stress level of 0.11 (Clarke 1993). There was a clear gradient in community structure from those on pure rocky habitats through those from mixed rock and mixed sand to sand (Fig. 4.2 B). A similar result was obtained after data were √√-transformed (Fig. 4.3 A & B). The only difference emerging was that the classification obtained after √√-transformation grouped some samples from pure rocky habitats and those from mixed rock in the cluster diagram (Fig. 4.3 A), although these were not evident in the MDS plot (Fig. 4.3 B). These were grouped separately after the presence-absence transformation (Fig. 4.2). The separation of mixed sand and sandy habitats was the same after both transformations.

There was a significant difference in community structure between pure rocky shore and mixed rock communities (2-way crossed ANOSIM, Global $r=0.951$, $p<0.05$) and pure sand and mixed sand communities (2-way crossed ANOSIM, Global $r=1$, $p<0.01$). The species that contributed to the dissimilarity between pure rock vs. mixed rock communities and pure sand vs. mixed sand communities are presented in Tables 4.1 and 4.2 respectively, which also show the species indicative of each shore type.

The average dissimilarity calculated using the SIMPER procedure, between pure rocky and mixed rocky habitats was 71.1%. Twenty-eight species contributed to 50% of the calculated dissimilarity, while a total of 124 species contributed to the total dissimilarity calculated. Only 7 species contributed more than 2% individually to the calculated dissimilarity. The isopod *Exosphaeroma truncatitelson* was the most important contributor to dissimilarity between pure rocky and mixed rocky habitats. The remaining six species that contributed >2% individually to dissimilarity were the alga *Gelidium pristoides*, the limpet *Patella cochlear*, the polychaete *Gunnarea capensis*, the chiton *Acanthochitona garnoti*, the barnacle *Tetraclita serrata* and the winkle *Oxystele variegata*.

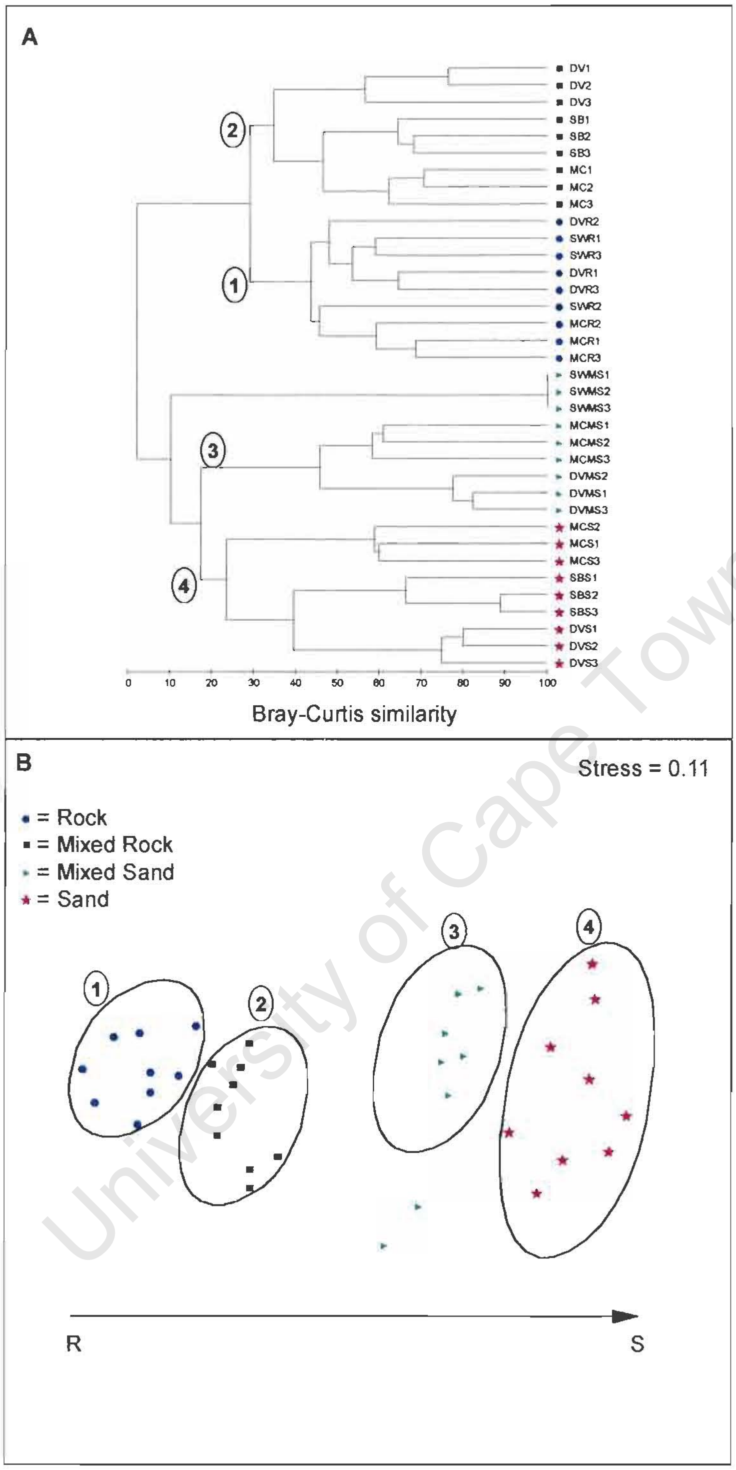

Figure 4.2. Dendrogram of Bray-Curtis similarities between samples (A) and 2-D MDS plot based on biomass data after transformation to presence/absence. Four groups are identified at approximately 25%, which correspond to habitat (1-4). The numbers after the site code (e.g. DV1) refers to individual transects.

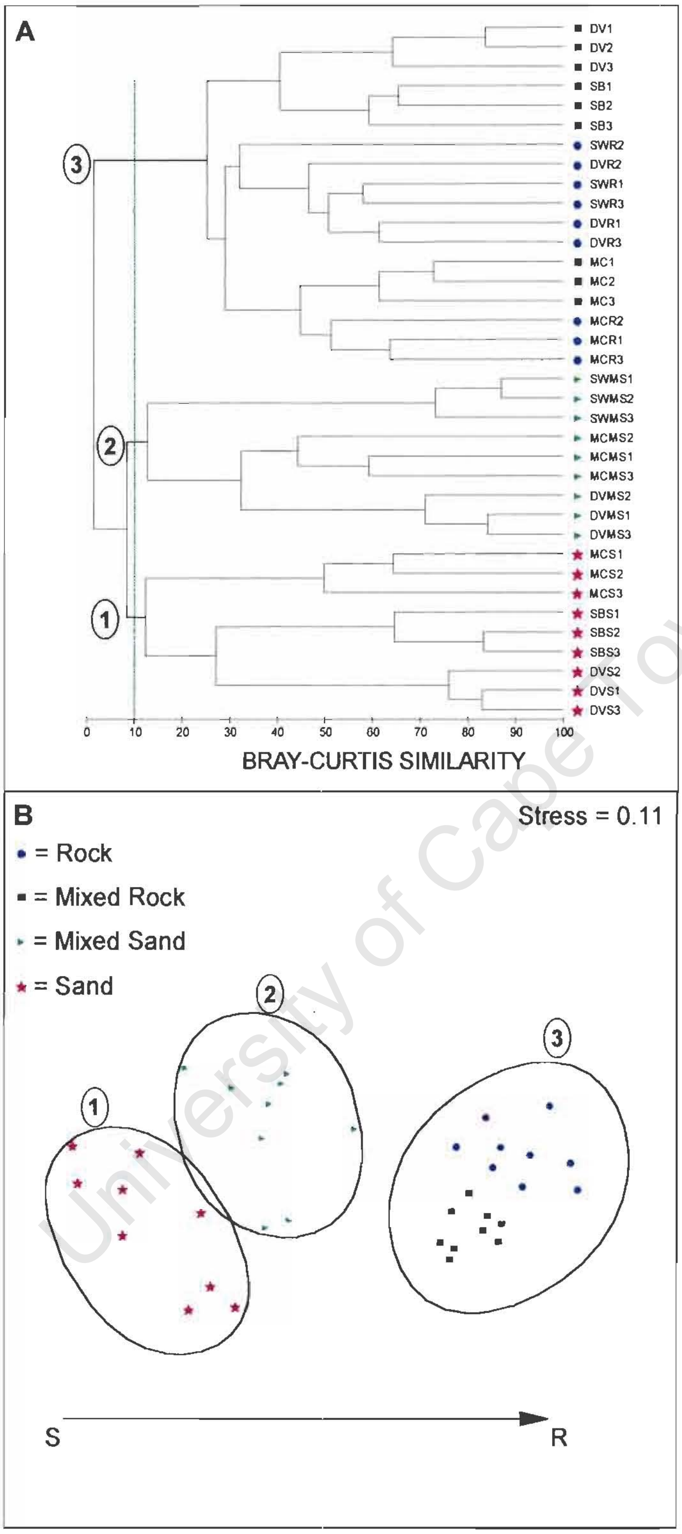

Figure 4.3. Dendrogram of Bray-Curtis similarities between samples (A) and 2-D MDS plot based on biomass data after root-root transformation. Three groups are identified at approximately 12% similarity, which correspond to habitat (1-3). The numbers after the site code (e.g. DV1) refers to individual transects.

Table 4.1. The 20 species that contribute 40% to average dissimilarity between pure rocky habitats and mixed rocky habitats. δ_i is the average contribution of the *ith* species to the dissimilarity between groups, δ_i /SD(δ_i) is the ratio between average contribution of the *ith* species (δ_i) and the standard deviation of the δ values for that species [SD(δ_i)] and Cum δ_i % the cumulative contribution to the total dissimilarity, re-scaled as a percentage. The species indicative of each shore type are indicated in Shore Type where MR = mixed rock and R = pure rock.

