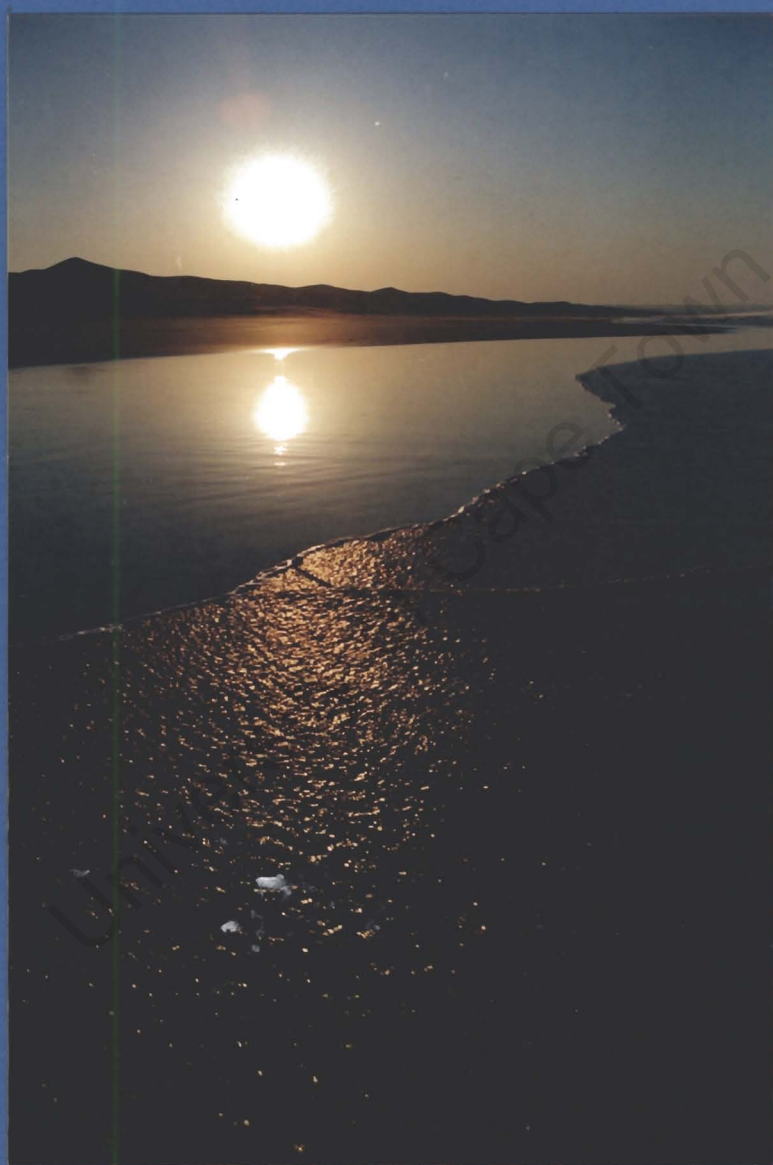


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PHYSICAL AND BIOLOGICAL FACTORS STRUCTURING SANDY BEACH MACROFAUNA COMMUNITIES

By

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requirements for the degree
Doctor of Philosophy

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 DECLARATION...

*I hereby declare that this thesis is my own unaided work.
It reports results of original research I carried out in the
Zoology Department, University of Cape Town.
This work has not been submitted for a degree
at any other university.*

Signed by candidate

Petronella Nel
1 September 2000

ABSTRACT

Previous sandy beach research described beach macrofaunal communities according to the *swash exclusion hypothesis* (SEH). This hypothesis stated that more species are present on fine grained, flat dissipative beaches due to a more benign swash climate. It suggested that, as beach morphodynamics change to reflective conditions, which is experienced on coarse, steep beaches, few species can survive; these beaches are therefore characterised by lower macrofaunal diversities, abundance and biomass. Furthermore, little proof has been obtained of biological interactions such as competition or predation, and beaches have been described as physically controlled environments. The aim of this investigation was therefore to redefine the SEH in more specific terms, preferably into a form that is experimentally testable, and to find evidence of biological interactions that could be important enough to modify/explain population or community structures. Furthermore, the study aimed to find experimental procedures to serve as alternatives to the previously correlative type approach.

Sampling 27 microtidal beaches along the southern African coastline tested the first aim. These microtidal beaches varied from reflective to dissipative, although most were in an intermediate state. The macrofauna was sampled using a triplicate transect design, of 10 or 11 stations between the low tide swash mark and the driftline. The physical factors measured were the parameters required by compound indices: beach morphodynamic state (Ω), relative tide range (RTR), the beach state index (BSI) and exposure (EXP). The biota was only significantly correlated to the conservative parameters, grain size (ϕ) and slope. The number of species also varied with biogeographical province and beach morphodynamic state. Multivariate analysis was used to identify the number of faunal zones. The number of zones was related to beach state and therefore also species richness. An increase in the number of species resulted in more faunal zones being present. The beaches sampled were considered as an adequate sample conforming to the general *swash exclusion hypothesis*.

During the transect sampling 26 swash and beach factors were measured at low tide. Many of these parameters co-vary, but the project aimed to elucidate the aspects of the co-varying factors to which beach macrofauna specifically respond. The factors that populations and the communities respond to are different. Grain size, swash period and frequency were identified as factors controlling macrofaunal communities, whereas individual populations responded to parameters related to their particular life style. The SEH was subsequently redefined.

Predictions of the *redefined swash exclusion hypothesis* (RSEH) was subsequently tested on three cold-temperate beaches. Fifty live and 50 dead beach clams (*Donax serra*) were placed on the effluent line of a steep gradient beach, two hours before high tide. This was repeated concurrently on a part of the same beach with a moderate gradient, and on a part with a low gradient. The same swash parameters were measured as for the 27 beaches sampled. The relative distribution of the clams was then correlated to the varying swash parameters. Passive animals 'reacted' as predicted by the RSEH, whereas live animals reacted to the swash parameters, but their response was better correlated to beach slope and effluent line crossings. It is therefore expected that the size, migratory patterns, and possible acoustic responses may be responsible for the deviation from the prediction.

The latter part of the thesis was aimed at finding evidence of biological interactions on beaches, after reviewing the possible interactions.

Competition for space was evaluated by testing for changes in the burial time of the beach clam, *D. serra*, of different sizes (< 15 mm, 15 - 55 mm and > 55 mm) into sediments containing different background densities (0, 15 and 30) of the same species. Burial times were not significantly different from the control, but differed between treatments. The slowest burial times were obtained for each size group burrowing onto sediments containing its own size, and fastest when smaller individuals were present in the sand. It is therefore concluded that significant changes in burial time should not occur unless *in situ* densities exceed 30 *D. serra* per 0.1m². This threshold density is also dependent on clam size, and individuals within the same size class (> 15 mm) are more likely to compete for surface space.

The possibility of interactions between adults and juveniles was also investigated over a longer time period. Nylon mesh cages, which allow emigration of juveniles clams but not adult clams, were placed in the intertidal. Stocking densities of adults were 0, 10, or 20 (or more) and 30 juveniles were allowed to burrow into sediment within the cages. After 24 hours, the cages were excavated to obtain the number of juveniles left within. The numbers of juveniles recovered were generally unrelated to adult stocking densities and appeared to have largely been determined by physical factors. It is also expected that the stocking densities of adults were too low and only once the *in situ* densities are higher than 30 per 0.1m² would there be any interference interaction.

This project further investigated interspecific interactions between cirrhitid isopods in the laboratory. This was conducted by obtaining the grain size preferences of three species in a range of grain sizes from 90 µm to 1000 µm. The isopods tested were *Excirolana natalensis*, *Eurydice kensleyi*, and *Pontogeloides latipes*. *E. natalensis* preferred coarse sand, *E. kensleyi* was catholic, occurring in almost equal frequency in all grain sizes, whereas *P. latipes* preferred medium to coarse sand. When the species were combined, two or more at a time, the preferences changed for all species. Incorporating macroscale distribution, it became apparent that physical factors seem to structure longshore distribution and abundance, whereas across-shore distribution is influenced by interference competition. *E. natalensis*, which is found higher on the shore than the other two species, seems to be the stronger competitor and is mostly limited by physical parameters. *E. kensleyi* frequents the bottom of the shore and has the highest abundance when *E. natalensis* is absent. *P. latipes*, which is found on the mid-shore, may be forced/influenced to occur between the other two species. It never reached abundance values close to those of the other two species.

The third aim of this study was to evaluate some of the current methodology in sandy beach research. Experimental techniques in this study have been applied with relative success. A series of swash parameters was constructed which describes the swash climate at low tide relatively accurately. Moreover, some of these measurements can be (and should be) included in studies evaluating the influence of swash factors on beach macrofauna. Techniques to test zonation and behavioural responses with respect to burial times and grain size preferences were applied, as well as caging techniques. Direct responses of animals were measured. These techniques can be applied to other studies occupied by other species, under different physical conditions.

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CHAPTER 1

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1.1 INTRODUCTION

Exposed sandy beaches can be defined as sediment deposits reworked by waves. The edges of this system are bound by the drift line which serves as the terrestrial margin and is formed by debris deposited by the highest wave run-up, while the point behind the surf zone where the waves do not exert any influence over the alluvium serves as the marine margin (Short, 1983). Sandy beach researchers have been investigating the interplay between these physical processes and biological communities on the shoreline, trying to understand the critical forces that are at work in shaping the intertidal soft-sediment fauna.

Oceanic beaches have often been referred to as marine deserts because of the apparent absence of intertidal life. However, beach research in the last few decades has demonstrated that, although beaches often appear to be barren, they harbour very distinct macrofaunal assemblages that occur nowhere else on earth. Moreover, the animals living on sandy beaches are behaviourally well adapted to cope with the rigors of the environment and they utilise the three-dimensionality of the system.

Intertidal sandy substrates vary widely in nature, ranging from low energy sand flats in estuarine mouths or tidal flats, to small pocket beaches or mixed shores, or to wide macrotidal beaches that stretch for kilometres and face into the oncoming swell. All these environments have distinct macrofaunal communities and it is therefore important to define the exact nature of the environment which this study is dealing with. This study aims to further our understanding of open ocean beaches formed by the interaction of waves, sand and tides.

1.2 THE PHYSICAL ENVIRONMENT

A sandy beach can be defined as the product of waves interacting with a sandy bed at the shoreline (Short and Wright, 1983). The interaction/influence of energy stretches across the nearshore area, through the surf zone¹ and to the landward limits of the swash zone² (Fig 1.1). The nature of these zones, but especially of the swash³ zone, is dependent on two parameters: firstly the wave energy (which controls the depth of the wave base), and secondly the sediment grain size, which influences sediment transport (Short and Wright, 1983). Using the interaction of these parameters, beaches are classified into low, moderate and high wave energy environments, each with very specific beach face characteristics. Wright *et al.* (1982b) combined the wave parameters and sediment characteristics into a dimensionless index to assist in the classification of beaches. The dimensionless fall velocity, Ω (also referred to as Dean's parameter), is defined as follows:

$$\Omega = H_b / (T_b \times W_s) \quad (1)$$

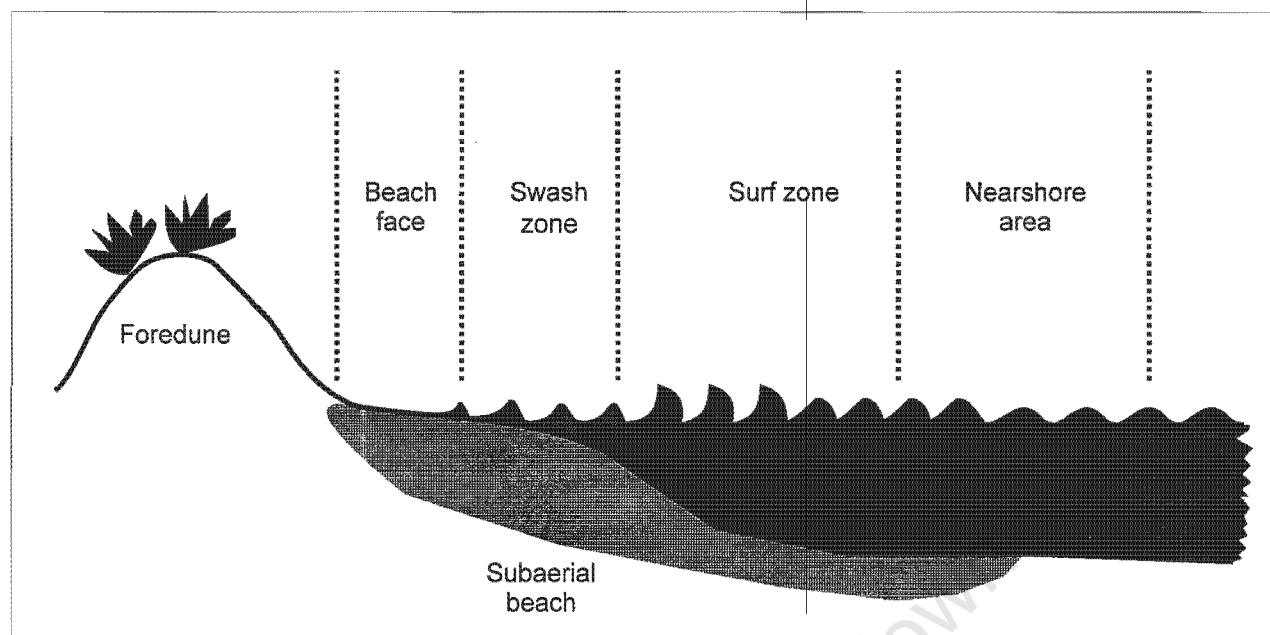
(where H_b is the breaker height in cm, T_b the breaker period in s, and W_s the sand fall velocity in cm.s^{-1} ; following Gibbs *et al.*, 1971).

Following the dimensionless fall velocity equation, beaches have been divided into three basic morphodynamic types: dissipative, intermediate and the reflective state. (The intermediate state has further been divided into four different types, but the discrimination between these intermediate states is considered unimportant in the scope of this thesis).

¹ **Surf zone:** is the area between the quasi-stationary mean sea level (tide level) and the wave break point.

² **Swash zone:** is the area between the tide level and the maximum run-up height.

³ **Swash:** is defined as the body of water that runs up and down the beach once a wave has broken on the shore. A wave that breaks is termed a bore, and as a bore collapses on the sand it turns into swash.

Fig 1.1 Beach ecosystem definitions (Brown and McLachlan, 1990).

1.2.1 Dissipative beaches

Dissipative beaches are characterised by persistently high waves (> 2.5 m), with breaker periods of 10 - 15 seconds, and fine sand ($< 200 \mu\text{m}$). Spilling breakers, which dissipate their energy across a generally wide surf zone, drive the dynamics of these beaches. The high waves, especially under storm conditions, cause beach erosion and beach profiles that are wide, with flat beach and swash zone gradients (Wright *et al.*, 1982b; Short and Wright, 1983; Short, 1996). Superimposed on the normal swashes, the wave action tends to have an infragravity surf beat⁴, which causes higher swash run-up, thereby allowing erosion of the back-beach and foredunes (Fig. 1.1). Typical periods for infragravity waves are 100 – 200 seconds (Wright *et al.*, 1982b). The modal beach state⁵ of dissipative beaches is relatively stable compared to other beach states, because of the compact, fine sand and the persistently high waves with long periods (Short and Wright, 1983; Short, 1996). In general, Ω -values greater than six are obtained for these type of beaches (Wright *et al.*, 1982b; Short and Wright, 1983).

⁴ **Infragravity surf beat:** is a dissipation of energy in such a way that the wave breaking causes incident/superimposed waves (with a period > 30 s). The surf beat can be observed as low frequency, long swashes (see Wright *et al.*, 1982b; Short and Wright, 1983; for more details).

⁵ **Modal beach state:** or most recurrent beach state, is when a beach is in dynamic equilibrium with the prevailing wave conditions.

1.2.2 Intermediate beaches

These beaches form the transition between dissipative and reflective states, and possess elements from both extremes. Intermediate beaches are characterised by variable wave heights, which result in dynamic beach morphologies. During times of high wave conditions the beach is eroded, sand is stored in the surf zone or seaward thereof, and when low wave conditions persist, the sediment is moved shoreward and stored on the subaerial beach (Short and Wright, 1983). This often leads to bar formation and hence the different intermediate beach forms (i.e. bar-trough, rhythmic bar, transverse bar and ridge –runnel). Beaches often move from one of these forms to another intermediate form, depending on the prevailing wave conditions (Short and Wright, 1983). The wave height generally ranges from 1 - 2.5 m, with medium sediments and slopes and moderate wave periods (Short, 1996). These beaches are generally moderately exposed and the surf zones display longshore⁶ variation characterised by different bar and rip topographies (Short and Wright, 1983). Infragravity standing waves can occur, with periods for these waves varying between 35 and 50 seconds (Wright *et al.*, 1982b). Ω -values that define intermediate conditions are 1 - 6.

1.2.3 Reflective beaches

Reflective beaches represent the other extreme, with waves reaching the beach instead of dissipating in a surf zone. These beaches are produced by low waves (< 1 m), particularly under coarse sediment conditions (median particle diameter > 600 μm) on open coasts, deep bays or protected environments, and are favoured by long wave periods (Short and Wright, 1983; Short, 1996). Waves tend to surge up the beach, or collapse over a step in the shallow subtidal (Wright *et al.*, 1982b). The intertidal gradient is steep, with a berm or a series of high tide cusps. Reflective beaches are unstable since any increase in wave height leads to beach erosion, but the 'recovery' to the modal beach form is rapid (Short and Wright, 1983). The Ω -values tend to be less than 1 (Wright *et al.*, 1982b).

⁶ **Longshore:** refers to running parallel to the horizon or shoreline.

There are many factors that complicate the application of these models in describing beach morphodynamic states, especially since this model only applies to single bar beaches in microtidal environments. Two factors that seem to be of great importance to beach communities are exposure and tide range, but neither are considered by Ω . The South African coast tends to be uniformly microtidal and exposed.

Headlands and megacusps are also important in structuring the surf environment, but since this project concentrates on the intertidal, their influence, although recognised, will not be discussed. See Short (1996) for a discussion of these factors.

1.3 EXPOSURE

The wave energy reaching the shore, generally visible in the height of the waves, is an indication of exposure. Most sandy beaches are characterised by turbulent surf zones where much energy is expended in the water column and on the sandy bed (McLachlan, 1980a; 1980c). This is not the case for reflective beaches, which generally lack a surf zone. Reflective beaches can develop under moderate to high energy exposed conditions, but the energy is dissipated on the shore. The beach faces of reflective beaches are therefore relatively exposed in comparison to the beach faces of dissipative beaches.

The reflective state is obtained when the wave height and period, combined with sand characteristics (by equation 1) results in an Ω -value < 1 . In the calculation of Ω the influence of wave energy becomes less pronounced if the sand is relatively coarse, even though the waves are relatively large. The coarse sand 'forces' the Ω -value to be small. For example, $\Omega < 2$ is obtained when $H_b = 1.5$ m (and $T_b = 13$ s), but the grain size equal to $450 \mu\text{m}$ (therefore $W_s = 6.1 \text{ cm.s}^{-1}$). The converse is also true. Exposure can change the beach state (temporarily from intermediate to dissipative) by increasing wave height while grain size is constant.

Exposure should be defined in terms of hydrodynamic forces experienced on the beach face and the resultant volumes of seawater percolating through the sand, and not necessarily the surf zone. However, this is difficult and impractical to fit into the sampling design of most beach projects. McLachlan (1980a) recognised these shortcomings in that there is no strict conformation of beach type to exposure, and designed a simple rating system to define exposure according to beach conditions. This system makes published literature on beach ecology more comparable.

McLachlan (1980a) used beach characteristics that are easily obtainable during a low tide sampling session to assess the degree of exposure. These were: wave action (which uses both wave height and surf zone width), sand particle size in combination with slope, sediment oxidation and macrofaunal burrows. The scores were rated from very sheltered⁷ (1 - 5) and sheltered⁸ (6 - 10), to exposed⁹ (11 - 15) and very exposed¹⁰ (16 - 20).

The importance of exposure is that it drives not only the sediment movement in swashes, but also the vertical/horizontal, and chemical and biological gradient, and sand nutrient exchanges in the system. Thus, apart from changing the morphology of the beach, it also determines nutrient exchanges in the interstitial system (McLachlan, 1989). Exposure is therefore extremely important in determining the structure and function of beach systems.

1.4 TIDE RANGE

The beach ecosystem has been divided into the nearshore, the surf zone, swash zone and beach face areas (Fig. 1.1). These areas are not static, but change with the rise and fall of the tides. For this reason, tidal variation is the most important parameter, after sand and

⁷ **Very sheltered:** means virtually no wave action, shallow reduced layers and abundant macrofaunal burrows.

⁸ **Sheltered** beaches: have little wave action, reduced layers present and usually some macrofaunal burrows.

⁹ **Exposed** beaches: experience moderate to heavy wave action, reduced layers are deep, if present, and no permanent macrofaunal burrows.

¹⁰ **Very exposed:** means heavy wave action, no reduced layers and only tough motile fauna present.

waves (or exposure), in structuring the physical intertidal environment. Wave action determines the morphodynamic state that prevails, whereas tide range influences swash and surf zone processes (Masselink and Short, 1993). Tide range may therefore have significant implications for the macrofaunal community.