Species	δ_i	δ_i /SD(δ_i)	**Cum** δ_i %	**Shore Type**
Exosphaeroma truncatitelson	2.09	3.32	2.94	MR
Gelidium pristoides	1.83	1.89	5.52	R
Patella cochlear	1.75	1.98	7.97	R
Gunnarea capensis	1.72	1.86	10.39	R
Acanthochitona garnoti	1.61	1.55	12.65	MR
Tetraclita serrata	1.60	1.61	14.91	R
Oxystele variegata	1.50	1.56	17.02	R
Burnupena cincta	1.39	1.20	18.98	MR
Gigartina radula	1.37	1.11	20.91	MR
Pseudonereis variegata	1.27	1.42	22.69	R
Fissurella mutabilis	1.27	1.38	24.48	R
Patella granularis	1.25	1.04	26.23	R
Dynamenella huttoni	1.25	1.70	27.98	R
Polysiphonia corymbifera	1.22	1.00	29.71	MR
Caulacanthus ustulatus	1.20	0.96	31.40	R
Cirolana venusticauda	1.16	1.03	33.04	MR
Siphonaria capensis	1.16	1.04	34.67	MR
Ulva sp.	1.16	0.99	36.30	R
Burnupena catarrhacta	1.13	0.95	37.89	R
Hymeniacedon perlevis	1.06	1.16	39.39	R

Pure sand and mixed sand habitats had an average dissimilarity between groups of 94.5%, calculated using the SIMPER procedure. Five species contributed 50% of this dissimilarity; viz. copepods, the mussel *Choromytilus meridionalis*, the amphipod *Talorchestia quadrispinosa*, the isopod *Eurydice Kensleyi* and the white mussel *Donax serra*. A total of 26 species contributed 100% of the calculated dissimilarity.

Table 4.2. The 10 species that contribute 75% to average dissimilarity between pure sandy and mixed sand habitats. δ_i is the average contribution of the *ith* species to the dissimilarity between groups, δ_i /SD(δ_i) is the ratio between average contribution of the *ith* species (δ_i) and the standard deviation of the δ values for that species [SD(δ_i)] and Cum δ_i % the cumulative contribution to the total dissimilarity, re-scaled as a percentage. The species indicative of each shore type are indicated in Shore Type where MS = mixed sand and S = pure sand.

Species	δ_i	δ_i **/SD(**δ_i**)**	**Cum** δ_i **%**	**Shore Type**
Copepoda	11.70	1.29	12.38	MS
Choromytilus meridionalis	10.06	0.91	23.03	MS
Talorchestia quadrispinosa	9.90	0.87	33.50	MS
Eurydice Kensleyi	7.80	0.98	41.75	MS
Donax serra	6.42	0.67	48.54	S
Mandibulophoxus latipes	6.31	0.80	55.21	MS
Pontogeloides latipes	6.26	0.79	61.84	S
Gastrosaccus psammodytes	6.09	0.76	68.28	S
Callianassa kraussi	4.66	0.68	73.21	S
Scololepis squamata	4.44	0.62	77.91	S

Community composition in the HIGH-shore zones of pure rock and mixed rocky habitats was more similar (i.e. lower *R*) than that of the LLOW-shore zones (Table 4.3). This pattern was not repeated on pure sand and mixed sand habitats (Table 4.3): the habitats were relatively similar to each other within each zone, with the exception of the MID zone (Table 4.3).

Table 4.3. The calculated similarity (***R***) between zones (**Zone**) on pure rock and mixed rock, and pure sand and mixed sand habitats. This test (see section 4.2) measures the level of dissimilarity between components, therefore, a lower R value indicates a higher level of similarity between the respective components.

ZONE	*R*
Rock vs. Mixed Rock	
HIGH	0.344
MID	0.398
LOW	0.592
LLOW	0.508
Sand vs. Mixed Sand	
HIGH	0.278
MID	0.792
LOW	0.298
LLOW	0.289

Mixed rock habitats had a greater total biomass (2868.8 ± 980.9 $g.m^{-2}$) of macrofauna than pure rock habitats (935.9 ± 215.7 $g.m^{-2}$) which were in turn greater than mixed sand (4.07 ± 1.47 $g.m^{-2}$) and sand habitats (3.83 ± 1.58 $g.m^{-2}$) which did not differ from each other (ANOVA, df=3, *F*=159.21, p<0.00001) (Newmann-Keuls α=0.05). The biomass of three functional groups, primary producers, herbivores and filter feeders constituted approximately 98% of the total biomass on rocky shores. On sandy shores two trophic groups, namely primary producers and herbivores were absent.

There was a significant difference in the biomass of filter feeders on certain habitats (Figs 4.4 & 4.5, ANOVA, df=3, *F*=82.38, p<0.0001). There was no difference between pure rocky habitats and mixed rock although both these differed from pure sand and mixed sand which differed from each other (SNK α=0.05). The biomass of herbivores (ANOVA, df=3, *F*=77.39, p<0.0001) and primary producers (ANOVA, df=3, *F*=34.67, p<0.0001) was greater on pure rocky habitats than on mixed rock habitats (Fig. 4.4). Primary producer biomass was, however, not independent of site and a significant interaction factor site x substrate (*F*=5.132, p=0.001) was calculated in the 2-way crossed ANOVA. A significant interaction effect (*F*= 5.67, p=0.0008) was also present for scavengers. Patterns in the biomass of these two groups were therefore complicated by between-site variability and these results should be viewed with caution. The biomass of omnivores was similar on pure rock and mixed sand but was different on pure sand and mixed rock (ANOVA, df=3, F=18.75, P<0.0001; SNK α=0.05). No differences in the biomass of detritivores (ANOVA df=3, F=0.95, P=0.43, SNK α=0.05) and carnivores (ANOVA, df=3, F=3.27, P<0.05; SNK α=0.05) were discernible between habitat types, although both were insignificant contributors to overall biomass. These data are all summarised in Table 4.4.

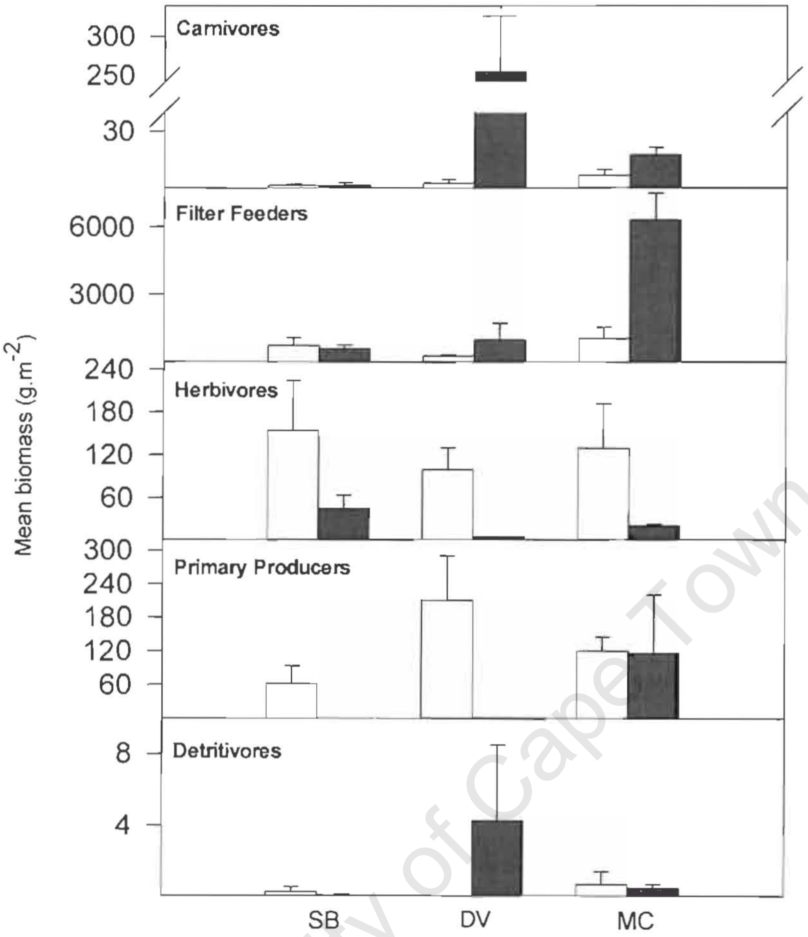

Figure 4.4. The biomass (g.m^{-2}) of trophic groups on pure rock (un-shaded) and mixed rock (shaded) habitats at Smitswinkel bay (SB), Dido Valley (DV) and Muizenberg Corner (MC)

Relative to pure rock, mixed rock was dominated by fewer species, having a shallower curve and thus a more uniform contribution to biomass than pure rocky habitats (Fig. 4.6). The pattern was different between samples from mixed sand and pure sandy habitats (Fig. 4.6), with mixed sand dominated by more species than pure sand. This result is possibly biased, however, by the presence of one large mollusc, i.e. *Donax serra*, which was the single biggest contributor to biomass in the samples from pure sand.

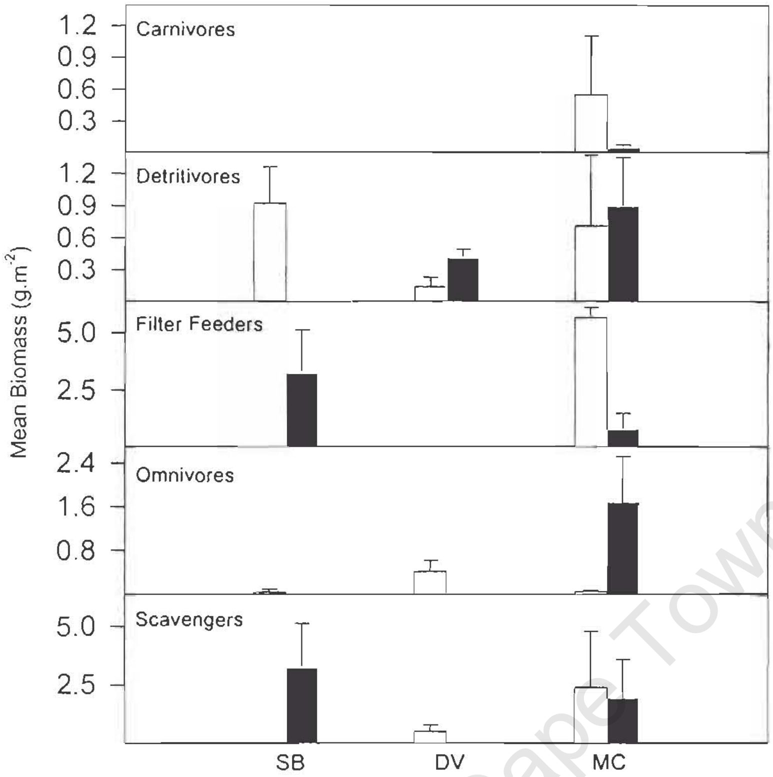

Figure 4.5. The biomass (g.m^{-2}) of trophic groups in mixed sand (un-shaded) and pure sand (shaded) habitats at Smitswinkel Bay (SB), Dido Valley (DV) and Muizenberg Corner (MC)

Figure 4.7 shows that the mean size of *Mytilus galloprovincialis* collected from pure rocky habitat was larger ($\bar{x}$ = 35.85 mm) than those from mixed rock ($\bar{x}$ = 29.59 mm) (Paired *t*-test, df = 2, *t*= -5.617, $p<0.05$).