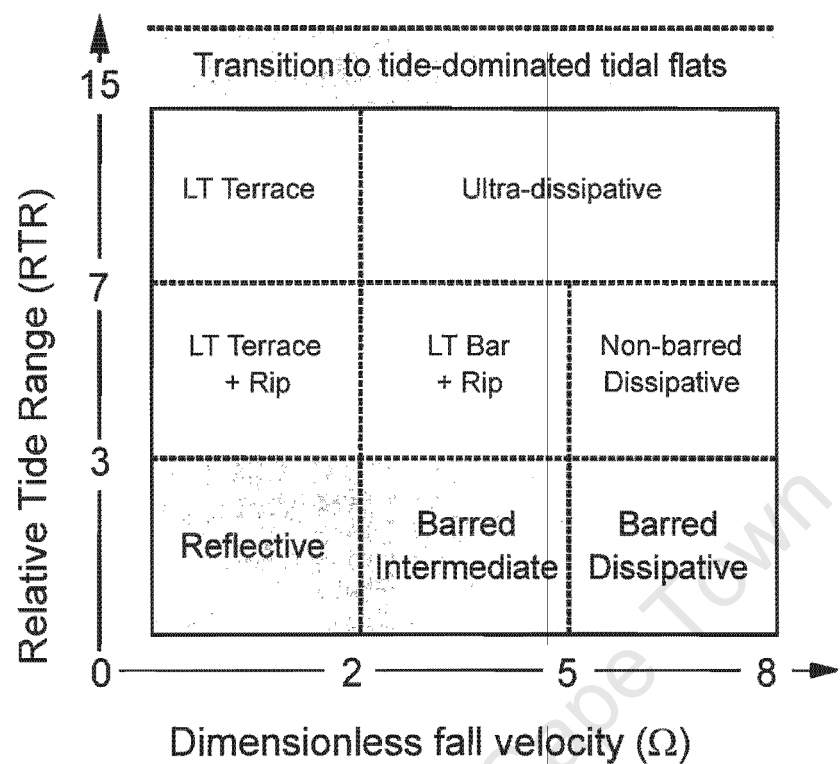
It was realised that the beach morphodynamic states, as described before, seem to apply only to a limited tide range. Davies (1964 cited by Masselink and Short, 1993) classified beaches as micro- (< 2 m), meso- (2 – 4 m), or macrotidal (> 6 m), depending on the tide range. It was found that the beach morphodynamic states are much more complex than simply applying the Ω -index to field data, and that macrotidal conditions make beaches more dissipative (Masselink and Short, 1993). Tide range may have a negligible influence on the beach morphology of microtidal beach states (Short, 1996).

The superparameter, wave height, should also be taken into account when trying to define all beach states, including tidal flats. Masselink and Short (1993) therefore incorporated these two factors into a single dimensionless parameter, the Relative Tide Range (RTR). This parameter depicts the ratio between the tide range (TR) and wave height (H_b) as follows:

$$\text{RTR} = \text{TR} / H_b \quad (2)$$

Using Ω in conjunction with the RTR, Masselink and Short (1993) defined nine beach states, which include tide dominated tidal flats. The interaction between RTR and Ω is presented in Fig. 1.2. Large values of RTR indicate tide dominance on beaches, whereas small values are obtained on wave dominated beaches (Masselink and Short, 1993). Thus, on single-barred micro-tidal beaches specifically ($\text{RTR} < 3$), waves drive the beach change, but within the 'boundaries' of the equilibrium Ω . In addition, when the RTR value is < 3 , the swash and surf zone processes dominate the entire intertidal and shallow subtidal zone (Masselink and Short, 1993). These factors are therefore expected to exert a significant influence on the macrofaunal community structure, although the primary use of these parameters is to describe the physical surf environment.

Fig. 1.2 The relative importance of beach morphodynamic state and RTR structuring the different beach types; LT = low tide (after Masselink and Short, 1993).



At the same time as when Masselink and Short (1993) redefined beach states, biologists were interested in fitting community patterns to the beach states as defined by Ω . McLachlan *et al.* (1993) found that it was useful to include some measure of tide range when community patterns from different biogeographical regions were compared.

The dimensionless fall velocity index was hence redefined into a dimensionless Beach State Index (BSI) incorporating tide range as follows:

$$BSI = \text{Log} \left(\left(\frac{H_b \cdot M}{W_s \cdot T_b \cdot E} \right) + 1 \right) \tag{3}$$

H_b , W_s and T_b as in the dimensionless fall velocity, M as the maximum tide range and E is the maximum theoretical equilibrium tide for the earth covered in water (= 0.8 m; McLachlan *et al.*, 1993).

Beaches with a BSI < 0.5 are reflective beaches, BSI-values between $0.5 - 1.0$ are low to medium energy intermediate, BSI of $1 - 1.5$ are high energy intermediate/dissipative beaches, $1.5 - 2.0$ are fully dissipative beaches and BSI > 2 are ultra-dissipative macrotidal beaches. The categories of this model are thus very similar to those using Ω , except for the high-energy intermediate/dissipative state and the ultra-dissipative extreme. The usefulness of this index is that variation in physical parameters, arising from variation in tidal range, is reduced (McLachlan *et al.*, 1993).

The test of whether or not the physical explanations are appropriate is their ability to predict the biological patterns found in the field. Most of these tests have involved correlative techniques, attempting to link physical and biological attributes of various beach types. As the fit of the curves improved so our understanding of the physical nature of beaches was assumed to have improved. One such example is the shift in the recognition of the importance of swash (and not only beach morphology) in the explanation of beach community structure (McLachlan, 1988; Brown and McLachlan, 1990; McLachlan *et al.*, 1993).

1.5 SWASH

It is evident that the morphologies of microtidal beaches ($RTR < 3$), and therefore also the swash environment and community patterns, are influenced by surf zone processes (Masselink and Short, 1993). McArdle and McLachlan (1992) argued that the swash climate on the beach face is the most important force/controlling factor experienced by the animals inhabiting exposed sandy beaches. Yet the factors controlling the swash climate on different beach types have not received nearly as much attention as beach and surf zone morphology. In fact, it is difficult to derive an appropriate definition for swash climate, and also to determine the critical factor/s that might control the swash environment.

The swash zone is defined as that part of the intertidal area that is periodically covered by water in response to the rise and fall of the tide and wave run-up (McArdle and McLachlan,

1992). The swash 'climate' is more difficult to define. Factors that are important in the swash environment are presented in Fig 1.3.

Parameters that should be taken into account when defining the swash climate (other than the obvious beach characteristics such as grain size and slope) are: frequency, time, distance, and speed of swash upwash¹¹ - and backwash¹², the number of effluent line crossings¹³, swash period and wave period : swash period ratio. McArdle and McLachlan (1992) tried to elucidate which of these factors would most likely have an influence on macrofauna, by correlating the swash parameters to beach state. The beach factors that control the swash were beach slope and wave height. The influence of these factors were therefore assumed to be the most important to beach communities.

The inter-relatedness of physical parameters describing beaches makes it difficult to determine which critical factors control beach macrofaunal communities, especially when using correlative techniques instead of cause and effect tests. After further investigation by McLachlan *et al.* (1993), the macrofauna community itself was found not to be best correlated with either slope or wave energy, which control the swash climate, but rather with beach morphodynamic state.

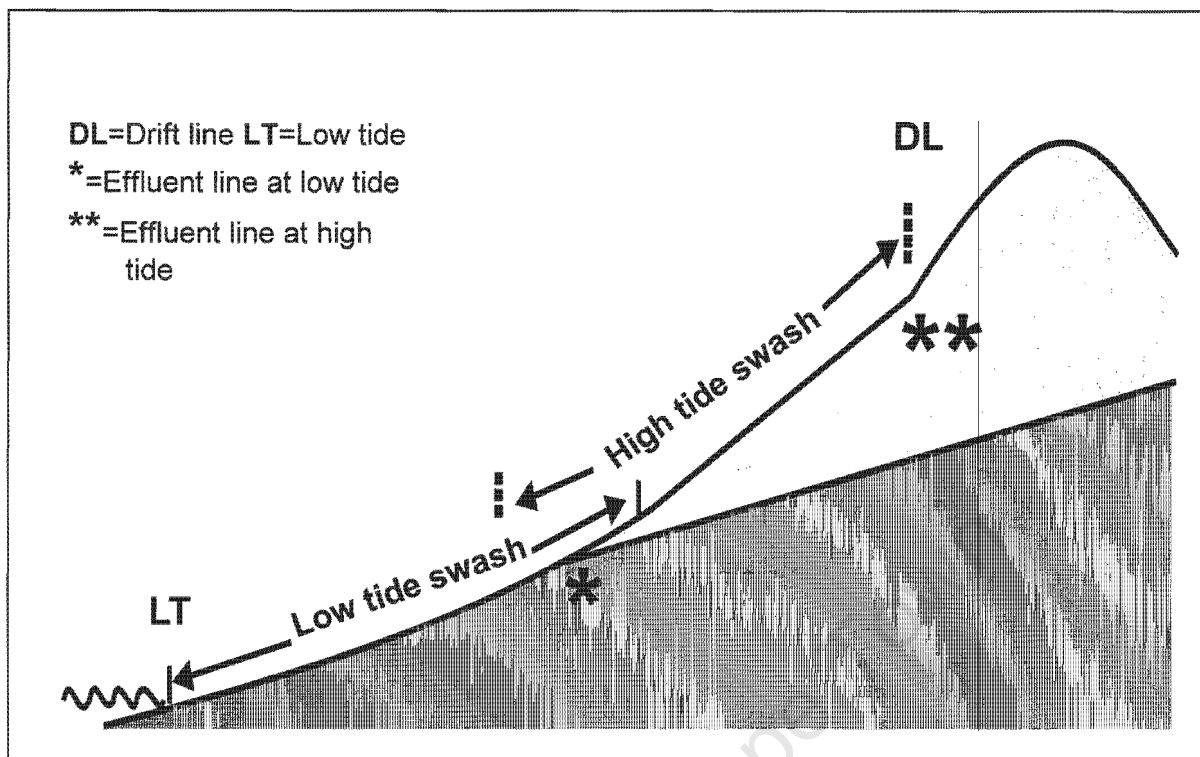
These factors (i.e. slope and wave energy) describe the beach morphology and surf zone processes, but not the swash. It has therefore become important to elucidate the relationship between the physical factors describing the swash climate and those describing beach macrofaunal communities.

¹¹ **Upwash:** is the movement of swash up the beach face until the leading edge, usually indicated by a line of foam, reaches maximum run-up.

¹² **Backwash:** is when the leading edge of the swash has stopped and starts the down-wash on the beach face, until it is overrun by the next wave.

¹³ **Effluent line:** is the intersection of the water table and the beach face, normally indicated as the edge of the 'glassy layer' / water table outcrop.

Fig. 1.3 Important swash parameters from an intertidal beach (after McLachlan, 1990; McArdle and McLachlan, 1992).



1.6 MACROFAUNA

Beaches have been described as marine deserts, largely because the beach fauna is mostly buried and very cryptic (Dahl, 1952). Other than large patches of feeding gastropods, or the odd ocypodid crab burrow, there is generally very little evidence of life on a beach surface. As a result beach animals have been relatively neglected by many ecologists.

A major feature of macrofaunal species on exposed sandy beaches is their high degree of motility (McLachlan, 1983a). These animals can generally rebury into the sand within seconds, or travel great distances by swash riding (Brown *et al.*, 1989; Brown and McLachlan, 1990; McLachlan *et al.*, 1995; Nel, 1995). All the major invertebrate taxa are represented on beaches (McLachlan, 1983a), but the dominant groups are polychaete worms, crustaceans and molluscs.

There is a continuous change in the distribution of macrofauna both along and across the shore. This is due to the great motility of these animals, in addition to tidal flux, swash sorting

and feeding aggregations, which cause patchiness in their distribution (McLachlan, 1983a; 1988; Brown and McLachlan, 1990). Beach communities are therefore referred to in terms of numbers per running metre¹⁴. Even with the continuous spatial and temporal variations in population structure, some clear distribution patterns have been obtained. Bally (1981) reported that there is a change in the abundance of macrofauna with a concurrent change in exposure. As exposure increases, diversity and abundance decrease, whereas individual size increases (McLachlan *et al.*, 1981). The highest biomass values are therefore obtained on very exposed beaches (McLachlan, 1977). The relative abundance of each of the dominant taxa varies according to exposure rating and beach type (McLachlan, 1983a).

1.6.1 Macroscale patterns

In recent years, community patterns have been described on both a macro¹⁵- and mesoscale¹⁶. McLachlan *et al.* (1981) described a general trend that indicated a significant relationship between biotic (species diversity and abundance) and abiotic (beach slope and particle size) variables, especially for high-energy microtidal beaches in South Africa (McLachlan *et al.*, 1981). When this was repeated after the introduction of the dimensionless fall velocity parameter (Equation 1), significant positive regressions were obtained between the community parameters (species richness and abundance) and beach morphodynamic type (McLachlan, 1990; Jaramillo and McLachlan, 1993; Jaramillo, 1994). Similar results were obtained using the BSI (Equation 3) for a wider range of beaches (McLachlan *et al.*, 1996a; Hacking, 1998). Biomass, on the other hand, is generally correlated with wave energy, increasing logarithmically with breaker height (McLachlan, 1990).

The conclusions from these studies always indicated that the swash climate on dissipative beaches accommodates more species, and in greater abundance, whereas only a few of the

¹⁴ **Numbers per running metre:** is the number of animals in a metre wide strip between the drift line and the low tide swash zone.

¹⁵ **Macroscale:** refers to patterns described *between* different beaches, which can generally be attributed to morphodynamic changes or biogeographical provinces.

¹⁶ **Mesoscale:** refers to changes *within* the same beach across the shore from the drift line to the swash zone.

'very large' crustaceans can survive on reflective beaches. This was termed the *swash control hypothesis* (McLachlan, 1990), later rewritten as the *swash exclusion hypothesis* (SEH; McLachlan *et al.*, 1993). This hypothesis states that:

"... the swash climate associated with dissipative beaches is sufficiently accommodating and varied to enable virtually all macrofauna species encountered on exposed beaches to maintain viable populations, but, as beach type changes through intermediate states towards reflective conditions, the increasingly inhospitable swash climate excludes more and more species until, in the fully reflective situation, only supralittoral forms (talitrid amphipods, Ocypode crabs, insects), which live 'outside' the swash climate, remain" (McLachlan *et al.*, 1993).

These trends have been obtained over a wide range of beach types, tide ranges and biogeographical provinces, and seems to hold under most conditions. However, the proponents of these hypotheses have realised not only the necessity of testing these ideas experimentally, but also the difficulty involved in doing so. The SEH is written in very general terms without understanding the mechanisms or exact parameters involved. This makes experimental testing almost impossible (McLachlan *et al.*, 1995). It has become imperative to describe the SEH in clear, testable terms.

1.6.2 Mesoscale patterns

Beach ecology virtually began with ecologists attempting to describe mesoscale patterns, and yet a satisfactory zonation pattern has not yet been found; this is probably because zones cannot be defined as clearly as is the case on rocky shores. Stephens (1929 cited by Wendt and McLachlan, 1985) was amongst the first to recognise that zonation existed on beaches. Dahl (1952) proposed the first zonation scheme, which was based specifically on crustacean distribution across the shore. He defined three zones; the subterrestrial fringe, the midlittoral zone and the sublittoral fringe. Salvat (1964 cited by Wendt and McLachlan, 1985) described four zones based on the physical conditions obtained on beaches; the zones of drying, retention, resurgence and saturation. Although these zonation schemes

appeared to be different in nature (one biological and the other physical), the similarity is considerable. The zones of resurgence and saturation can be considered to make up the sublittoral area from Dahl's scheme (McLachlan and Jaramillo, 1995). However after these studies, many beach ecologists dealt with across-shore patterns (Wendt and McLachlan, 1985; Jaramillo *et al.*, 1993; Jaramillo and McLachlan, 1993; Jaramillo, 1994; McLachlan and Jaramillo, 1995; James and Fairweather, 1996; McLachlan *et al.*, 1996a), with no single answer or zonation scheme, but generally a variation of Dahl (1952) and Salvats' schemes (cited by McLachlan and Jaramillo, 1995). The simplest zonation pattern, and probably the most broadly applicable, is the zonation scheme proposed by Brown (McLachlan 1983a; Brown and McLachlan, 1990). This includes only two zones that are always present on beaches: i.e. air-breathing fauna at the top of the shore and water breathers below the driftline. Raffaelli *et al.* (1991) confirmed this to be the only universal zonation scheme.

It is important to define what a 'zone' means, since this definition could change the proposed zonation schemes. McLachlan and Jaramillo (1995) stated that *"a zone should include the centre of gravity of at least one characteristic species and should be visible without the use of sophisticated statistics. It should be reasonably obvious from kite diagrams, otherwise it is merely a statistical separation in a continuum"*. This is probably a bit oversimplified, since a centre of gravity can be obtained for most species on most beaches but with a shifted overlap with other species. According to this limited definition of a zone, it is thus a subjective decision which of the species would be characteristic of a zone.

The greatest problem with defining zones on a sandy beach is thus the 'blurring' of the edges of the zones. The dynamic nature of the environment cause the animals to move around, sometimes outside the 'centre of gravity'. McLachlan and Jaramillo (1995) further described the reasons for the overlap of species between zones. These include the rhythmic responses of animals to tidal, diel and semi-lunar cycles. However, the assumption is made that other factors that affect the intertidal distribution of sandy beach animals are stronger than the forces causing overlap of species and these are the factors causing zonation. These factors are: intraspecific zonation caused by size, predation, competition for food,

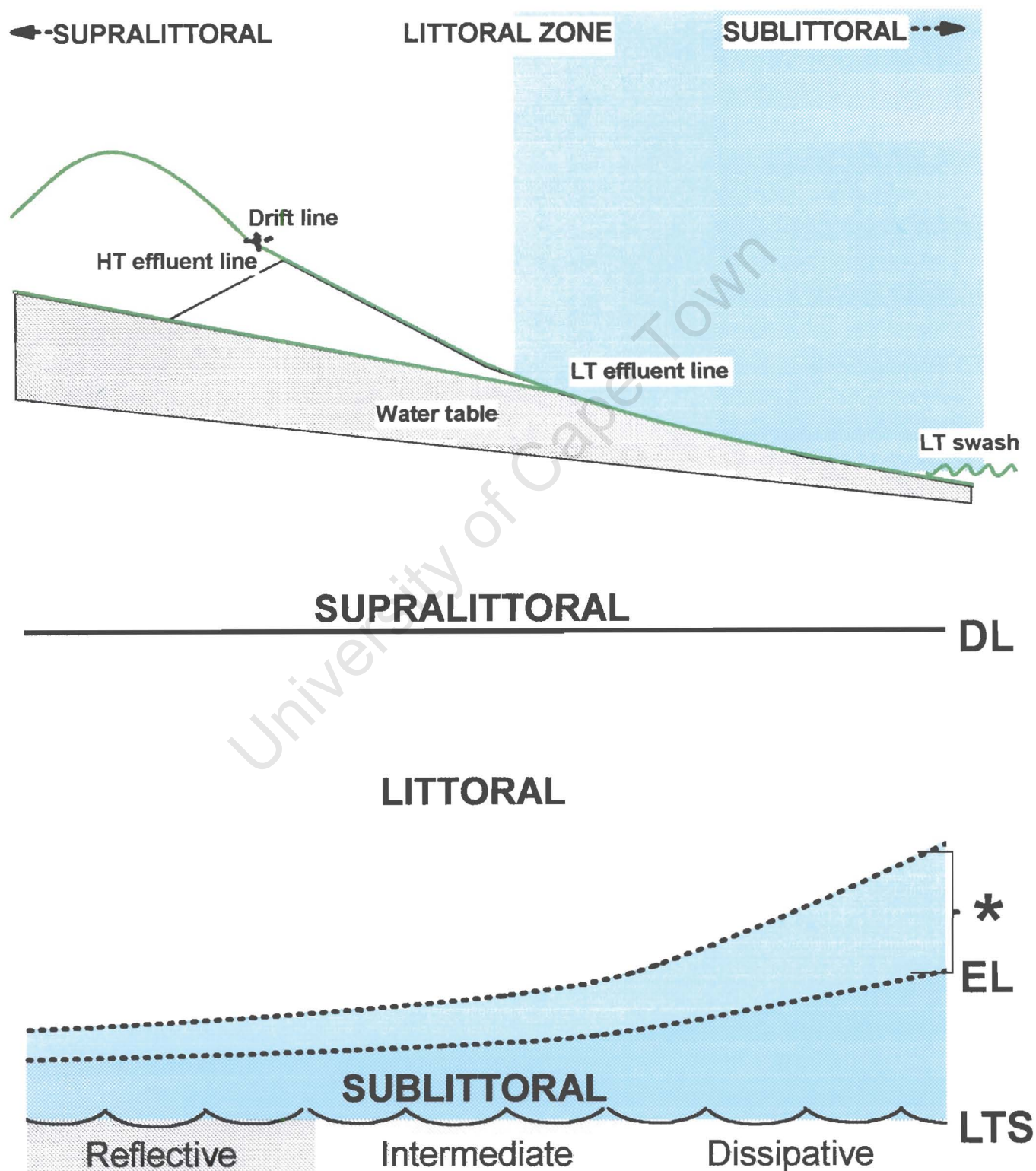
differences in physical tolerances and sand particle and moisture preferences (McLachlan and Jaramillo, 1995). The description of zonation patterns has been limited to low tide patterns. Only Hacking (1996) has investigated the change of zonation at different points during the tidal cycle.

McLachlan and Jaramillo (1995) described a zonation scheme that may exist on most beaches during low tide. This scheme is compiled from our current understanding of beaches and does not focus on only the physical environment or the biota. It comprises three zones. These zones are the same as the zones suggested by Dahl (1952), with an optional extra in the resurgence zone characterised by species different to those from the swash zone or subtidal. This extra zone may be present on dissipative beaches, which appear to be more benign, with more niches present. Even the number of zones is thus dependent on beach state (Fig. 1.4).

1.7 BEACH ECOSYSTEMS

There are two main biotic components to the beach ecosystem. The macrofauna and the interstitial fauna form two separate communities, with little or no energy flow between them (McLachlan, 1980b; 1983a). Dissolved and particulate organic matter is imported into the interstitial environment by means of water filtration driven by the swash and backwash processes (McLachlan *et al.*, 1985). Maximum water percolation takes place through the swash on microtidal, reflective beaches with nutrient levels higher in the interstitial waters than the swash (McLachlan *et al.*, 1985). This confirms the large amount of mineralization of organic matter that takes place in the interstitial environment. These minerals leach back into the surf zone where they are utilised by the surf phytoplankton, to start the 'macrofauna loop'. McLachlan (1980c) referred to a semi-exposed beach system, especially utilising surf zone phytoplankton, as a semi-closed ecosystem with few imports and exports. Other than

Fig 1. 4 A zonation scheme describing the possible zones on most microtidal beaches. As conditions become more dissipative, areas around the effluent line may have distinct faunal groups. **HT** = High tide; **LT** = Low tide; **DL** = Driftline, **EL** = Effluent line, **LTS** = Low tide swash. *May become a distinct zone in ultra-dissipative conditions. (After McLachlan and Jaramillo, 1995).



macrophytes all the components on a typical intertidal community, with the associated trophic structures, are present within such systems.

1.8 COMPLICATIONS IN BEACH ECOLOGY

1.8.1 Introduction

Beach work has often been described as a pseudo-replicated¹⁷, snapshot, bucket-and-spade science, and this is quite often true! Few other systems, even though sampled with a similar sampling regime (for instance a transect survey along a rocky shore) are ever described in the same fashion. Fixed samples across the intertidal gradient are accepted as an adequate strategy to describe the community of a more stable environment, such as a rocky shore. However, the beach fauna on an exposed sandy beach has probably changed in absolute distribution, abundance and biomass by the end of the next tide, let alone before by the time the analysis is completed in the laboratory (Hacking, 1996). It is therefore necessary to take inventory of the information that is obtained from typical beach survey strategies, and to understand the descriptive and predictive value of this information.

1.8.2 Beach ecosystem *per se*

Beaches are physically complex systems, because they are formed as an interface between terrestrial and marine environments. Since the beach boundaries fluctuate between the spring high and low water levels, they are inherently unstable. The dynamics of the system are enhanced by the changing wave action, which is largely affected by season and geographic position. And unlike rocky shores, the substratum is mobile and is rearranged by virtually every wave. The typical beach face that fauna have to respond to, is a function of many wave action parameters (manifested in swash period and intensity), grain size, water

¹⁷ **Pseudo-replication:** is defined as: "the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent" (Hurlbert, 1984).

table position and slope (McLachlan, 1988). Community structure of one day may not necessarily be the same the following day.

1.8.3 Interdependence of physical parameters

Studies that have relied on regression of biotic variables, such as of diversity, abundance and biomass against physical parameters have often concluded that the control of beach faunal characteristics is complex and determined by overall morphology and dynamics of the beach, rather than any single parameter (Brown and McLachlan, 1990). Individually, particle size or wave energy cannot characterise a beach (Brown and McLachlan, 1990). Biomass is best correlated with wave energy, and abundance and diversity are best correlated with compound parameters (such as Ω), which are related to the overall beach morphodynamic state (Brown and McLachlan, 1990; McLachlan *et al.*, 1996a). These studies, however, do not explain the processes involved. A change in wave height or grain size, for example, causes a concurrent change in a suite of physical parameters and it becomes very difficult to elucidate which of these parameters are critical to the macrofaunal populations.

1.8.4 Macrofauna

A valuable adaptation of beach macrofauna is their mobility. But the gregarious nature of beach macrofauna poses an inherent problem in studies explaining distribution patterns according to swash sorting or physical regimes. Species tend to aggregate in favourable positions, resulting in patchy distributions along the shore. The scale of variation in distribution is often not addressed by the sampling methodology, especially in terms of recruitment patterns that may vary across kilometres (Defeo, 1996, Lastra and McLachlan, 1996; Schoeman, 1997). Macrofauna is not evenly distributed throughout cusps¹⁸ and different taxa tend to aggregate in different parts depending on the swash climate (McLachlan, 1988). Sampling should take this into account. Biological reasons for

¹⁸ **Cusps:** "are scallops or undulations along the beach which breaks the beach face into a series of bays" (McLachlan and Hesp, 1984), that are formed along the shore with steep cusps horns and generally flatter centres. The sizes of the cusps can vary from a few metres across, to hundreds of metres depending on the beach state (see McLachlan and Hesp, 1984; McLachlan, 1983a; 1988).

patchiness in distribution include feeding or breeding aggregations of animals (e.g. *Bullia rhodostoma* around carrion), or to avoid predation (McLachlan, 1988). These aggregations are often observed, but avoided during sampling sessions. Therefore, community descriptions are relative estimates of population sizes and distributions, and may be biased. Additionally, transect sampling is restricted to the period of low tide (with the exception of a study by Hacking, 1996). The behaviour of the fauna and the distribution thereof during high tide remain matters of speculation.

1.8.5 Recruitment estimates

Defeo (1996), concluded that there can be no reliable predictions of recruitment to beaches. The four reasons explaining this can directly be applied to adult macrofauna populations on sandy beaches. Firstly, Defeo (1996) reported on the inherent difficulties in sampling and experimentally manipulating generally small and mobile fauna. Secondly, unlike rocky shores, the third dimension available on beach sediments causes vertical and horizontal space partitioning, which makes biological interdependence unrecognisable/unobservable. Thirdly, a general lack of long-term data exist for most beach studies, since they are usually sampled infrequently. Lastly, Defeo (1996) commented on the scarceness of information on scale-dependence of processes and patterns structuring beach populations.

1.8.6 Broad questions (in ecology)

Researchers have not been able to answer some basic questions involved in beach ecology, i.e. what are the roles of sand and waves (or ultimately swash parameters) in controlling beach communities? McLachlan (1988) suggested that on fully reflective beaches the harsh swash climate excludes the establishment of intertidal macroinfaunal species. Good correlations have been obtained between these physical parameters and the communities, yet nothing is known about the mechanism involved. Questions are asked such as whether the SEH applies broadly over biogeographical provinces (Jaramillo, 1994; McLachlan *et al.*, 1996a), when a clear, testable definition of this hypothesis cannot be given for a single region over morphodynamic states. The trend therefore is to explain what happens on a

macroscale, between biogeographical provinces without sufficient understanding of processes structuring mesoscale, across-shore distribution patterns, or even knowing basic physiological requirements or tolerances. This is potentially driven by the pressure for applied rather than theoretical/empirical science.

1.8.7 Methodology

Rocky shores are more tractable ecosystems for biological modelling than sandy beaches (Peterson, 1991). Sampling on sandy beaches is generally only possible during spring low tides and is labour intensive. Sampling design should reconsider the size of samples and the number of samples, but also the sampling depth. Hacking (1997) calculated the number of samples required (with a quadrat size of 0.1 m^2 to a depth of 35 cm), at different levels of the intertidal, to have a relatively acceptable level of precision ($D = 0.2$). It was reported that about 50 samples should be obtained across the shore (but with concentrated effort on the lower shore) to obtain an accurate estimate of species richness, and about 150 samples are necessary to obtain an accurate estimate of abundance for these species (also with a concentrated effort on the lower shore). It may be possible to obtain a sample size large enough for an acceptable estimate of species richness, but it is impossible to increase the sample size to estimate abundance sufficiently with limited resources (Hacking, 1997). The sampling designs used in macrobenthos studies include few spatial scales, are usually poorly replicated at each scale and are often inadequate for addressing the questions asked (James and Fairweather, 1996).

Beach sampling has often been described (mostly by non-beach biologist) as pseudo-replicated. Keeping the difficulties of sampling methodology in mind, it is very important to remember the constraints during the analysis. Diversity, abundance and biomass values obtained from triplicate transects should not be extrapolated to larger scales. The spatial arrangement of benthos obtained is specific to the width of the transect only, and to the physical parameters obtained within the area. Values should therefore not be used to extrapolate to the whole beach (Hurlbert, 1984). Thus, to make unequivocal comparisons

among beaches or along a single beach, adequate descriptions of spatial variation within beaches are not provided by triplicate transect sampling design (generally with 10 – 15 equidistant stations). Unconfounded comparisons among beaches are therefore impossible (James and Fairweather, 1996). Beach studies comparing transects should thus bear in mind that the sample might be a representative point sample, but that this is specific in time and space.

1.8.8 Correlative type approach

Most beach ecological research has taken a correlative type approach, instead of an experimental one. Because most parameters seem highly confounded, guidelines in terms of critical (physical) parameters, do not yet exist. The physical and biological environment is generally well correlated. However, the goodness of fit of these models is often variable, depending on the study and care taken in measuring the physical environment. Some studies reported slope to be the most important factor in structuring beach communities (McArdle and McLachlan, 1991), while Jaramillo and McLachlan (1993) obtained the best fit between the number of species and the dimensionless fall velocity, while grain size was found to determine the abundance and biomass. The physical variables are, however, highly correlated/confounded and a change in the one factor often results in a concurrent change in a suite of other physical parameters. For example, a change in grain size will result in a change in slope, which in turn will affect swash parameters. Understandably the best fit between the biotic structure and the abiotic environment is thus obtained when compound indices, incorporating several of the variables, are used.

1.8.9 General lack of knowledge

It is, however, important to remember that beach ecology is a recent science (compared to ecological studies of most other accessible systems) and with a comprehensive approach dating only from the time of Dahl (1952). Since the fauna of this ecosystem is not of great economic or ecological importance (in the sense of having few economically important and rare/endangered species), it has received little attention. In contrast to the recreation and

tourism industry, which has expanded dramatically, the science around beaches has developed slowly. Brown (1996) reported that the overall picture of the ecophysiology of sandy beach macrofauna has not changed dramatically since the Sandy Beach Conference, 1983 (McLachlan and Erasmus, 1983). This shortcoming must be addressed. It has been shown that many beach animals can burrow in a wider range of sand particle sizes than they would encounter in nature (Brown and McLachlan, 1990; Nel, 1995). Yet, the effect of grain size on beach macrofauna has not been studied, and optimum grain size ranges, or their effect on field distribution for most species are unknown. Knowledge of the taxonomy of beach fauna is adequate, but some problems still exist. For example, the isopod *Eurydice longicornis* has apparently been incorrectly identified in South Africa for about three decades, and a recent study has described this 'species' as possibly four different species (Bruce and Soares, 1996). These types of complications and confusions have added to the dynamics of beach ecology, but have also hindered progress.

1.9 AIMS

The objective of this study is to attempt to resolve some of the above problems involved in sandy beach ecology. This project tries specifically to take an alternative approach to previous work. Instead of looking for correlations between the abiotic environment and the biotic communities, it will take an experimental approach and evaluate some of the ideas that have been published in the sandy beach literature. The title of the thesis is very broad, indicating investigation of both the physical factors and biological interactions present on exposed sandy beaches. More specifically the aims are to:

1. Identify critical parameters in the swash climate that are responsible for the structure of beach macrofaunal communities, and hence allow redefinition of the SEH.
2. Test the validity of the assumption prevalent in the literature that biological interactions play no role in the macrofaunal community structure on exposed sandy beaches.
3. Expand the experimental approach in beach studies.



CHAPTER 2

University of Cape Town

2.1 INTRODUCTION

Few environments have as little stability or biological structure as exposed sandy beaches. These beaches are characterised by the constant interaction between waves and the substratum in such a dynamic way as to create this physically harsh environment (McLachlan, 1988). Consequently this interface between terrestrial and marine systems supports a fauna of low diversity (McLachlan *et al.*, 1995). Intertidal animals on exposed beaches are well adapted to such conditions and find compensation in the three dimensionality of the system. The hallmark of all inhabitants of these dynamic systems is a very high degree of motility and the ability to burrow rapidly (McLachlan, 1988). However, on some beaches these adaptations are not sufficient to ensure successful use of the habitat.

The aim of this study is to investigate the changes in the biological community with changes in the physical environment and to determine whether similar trends to those reported in previous studies are found. This was done in four steps. Firstly, to determine whether the beaches that were sampled came from a range of beach morphodynamic types, from dissipative to reflective, as described by Short and Wright (1983). Secondly, to determine whether the communities of these beaches conform to the general trends as found by McLachlan and co-workers, i.e. that there is a linear increase in species richness from dissipative to reflective beaches, and a logarithmic increase in abundance and biomass along this continuum (McLachlan, 1988; 1990; McLachlan *et al.*, 1993). Thirdly, to determine whether the beach communities sampled could be characterised in terms of biogeographical provinces. And lastly to test for any consistent trends in terms of faunal zones present on

these beaches. An investigation is also made into the appropriateness of the current indices used to define beaches and their associated communities.

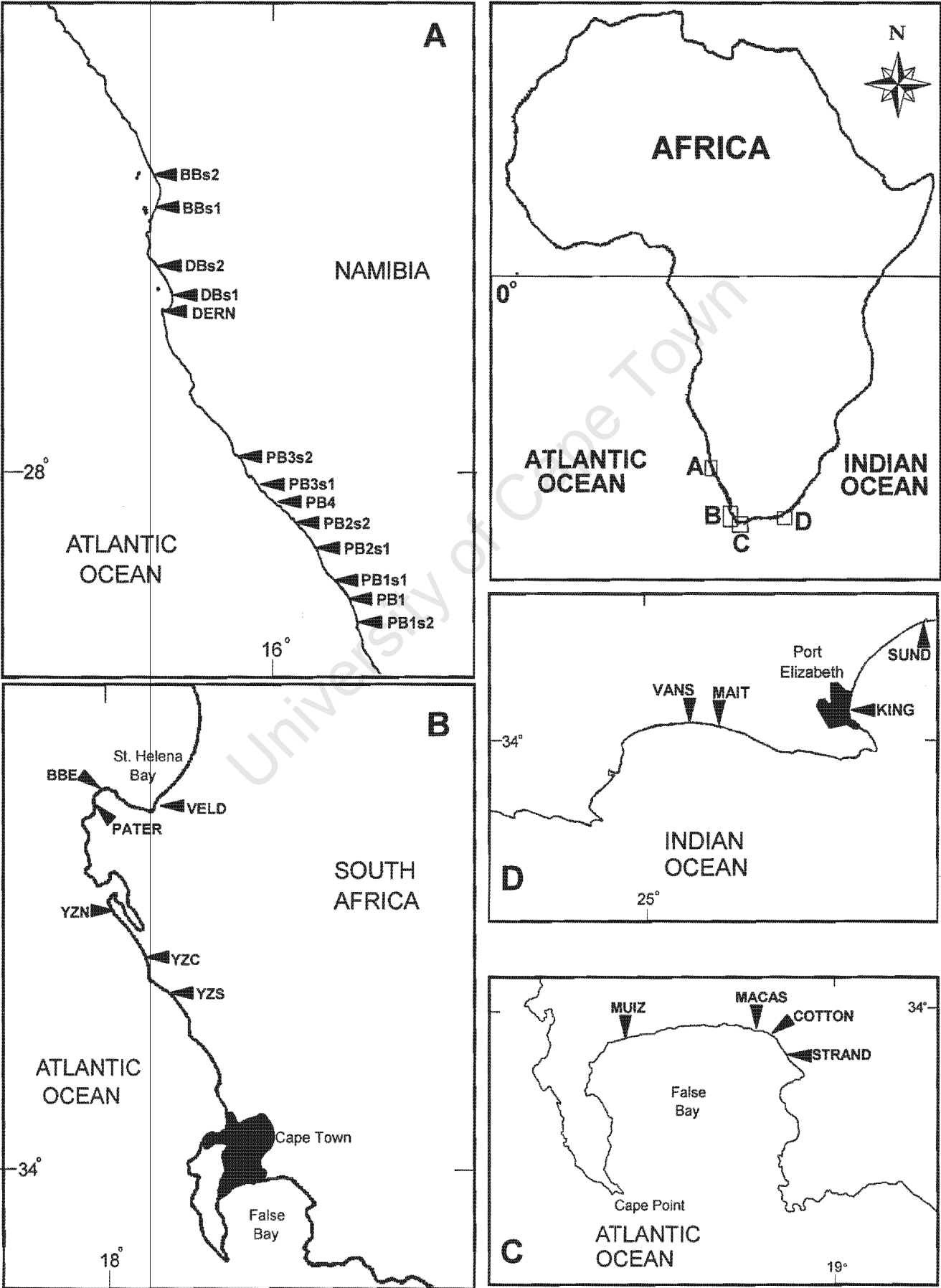
2.2 METHODS

2.2.1 Sampling

Twenty-seven beaches were sampled during spring low tides between August 1997 and September 1998. These beaches ranged from Sundays River beach in the Eastern Cape to Dernberg Bay in southern Namibia (Fig. 2.1). The sampling methods and the statistical analyses employed reflected those of previous beach workers. Standard methods were used both for the sake of comparison, and to optimise the sampling success with the smallest effort (Jaramillo, 1994; Hacking, 1997; Jaramillo *et al.*, 1998). Most of the beaches are considered pristine, with little human impact and low pollution. Beaches were chosen haphazardly, without favouring any particular morphodynamic characteristic, or biogeographic province.

Each collection was conducted along a transect with either 10 or 11 stations, depending on the coast. On the beaches west of Cape Point an 11th station was sampled to include an estimate of the potential adult beach clam (*Donax serra*) population that might have existed in the surf on those beaches. At each station, three replicate quadrates (0.1 m²) were collected, to a depth of 30 cm and sieved through a 1 mm mesh bag. The replicates were 5 m apart. Station 1 was located on the driftline and Station 10 was situated on the spring low water mark (SLWM) as indicated by bore collapse. Station 11 was below the SLWM. The other eight stations (between 1 & 10) were arranged equidistant from one another. On beaches where a large fraction of sediment was retained in the sieve bags, sediments were

Fig. 2.1 The 27 beaches sampled along the southern African coastline.



elutriated¹ until three consecutive decants were empty. The retained sediments were hand-sorted on the shore for heavier biota.

The collected macrofauna was preserved in 5 – 10% formalin in sea water. In the laboratory, animals were identified to species level, dried (at 60 °C for 24 h) and weighed in the shells. The number of species per transect was determined as well as abundance and biomass values per running meter of beach. Large molluscs, such as the bivalve *Donax* and the gastropod *Bullia*, which were abundant on some shores, were counted and measured on site. The measurements obtained were maximum shell length to the nearest 1 mm. Biomass values for these species were obtained from previously determined dry weight - length regressions (Schoeman, unpublished data; Nel, unpublished data).

2.2.2 Analysis

The beaches

A series of physical parameters was measured within half an hour around the time of low tide. The low tide beach state was used to facilitate comparison with earlier beach studies. It is realised that the beach states tend to be more 'reflective' by having steeper beach slopes at high tide (McLachlan, pers. comm.). The physical parameters were chosen to characterise the wave action in the surf zone and the intertidal beach parameters. Wave action is described by surf zone width², number of breakers³ in the surf zone, maximum wave height⁴

¹ **Elutriate:** is when the biota, with a lower density than the sediments and shell fragments, are washed out of the sample by stirring the sample sediment and water mixture, and then pouring the water through a fine mesh sieve. The biota is retained in the mesh bag.

² **Surf zone width:** obtained as a visual estimate, in metres, from the SLWM to the breaker furthestmost from the shore.

³ **Number of breakers:** as a count of the number of breakers at a particular point in time, in the surf zone.

⁴ **Maximum wave height:** as measured with a graduated measuring stick (to the nearest 10 cm), as the distance between the trough and the maximum height obtained by the wave, as it starts to break (McLachlan, 1988).

(m) and wave period⁵ (s). The beach parameters measured were intertidal slope and grain size. Sediment samples (5 cm deep) were taken from the driftline, midshore and SLWM. In the laboratory, the sand was dried and passed thorough a series of sieves to obtain mean grain size, sorting and skewness per sample. Settling velocities were calculated as by Gibbs *et al.* (1971). The beach morphodynamic state was calculated (using Equation 1), as well as the RTR (Equation 2) and BSI (Equation 3).

Macrofaunal component

Species richness, abundance and biomass

The biological data were explained in terms of the physical factors that are thought to structure beach communities. Regressions (using the Multiple Regression Module, STATISTICA '98) were constructed between the number of species per sample site, the abundance and biomass values (as $\text{Log}_{10} \text{ no.m}^{-1}$ or $\text{Log}_{10} \text{ g.m}^{-1}$ of beach) and the slope, mean grain size, RTR, EXP and Ω (Zar, 1984; 1996).