Mixed rock contained a greater biomass of siphonarid limpets relative to patellid limpets than pure rock. The ratio of *Siphonaria* to *Patella* biomass was greater on mixed rock than on adjacent pure rock (Fig. 4.8 Mann- Whitney *U* test, *U* = 2.00, $p<0.05$).

Table 4.4. Summary of the differences between biomass of functional groups on the four different habitat types, rock (R), mixed rock (MR), sand (S) and mixed sand (MS) identified by Student Newman-Keuls tests (α=0.05) after 2- way crossed ANOVAs. Sites marked XX in each of the columns a, b or c indicate that they were statistically indistinguisable.

Trophic Compartment		a	b	c
Total Biomass	MR	XX		
	R		XX	
	MS			XX
	S			XX
Filter feeders	R	XX		
	MR	XX		
	MS		XX	
	S			XX
Herbivores	R	XX		
	MR		XX	
	S			XX
	MS			XX
Primary producers	R	XX		
	MR		XX	
	S		XX	
	MS		XX	
Scavengers	R	XX		
	MR	XX		
	S	XX	XX	
	MS		XX	
Carnivores	R	XX		
	MR	XX		
	S	XX		
	MS	XX		
Detritivores	R	XX		
	MR	XX		
	S	XX		
	MS	XX		
Omnivores	R	XX		
	MS	XX		
	S		XX	
	MR			XX

Mean grain size did not differ between mixed sand and pure sandy habitats sampled (Mann-Whitney *U* test, *U* = 18.5, *p*>0.05). Sand particle size on all pure sandy habitats and mixed sand habitats decreased with height up the shore (with the exception of Muizenberg mixed sand mid (MCMSM) Table 4.5). However, sorting and skewness of sediments varied randomly among heights and sites (Table 4.5).

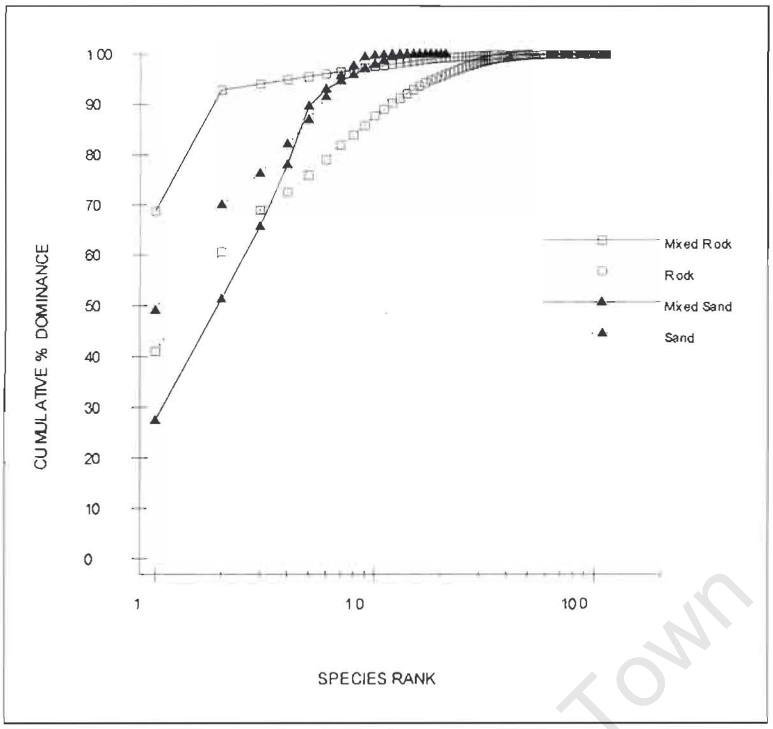

Figure 4.6. K-dominance curves (based on biomass data) for pure rock, mixed rock, mixed sand and pure sand

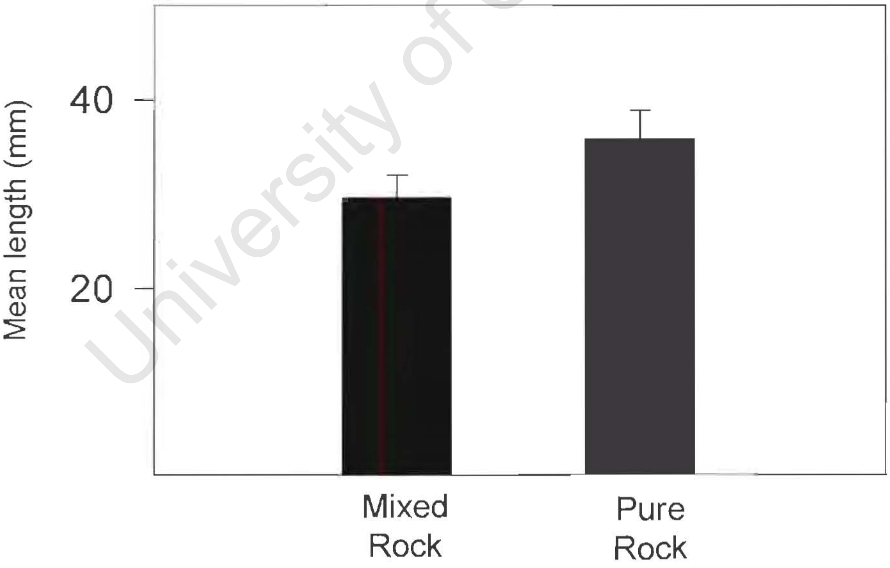

Figure 4.7. The mean length (mm) of *Mytilus galloprovincialis* on mixed rock and pure rock habitats. Error bars are standard error.

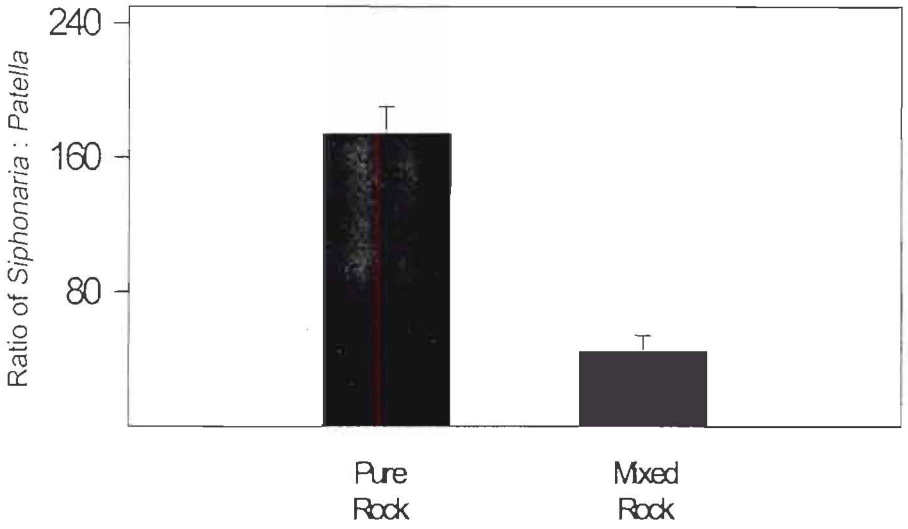

Figure 4.8. The ratio in biomass of the genera *Siphonaria* to *Patella* (i.e. 1 g.m^{-2} *Siphonaria*:y g.m^{-2} *Patella*) on pure rock and mixed rock habitats.

Table 4.5. Sand particle analysis of samples from pure sand and mixed sand habitats. Mean and median particle diameter are presented in both Phi units and µm. Sorting (Inclusive graphic standard deviation) (Good, Moderate Mod and Poor) and Skewness (Inclusive graphic skewness) (Coarse, Normal and Fine) are also presented. Samples are identified by shore, substrate and height (*e.g.* DVSL is DV = Dido Valley, S = Pure Sand and L = Low).

Sample	Mean (Phi)	Mean (µm)	Median (Phi)	Median (µm)	Sorting		Skewness	
DVSL	1.59	330.6	1.60	329.8	0.533	Mod	-0.053	Coarse
DVSM	1.50	353.5	1.48	358.5	0.349	Good	-0.649	Normal
DVSH	1.26	415.6	1.25	420.5	0.649	Mod	0.014	Normal
SBSL	1.50	351.9	1.49	356.0	0.476	Good	0.040	Coarse
SBSM	1.47	360.2	1.47	361.0	0.516	Mod	-.001	Coarse
SBSH	1.20	434.3	1.18	441.4	0.661	Mod	0.031	Normal
MCSM	1.24	423.4	1.12	460.1	1.516	Poor	0.080	Normal
MCSH	1.12	460.1	0.82	566.4	1.481	Poor	0.236	Fine
MCMSL	2.89	134.3	2.99	125.9	0.547	Mod	-0.395	Coarse
MCMSM	3.00	125.0	3.09	117.4	0.434	Good	-0.405	Coarse
MCMSH	1.34	394.1	1.32	400.5	0.501	Good	0.080	Normal
DVMSL	1.24	423.4	1.32	400.5	0.934	Mod	-0.164	Coarse
DVMSM	1.57	336.8	1.63	323.1	0.650	Mod	-0.167	Coarse
DVMSH	1.81	285.2	1.82	283.2	0.435	Good	-0.064	Normal
SBMSL	1.15	449.6	1.13	456.9	0.600	Mod	0.013	Normal
SBMSM	1.52	347.1	1.54	344.0	0.477	Good	-0.058	Normal
SBMSH	1.63	321.6	1.66	316.4	0.428	Good	-0.022	Normal

4.4 Discussion

The species composition of the individual habitats that constitute mixed shores i.e. mixed sand and mixed rock, was different from their respective pure shore types. The presence of sand or rock fundamentally effects community structure, and differences in species composition, trophic partitioning of biomass, size structure of mussels and species dominance occurred as a result of the presence of these 'disturbance agents'.

Species that live on rocky substrates differ in their ability to tolerate disturbance by sand (Seapy & Littler 1982, Taylor & Littler 1982, Littler *et al.* 1983, Stewart 1983, D'Antonio 1986, Marshall & McQuaid 1989, Dower 1989, McQuaid and Dower 1990, Brown *et al.* 1991, Kendrick 1991). Certain species are intolerant of the stress associated with sand inundation and scouring and are absent under these conditions. In this study, the most important group of intertidal organisms affected by sand was the patellid limpets. As discussed in Chapter 3, *Patella cochlear* was absent from the Cochlear zone on all mixed shores investigated in this study. Patellid limpets are intolerant of sand inundation, as they are unable to tolerate hypoxia caused by inundation (Marshall & McQuaid 1989). Patellid limpets contribute significantly to the grazer biomass on rocky shores in regions not influenced by sand. The biomass of grazers was significantly lower on mixed shores than on rocky shores, due mainly to the absence of *P. cochlear*.

The dominant space-occupying species on both rock and mixed rock habitats were the black mussels *M. galloprovincialis* and *C. meridionalis.* Since the invasion of *M. galloprovincialis*, which now occupies large proportions of primary rock surface on the west coast of South Africa (Bustamante 1994, Bustamante & Branch 1996a & b, Bustamante *et al.* 1997), *C. meridionalis* now occurs almost exclusively in sanded mixed-shore habitats. In heavily sanded environments, *C. meridionalis*, which is a psammophile, is able to tolerate prevailing conditions better than *M. galloprovincialis*, possibly even out-competing it in these areas. Alternatively, *M. galloprovincialis* may simply be unable to survive in these areas. Thus, sandy environments provide a refuge for *C. meridionalis*. Marshall & McQuaid (1989) have shown that *C. meridionalis* is better able to tolerate hypoxia than the brown mussel *Perna perna* that occurs in the warmer waters of the Eastern Cape and KwaZulu-Natal. Although a direct comparison between the tolerances to hypoxia of *C. meridionalis* and *M. galloprovincialis* has not been made, it is likely that *C. meridionalis* will prove to be more tolerant of hypoxia than *M. galloprovincialis* as it is able to survive better than this species in sanded habitats.

The mean size of *M. galloprovincialis* was smaller on mixed shores than on rocky shores. Of many possible explanations, two are most likely. Firstly, the presence of sand may interfere with the animals' filter-feeding by clogging its filtering apparatus. This would result in a slower growth rate, as filtration efficiency would be reduced (Van Erkom Schurink & Griffiths 1992 & 1993). Secondly *M. galloprovincialis* on mixed shores may be constantly killed by sand inundation. The average age of the *Mytilus* population could thus be younger than those on rocky shores and hence size would be smaller.

Species composition differed between pure sand and mixed sand habitats, even though there was no difference in mean grain size, which is one of the most important factors affecting beach macrofauna (McLachlan 1990, Jaramillo 1994). It has been suggested that the presence of rocks on intertidal sandy substrates interferes with the swash climate and thus effects migrating sandy beach macrofauna, often resulting in the absence of many regular sandy beach species (Brown *et al.* 1991). Mean biomass did not differ between these substrates, however, possibly due to the nature of the sandy beaches that were sampled. With the exception of Muizenberg Corner, the two sandy beaches sampled were extremely short (tens of meters), and shore length is known to affect species composition and biomass (R. Nel pers. comm.). But even though two of the pure sandy beaches used in the comparison were pocket beaches rather than open-ocean beaches, they still contained different species from sites with mixed sand. In particular copepods, *Choromytilus meridionalis* (which must initially have been attached to nearby rocks) and *Talorchestia quadrispinosa* were all more abundant on mixed-sand habitats. Conversely *Donax serra*, *Pontogeloides latipes*, *Gastrosaccus psammodytes* and *Callianassa kraussi* were all more prevalent on pure sandy shores. The most obvious difference between these two groups is their vertical distribution up the shore. Most of the fauna in sand occupied the LOW and LLOW zones. In these zones, the presence of rocks greatly affects the swash climate, which many workers argue is critical to beach macrofauna (McLachlan 1988, McArdle & McLachlan 1992). Higher up the shore, the disturbance from rocks is probably less marked. Scavengers like *Talorchestia*, which is very abundant on mixed sand, may even benefit from the proximity of kelp, which is present on rocky areas in the immediate subtidal area and often stranded as drift nearby.

The effects of sand or rock seem to follow a similar pattern up the shore. In the low shore the effects of the disturbance by sand or rock were more marked, and it was in these zones where the greatest differences between mixed and pure habitats were noted. As was discussed in Chapter 3, zonation patterns are controlled by different factors at different heights up the shore. Lower limits of most species' distribution seem to be limited by competition or predation, while the upper limits seem to be driven by physical factors (Newell 1979, Barnes & Hughes 1982). The high-shore zones on mixed shores are more similar to pure rock and sand than the low-shore zone. The few species of fauna and flora in these high-shore areas are resistant to harsh environmental conditions. The limited communities that can tolerate such conditions make the high-shore zones similar. Similar results have been noted among shores exposed to different wave exposure: low-shore zones were found to differ substantially, yet high-shore samples tended to be more similar (Bustamante *et al.* 1997)

The response of the entire community on rocky habitats to disturbance is probably best demonstrated by the dominance curves in Figure 4.6. In mixed rock the curve is steeper than that for pure rock. This means that a few tolerant species or rapid recolonisers dominate community biomass. On mixed rock and pure rock habitats, it is likely that this pattern is driven by tolerant species, rather than rapidly recolonising species, as few opportunistic recolonisers other than *Ulva* sp. were noted during sampling. In particular, on mixed rocky habitats the shape of the dominance curve was driven by the large biomass of *C. meridionalis*. Mixed sand did not show a similar pattern in dominance (Fig. 4.6). In this case the curve for mixed sand began below and subsequently crossed that of pure sand. The results for sandy habitats were not conclusive therefore, although it is possible that the proximity of rock lends stability to the mixed sand habitat.

In conclusion, it appears that the biota on both sand and rock components of mixed shores are significantly different from those in adjacent areas of pure rock or sand. One factor that has not been discussed in this Chapter is the disturbance effects that rock and sand have on the diversity of macrofauna and flora on the shores in question. This is the topic of Chapter 5, where patterns in diversity are discussed with particular reference to the intermediate disturbance hypothesis.

CHAPTER FIVE: DIVERSITY ON MIXED SHORES: DO MIXED SHORES FIT THE INTERMEDIATE DISTURBANCE HYPOTHESIS?

5.1 Introduction

Diversity is one of the most commonly used univariate measures of community structure. Many authors have used diversity indices to measure the effects of pollution and disturbance by various agents on marine communities (see Washington 1984). Measures of diversity also underpin one of the best-known theories in ecology, namely the *intermediate disturbance hypothesis* (Connell 1978). This hypothesis predicts that communities will have higher diversity under an intermediate intensity or frequency of disturbance (Connell 1978, Abugov 1982, Miller 1982, Petraitis *et al.* 1989).

It is pertinent at this stage to examine what is meant by the term diversity. The Oxford dictionary defines diverse to mean "different in character or quality; not of the same kind". Diversity is often equated with variety and complexity. Margalef (1958) provides a useful definition of ecological or species diversity: a function of the number of species present and the evenness with which the individuals are distributed among these species. Thus, a community that has more species with individuals evenly distributed among them has a greater diversity.

Measures of diversity vary from a simple count of species number (generally referred to as species richness) to calculations based on the relative abundance of each species or taxon. There has been much debate in the literature about which measure of diversity best summarises the community, with different measures weighted towards different aspects of the community (see review by Washington 1984). For instance, some measures, such as species richness are heavily weighted toward rare species, while others, such as Shannon-Wiener's H', are weighted toward the dominant species in the community.

Diversity can also be studied at various scales namely: α-, β- and γ-diversity. α-Diversity is related to the diversity or species richness in small homogeneous areas, β-diversity compares species turnover along an environmental gradient and γ-diversity compares species between different geographical regions.

Many authors suggest that diversity is strongly linked to environmental stability or spatial and temporal heterogeneity of a habitat. Environmental stability can be defined as the physical nature of an environment remaining reasonably constant over time. Previously, studies have examined the effects of various disturbances on the diversity of intertidal shores (e.g. Menge & Sutherland 1976, Lubchenko & Menge 1978, Sousa 1979a & b, Whethey 1985, Menge & Sutherland 1987, Menge & Farrel 1989, Thompson *et al.* 1996, Archambault & Bourget 1996). However, the effects of recurrent sand deposition have relatively seldom been studied (Daly & Mathieson 1977, Taylor & Littler 1982, Littler *et al.* 1983, Dower 1989, McQuaid & Dower 1990).

Sand can occur on shores in various forms. Most obviously, it can constitute the entire substrate such as on a sandy beach. However it also occurs as semi-permanent deposits amongst rocks on mixed shores (Bally *et al.* 1984, McQuaid & Dower 1990, Brown *et al.* 1991). Finally sand can be deposited and removed on a seasonal or even more rapid cycle (Daly & Mathieson 1977, Littler *et al.* 1983, Stewart 1983, Bally *et al.* 1984, Zitha 1994).

In this chapter diversity was compared at two scales, namely between habitats i.e. mixed rock vs. pure rock and mixed sand vs. pure sand (α-diversity), and how diversity changes between whole shores namely mixed shore vs. pure rocky shore and pure sandy beaches (β-diversity). In particular, I examined mixed shores to see how sand deposits affects diversity on rocky substrata and *visa versa.* Special reference is made to the concepts of environmental heterogeneity, environmental stability and disturbance - and the roles that these factors play in determining both α- & β-diversity.

5.2 Methods

Three transects consisting of one $0.1 m^{-2}$ quadrat in each of the four zones identified in Chapters 3 and 4 were surveyed from four habitats (Rock = R, Mixed Rock = MR, Mixed Sand = MS; Sand = S) on three shores Smitswinkel Bay, Dido Valley and Muizenberg Corner. Total species number and species number for each habitat on each shore were obtained by summing all species in all transects for each case. The number of species present was then counted. Before analysis, the mean biomass of each species in each transect was calculated. These data were then used in the calculation of the Shannon-Wiener diversity index H' (eqn 2.1) and Pielou's evenness index J' (eqn 2.2).