Biogeographical province and zonation

The beaches were initially separated into different beach types and by biogeographical province, based on abundance per species for each beach. This was done by constructing a dendrogram (based on Bray-Curtis similarities, using PRIMER ver. 3.1) and a non-metric multidimensional scaling-plot (MDS using the default settings without transforming the data, PRIMER, ver. 3.1). Clusters indicated similar beach states per biogeographical province.

Zonation per beach state (per region) was subsequently obtained by choosing three 'representative' beaches from these clusters. These samples were selected using two

⁵ **Wave period:** is the reciprocal of the number of waves that pass a particular point in the surf zone, in a minute.

criteria: (1) to span the greatest range of species richness, and (2) to include the largest possible range of species. The beaches used were subsequently selected as the beaches with the least, second highest and highest number of species. A dendrogram (using Bray-Curtis similarity) and MDS-plot were constructed for each beach, using abundance (per m²) per species, per level on the beach (excluding all empty stations). A total of 15 beaches were analysed this way. Kite diagrams were constructed for these 15 beaches based on abundance (per m²), per station for each species. Faunal zones were *post hoc* defined as relatively similar, consecutive (or second consecutive⁶) stations.

2.3 RESULTS

2.3.1 Beach morphodynamics

The beaches that were sampled varied greatly in physical and biological characteristics. Although all the beaches receive swell predominantly from a south-westerly direction, there was great variation in breaker height (H_b) both among and within sites, at the times of sampling. Since wave height shows great temporal variability, more stable physical parameters such as grain size and slope, were also used to characterise these beaches. The sandy beaches of this study were mostly composed of fine (10 beaches) to medium (17 beaches) grained sand. The beach with the finest sand had a mean particle diameter of 137 μm , and the coarsest beach had 452 μm sand (Table 2.1). Slopes ranged from a steep 1/10 to a flat 1/64, although most beaches had a medium gradient 1/25 – 1/40 (Table 2.1). Beach widths were not exceptionally large. The beaches were classified as exposed to very exposed (i.e. having an EXP > 10 - 15). A few beaches did not score values greater than 10 but are generally located in large bays and not facing directly into the predominant swell direction.

⁶ **Second consecutive:** meaning that stations that were included can be separated by one or two stations only, for example station 1, 2 and 4 can make up a faunal zone, but not stations 1, 2 and 5.

According to the dimensionless fall velocity values (Ω), only three truly dissipative beaches were sampled (PB3s2, PB4 and STRAND i.e. $\Omega > 6$) and one reflective beach (VELD with $\Omega < 1$). The other 23 beaches were all in the intermediate range. Using the BSI index (incorporating tide range) as an alternative way to define the beach states, the findings were slightly different to the beach states defined by Ω . Since all the beaches sampled are microtidal beaches (i.e. having a tidal range of less than 2 m) the BSI and RTR had little variation (Table 2.1). Using the categories strictly as outlined by Masselink and Short (1993), four beaches were classified as reflective (i.e. PB3s1, DBs2, BBs1 and VELD having BSI < 0.5) and five beaches were described to be high energy intermediate to dissipative (i.e. PB3s2, PB4, YZC, YZS, STRAND having BSI of 1.0 - 1.5, Table 2.1). The other 18 beaches are described as low to medium energy, intermediate beaches (Table 2.1). A range of microtidal beaches was thus sampled (according to the RTR, BSI, or Ω -values), of which most of the beaches were of an intermediate type.

All of these indices (RTR, BSI, or Ω) incorporate wave height as a parameter. Wave height is highly variable, especially on a seasonal basis. The index values are exceptionally high for some beaches and probably not representative of the modal beach state. This can be seen in the mean wave height values obtained for DERN, PB1 and PB4, which range 3 - 3.1m (Table 2.1). This sampling event was during August 1997. These beaches were resampled⁷ in a different season (April 1998) as DBs1, PB1s1 and PB3s1 with wave height values 33 – 50% of the previous season. A concurrent change in grain size resulted in an order of magnitude change in the Dean's values obtained for PB4 ($\Omega = 11.4$) and then sampled as PB3s1 ($\Omega = 1.8$) between the different seasons. The number of species, however, only increased from nine in winter to 10 during summer. The beach state value of 11.4 is considered as an exception since this is a microtidal beach in Namibia, with medium grained

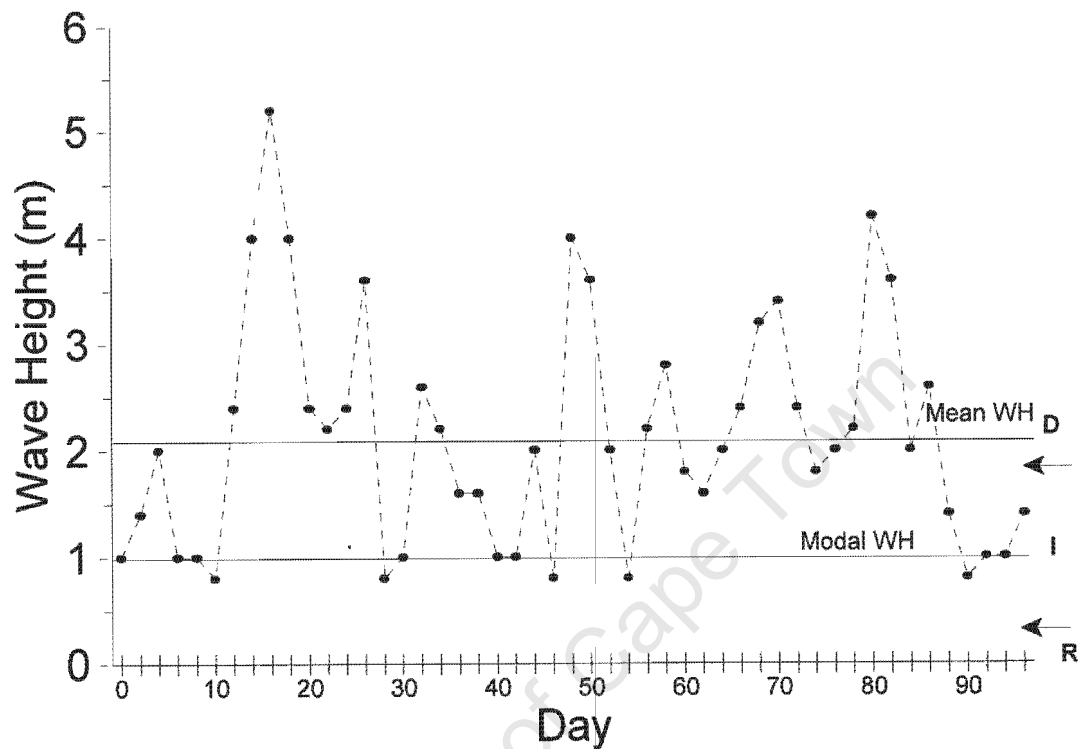
⁷ **Resampled:** meaning that the same three beaches were sampled again, but not in exactly the same location ($\pm 150 - 200$ m variation along pocket beaches spanning 2 – 7 km). The beaches are hence treated as different samples because of spatial variation but also the seasonal change.

sand and a moderate slope. The high waves resulted in the exceptionally high Ω -value. This is an indication of the variation that is possible within a beach, between seasons.

In addition the 'modal' beach state is also dependent on calculation of the beach state. Fig. 2.2 represents measurements of wave height obtained for Sundays River Beach over a 96 day period, as measured every second day by Donn *et al.* (1986). They related changes in the populations to changes in physical conditions, but also highlighted the extreme variation in wave height. On one occasion during the 96 day of sampling, wave height changed from 0.8 m to 5.2 m in 6 days. During the whole 96 days of sampling, identical wave heights for consecutive sampling events were only obtained on four occasions (Fig. 2.2). The modal wave height (which was calculated as 1 m) was only encountered on seven occasions out of 47 sampling events. Moreover, mean wave height was calculated as 2.1 m. This is more than double the modal wave height. Beach morphodynamic state values (Ω) were calculated from this data. This was done using the reported grain size value by Donn *et al.* (1986), and the wave period obtained for Sundays River Beach (as one of the 27 beaches sampled in the current study) as a 'theoretical' wave period value. The Ω -values ranged 1.5 - 10.3, which spans from almost completely reflective to dissipative. The mean Ω -value was calculated as 4.2, whereas the modal Ω was 2.0. This emphasises the limitations of 'snapshot' sampling, and especially in the estimation/measurement of modal beach state.

Being aware of the constraints involved using the indices, the 27 beaches are considered a representative sample, having dimensionless fall velocity values 0.65 - 7.26 (with the exception of PB4). A range of microtidal beaches was thus sampled spanning a fair range of morphodynamic types (although mostly intermediate) with variable amounts of wave energy. It is expected that there will be a concurrent change in the macrofaunal communities along these beach types.

Fig. 2.2 Variation in wave height on Sundays River Beach as measured by Donn *et al.*, (1986), over a 96 day period. **Mean WH** = mean wave height (or H_b) calculated over the 96 days, and **Modal WH** = mode of wave height measured for the 96 days. The theoretical limits for dissipative (D), intermediate (I) and reflective (R) wave climates (as calculated by Donn *et al.*, 1986; according to Short and Wright, 1983) are indicated by the arrows.



2.3.2 Macrofaunal component

Species richness, abundance and biomass

The species richness ranged 5 - 21 species (Table 2.1), with VELD and PB1 as exceptions where only two and three species were found, respectively. The abundance and biomass values ranged from very poor on some beaches to extremely rich (especially in the South African context) on other beaches (Table 2.1). In attempting to relate the community parameters to the physical environment very few significant correlations were obtained. The species richness and log abundance per running meter were both significantly correlated (at $P < 0.05$) to grain size (in ϕ -units) and to slope (Fig. 2.3), but not to Ω , BSI or EXP. Log biomass was not significantly correlated to slope (Fig. 2.3) or any of the indices (at $P = 0.05$).

Table 2.1 Physical and biological parameters of 27 oceanic beaches sampled.

Beach	H _b (cm)	T _b (s)	W _s (μ m)	Dean's (Eq.1)	Slope (1/H)	BWIDTH (m)	RTR (Eq.2)	BSI (Eq.3)	*EXP	No.SPP	ABUN	BIOM
1. PB1s1	147.5	9.2	313	3.9	16.4	56	0.55	0.69	15	8	13	10
2. PB1s2	204	12.5	401	2.98	15.3	53	0.73	0.81	14	6	16	40
3. PB2s1	144	9.4	370	3.21	19.4	55	1.17	0.89	15	9	50	57
4. PB2s2	196	13.6	384	2.8	18.1	41	0.91	0.86	12	8	54	432
5. PB3s1	86	10.7	342	1.81	26.1	75	0.90	0.44	13	8	112	49
6. PB3s2	185	9.4	240	7.26	43.1	88	0.89	1.20	9	8	57	36
7. DBs1	62	11.5	245	1.98	25.9	51	2.31	0.66	12	7	32	27
8. DBs2	96	10	346	2.16	19.2	58	0.68	0.44	17	9	15	15
9. BBs1	48	15	226	1.34	45.5	105	2.40	0.47	14	11	157	91
10. BBs2	78	6.5	214	5.02	27.7	74	1.12	0.81	15	8	71	18
11. DERN	310	9.7	408	5.84	57	98	0.27	0.85	12	7	118	116
12. PB1	300	10	452	4.86	12.5	36	0.37	0.89	17	3	73	6
13. PB4	310	10	255	11.41	32	72	0.45	1.32	14	11	9	79
14. YZN	195	15.8	285	3.63	24.4	100	0.70	0.86	13	15	225	279965
15. YZC	118	10	210	5.74	30	110	1.14	1.03	13	15	1179	11690
16. YZS	220	13.6	334	5.93	46.1	88	0.59	1.02	12	5	138	148
17. BBE	71	15	247	1.74	27.8	62	1.89	0.59	12	12	73	688
18. PATER	50	15.8	195	2.21	17.9	50	2.58	0.66	10	12	196	325
19. VELD	30	10.3	342	0.65	10.1	30	4.50	0.32	9	2	4	6
20. SUND	190	16.7	232	3.8	35.7	81	0.80	0.91	16	19	102	1391
21. VANS	170	11.5	252	4.39	34.2	90	0.89	0.97	15	18	193	2946
22. MAIT	144	11.5	268	3.72	40.4	120	1.08	0.92	14	13	204	3112
23. KING	46	12.5	220	1.39	30.3	76	3.00	0.53	12	12	12	172
24. STRAND	78	9.4	137	6.29	64.4	130	1.90	1.10	8	19	756	232
25. MACAS	70	10	174	3.55	43.4	106	2.00	0.61	8	20	219	71
26. COTTON	52	10.3	170	3.07	34.5	86	2.90	0.83	9	21	105	247
27. MUIZ	62	11.5	362	1.05	33.3	81	2.35	0.46	14	17	38	458

*Exposure Rating System following McLachlan (1980a), **No.Spp** = Number of species; **ABUN** = Abundance ($10^2.m^{-1}$); **BIOM** = biomass ($g.m^{-1}$).

The physical parameters that appear to differentiate the communities on a macroscale (even within the limited microtidal range) are grain size and slope. Thus, beach morphodynamic state *per se* (as per Ω or BSI) does not seem critical to the community structure on these beaches. This is probably due to the continuous, high variability in wave height, but also since only microtidal beaches spanning three (out of a possible nine) beach types were sampled. Furthermore, most of the beaches were of the intermediate type.

Biogeographical provinces

The macrofauna present were typical of the biogeographical areas in which each beach was located. The macrofauna found on the south coast beaches were characteristic of the warm-temperate coast (including gastropods such as *Bullia pura*), while typical cold-temperate beach species were found on the west coast, e.g. *Hyale saldanha* (Day, 1969; Branch *et al.*, 1994). There were few species that occurred around the entire coast, inhabiting beaches in both the warm and cold temperate provinces (*sensu* Brown and Jarman, 1978). Specifically, beaches east of Cape Point harboured species such as *Bullia rhodostoma*, *B. pura* and *Donax sordidus*, while *Tylos granulatus* was present on one beach in False Bay and on most of the Namibian beaches. The sandhoppers, *Talorchestia australis* and *T. quadrispinosa*, were found on the Western Cape and Namibian beaches, while *T. capensis* only frequented the beaches of the Eastern Cape. Cirolanid isopods occurred on beaches throughout this biogeographical range and were not specific to any particular area. Five different cirolanid species were found, one of which, *Eurydice* sp., is considered to be a new, undescribed species (see *Appendix 1* for a complete species list).

Multivariate analysis was used to determine whether the macrofaunal communities can be separated, and if so whether the separations are based on physical parameters such as beach type and/or biogeographical province. Three large clusters were identified on the

MDS-plot, which seem to be related to the species composition and abundance per beach (Fig. 2.4). The cluster (REFL) containing only three beaches i.e. VELD, PB1 and YZS, had very low species diversities, with only 2, 3 and 5 species respectively. The larger centre cluster (COLDTEMP) constitutes beaches with intermediate species diversities (6 - 15 species), while the right hand cluster (WARMTEMP) is based on beaches with the highest species diversities (12 - 21 species). The two left clusters (containing beaches #1 - #19) are all from the west coast region, while the cluster on the right constitutes beaches from the south coast, with the exception of Paternoster (#18, Fig 2.4). This separation between the two coasts is not surprising, since many of the species are characteristic of the specific coast, but there is a consistently higher species richness on the warm-temperate beaches of the south coast. The clusters therefore broadly separate beaches in terms of geographical region based on species richness and composition.

A further separation within biogeographical provinces was investigated, to elucidate whether the species richness within each region was related to physical beach characteristics (Fig. 2.5). The two larger clusters (COLDTEMP and WARMTEMP), constituting each temperate region, could be separated into two smaller clusters (Fig. 2.5). The two smaller clusters within each region also appear to be based on differences in species richness on these beaches.

In the warm-temperate area, the beaches #20 - #23 (Fig. 2.5) which are all situated around Port Elizabeth (Fig. 2.1), seem to have different beach communities from those of beaches #24 - #27 (all from False Bay). This is probably not only because of spatial separation, but also because of different physical conditions between these groups, and specifically different exposure and to a lesser extent, Ω . The beaches around Port Elizabeth range from exposed to very exposed, whereas the beaches from the eastern side of False Bay are all sheltered (McLachlan, 1980a). Semi-permanent burrows harbouring *Abaranicola* (a polychaete) and *Callianassa kraussi* (sand prawns) were observed in False Bay during sampling, which is an indication of the lower exposure.

The separation between the cold-temperate beaches #1 - #13 (which are Namibian beaches) and #14 - #18 (excluding #16), which are found along the west coast of South Africa, is less obvious. Community patterns seem to be related to region (i.e. northern and southern west coast), but also a combination of grain size, slope and beach morphodynamics. The Namibian beaches shared species characteristic of coarse sand beaches with steep slopes, rather than species common to the physical conditions encountered on the southern west coast beaches. The biota can be separated based on the absence of species such as *B. digitalis*, some coleopterans, and the polychaetes *Nephtys capensis* and *Scolecopsis squamata*, from the Namibian beaches (Appendix 1). In combination, the Namibian beaches appear to have greater Ω -values, as a result of the wave heights encountered during the sampling periods.

An evaluation of the distribution pattern of all the beaches on the MDS-plot (as obtained in Fig. 2.4), and the physical parameters, indicated that there is no single physical parameter that broadly explains the specific community patterns across the biogeographical regions. Grain size (ϕ) seems to yield the best explanation (Fig. 2.6). Sediment particle size is generally larger on the west coast, with corresponding low number of species. As the grain size decreases on the beaches sampled in False Bay (FB) and Port Elizabeth (PE), the number of species concurrently increased. However, none of the indices in isolation gave a satisfactory explanation of the distribution of the biota (Fig. 2.6).

A regression of the number of species *versus* grain size (in ϕ -units), or *versus* beach state (Ω) indicated a separation between the two biogeographical provinces (Fig 2.7). Although, only the regression between the number of species of the west coast and grain size was significant ($P=0.004$, $R^2=0.397$ $n=19$; Fig 2.7), it is important to realise that this possible separation exists. The sample size of the south coast was small (only seven beaches). If the

Fig. 2.3 Significant regressions obtained between the community parameters i.e. species richness, abundance ($\text{Log}_{10} \text{ no.m}^{-1}$) and biomass ($\text{Log}_{10} \text{ g.m}^{-1}$), and the physical environment.

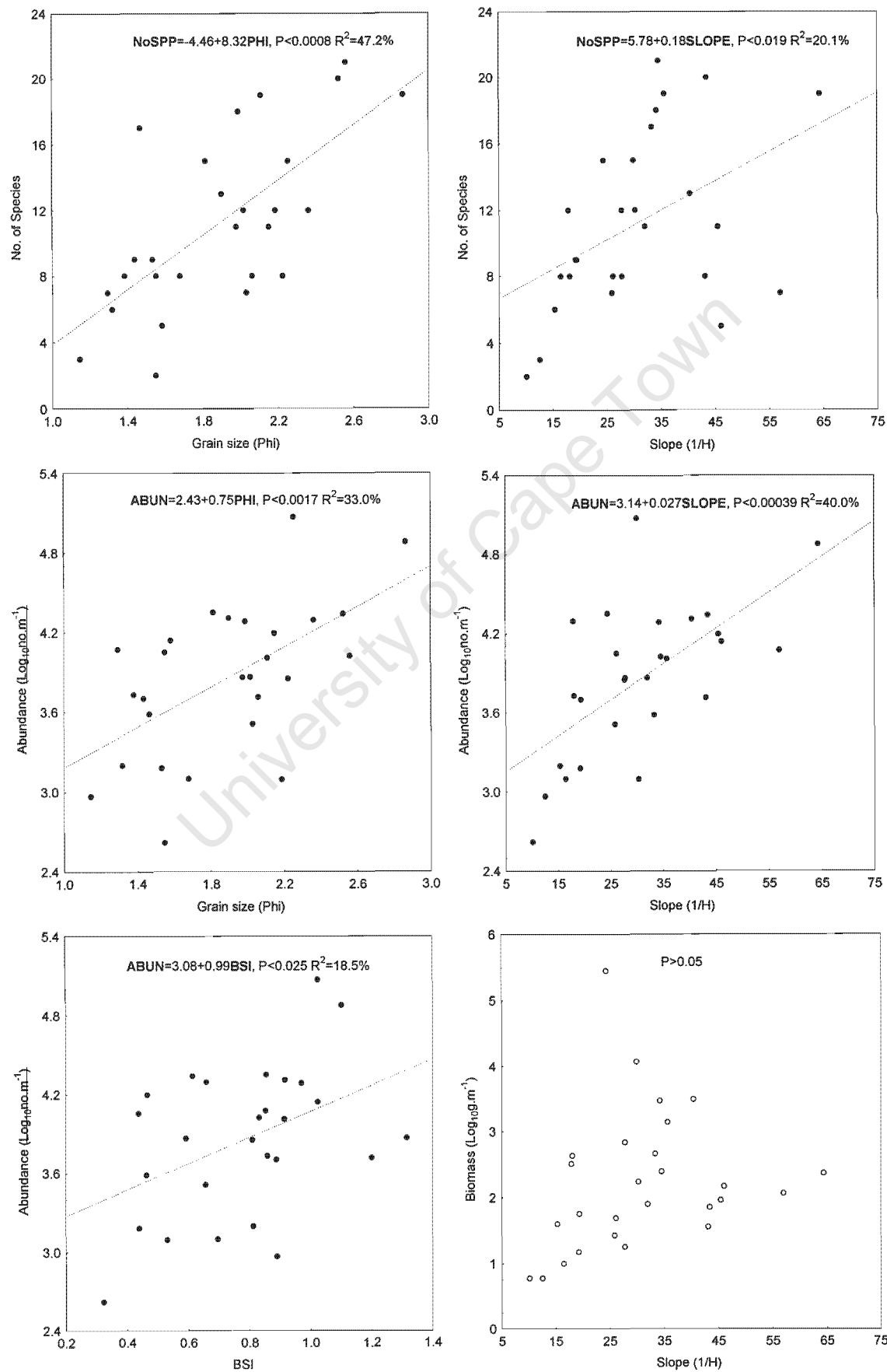
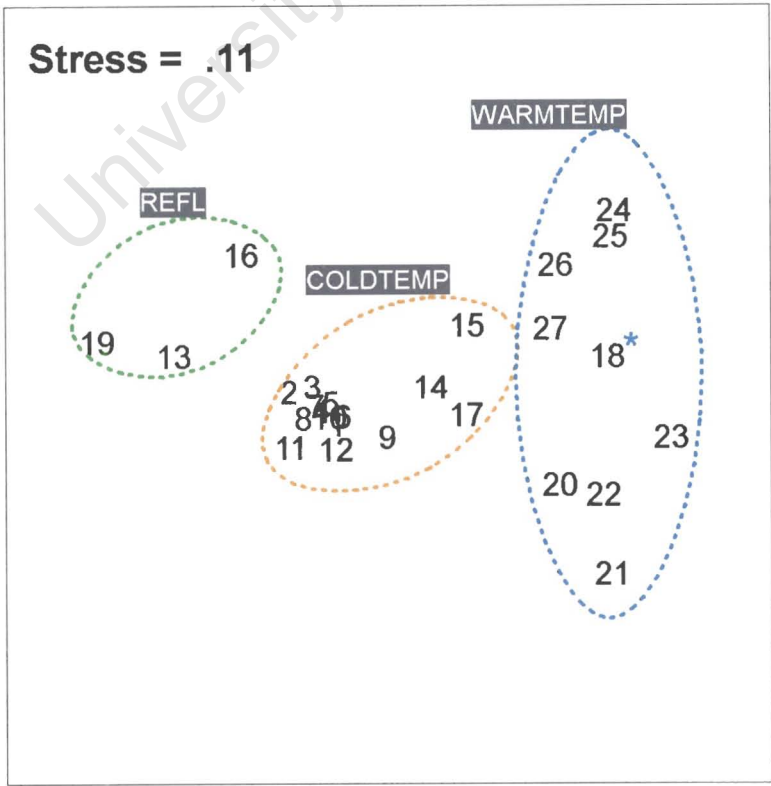
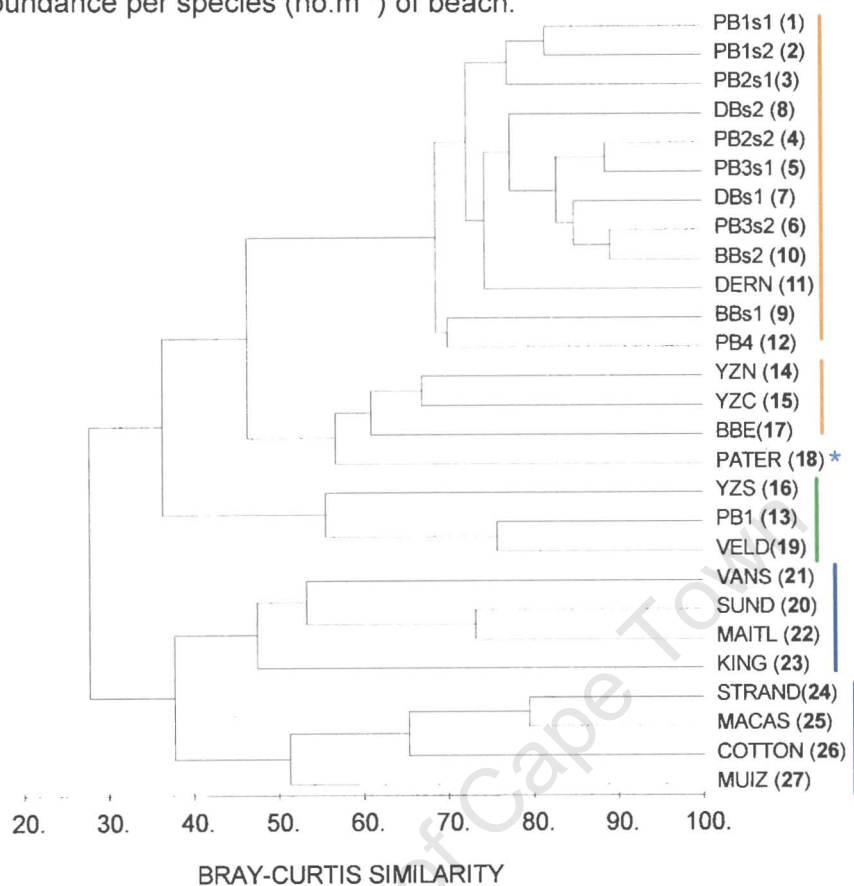


Fig. 2.4 Beaches separated into beach morphodynamic types and biogeographical province by means of multivariate analysis, using dendrograms and non-metric MDS, based on abundance per species (no.m⁻¹) of beach.



*PATER = Paternoster, which is a west coast beach clustering with east coast beaches from PE and FB.

Fig. 2.5 Physical factors superimposed on the MDS-plot of the beach communities across the biogeographical regions. The magnitude of the physical parameters of the warm-temperate region is proportional to the size of the circles, whereas the relative magnitude of the physical parameters of the cold temperate beaches is indicated by the size of the hexagons.

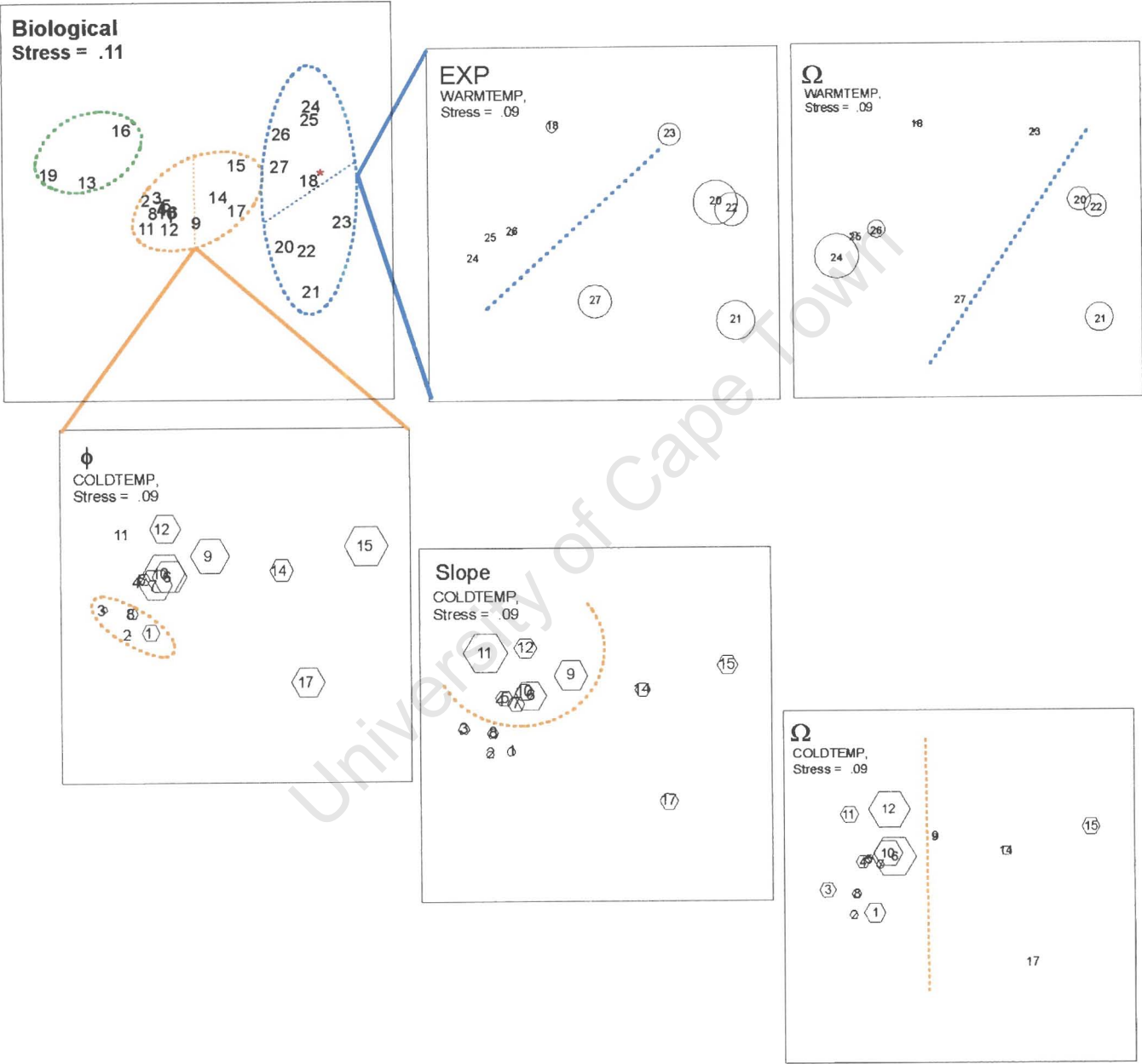


Fig. 2.6 MDS-plot of the beach community, and the physical parameters that seem responsible for the changes in the biota across different biogeographical provinces. These factors are grain size (ϕ), tide range (RTR), exposure (EXP) beach morphodynamics (Ω) and combined beach state and tide range (BSI). The size of the symbol is proportional to the magnitude of the parameter for that particular sample.

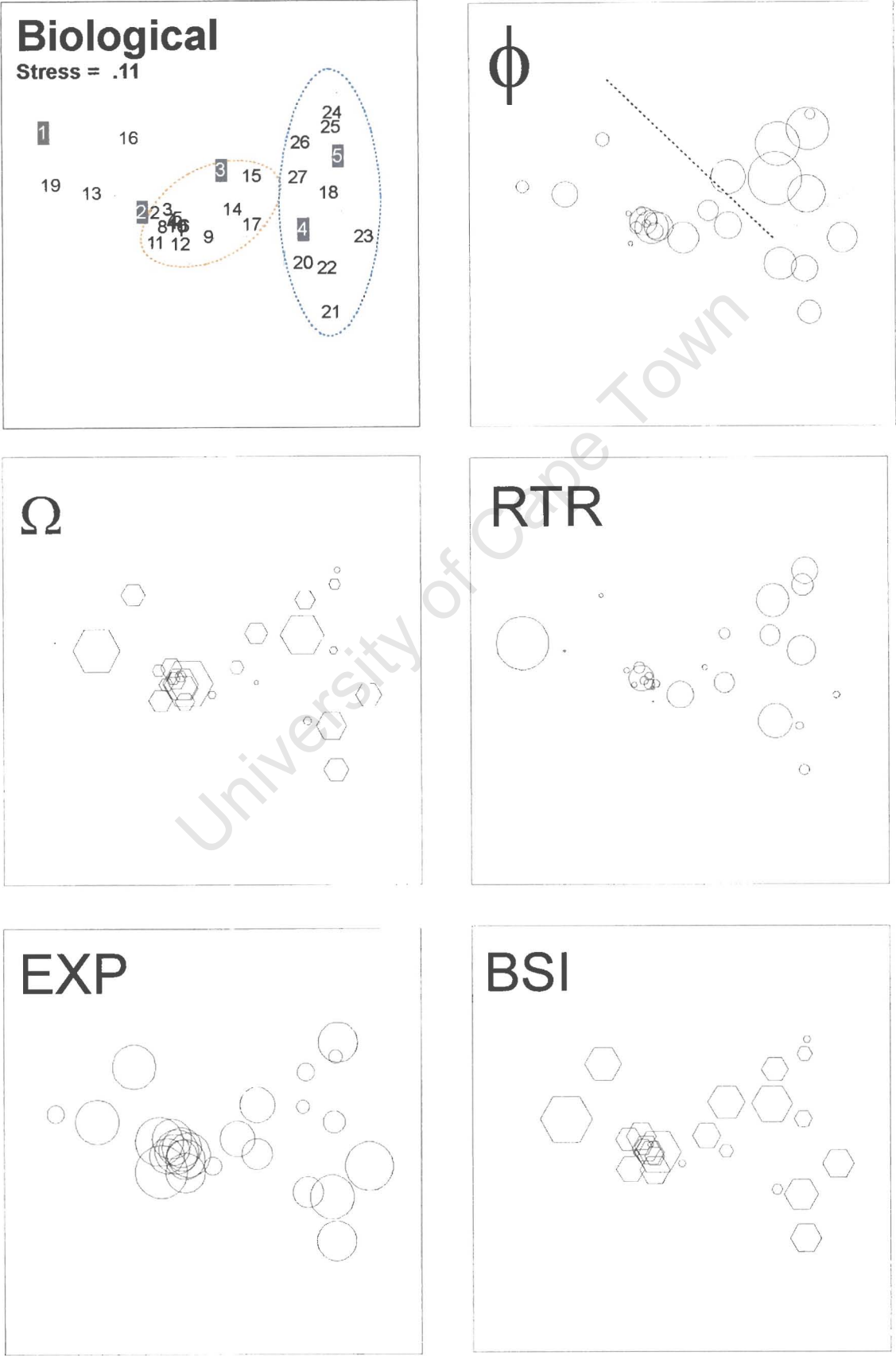
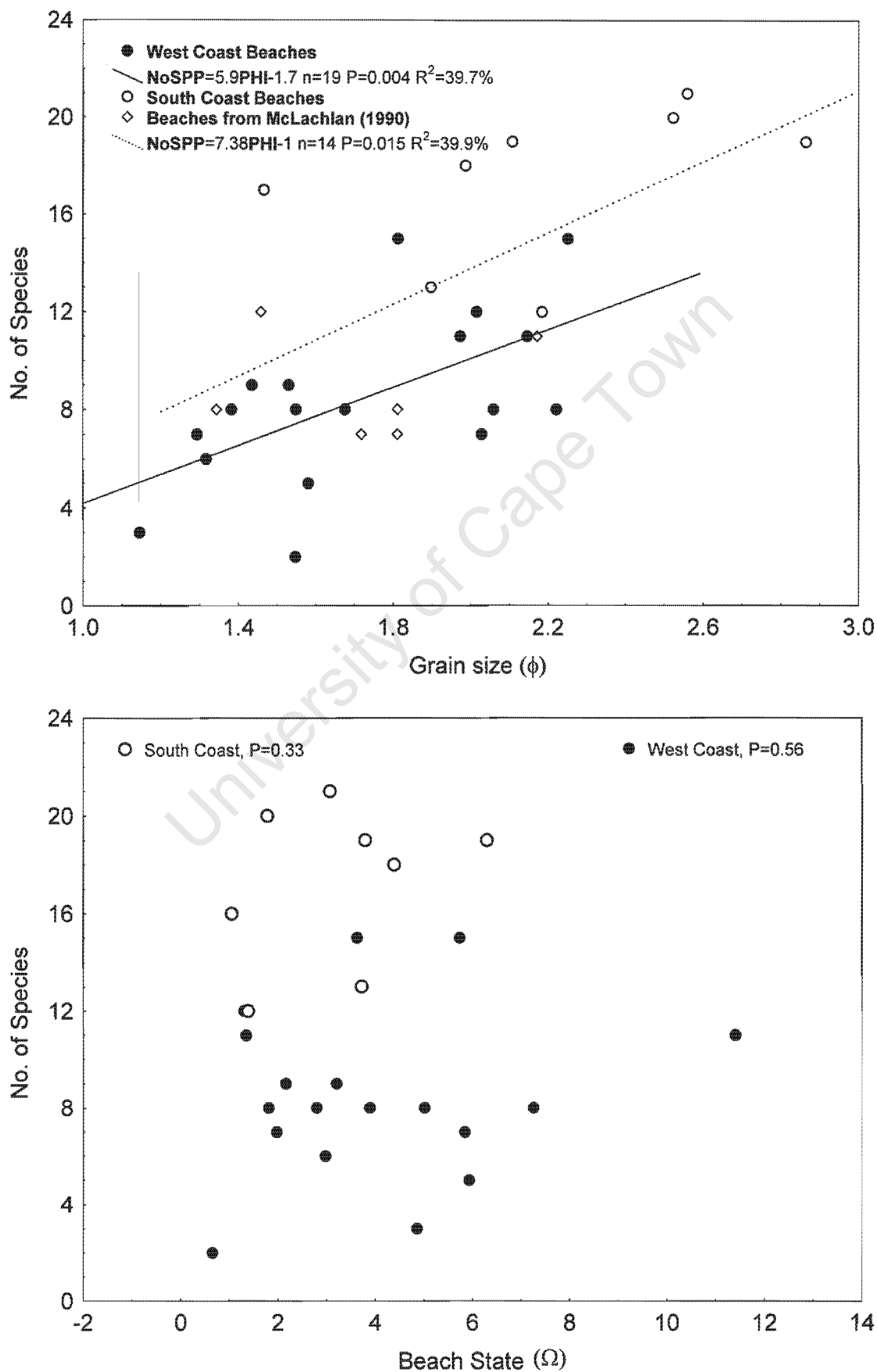


Fig. 2.7 Regressions of the number of species vs. grain size (ϕ) and beach state (Ω), between two different biogeographical provinces.



sample size for the south coast is augmented by including values from McLachlan (1990), a significant regression ($P=0.015$, $R^2=0.399$ $n=14$; Fig. 2.7) is also obtained for the number of species and grain size (Fig. 2.7). A comparison of slopes and elevations between the south coast and west coast beaches indicated no difference between slopes, but a significant difference between the elevations (Student $t_{0.05(2),30}=2.82$ $P=0.0085$; Zar, 1984). The south coast therefore has more species per grain size, than an equivalent beach would have on the west coast. No significant regressions (with or without an augmented data base) could be obtained for the number of species and beach morphodynamic state, but the east coast scored consistently higher in terms of the number of species per Ω -value (Fig. 2.7).

Zonation

Mesoscale

The possibility of specific zonation patterns was investigated according to the five small clusters since there seems to be a very specific community associated with each cluster in Fig. 2.6. Only three beaches per geographical-morphodynamic group were used in order to simplify this analysis. The beaches with the lowest, highest and second highest number of species, were selected per cluster. This should include the most diverse communities for each of the regions. The beaches are discussed according to geographic-morphodynamic type.

i. West coast - reflective beaches

Characteristic of these beaches was the exceptionally low number of species per beach. VELD (beach #19) had only two species, while PB1 (beach #13) had three species and YZS (beach #16) five species (Fig. 2.8). These beaches are dominated by the same small crustaceans. These were *Talorchestia* spp. occurring on the top of the shore and *Excirolana natalensis* at the mid-shore (Fig. 2.8). PB1 and YZS had an additional cirolanid isopod, namely *Eurydice kensleyi*, that occurred at the bottom of the shore. The species richness of

YZS was increased by two air-breathing species that occurred at the top of the shore, commonly found on the driftline of beaches, but not limited to shores. These were insect larvae and a yellow beetle.