The number of species, H' and J' were compared among substrates using a Kruskal-Wallis non-parametric ANOVA (Zar 1984), after Bartlett's test (Zar 1984) showed that variances were not equal. Data were entered as mean biomasses of each species per transect. That gave three replicates at each site on each substrate.

Data from mixed shores were combined. The mean biomass of each species was obtained from all transects, both mixed rock and mixed sand, and these data were then used to calculate total species number, H' and J'. The data presented in Table 5.2 are not means therefore, but are rather values of H' and J' calculated for the whole shore type.

Shannon-Wiener and Pielou's evenness indices were calculated using PRIMER v3.1a (Plymouth Routines in Multivariate Ecological Research, Carr 1994). All other statistics were calculated using STATISTICA (Statsoft Inc., Tulsa, USA 1996).

5.3 Results

A total of 168 species, from all four habitats and all three sites, was recorded in this study. Pure rock had the most species with 113 species recorded. Mixed rock followed with 72 species while mixed sand and pure sand had 21 species each (Fig. 5.1 Kruskal-Wallis, H=27.71, p<0.01). Ninety one species were recorded in total on mixed shores (combining mixed rock and mixed sand). The number of species found at each site in each habitat is presented in Table 5.1.

Table 5.1. The total number of species found on each habitat, at each site (i.e. α-diversity).

	Rock			Mixed Rock			Mixed Sand			Sand		
Site	SB	DV	MC	SB	DV	MC	SB	DV	MC	SB	DV	MC
Sp. #	79	66	54	49	20	48	2	11	18	7	8	15

Pure rock had the highest mean H' value, followed by mixed sand, pure sand and mixed rock (Fig. 5.2; Kruskal-Wallis, H = 13.13, p<0.01). Mean J' was highest on mixed sand, followed by pure sand, pure rock and mixed rock (Fig. 5.3; Kruskal-Wallis, $H = 14.45$, $p<0.01$).

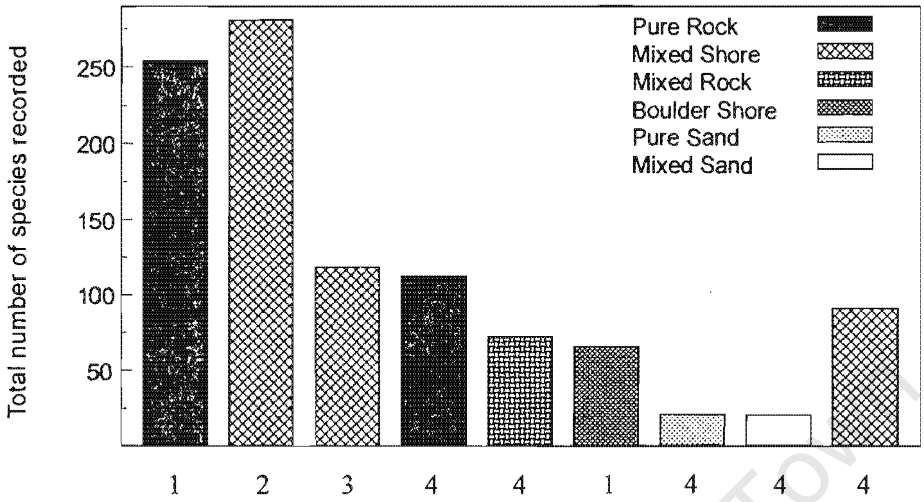

Figure 5.1. Comparison of the total species richness recorded on different shore types by different workers: 1 = McQuaid (1980), 2 = McQuaid & Dower (1990), 3 = Brown *et al.* (1991) and 4 = This study.

When diversity was compared among whole shores, i.e. β-diversity, rocky shores had the highest values of H' followed by sandy shores, while mixed shores had the lowest values recorded. J' was highest on sandy shores and decreased on rocky shores, with mixed shores again having the lowest mean values (Table 5.2).

Table 5.2. Shannon-wiener's H' and Pielou's evenness index J' for the three shore types (i.e. β-diversity) namely rock, sand and mixed shore (combining mixed rock and sand), based on the mean biomass of species in all quadrats sampled.

	Rock	Mixed shore	Sand
H'	2.33	0.997	1.61
J'	0.493	0.217	0.529

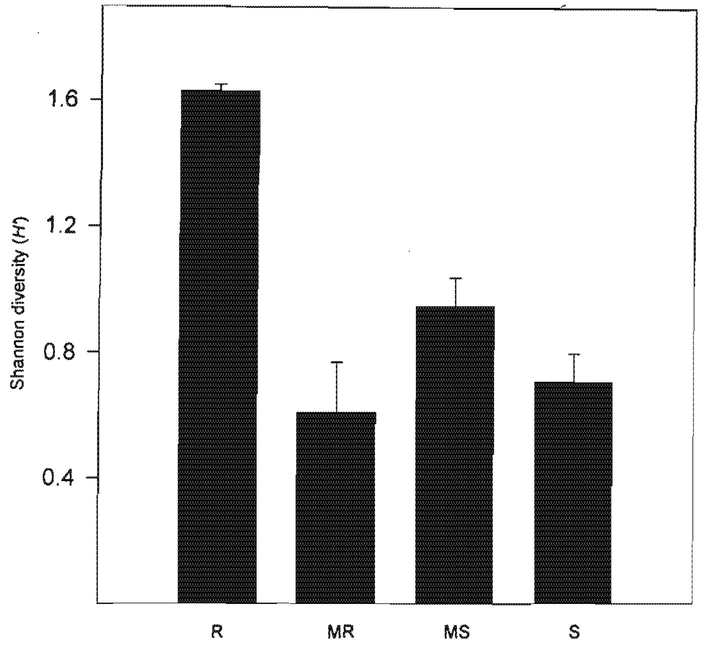

Figure 5.2. Mean ± standard error of Shannon diversity (H') for different habitats, R = pure rock, MR = mixed rock, MS = mixed sand and S = pure sand.

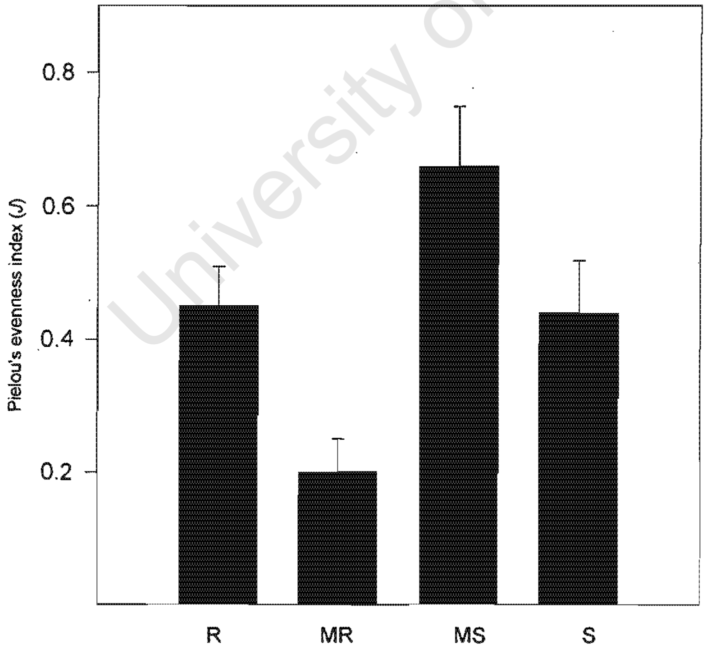

Figure 5.3. Mean ± standard error of Pielou's evenness index for different habitats, R = pure rock, MR = mixed rock, MS = mixed sand and S = pure sand.

5.4 Discussion

Environmental stress is difficult to define and evaluate, especially since the inevitable result of natural selection is to minimise the effects of such stress on an organism. However, a reduction in species numbers and diversity in harsh environments has been well-documented (Barrett & Rosenberg 1978, Brown & McLachlan 1990, Clarke & Warwick 1994, Hawkins *et al.* 1994 as cited by Caraballo *et al.* 1996, Warwick & Clarke 1994). The intermediate disturbance hypothesis proposes that intermediate disturbance, in terms of severity or frequency, increases heterogeneity and patchiness of communities. This allows certain disturbance-tolerant yet competitively inferior species to coexist with other less tolerant but competitively dominant species, hence increasing diversity (Connell 1978).

The results of the present study show that mixed shores in False Bay harbour fewer species than their neighbouring rocky shores. This result was similar for both scales of diversity, i.e. α- and β-diversity. This is contrary to the findings of Dower (1989) and McQuaid & Dower (1990) who suggested that diversity on mixed shores should be high as predicted by the intermediate disturbance hypothesis. Furthermore McQuaid & Dower (1990) suggest that the addition of sand leads to an increase in habitat heterogeneity, and that this was the reason for higher levels of diversity on the mixed shores in their study. As such, sand constitutes an additional temporal and spatial variable on mixed shores, thereby increasing heterogeneity. However their comparisons, were made among samples collected by different workers following different protocols and even among different biogeographical provinces, and are thus not ideal. It was for this reason that I standardised procedures and worked on matched sites, allowing comparisons between adjacent pure rock, pure sand and mixed shores. Comparing the results of my study with those of McQuaid (1980), certain interesting patterns emerge. McQuaid noted that on boulder beaches in False Bay there were far fewer species than on nearby rocky shores. He ascribed this difference to the effects of disturbance and the instability of the environment, as per Sousa (1979a). What is interesting is that the species numbers recorded by me on mixed rock in False Bay are similar to these boulder shores (Fig. 5.1).

Species richness on mixed shores (mixed sand and mixed rock samples combined) surpassed those of the boulder shores reported by McQuaid (1980). This however, was to be expected, as habitat diversity or heterogeneity increases to encompass large patches of rock that tend to function like rocky shores not affected by sand, patches of rock heavily influenced by sand and pure sandy substrate. Increased habitat heterogeneity on mixed shores did not, however, result in a higher diversity when compared to adjacent pure rocky shores (i.e. β-diversity). This is the direct opposite of the pattern recorded by Dower & McQuaid (1990) on the East Coast. One possible explanation is that the level of disturbance by sand on shores in False Bay was severe, placing these shores on the species poor, 'severe side', of the theoretical curve proposed by the intermediate disturbance hypothesis. Thus, despite an increase in habitat heterogeneity, overall species diversity on mixed shores never reached the levels experienced on pure rocky shores.