Two clusters can consistently be identified on the MDS-plots from each of these beaches (Fig. 2.8). These clusters do not always constitute the same species, but they tend to be one from the top of the shore containing the air-breathing *Talorchestia*, and a second lower-shore species, with either *Excirolana natalensis* or *Eurydice kensleyi*. There thus appear to be two zones on these reflective beaches.

ii. Namibian - intermediate beaches

Based on the communities involved, this would include beaches #1 - #12. The three beaches that were investigated for zonation were PB1s2, PB4, BBs1 (i.e. beaches #2, #12 and #9 from Fig 2.4). Two to three zones appear to be present on these harsh intermediate beaches (without considering single stations as zones; Fig. 2.9). The zones represent high-shore (stations 1 - 3), mid-shore (stations 4 - 6) and low-shore (stations 7 - 11) components (Fig. 2.9). It was difficult to identify a third zone on PB1s2, because the dendrogram indicate stations 7 and 8 to be only 40% similar whereas the MDS-plot place these stations relatively close together. Furthermore, only five species were present on PB1s2, resulting in empty stations. Stations 7, 8 and 11 shared some species, but not sufficient to identify it as a zone (according to the definition of consecutive stations used in this study). Generally, the high-shore was characterised by sand hoppers, *Talorchestia quadrispinosa*, and *Excirolana natalensis*, while the mid-shore was dominated by *Pontogeloides latipes*. The faunal communities on the low-shore of PB4 and BBs1 were diversified, with amphipods, polychaetes, cumaceans or gastropods being present. The low shore was, however, dominated by the nemertean *Cerebratulus fuscus*, the mysid shrimp, *Gastrosaccus psammodytes*, the amphipod *Mandibulophoxus latipes*, and the cirrolanid isopod *Eurydice*

kensleyi. It was therefore concluded that the number of faunal zones is a function of species diversity.

iii. West coast – intermediate/dissipative beaches

Three to four faunal zones can be identified on the representatives of this beach state (Fig. 2.10), which are YZN, YZC and BBE (i.e. beaches #14, #15 and #17, respectively, from Fig. 2.4). These groups range from the high-shore, to mid- and lower-shore, plus an additional zone in the swash. Using YZN-beach with 15 species as an example, it appears as if the high-shore stations were dominated by the air-breathers (i.e. *Talorchestia quadrispinosa*, *Tylos granulatus*, coleopterans and insect larvae). The mid-shore was dominated by the three cirolanid isopods (*Excirolana natlensis*, *P. latipes* and *Eurydice kensleyi*) although *E. kensleyi* extended all the way across the shore on this particular beach. *G. psammodytes*, *S. squamata* and *M. latipes* had peak abundances on the low shore, while the swash zone was characterised by the presence of *C. fuscus* and the molluscs *D. serra* and *B. digitalis*.

iv. South Coast - high energy intermediate beaches

These beaches were sampled around Port Elizabeth (i.e. beaches #20, #21 and #23 in Fig. 2.4). Species very typical of the area were encountered, i.e. a variety of polychaetes and amphipods but especially swash riding molluscs. It was, however, difficult to identify consistent faunal zones for these species, and either two or three zones could be identified for the beaches if single stations are not considered as zones (Fig. 2.11). There was a general absence of high-shore species on KING (Kings beach, #23), hence only two faunal zones. This may be due to a lack of organic input on the driftline and macrophyte accumulations being restricted to the surf zone (Van der Merwe and McLellan, 1987). Moreover, this is an urban beach which is regularly cleaned and organic input is removed.

Additionally, the beach is characterised by regular overtopping⁸ during spring tides, with large pools of water accumulating on the back-beach, which would make it difficult for air-breathers to survive. Most fauna on Kings Beach can be grouped as either mid- or low-shore species (Fig. 2.11).

It is peculiar that the macrofauna of VANS and SUND (i.e. Van Stadens and Sundays River Beaches) are divided into a high shore component, generally constituting stations 1 and 2, and an intertidal component, with large overlap between species of the lower shore. This is probably due to the molluscs, such as *D. serra* and *B. rhodostoma*, which occur almost across the entire beach face. Size segregation, however, occurs within these species, across the shore, but this is not selected for by the MDS-plots, dendrograms or kite diagrams. Despite the wide distribution of the species, each of these species has a level of peak abundance, which makes it possible to identify faunal zones, especially if the dominating influence of the top-shore stations (1 and 2) is eliminated.

A second MDS-plot including only stations 3 - 10 of VANS (#21), showed a mid-intertidal zone as stations 4 - 8, and a low-shore zone with stations 9 and 10. It is concluded that there are generally three faunal zones on south-coast intermediate beaches, with a clear separation between the air-breathers of the top-shore and the two weaker intertidal zones dominated by swash riding molluscs in the mid-shore, with polychaetes, amphipods and a nemertean species dominating the low shore.

v. South coast – low energy intermediate/dissipative beaches

These beaches were sampled along the northern shore of False Bay (FB), and are sheltered from the predominant swell by the Cape Peninsula and shallow reefs. Although these beaches are spatially far apart from the other south coast beaches, they occur in the same

⁸ **Overtopping:** can be observed on beaches with a flat back-beach area (often as a result of beach accretion) with spring high tides washing over the berm, and pools of sea water collect at the back of the beach above the driftline (pers. obs).

biogeographical province (as those from Port Elizabeth, just at the opposite end of the province; Fig. 2.1). Since they are from the same biogeographical region they share most of the species with the PE beaches, but the species richness is higher on the FB beaches (16 - 21 species). This is primarily due of a lack of exposure, which results in the unique presence of burrow formers, such as the sand prawn *Callianassa kraussi* and the polychaete *Abarenicola* sp., in the intertidal. Yet, 'high-energy' species such as *D. serra*, *D. sordidus* and *B. digitalis* were present, although in relatively low numbers compared to other beaches in the area and high energy beaches around Port Elizabeth.

Three or four faunal zones were identified on these sandy shores (Fig. 2.12). The zones that appeared consistently for all three beaches were the zones that can be related to Salvat's (1964 cited by McLachlan, 1988) zones of retention, resurgence and saturation. The air-breathing component appears to be limited to the top station (except on MACAS where flying insects were found at the bottom of the shore, since it was sampled during strong offshore winds). The zone of drying (according to Salvat's scheme) is thus probably under-represented in this sampling. There are three consistent faunal zones present in the intertidal.

Macroscale

It is difficult to identify one single zonation scheme that can explain the distribution of all species on all of these beaches. Since they are from different biogeographical provinces, wave regimes and different beach morphodynamic types, different numbers of zones are present. Two trends seem apparent. Firstly, the number of zones present increases with a general increase in species richness. Secondly, there seems to be an increase in the number of zones from the most reflective states (which was two) to the beaches with more dissipative states (with three or four zones), for both geographical regions. The air-breathing fauna of the reflective beaches tend to span a greater number of physical zones than on the more

Fig. 2.8 MDS-plots, dendrograms and kite diagrams for reflective beaches on the west coast. Clusters indicate faunal zones based on stations along a transect (with station 1 on the driftline and station 10 or 11 at SLWM). Kite diagrams indicate faunal abundance (m^{-2}).

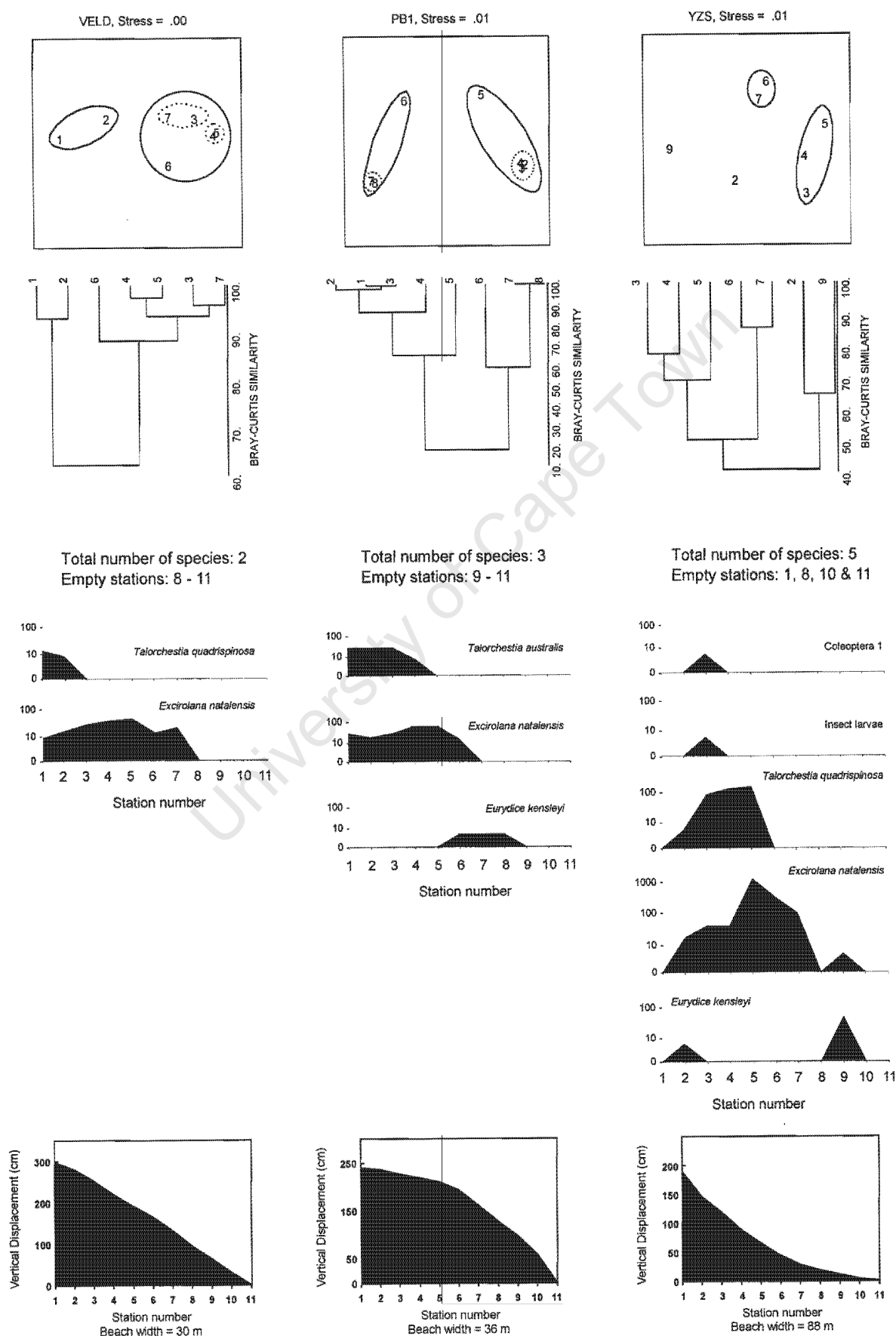


Fig. 2.9 MDS-plots, dendrograms and kite diagrams for Namibian intermediate beaches. Clusters indicate faunal zones based on stations along a transect. Kite diagrams indicate faunal abundance (m^{-2}) across the shore.

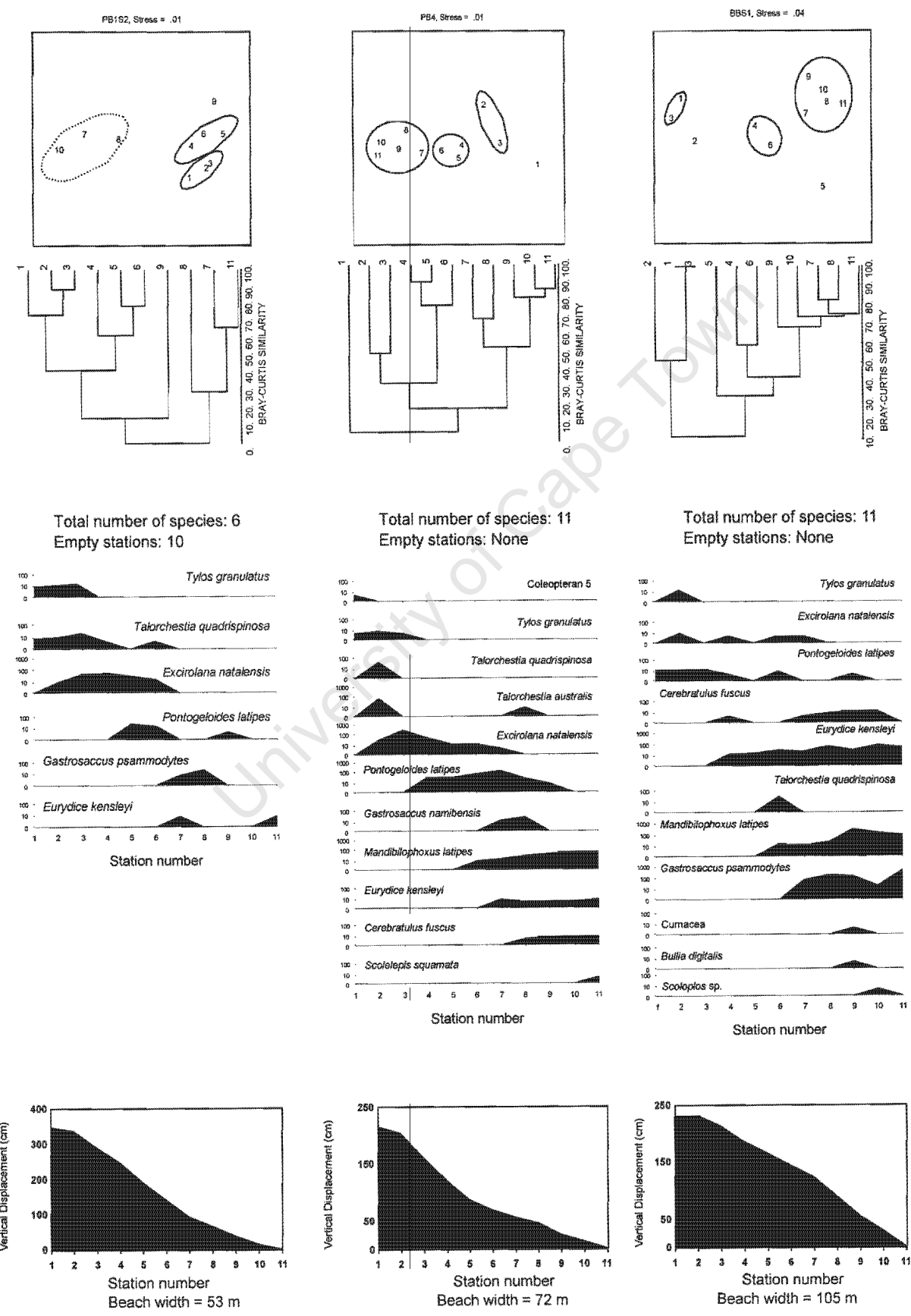


Fig. 2.10 MDS-plots, dendrograms and kite diagrams on beaches indicated as high energy intermediate-dissipative along the west coast. Clusters indicate faunal zones and kite diagrams indicate faunal abundance (m^{-2}) across the shore.

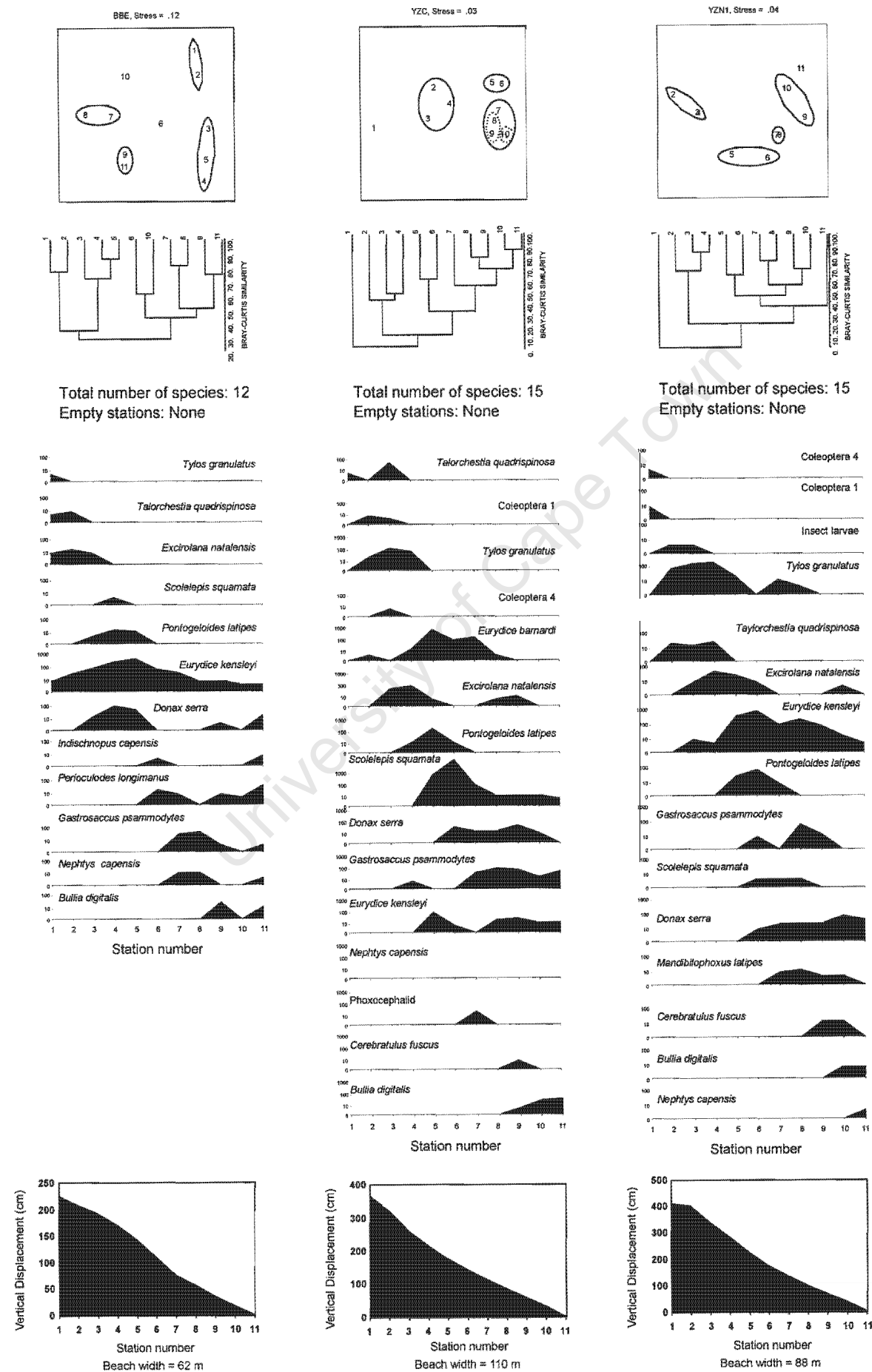


Fig. 2.11 MDS-plots, dendrograms and kite diagrams for high energy, intermediate beaches along the south coast. Clusters indicate faunal zones based on stations along a transect. Kite diagrams indicate faunal abundance (m^{-2}), across the shore. (Species with a bimodal distribution such as *D. serra* complicate the identification of strict zones).