The effects sand inundation has on individual species may heavily influence this result, however. One of the central ideas of the intermediate disturbance hypothesis is that disturbance events interfere with competitively dominant species, and thus allow less competitive species to survive. In essence, disturbance precludes the development of a species-poor climax community (Connell 1978). On mixed shores in False Bay, sand inundation promoted populations of *Choromytilus meridionalis* (see Chapter 3 and 4), which is a competitively dominant species. Thus the presence of sand promoted, rather than hindered, a competitively dominant space-occupier on these shores. Even in the low-shore zone where disturbance was presumably highest, *C. meridionalis* was prevalent. Here the normally diverse algal fringe was inhibited by sand inundation. Low H' and J' values obtained for mixed rock (α-diversity) and for mixed shores (β-diversity, MR and MS combined) indicated a community that was dominated by one (or few) species. The nearby rocky shores had the highest values of H' recorded in this study, indicating that the biomass on these shores is more evenly distributed across more species. This was clearly illustrated in the ANOSIM and SIMPER procedures (see Chapter 4) where about 50 species contributed significantly to the calculated dissimilarity between samples. The relative shapes of the dominance curves plotted for these shores (Chapter 4, Fig. 4.6) also demonstrated this.

Pure sand and mixed sand habitats had similar numbers of species, which was surprising considering the results obtained in Chapter 4. In Chapter 4 these habitats were clearly separated on cluster and MDS plots, indicating that species composition was different in these two substrates. Biomass was, however, lower on mixed sand than on adjacent sandy beaches. At first glance it appeared that rocky outcrops did not disturb sandy beach macrofauna as severely as had been suggested by Stephen (1929) and Brown *et al.* (1991). However, many species sampled in mixed sand were probably associated with the nearby rocks – which would account for the dissimilarity in community composition. The presence of rocks seemed to interfere more with species that occupied the low-shore surf zone than those in the high shore. For example, no *Bullia digitalis* or *Donax serra* were obtained on mixed shores although they were encountered on sandy beaches nearby. Both these species rely on the swash climate: *B.*

digitalis scavenges, surfing along the beach in search of food using the swash while *D. serra* filters particles from the passing water. The swash climate is possibly the most important general determinant of sandy beach macrofauna communities, as advocated in the *swash exclusion hypothesis* (McArdle & McLachlan 1991 & 1992, Jaramillo & McLachlan 1993, Masselink & Short 1993, McLachlan *et al.* 1993, Giménez & Yannicelli 1997). Disruption of the smooth laminar flow of the swash may influence both these species, interfering with the surfing of *B. digitalis* and the filter feeding of *D. serra* (Brown *et al.* 1989, Brown & McLachlan 1990 and R. Nel unpublished data) and could explain their absence from mixed shores.

Sandy beaches are extremely dynamic environments, often with large changes occurring to the nature of the beach over short time periods. It is thought that this harsh environment results in the low diversity of macrofauna on sandy beaches. Rocky outcrops within this environment interfere with certain species, but probably do not cause a disturbance of any great significance compared with the prevailing harsh conditions. Rocks do affect the sand that surrounds them by preventing certain 'typical' sandy beach species from establishing themselves in this mixed sand habitat, and by promoting other species (such as *Choromytilus meridionalis* and *Exosphaeroma truncatitelson*) that do not normally occur on open sandy beaches.

The effects of sand inundation did not promote an increase in species richness or diversity on mixed shores. This agrees with the results of Seapy & Littler (1982) from California, Engeldow & Bolton (1994) form Namibia and Brown *et al.* (1991) from mixed shores in False Bay, but contradicts those of Littler et al. (1983), Dower (1989), McQuaid & Dower (1990) and Airoldi & Cinelli (1997). Brown *et al.* (1991) questioned the validity of the shores used in the comparisons of Dower (1989) and McQuaid & Dower (1990), suggesting that if more appropriate shores (i.e. from the same biogeographical province and similar physical conditions) were used in their comparisons they would find different patterns. The present study indicates that the effect of sand on dominant competitors needs to be considered. In this study, *C. meridionalis*, a dominant competitor for primary space is tolerant of sand inundation, whereas none of the tolerant species in the studies on the East Coast seemed to be dominant space occupiers. This could be one of the most important differences between shores in False Bay and those on the East Coast. Furthermore, this difference could explain why McQuaid & Dower's (1990) results do not agree with neither my nor previous studies in the Western Cape.

The results of this work highlight that caution needs to be exercised when examining general hypotheses such as the intermediate disturbance hypothesis. Although this hypothesis appears to apply generally to the study of disturbances, cognisance should be taken of the effect of different disturbance situations. In this study for instance, disturbance on mixed shores does not reduce populations of the competitively dominant species and hence does not make free space available for new colonists. Moreover, although the presence of sand did increase habitat heterogeneity on a spatial and temporal scale, this did not result in an increased diversity when compared to pure rocky shores. As a general hypothesis, I would predict that under a regime of disturbance, species diversity will decrease if a competitively dominant species is either a) not affected by or b) actively promoted by the disturbance factor.

CHAPTER SIX: SYNTHESIS

6.1 General Discussion

The Community structure of mixed shores in False Bay differed from nearby rocky shores and sandy beaches. The two distinct habitats that constitute mixed shores in the region, namely mixed rock and mixed sand were also found to differ from their nearby pure habitat types. These results were similar to those obtained by other workers on mixed shores in the region (Brown 1989, Brown *et al.* 1991), nationally (Bally *et al.* 1984, Dower 1989, McQuaid & Dower 1990) and internationally (Daly & Mathieson 1977, Devinny & Volse 1978, Taylor & Littler 1982, Littler *et al.* 1983, D'Antonio 1986, Engeldow & Bolton 1994), although certain unique characteristics of the shores investigated in this study were observed.

Filter feeders dominated the biomass on mixed shores (Chapter 3). Two species of bivalves, the black mussel *Choromytilus meridionalis* and the Mediterranean mussel *Mytilus galloprovincialis* were responsible for this. *Choromytilus meridionalis* is tolerant of sand inundation and survives, indeed thrives, in the conditions found on these mixed shores. Between them these two species dominated the primary rock surface and it is hypothesised that it is the ability of *C. meridionalis* to withstand inundation that largely results in the different community structure and in particular the low diversity found on these mixed shores.

The inability of patellid limpets to withstand sand inundation also led to differences in intertidal zonation patterns. In particular *Patella cochlear* was absent from mixed shores and the cochlear zone was thus in turn also absent. This zone was replaced on mixed shores by a mussel-dominated band. The sublittoral algal fringe was also poorly represented on mixed shores, once again being replaced by mussels (Chapter 3).

This pattern was confirmed in comparisons of the biomass of primary producers and grazers on mixed rock and pure rock habitats. The biomass of these two functional groups was lower on mixed rock than on nearby pure rock, while the biomass of filter feeders on mixed rock was similar to, or greater than those found on pure rock (Chapter 4).

Although less marked, differences were also noted between mixed sand and pure sand habitats. Most notably, the absence of two characteristic sandy-beach molluscs, namely *Bullia digitalis* and *Donax serra*, was ascribed to the disruption caused to the swash climate by emergent rocks (Chapter 4).

High-shore communities on mixed rock and pure rock, and on mixed sand and pure sand were more similar to each other than low-shore communities. These results, lend further weight to the arguments of Bustamante *et al.* (1997), who suggest that relative to high-shore communities, those in the low-shore are more susceptible to prevailing physical conditions - in their case wave exposure, and in my study, sand inundation (Chapter 4).

The scales of diversity examined in this thesis showed that mixed rock (α-diversity) and mixed shores as a whole (β-diversity) were less diverse, having lower species richness than nearby pure-rock habitats and whole rocky shores (Chapter 5). This was not the case with mixed sand and pure sand habitats, which had equal species richness, although mixed shores as a whole had far greater species richness than sandy beaches.

This was to be expected however as the inclusion of mixed-rock species far outweighed those from sand.

These results, in conjunction with the recorded patterns of dominance (Chapter 4), suggest that mixed rock was severely disturbed by the frequent inundation of sand. Furthermore it is likely that this disturbance occurs with sufficient severity or frequency to depress diversity in this habitat. Hence, mixed rock can be plotted on the severe side of the theoretical curve proposed by the intermediate disturbance hypothesis (Fig. 6.1). This was similar to the results of Seapy & littler (1982) who found that the environmental conditions of their study sites in California, subject to sand inundation and aerial exposure, exceeded the optimal intermediate level of disturbance described in the intermediate disturbance hypothesis. Engeldow & Bolton (1994) have also recorded lower diversity on intertidal rocky communities in southern Namibia, which are subject to sand inundation and wave exposure.

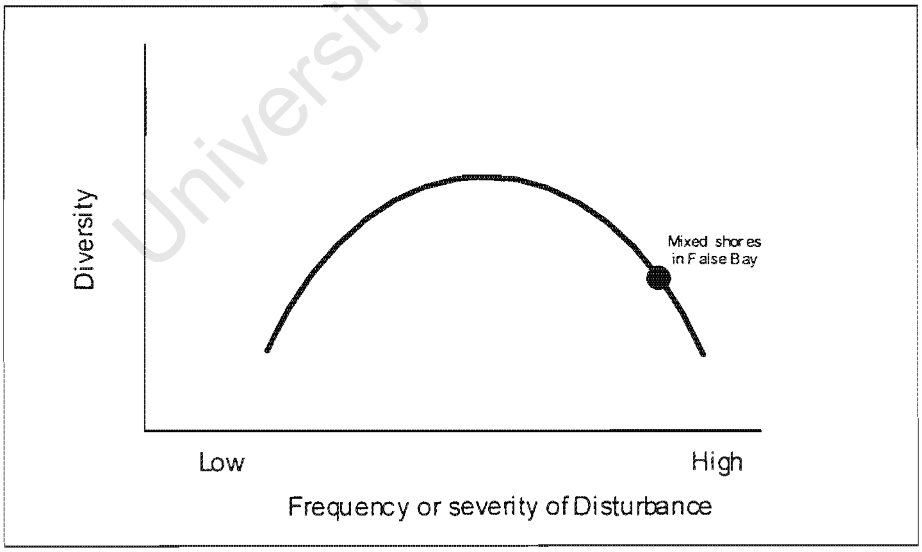

Figure 6.1. Schematic representation of the intermediate disturbance hypothesis (Connell 1978) placing mixed shores in False Bay on the severe side of the optimum disturbance required for maximum diversity.

Results were less clear for mixed sand, and the possibility that emergent rock lends stability to this habitat should not be discounted. Indeed this needs to be examined further as it has been suggested both in this thesis and by other workers (Bally *et al.* 1984, Brown *et al.* 1991) that emergent rock disrupts the swash climate thereby influencing sand-dwelling macrofaunal species.

At a larger scale (β-diversity) the increase in habitat heterogeneity on mixed shores (encompassing both mixed rock and mixed sand) did increase diversity relative to that in these individual habitats. However, this diversity was still lower than the diversity of nearby pure rocky shores. This was true even though the comparison of diversity was conservative in that diversity on mixed shores was calculated by averaging over six transects, whereas rocky shore diversity was based on only three transects. These results are contrary to those of many authors (Fig. 6.2 Taylor & Littler 1982, Littler *et al.* 1983, McQuaid & Dower 1990, Zitha 1994, Airoldi & Cinelli 1997).

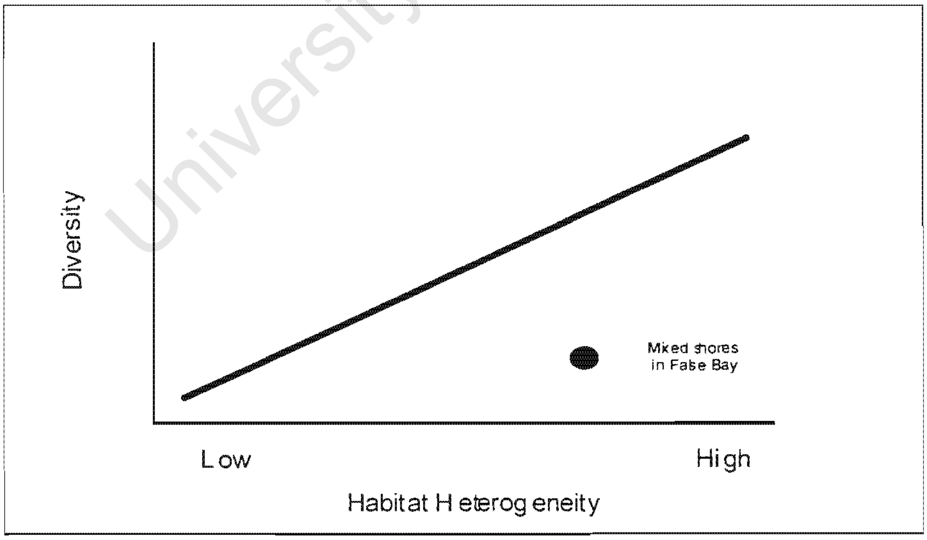

Figure 6.2. Schematic reprensentaion of the predicted increase in diversity with increasing habitat heterogeneity, placing mixed shores in False Bay below the predicted level.

McQuaid & Dower (1990) found that increased habitat heterogeneity increased diversity on mixed shores on the East Coast of South Africa. Unlike these workers, the comparisons in this study were based on adjacent shores, which were influenced by identical regimes of wave action and sea temperature, and upon a standardised sampling protocol. It is suggested, however, that the depressed diversity recorded on mixed shores in False Bay is primarily due to the response of *Choromytilus meridionalis* (which is also a dominant competitor) to sand inundation. It is proposed that the ability of this species to monopolise space on mixed shores following sand inundation leads to lower diversity. Hence a general prediction is put forward that diversity will be lower following a disturbance should a dominant competitor be either: a) tolerant of the disturbance or b) able to recolonise the habitat more rapidly than other less able competitors.

In sum, there are three central issues influencing the diversity of mixed versus pure shores: (1) the magnitude and frequency of disturbances imposed by sand on rocky shores or rock on sandy beaches; (2) the degree to which this alters habitat heterogeneity spatially and temporally; and (3) whether the disturbance promotes or inhibits competitive dominants.

6.2 The way forward

In keeping with most postgraduate studies, this thesis has probably raised more questions than solutions. Further work needs to be directed at both ecological and physiological levels towards mixed shores. Why *Choromytilus meridionalis* is better able to endure sand inundation than *Mytilus galloprovincialis* remains unanswered. However it is predicted that *C. meridionalis* has probably evolved superior anaerobic pathways in order to deal with the anoxia associated with inundation. Furthermore, the relevant competitive abilities of these two species has remained untested, although many assume that *M. galloprovincialis* has the ability to out-compete *C. meridionalis.* Further work is also required on the fragmented nature of the habitat, possibly examining emergent rocks with island biogeography theory in mind. It is likely that the size and height above sand of these 'islands' plays a role in determining the eventual community structure on mixed shores. The immediate subtidal areas of mixed shores have also received little attention, although many fishers claim that catches are often better in these areas (Lechanteur pers. comm. Clarke pers. comm.). It is likely that recurrent sand deposition constantly crates space for new recruits, which are often the preferred prey of various fish species.

6.3 Conclusion

This study highlights that in any research on the effects of disturbances on intertidal biota, cognisance should be given to species-specific responses. It shows that the abilities of a single disturbance-resistant species may have important ramifications for the applicability of general models, for example the intermediate disturbance hypothesis and the habitat heterogeneity hypothesis. This thesis contributes therefore, to our understanding of the role disturbance plays in determining intertidal communities, in that it highlights the consequences of the presence of a disturbance-resistant, dominant competitor – *Choromytilus meridionalis.*

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APPENDIX 1

Appendix 1. Mean biomass (P = mass < 0.05 g.m^{-2}) of all species sampled at each site and on/in each habitat (R = pure rock, MR = mixed rock, MS = mixed sand, S = pure sand). Also shown are the class (a = Algae, c = Crustacea, e = Echinodermata, fw = unsegmented worms, m = Mollusca, n = Cnidaria, t = Ascidiacea) and trophic group (C = carnivore, D = detritivore, F = filter feeder, H = herbivore, P = primary producer, S = scavenger) to which each species belongs.

Site:			Muizenberg Corner				Dido Valley				Smitswinkel Bay			
Habitat:	Class	Group	R	MR	MS	S	R	MR	MS	S	R	MR	MS	S
Acanthochitona garnoti	m	H	3.2	13.6	0.0	0.0	1.6	0.0	0.0	0.0	1.3	0.0	0.0	0.0
Amaryllis macropthalma	c	D	0.0	0.6	0.0	0.0	P	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Amphiroa ephedraea	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	172.2	0.0	0.0
Ampelisca excavata	c	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Amphilochidae	c	D	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anatanais gracilis	c	C	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arabella iricolor	w	C	0.9	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Arenicola loveni	w	D	0.0	0.0	0.9	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0
Aristothamnion collabens	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0
Aulacomya ater	m	F	P	7.0	0.0	0.0	36.8	0.0	0.0	0.0	27.6	0.4	0.0	0.0
Bifurcaria brassicaeformis	a	P	0.0	0.0	0.0	0.0	319.3	0.0	0.0	0.0	122.9	0.0	0.0	0.0
Bullia digitalis	m	S	0.0	0.0	P	9.6	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0
Bunodactis reynaudi	n	C	26.2	33.0	0.0	0.0	12.5	63.0	0.0	0.0	1.5	0.7	0.0	0.0
Bunodosoma capensis	n	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
Burnupena catarrhacta	m	S	27.0	21.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.7	0.0	0.0
Burnupena cincta	m	S	6.3	168.4	0.0	0.0	15.9	0.0	0.0	0.0	1.9	0.0	0.0	0.0
Burnupena lagenaria	m	S	0.0	368.6	0.0	0.0	P	0.0	0.0	0.0	1.4	1.1	0.0	0.0
Callianassa kraussi	c	D	0.0	0.0	P	2.7	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Capitella capitata	w	D	0.0	0.0	1.9	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cardita variegata	m	F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0
Carpoblepharis flaccida	a	P	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Caulacanthus ustulatus	a	P	76.7	54.8	0.0	0.0	3.0	0.0	0.0	0.0	0.4	2.5	0.0	0.0
Centroceras clavulatum	a	P	27.7	P	0.0	0.0	P	0.0	0.0	0.0	1.3	0.0	0.0	0.0
Ceramium sp.	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	26.5	0.0	0.0
Cerebratulus fuscus	n	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0
Chaetopleura papilio	m	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Champia compressa	a	P	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chiton tulipa	m	H	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Choromytilus meridionalis	m	F	4012.5	27172.8	2.5	0.0	1112.5	467.1	0.1	0.0	0.0	860.4	13.0	0.0
Cirolana cranchii	c	C	0.0	2.5	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0
Cirolana venusticauda	c	C	2.2	11.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.0	0.0	0.0
Cladophora capensis	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.1	0.0	0.0
Copepoda sp.	c	?	0.0	0.0	3.9	P	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0
Corallina sp.	a	P	0.0	0.0	0.0	0.0	10.9	0.0	0.0	0.0	8.1	1.7	0.0	0.0
Coropiidae sp.	c	?	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crepidula porcellana	m	H	0.0	1.2	0.0	0.0	2.5	0.0	0.0	0.0	2.8	0.0	0.0	0.0
Chthamalus dentatus	c	F	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Cymodocella sublevis	c	S	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.2	0.0	0.0
Dendropoma corallinaceus	m	F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	385.8	0.0	0.0	0.0
Donax serra	m	F	0.0	0.0	0.0	22.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Donax sordidus	m	F	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dynamenella australioides	c	S	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dynamenella huttoni	c	S	0.3	1.6	0.0	0.0	1.9	0.0	0.0	0.0	0.4	0.1	0.0	0.0
Ecklonia maxima	a	P	0.0	0.0	0.0	0.0	243.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Elasmopus japonicus	c	F	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	P	0.0	0.0	0.0
Epidiopatra gilchristi	w	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0