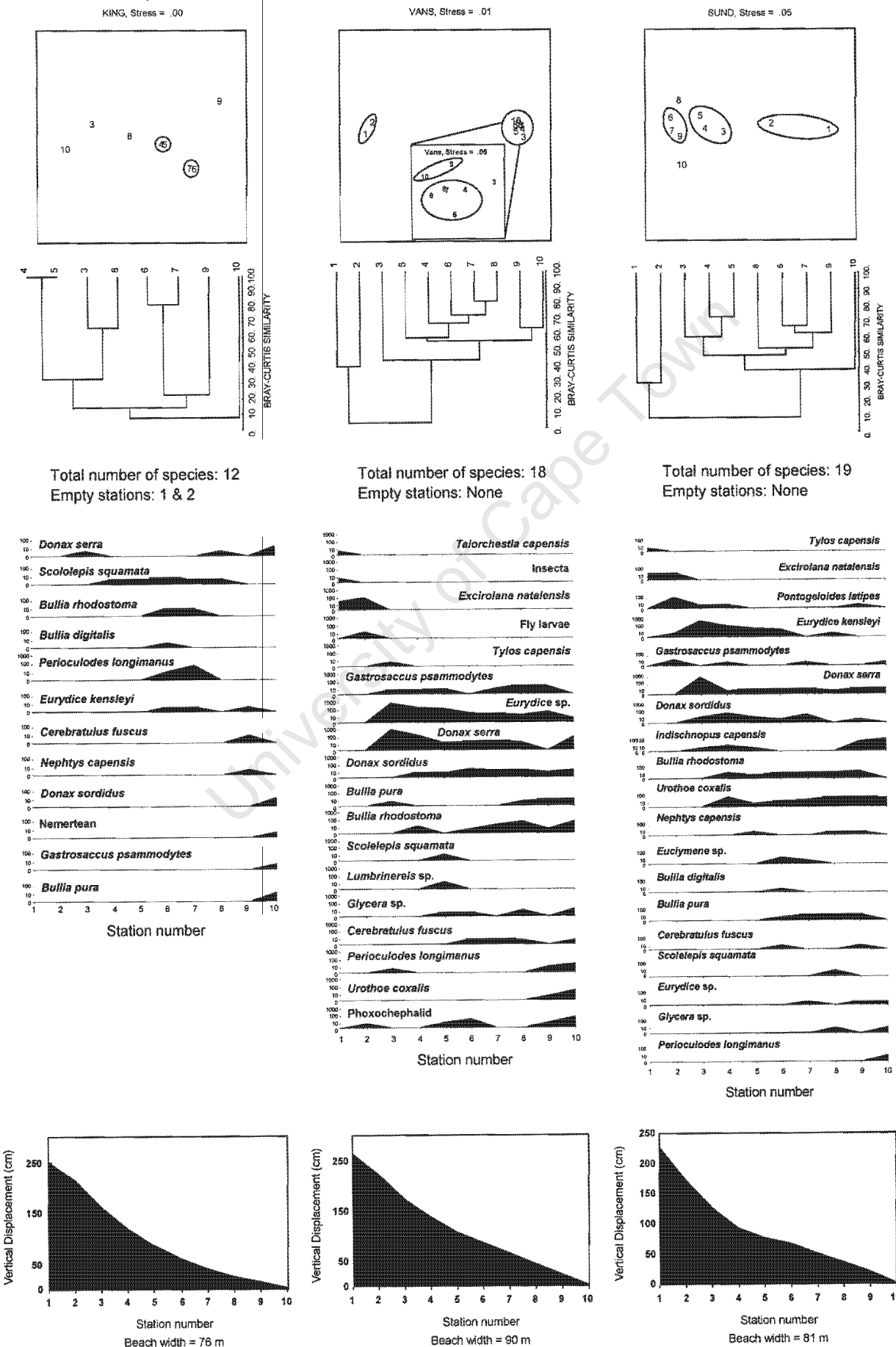
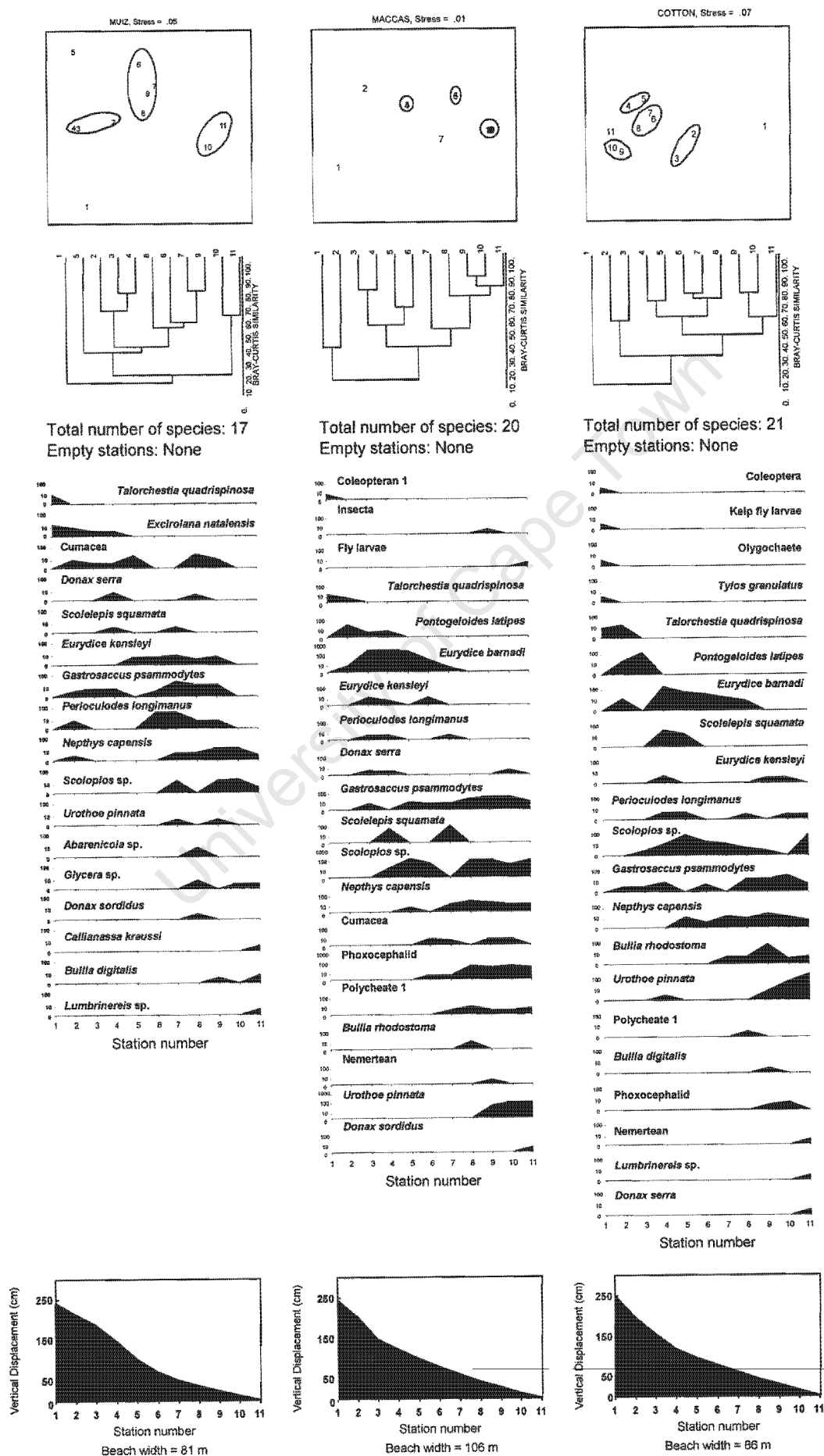


Fig. 2.12 MDS-plots, dendrograms and kite diagrams of the low energy intermediate/dissipative beaches in False Bay. Clusters indicate faunal zones based on stations along a transect. Kite diagrams indicate faunal abundance (m^{-2}) across the shore.



dissipative states. *Talorchestia* individuals were found down to station 5 and 6 on PB1 and YZS, which are reflective beaches, whereas this species was found only in stations 1 and 2 on MACAS and COTTON, which are dissipative beaches in False Bay.

If the air-breathing fauna is excluded (and hence fauna of the drying zone according to Salvat), and only the intertidal zones are taken into account, then the following appear to be the case: reflective beaches have only one intertidal faunal zone, whereas intermediate beaches tended to have two faunal zones, and dissipative beaches three faunal zones. It is difficult to determine which of the two trends (i.e. an increase in zones with species richness or an increase of zones according to beach state) is the cause and which the effect. The most likely mechanism is probably that dissipative conditions (as stated by SEH) can harbour more species, and hence should have more faunal zones.

2.4 DISCUSSION

The beaches that were sampled varied greatly in wave height, grain size and slope, and exposure. When these variables are used to define the beaches in terms of the dimensionless fall velocity (equation 1), RTR (equation 2) and BSI (equation 3) examples of all morphodynamic types are obtained.

Some beaches had artificially high Dean's (Ω) values because of exceptional wave heights during sampling. These indices, especially beach state (as Ω), are thus only approximations of the modal beach states, since they are highly influenced by factors that vary greatly on a small temporal scale. Dean's parameter (Ω), and therefore the calculated beach state, varies considerably with changes in wave height, which in turn is affected by strong winds or storm events (Wright *et al.*, 1982b). McLachlan (1990) found the Dean's value for Kings Beach to

be $\Omega = 3.8$, whereas McArdle and McLachlan (1992) obtained $\Omega = 5.6 - 7.3$ for the same beach. The measured wave height for the first study was 0.8 m, and ranged 1.4 - 1.6 m for the second study. The present study measured $\Omega = 1.4$ for Kings Beach with a mean wave height of 0.5 m. This is a considerable variation in both wave height and Ω . Yet, all these studies classified Kings Beach to be an intermediate beach. Single sample events therefore tend to be unreliable, especially if the absolute Ω -value is important (such as for a regression).

The theoretical beach morphodynamic state is also greatly affected by the use of either mean wave height or modal wave height, as illustrated using long term wave height measurement values (published by Donn *et al.*, 1986). Mean wave height can be double that of the modal wave height, which accounts for a doubling in Ω -values, even though the sampling has been done over a long term (i.e. 96 days). Long-term studies are very difficult to do and may not necessarily yield more accurate estimates of the beach state or communities (Jaramillo *et al.*, 1996). These complications emphasise the dynamic nature of the beach environment, with the only constant factor being the variability in the physical environment. For this study, it is accepted that some of the Ω -values are not good estimates of the modal beach states, since the sampling was once-off with no replication per beach. Sampling was also conducted in different seasons (although mostly during winter). However, it is also argued that replication would not have yielded better results. Keeping the limitations in mind, it was inferred that this is a representative sample spanning a range of microtidal beach types. Using a 'snapshot' beach state and its associated fauna, the relationship between the physical parameters and the community response was investigated.

In relating the biological community structure to the physical parameters it became evident that significant correlations were only obtained between the biological communities and single parameters (i.e. grain size and slope) which are relatively stable over a small temporal

scale (Fig.2.3). This study positively correlates species richness and abundance with slope and grain size. Previous studies (McLachlan *et al.*, 1981; McLachlan, 1983a) also showed an increase in both total abundance and species diversity (as richness) with a decrease in slope or grain size over a range of intermediate beaches in southern Africa. None of the macrofaunal community parameters (i.e. species richness, abundance or biomass) were significantly correlated to the compound indices (equations 1 - 3) other than abundance with BSI. Other beach studies found similar results, but generally stronger correlations between compound indices, such as species diversity and Dean's index (Ω), rather than grain size or slope (McLachlan, 1990; Jaramillo and McLachlan, 1993; McLachlan *et al.*, 1993; Jaramillo, 1994). Since the deviation from the modal beach states on some beaches in this study is too large, they are not expected to have a strong correlation with community parameters. It is, however, concluded that the communities investigated are responding to the physical environment, and in a fashion similar to what previous studies claimed, i.e. an increase in the species richness and abundance from coarse sand, steep reflective beaches to fine grained, flat, dissipative beaches (McLachlan, 1983a; 1988).

An additional reason for the lack of insignificant trends in this study, as opposed to the significant trends obtained by other beach ecologists, is evident when the study area is compared to those of McLachlan and co-workers (1983a; 1990; 1993; 1996a). It is clear that the present study uses a limited range of beaches i.e. microtidal beach states. Previous studies (Jaramillo and McLachlan, 1993; Jaramillo, 1994) either used a smaller number of beaches (± 10), spatially not very far apart (probably experiencing similar conditions within the same faunal provinces), or included data from other studies, spanning reflective to ultra-dissipative beaches from different continents (McLachlan *et al.*, 1993; McLachlan *et al.*, 1996a). The first method may be advantageous, because it limits variability in the study, whereas the latter replicates variability more substantially but generally spans a greater tidal range. This study lacks the biases of both of these two scenarios.

The correlations between macrofaunal community structure and biogeography indicated that the number of species was higher on the warm-temperate south coast than the cold-temperate west coast. The number of species was significantly higher on a warm-temperate beach than for a beach with a similar grain size on the cold-temperate west coast (Fig. 2.7). Hacking (1998) also reported a significant increase in species richness per beach state (using the BSI), on warm-temperate beaches of North South Wales, in comparison to the species richness (per BSI) along the Oregon coast, southern Africa and Western Australia. Further, McLachlan *et al.* (1996a) reported an elevated number of species on tropical beaches when compared to temperate beaches. This suggests that the number of species 'available per beach state' is dependent on biogeographical province, and seems higher in warmer climates.

Many researchers have discussed reasons for zonation patterns on beaches. Among them are: competition for space and food (McLachlan, 1988; Peterson, 1991), tidal flux (Dahl, 1952; Dexter, 1984; Peterson, 1991; Jaramillo, 1994), predation, physical or biological disturbance (Bally, 1983a 1983b; Defeo *et al.*, 1992; McLachlan, 1983a; 1988; Borzone *et al.*, 1996) or recruitment variability (Jaramillo *et al.*, 1987; Defeo, 1996). However, few studies have indicated cause-and-effect relationships between any one of these factors and zonation. Reasons for the zonation patterns obtained from this study are dependent on the physical environment, and seem to be effected by morphodynamics. Although the different geographical regions supported different numbers of species on them, the distribution of species, and the number of zones within each beach type, appeared to be related to both the amount of energy reaching the beach (i.e. exposure), and beach morphodynamic state.

The three beaches considered to be reflective had few species, which were separated into a high shore and low shore fauna. In both biogeographical regions, the number of zones increased to three or four, as the community became more complex. Considering the zonation scheme proposed by Dahl (1952) with three zones, Salvat's (1964 cited by

McLachlan 1988; Brown and McLachlan 1990) with four zones, or the simplest by Brown (in Brown and McLachlan, 1990) with only two, none of these schemes seem appropriate. Although the most broadly applicable scheme is that of Brown (McLachlan, 1983a; Brown and McLachlan, 1990), with the air-breathing component and intertidal component, the best approach seems to be that of McLachlan and Jaramillo (1995). Their zonation scheme suggested three or four zones, depending on the beach state, and therefore, the number of niches, which seems to increase as beaches become more dissipative. This zonation scheme (with a supralittoral, a littoral and sublittoral zone) is partly based on the biological zones as proposed by Dahl (1952), but also acknowledges that more species tend to be present under more dissipative conditions. It hence allows subdivision of the sublittoral zone under dissipative conditions. However, this scheme does not really explain the occurrence of only two zones found here on the reflective extreme, other than giving evidence of impoverished faunas on other reflective beaches. Nevertheless because it is based on both physical and biological characteristics, it should be able to acknowledge that the physical zone can be present but not occupied by any fauna. The first option is probable on the reflective beaches in this study, resulting from the very low diversities (for example 2, 3, and 5 species; Fig. 2.8). The latter case seems to be the option for study, i.e. investigating if an extended down-shore distribution of air-breathing fauna into the upper-intertidal is possible.

Using the correlative-type approach that has been very typical of beach work, it seems that this study broadly supports the SEH (McArdle and McLachlan, 1992), but does not explain any of the mechanisms involved. The number of species, abundance (log-transformed) and, probably, biomass (also log-transformed), increase from the steeper beaches (generally coarse sand reflective) to the flatter, finer (dissipative) extreme. The number of faunal zones also seems to increase towards the finer, flatter extreme, which harbours more species, even across two different geographic regions. However, this does not contribute to our understanding of the mechanism involved in swash exclusion. It is thus necessary to

continue this investigation into the physical factors, and especially swash factors that may be structuring beach communities.



University of Cape Town

CHAPTER 3

University of Cape Town

3.1 INTRODUCTION

The *swash exclusion hypothesis* (i.e. a general increase in species richness, abundance and biomass on beaches towards the dissipative extreme due to a more benign swash climate; SEH), had been applied in many forms even before it was formally stated by McArdle and McLachlan (1992). It was recognised that the swash climate on dissipative beaches is such that the low swash periods allow time for slower moving animals to feed, breed and maintain position in the intertidal (McLachlan, 1983a; 1990). Brown *et al.* (1989) described the patchy long-shore distribution of *Donax serra* and *Bullia digitalis* according to varying substratum, slope and wave conditions. It was suggested that, in the extreme, these factors preclude fauna because they afford insufficient time to burrow between swashes (because of sediment compaction), their slopes are too steep, or they have unfavourable wave action conditions. McArdle and McLachlan (1992) suspected that the behaviour patterns of swash riders such as *Donax* spp. or *Bullia* spp. were affected by swash periods and speeds. The inverted zonation of *D. serra* on the south and west coasts of South Africa has been attributed to (among other factors) the probability that the adults on the west coast cannot burrow fast enough between swashes (< 48 s) and are consequently excluded from the intertidal (Donn and Els, 1990; Donn, 1990a; 1990b). McArdle and McLachlan (1991) suggested that dissipative conditions are most conducive to the life of slow burrowers and small, less robust animals. Fauna on reflective beaches seem to have an increased risk of being stranded or swept above the effluent line, and the conditions are less favourable to move and feed (McArdle and McLachlan, 1991). This is true even if these conditions exist on a small scale, such as in beach cusps (McLachlan and Hesp, 1984).

The SEH may hold true over a range of beaches from different continents and provinces (McLachlan, 1990; McLachlan *et al.*, 1993; Jaramillo, 1994). Even though good correlations between beach state and the biota have been obtained, McLachlan *et al.* (1996a) speculated that it is not beach state *per se* that structures macrofauna, but rather the associated swash climate. McArdle and McLachlan (1991), investigated how swash factors were related to beach morphodynamic type and described the typical swash climate associated with each beach state. They found that beach slope and wave height were the most important factors controlling the swash climate. More specifically, wave height was the most important factor on dissipative beaches, while beach slope was the dominating factor on both intermediate and reflective beaches (McLachlan *et al.*, 1993). However, no investigation has shown how the macrofauna responds to these swash factors. Nevertheless, swash distance and period seem to be the most likely parameters to ultimately control beach macrofaunal communities (McArdle and McLachlan, 1991).

The aim of this study was to define the *swash exclusion hypothesis* (SEH) in more specific terms. Firstly, to determine which specific swash factors the beach macrofaunal community as a whole responds to; and secondly, to determine if these correlations also hold at a population level. The final aim is to elucidate whether the community response to swash is a sum of the individual species or population responses.

3.2 METHODS

This study was initially attempted in the laboratory, by using a model beach system (similar to that proposed by Pugh, 1975). It was possible to create a sheltered 'beach' with the associated interstitial environment in a wave tank (14 m long x 1.5 m deep x 1 m wide), but it was difficult to obtain swash periods, speed and distances that remotely resembled conditions on an exposed reflective beach, let alone the dissipative extreme. After extensive

manipulation, the laboratory experimental approach was abandoned in favour of *in situ* measures using a longer-term correlative type approach. Apart from a greater range of physical parameters that could be measured, the populations were also well established, reflecting more representative effects.

The same biological data, i.e. number of species, abundance (as $\text{Log}_{10}\text{no.m}^{-1}$) and biomass ($\text{Log}_{10} \text{g.m}^{-1}$) of the 27 beaches that were sampled for the previous chapter, are used for this study. A series of swash parameters were measured simultaneously during the sampling of these beaches, with readings being taken within half an hour of the low tide. These physical parameters characterise the wave action, swash climate and some other intertidal beach parameters.

Wave action is described by the surf zone width (m; **SURFZ**), number of breakers across the surf zone (**No.WAVE**), maximum wave height (cm; **WAVEH**), wave frequency (min^{-1} ; **WAVEF**), and wave period (s; **WAVET**). These parameters were obtained as described in Chapter 2 (also see Appendix 2).

The swash climate was defined by haphazardly selecting swashes and measuring the swash upwash and backwash parameters. Due to the large number of factors that needed to be measured around the time of low tide, five measurements were obtained per swash or wave parameter. The swash parameters measured were:

- *swash upwash distance* (m; **SUD**): as the distance that each of the swashes travels up onto the beach past the spring low water mark (SLWM), until the point where it stops and begins to run back;
- *swash upwash time* (s; **SUT**): as the time that it takes the swashes of a measured distance to run up-shore;
- *swash upwash velocity* (m.s^{-1} ; **SUV**): as the swash upwash distance divided by swash upwash time;

- *swash backwash distance* (m; **SBD**): as the distance from the turning point of the swash when it starts the backwash, until it is over-run by the next swash;
- *swash backwash time* (s; **SBT**): as the time that it takes the measured backwash from the turning point until it is over-run by the next swash;
- *swash backwash velocity* (m.s⁻¹; **SBV**): as the swash backwash distance divided by swash backwash time;
- *mean swash time* (s; **MEANST**): the mean swash upwash time + mean swash backwash time;
- *mean swash distance* (m; **MEANSD**): as mean swash upwash distance + mean swash backwash distance.

Other swash factors that were obtained are the number of *low tide effluent line crossings* (no.min⁻¹), which is the frequency of swashes passing the glassy layer boundary per minute during low tide (**EFFCROS**), the frequency of swashes passing SLWM as a measure of *swash frequency* (no.min⁻¹; **SWASHF**), and *swash period* (as 1/SWASHF, **SWASHT** in seconds).

The beach parameters measured are vertical displacement¹ (i.e. the vertical height difference between the SLWM and the drift line), the beach width (**BWIDTH** in meters) and water table depth (in centimetres from the sand surface) at each station to obtain the mean water table depth. The importance of grain size, slope and beach state (Ω), RTR, BSI and exposure were mainly discussed in the previous chapter.

The analysis was conducted by means of single and multiple regressions (STATISTICA '98) by regressing the biotic parameters against physical factors. The community parameters

¹ **Vertical displacement**: was obtained placing two ranging staffs at two consecutive transect stations. The height difference was obtained by lining two points, one on each measuring staff, with the horizon. Placed next to each other the relative height difference was obtained, and the sum of all the differences = VERTDIS.

were species diversity/richness, abundance ($\text{Log}_{10}\text{no.m}^{-1}$) and biomass ($\text{Log}_{10}\text{g.m}^{-1}$). Simple regressions were firstly performed, and all the significant factors were then used in multiple regressions. The multiple regression was hence a combination of step-up and step-down procedures (Zar, 1984).

A group of species were then selected to test their responses as individual populations to the same swash factors and some beach morphodynamic variables, and to compare these responses to that of the whole community. The species tested were selected by two criteria: (i) the species must occur in both biogeographical provinces, and (ii) it must occur on more than 10 of the 27 beaches sampled to have a reasonable sample size. The analysis entailed correlating the abundance ($\text{Log}_{10}\text{ no.m}^{-1}$) and biomass ($\text{Log}_{10}\text{ g.m}^{-1}$) of each of the selected species to the same series of wave, swash and beach parameters. This was conducted to determine if the species individually responded to the same factors that the community, as a whole, responded to.

3.3 RESULTS

3.3.1 Community Response

Features of the biological community seem to be strongly correlated with wave and swash parameters. Significant correlations were obtained for species richness (7), log abundance (7) and log biomass (10), with the various physical variables tested in this study. These parameters are not consistent, although there are some common parameters (Table 3.1). The number of species and abundance particularly had correlations with the following features: the number of waves in the surf zone (No.WAVE), swash upwash time (SUT and MEANST) and beach width (BWIDTH). It is therefore suggested that the time that animals are covered by swashes at low tide and the space that they can occupy are important structuring forces. Particularly, the longer the time that each animal is covered (but not the

frequency of covering events) and the more space available to individuals appear to favour both a greater number of species and greater abundance. Biomass and abundance are similarly correlated with swash period (SWASHT), swash backwash distance (SBD) and beach width (Table 3.1). The critical factors leading to increased biomass therefore seem to be the period (or the inverse of frequency) for which animals are covered, as well as the distance of the intertidal covered by each swash (affected by SUD, MEANSD and BWIDTH). Each of the biological variables have some correlation with some wave energy parameter (i.e. No.WAVE / SURFZ / WAVEF / WAVET), a swash frequency parameter (EFFCROS / SWASHT / SWASHF) and swash time or distance (SUT / SUD / SBD / MEANSD / MEANST).