Site:			Muizenberg Corner				Dido Valley				Smitswinkel Bay			
Habitat:	Class	Group	R	MR	MS	S	R	MR	MS	S	R	MR	MS	S
Epymenia capensis	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.9	0.0	0.0
Eulalia trilineata	w	O	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Eurydice natalensis	c	O	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurydice barnardi	c	O	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurydice kensleyi	c	O	0.0	0.0	6.7	0.1	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.2
Exosphaeroma kraussi	c	S	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Exosphaeroma pallidum	c	S	0.0	2.1	0.0	0.0	0.0	P	0.0	0.0	0.0	0.5	0.0	0.0
Exosphaeroma truncatitelson	c	S	0.0	4.9	0.0	0.0	P	2.9	0.0	P	0.0	1.2	0.0	0.0
Fissurella mutabilis	m	H	0.9	0.0	0.0	0.0	2.6	0.0	0.0	0.0	2.5	0.0	0.0	0.0
Gastrosaccus psammodytes	c	D	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8
Gelidium pristoides	a	P	119.6	0.0	0.0	0.0	74.0	0.0	0.0	0.0	45.3	0.0	0.0	0.0
Gibbula cicer	m	H	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gibbula zonata	m	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Gigartina radula	a	P	100.5	235.3	0.0	0.0	17.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gigartina scutellata	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	266.3	0.0	0.0
Glycera sp.	w	C	0.0	0.0	0.2	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gnathia sp.	c	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Golfingia capensis	w	D	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gregariella petagnae	m	F	0.1	0.0	0.0	0.0	0.4	0.6	0.0	0.0	0.1	5.6	0.0	0.0
Gunnarea capensis	w	F	3.1	0.0	0.0	0.0	0.8	0.0	0.0	0.0	4.6	0.0	0.0	0.0
Gymnogongrus complicatus	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.8	0.0	0.0
Gymnogongrous polycladus	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	481.8	0.0	0.0
Haliotus spadicea	m	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	32.9	0.0	0.0	0.0
Helcion dunkeri	m	H	P	1.2	0.0	0.0	P	0.0	0.0	0.0	P	1.5	0.0	0.0
Helcion pectunculus	m	H	1.2	15.9	0.0	0.0	0.3	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Helcion pruinosus	m	H	0.5	10.8	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Hiatella artica	m	F	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Hildenbrandia rubra	a	P	0.0	0.1	0.0	0.0	0.0	1.4	0.0	0.0	0.0	67.1	0.0	0.0
Hyale grandicornis	c	H	0.4	0.1	0.0	0.0	0.1	0.0	0.0	0.0	P	0.8	0.0	0.0
Hyale sp.	c	H	P	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Ianiropsis palpalis	c	S	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Indishchnopus capenis	c	D	0.0	0.0	P	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Ischnochiton bergoti	m	H	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ischyrocerus carinatus	c	D	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0
Jania sp.	a	P	1.1	0.0	0.0	0.0	15.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lasaea adansoni turtoni	m	F	0.0	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.1	P	0.0	0.0
Laurencia sp.	a	P	0.0	0.0	0.0	0.0	101.5	0.0	0.0	0.0	12.5	0.0	0.0	0.0
Lepidonotus semitectus clava	w	C	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Ligia dilatata	a	P	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris hartmanni	w	C	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrineris tetraura	w	C	0.0	4.3	P	2.2	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Lysianassa ceratina	c	D	0.1	P	0.0	0.0	0.1	0.0	0.0	0.0	0.1	P	0.0	0.0
Lysidice natalensis	c	D	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.8	0.0	0.0	0.0
Membranipora membranacea	b	F	0.0	P	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0
Mandibulophoxus latipes	c	D	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9
Marphysa depressa	w	C	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mytilus galloprovincialis	m	F	60.0	214.6	0.0	0.0	308.4	6536.6	0.0	0.0	2076.2	3268.2	0.0	0.0
Naineris laevigata	w	D	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	1.8	0.0	0.0
Nassarius capensis	m	S	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Natica tecta	m	C	0.0	20.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematodes			0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0
Nephtys sp.	w	O	0.0	P	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nermetea sp.	n	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0
Nicolea macrobranchia	w	D	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nicolea venusticauda	w	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Nodilittorina Africana knys.	m	H	1.9	0.2	0.0	0.0	5.9	20.1	0.0	0.0	11.8	59.5	0.0	0.0
Nothogenia erinacea	a	P	0.0	95.5	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Notomastus latericeus	w	D	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomegabalanus algicola	c	F	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Notoplana patellarum	fw	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0

Site:			Muizenberg Corner				Dido Valley				Smitswinkel Bay			
Habitat:	Class	Group	R	MR	MS	S	R	MR	MS	S	R	MR	MS	S
Nucella cingulata	m	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Nucella dubia	m	C	1.5	1.3	0.0	0.0	0.2	0.0	0.0	0.0	0.9	5.4	0.0	0.0
Octomeris angulosa	c	F	0.0	0.0	0.0	0.0	229.1	0.0	0.0	0.0	12.6	0.0	0.0	0.0
Oligochaete sp.			0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ophiactus carnea	e	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Ophionereis dubia	e	D	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orbinia anrgapequensis	w	D	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0
Oxystele impervia	m	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Oxystele sinensis	m	H	0.0	0.0	0.0	0.0	4.3	0.0	0.0	0.0	45.2	0.0	0.0	0.0
Oxystele tigrina	m	H	0.5	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxystele variegata	m	H	1.1	0.0	0.0	0.0	9.5	0.0	0.0	0.0	20.3	5.6	0.0	0.0
Paramoera capensis	c	S	P	2.9	0.0	0.0	0.1	0.0	0.0	0.0	P	P	0.0	0.0
Parisocladus perforatus	c	S	P	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	P	0.0	0.0
Parisocladus stimpsoni	c	S	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Patella argenvillei	m	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.0	0.0	0.0	0.0
Patella barbara	m	H	0.0	0.0	0.0	0.0	11.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Patella cochlear	m	H	441.0	0.0	0.0	0.0	236.9	0.0	0.0	0.0	352.7	0.0	0.0	0.0
Patella granatina	m	H	31.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	13.3	65.1	0.0	0.0
Patella granularis	m	H	17.2	54.5	0.0	0.0	98.5	0.0	0.0	0.0	42.6	105.4	0.0	0.0
Patella longicosta	m	H	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0
Patella miniata	m	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.0	0.0	0.0	0.0
Patella oculus	m	H	0.0	0.0	0.0	0.0	16.1	0.0	0.0	0.0	32.5	0.0	0.0	0.0
Patiriella exigua	e	H	0.2	1.0	0.0	0.0	0.6	0.0	0.0	0.0	2.9	0.0	0.0	0.0
Perinereis capensis	w	O	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Perinereis falsovariegata	w	O	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Perioculodus longimanus	c	D	0.0	0.0	0.0	P	0.0	0.0	0.0	P	0.0	0.0	0.0	P
Perna perna	m	F	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0
Petalonia debilis	a	P	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pharyngeovalata natalensis	w	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Phoxocephalidae sp.	c	D	0.0	0.0	P	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	P
Plagusia chabrus	c	S	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.9	0.0	0.0	0.0
Platynereis dumerilii	w	H	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Plocamium cornutum	a	P	0.0	0.0	0.0	0.0	104.0	0.0	0.0	0.0	54.1	0.0	0.0	0.0
Plocamium rigidum	a	P	12.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polyopes constrictus	a	P	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.6	0.0	0.0
Polysiphonia corymbifera	a	P	2.4	8.7	0.0	0.0	0.0	4.4	0.0	0.0	0.0	1.6	0.0	0.0
Pontogeloides latipes	c	S	0.0	0.0	7.0	0.0	0.0	0.0	P	2.1	0.0	0.0	0.0	0.1
Porphyra capensis	a	P	8.2	0.0	0.0	0.0	17.2	0.0	0.0	0.0	0.0	72.1	0.0	0.0
Pseudonereis variegata	w	O	2.5	0.0	0.0	0.0	18.4	0.0	0.0	0.0	22.3	0.5	0.0	0.0
Pyura stolonifera	t	F	0.0	0.0	0.0	0.0	70.5	0.0	0.0	0.0	296.7	0.0	0.0	0.0
Scololepis squamata	w	D	0.0	0.0	P	P	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Scoloplos sp.	w	D	0.0	0.0	0.0	P	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0
Scoloplos armiger	w	D	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scoloplos johnstonei	w	D	0.0	0.4	0.0	0.0	0.0	P	0.0	0.0	0.0	0.3	0.0	0.0
Siphonaria aspera	m	H	0.0	1.0	0.0	0.0	0.0	7.2	0.0	0.0	0.0	10.1	0.0	0.0
Siphonaria capensis	m	H	1.0	0.0	0.0	0.0	4.4	0.3	0.0	0.0	0.6	21.2	0.0	0.0
Siphonaria concinna	m	H	1.7	1.5	0.0	0.0	1.3	0.0	0.0	0.0	0.2	1.8	0.0	0.0
Sphaeramene polytylotos	c	S	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spionidae sp.	w	D	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Splachnidium rugosum	a	P	0.0	0.0	0.0	0.0	9.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hymeniacedon sp.		F	0.1	0.0	0.0	0.0	51.6	0.0	0.0	0.0	37.2	0.0	0.0	0.0
Streblocladia sp.	a	P	8.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syllis spongicola	w	C	0.0	P	0.0	0.0	P	1.0	0.0	0.0	0.0	P	0.0	0.0
Talorchestia quadrispinosa	c	S	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.0	0.1
Tanystylum brevipes	sp	C	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tayloriella tenebrosa	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0
Tellina gilchristi	m	F	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tellina ponsonbi	m	F	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0
Telmatogeton larvae	i	H	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0
Tetraclita serrata	c	F	61.8	49.3	0.0	0.0	361.2	0.0	0.0	0.0	2.7	0.0	0.0	0.0

Site:	Class	Group	Muizenberg Corner				Dido Valley				Smitswinkel Bay			
Habitat:			R	MR	MS	S	R	MR	MS	S	R	MR	MS	S
Thais castanea	m	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	0.0	0.0	0.0
Thamnophyllis discigera	a	P	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.8	0.0	0.0
Timarete capensis	w	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	P	2.6	0.0	0.0
Timarete tentaculata	w	D	5.5	P	0.0	0.0	0.1	P	0.0	0.0	0.3	0.0	0.0	0.0
Tricolia capensis	m	H	17.6	89.7	0.0	0.0	0.3	1.4	0.0	0.0	P	0.4	0.0	0.0
Ulva sp.	a	P	56.4	91.0	0.0	0.0	46.7	0.7	0.0	0.0	0.1	0.1	0.0	0.0
Unknown Biavalve A	m	F	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.8	0.0	0.0
Urothoe pinnata	c	D	0.0	0.0	0.0	P	0.0	0.0	P	0.0	0.0	0.0	0.0	0.0
Venerupis corrugatus	m	F	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0