Table 3.1 The wave and swash variables correlating with species diversity, abundance and biomass on 27 beaches. (The n=27 and n=24 for EFFCROS, Negative P values indicate negative correlations; values in **Bold** indicate the strongest correlations, while those in *Italics* refer to the significant beach parameters obtained in Chapter 2).

Number of Species			Log Abundance			Log Biomass		
Variable	P	R ²	Variable	P	R ²	Variable	P	R ²
No.WAVE	0.034	0.167	No.WAVE	0.046	0.150	WAVEF	-0.029	0.177
WAVET	0.047	0.148	SWASHT	0.012	0.227	WAVET	0.045	0.150
SUT (s)	0.003	0.292	SUT (s)	0.002	0.322	SURFZ	0.014	0.218
SWASHF	-0.029	0.177	SBT	0.010	0.235	SWASHT	0.001	0.356
MEANST	0.012	0.223	SBD (s)	0.015	0.214	SUT (s)	0.004	0.281
EFFCROS	-0.012	0.257	MEANST	0.002	0.324	SUD	0.015	0.213
BWIDTH	<0.001	0.392	BWIDTH	<0.001	0.614	SBD	0.012	0.223
<i>Slope</i>	<i>0.019</i>	<i>0.201</i>	<i>BSI</i>	<i>0.025</i>	<i>0.185</i>	MEANSD	0.009	0.241
<i>Phi</i>	<i>0.001</i>	<i>0.472</i>	<i>Slope</i>	<i><0.001</i>	<i>0.400</i>	SWASHF	-0.039	0.158
			<i>Phi</i>	<i>0.002</i>	<i>0.330</i>	BWIDTH	0.004	0.286

None of the biological parameters were correlated with either the swash upwash or backwash speeds encountered in this study. This is probably because of the variability in this parameter since in reality the swash speed changes with distance up and down the intertidal.

The strongest single correlations were obtained between the biotic factors and beach width. An increase in space correlates with more species, greater abundance and biomass being present on the beach (Table 3.1 & Fig. 3.1). Abundance and biomass *per running metre* though, is a function of beach width and this confounded relationship is expected to be strong. A similar significant result, however, has been obtained for the number of species *versus* beach width, although species richness is not calculated or expressed per running metre of beach and hence not confounded by it. In fact the number of species on broad beaches may rather be underestimated because of the sampling design. The correlation of beach width and number of species may even be stronger. It is therefore likely that species richness is a function of space. The mechanism or reason for this relationship is uncertain. When abundance and biomass were expressed as (Log_{10}) numbers or mass per square meter, the correlations are not as strong, but a significant result was still obtained between abundance ($\text{Log}_{10}\text{no.m}^{-2}$) and beach width (Fig. 3.2). It is hence suspected that at least abundance, but probably also biomass, is significantly influenced by beach width. The number of species, and the number of individuals per species, therefore increases with an increase in beach width.

Wave frequency, swash frequency and effluent line crossings generally had a negative correlation on diversity, abundance and biomass (Table 3.1 & Fig. 3.3). It appears as if the biota responded positively to the increase in the time that the intertidal is covered by water, but not if it means an increase in the frequency of covering. The frequency of covering seems to be a disturbance factor.

Combining, all the biological parameters, only two physical factors show a significant correlation with all three biological factors (Table 3.1). These are positive correlations of species richness, abundance and biomass with both swash upwash time (SUT) and beach width (BWIDTH). It is thus suggested (using only single linear regressions) that the critical swash parameters controlling beach macrofaunal communities include the time that the

intertidal is covered by swashes at low tide (Fig. 3.3) and the space available to biota (Fig. 3.1), with positive correlations to both these physical parameters. These factors allow for an increased amount time for beach organisms to feed, breed and move.

Beach width, swash time and frequency, in addition to the overall beach factors (such as slope and grain size discussed in the previous chapter), thus seem to have some importance to communities as a whole. The next issue which arises is to evaluate the relative importance (to the community) of each of these swash factors, and the importance of the beach and swash factors in combination.

Table 3.2 Multiple correlation incorporating all the significant swash factors, and then all the beach and swash factors (that are not confounded). **No.SPP** = number of species; **ABUN** = abundance ($\text{Log}_{10} \text{no.m}^{-1}$); **BIOM** = biomass ($\text{Log}_{10} \text{g.m}^{-1}$).

	Equation	F	P	R ²
+BWIDTH	No.SPP = 6.30-0.76 SWASHT +0.12 BWIDTH	$F_{2,21}=11.25$	0.00047	51.7
	ABUN = 2.37+0.018 SWASHT +0.015 BWIDTH	$F_{2,24}=33.87$	0.00000	73.8
	BIOM = 1.97-0.28 WAVEF +0.054 SWASHT +0.075* SUD -0.16 SUT +0.022 BWIDTH	$F_{5,21}=9.84$	0.00006	70.1
Swash only -BWIDTH	No.SPP = *Not confounded			
	ABUN = 2.62+0.09 No.WAVE +0.025 SWASHT +0.029 SBD	$F_{3,23}=9.54$	0.00028	55.5
	BIOM =1.99+0.0047 SURFZ -0.27 WAVEF +0.046 SWASHT +0.039 SBD	$F_{4,22}=10.32$	0.00007	65.3
Beach + Swash +BWIDTHH	No.SPP = -4.24+8.25 PHI	$F_{1,22}=16.84$	0.00047	43.4
	ABUN = Same as swash only			
	BIOM = No significant beach parameters			
Beach + Swash -BWIDTH	No.SPP = *Not confounded			
	ABUN = 2.65 +0.025 SWASHT +0.027 SLOPE	$F_{2,24}=20.96$	0.00001	63.6
	BIOM =No significant beach parameters			

* Not confounded, because the number of species is not calculated as be a function of beach width, but the absolute value as sampled per transect.

Fig. 3.1 Linear regressions between species richness, abundance ($\text{Log}_{10}\text{no.m}^{-1}$) and biomass ($\text{Log}_{10}\text{g.m}^{-1}$) and beach width.

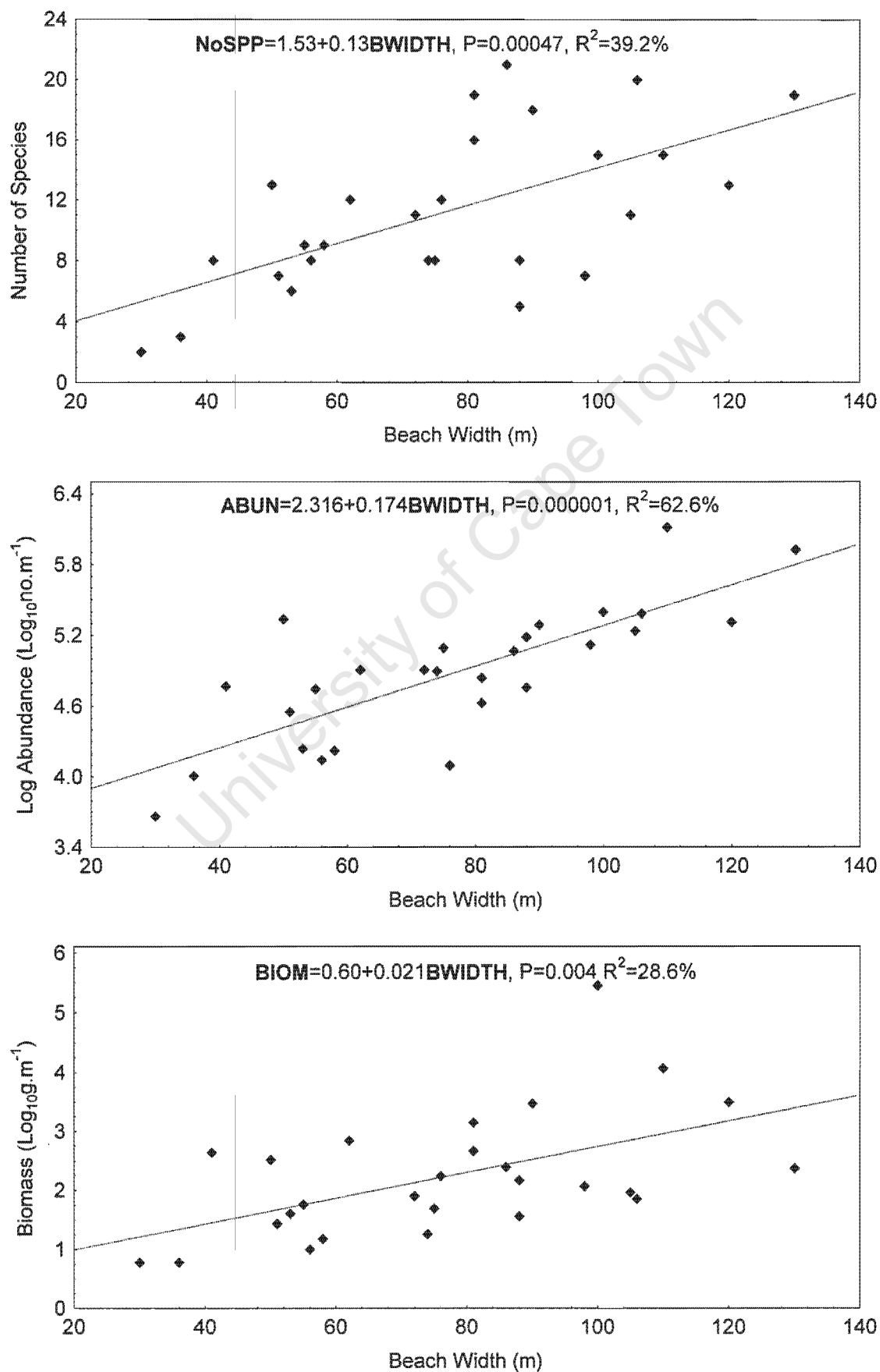


Fig. 3.2 Comparison of abundance ($\text{Log}_{10}\text{no.m}^{-1}$) and biomass ($\text{Log}_{10}\text{g.m}^{-1}$) indicating the dependence on units per running metre or square metre, against beach width.

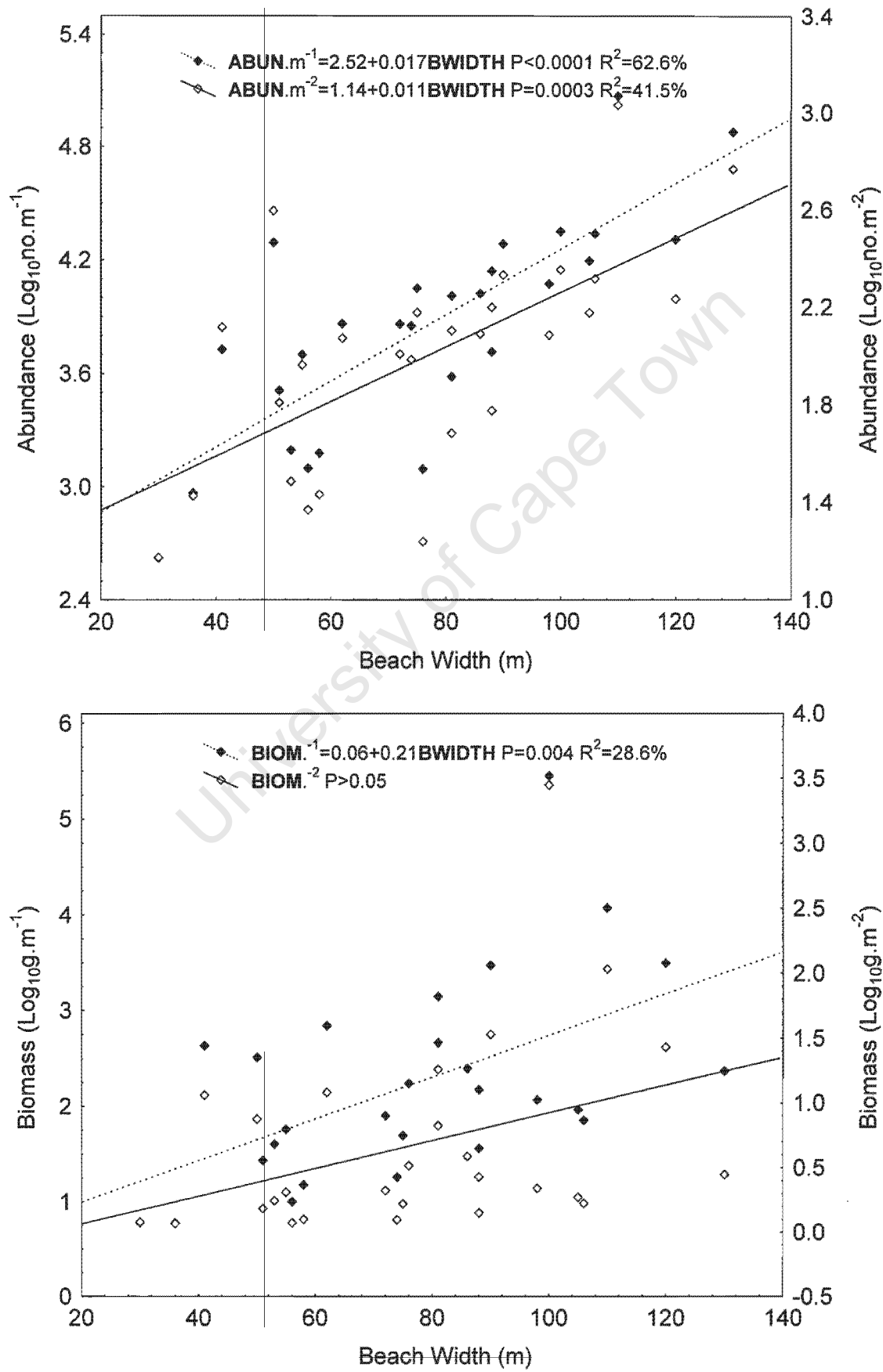
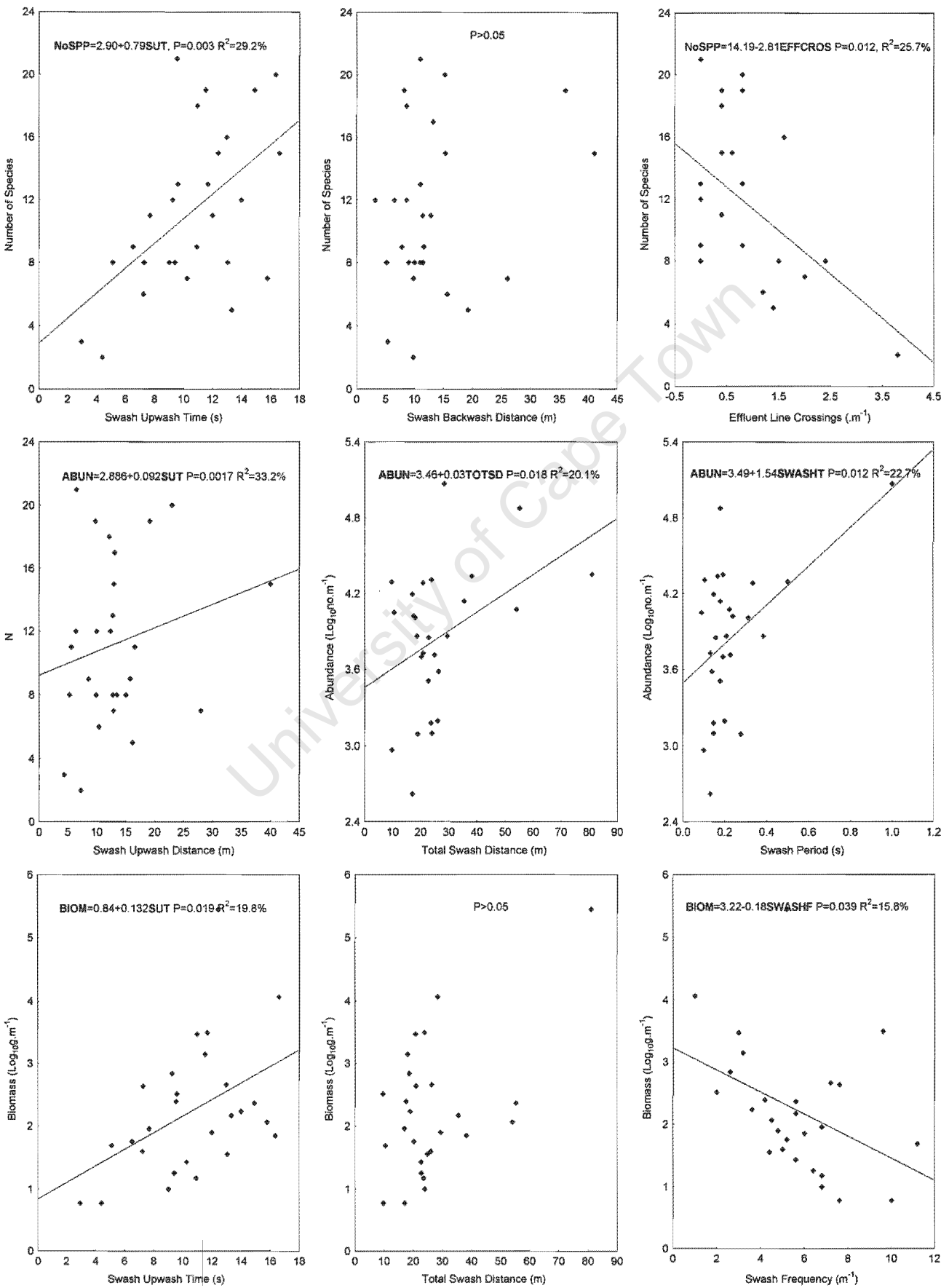


Fig. 3.3 Regressions between species richness, abundance ($\text{Log}_{10}\text{no.m}^{-1}$) and biomass ($\text{Log}_{10}\text{g.m}^{-1}$) vs. swash upwash time, swash backwash or total swash distance and a disturbance factor, such as effluent line crossings, swash period or swash frequency.



The low values of the correlation coefficients (R^2) in the single regressions (from Table 3.1 & Fig. 3.3) suggest that none of these variables individually structure communities and that it is probably a combination of these (or some other untested factors) that influence community patterns. Multiple regressions² were therefore employed to test whether a larger amount of variation can be explained by relating the biota to different combinations of swash parameters.

More of the variation within the biotic parameters were accounted for when the swash parameters were used in concert (Table 3.2). However, no single suite of parameters explained all of the variation. Two factors - beach width and swash frequency/period - occurred consistently as correlative factors in the community attributes, indicating these factors (or some factor/mechanism regulated by them) to be important. Since BWIDTH dominates both the single and multiple regressions, but is also confounded in the calculation of abundance and biomass per running metre, it was eliminated from the analysis. Apart from swash frequency/period, the same components, i.e. wave energy parameter (No.WAVE / SURFZ; as well as a swash time/distance parameter SBD) were significant (Fig. 3.2). About 70 – 73% of the variation is explained by these factors, but this drops to 50 – 65% with the exclusion of beach width.

The same procedure was employed to test the influence of the significant beach factors in combination with the swash parameters. Since no significant regressions were obtained between biomass and beach parameters, it was excluded from this part of the analysis (Table 3.2). Using both the beach and swash parameters to predict the number of species, the strongest correlative factor is still grain size (ϕ). The swash parameters, including beach width, which is highly significant in a single regression, cannot significantly add to explaining

² **Multiple regression:** assumes that the predictor variables are independent from each other (Zar, 1984). Thus, obviously correlated/confounded variables, such as swash period and swash frequency, were not both included in the analysis.

of species distribution by physical factors. It seems questionable to single out factors that the community responds to as a *whole*, or to isolate 'superparameters' that regulate the biota of a beach. However, species richness seems to be structured primarily by grain size. Furthermore, the number of species seems to be related to the space available on the beach and the frequency, by which these animals are covered, keeping in mind that the swash frequency has a negative correlation with species richness. Incorporating the entire set of single and multiple regressions suggests that wide, fine grained beaches will harbour the largest number of species. These are dissipative beaches with a large number of breakers in the surf zone and long swash upwash times, of low frequency.

Abundance, on the other hand, was still best explained with only swash parameters, i.e. SWASHT and BWIDTH (Table 3.2). Macrofaunal abundance on the beach is positively and very strongly related ($P < 0.001$; Fig. 3.1 & Fig. 3.2) to the space available. However, when this confounding effect is eliminated, swash frequency and slope mostly 'control' abundance. It is therefore expected that high abundance values would be obtained on broad, flat beaches aided by the long swash times associated with these beaches.

The macrofaunal biomass on beaches seems to be correlated exclusively with swash and wave parameters, rather than being a function of the intertidal conditions such as grain size or slope. Beaches with slow, infrequent swashes moving over a wide, flat face should therefore have the highest biomass values.

3.3.2 Population response

An investigation into the effects of physical factors on individual populations indicated that component species may respond differently to wave, swash or beach factors than the community as a whole (Table 3.3).

The abundance (as $\text{Log}_{10} \text{ no.m}^{-1}$) of nine species was significantly correlated ($P=0.05$) to each of 14 different variables, with a total of 42 significant correlations (Table 3.3). Biomass ($\text{Log}_{10} \text{ g.m}^{-1}$) was also correlated with each of 14 different variables (of which three differ from those relating to abundance) with a total of 38 significant correlations (Table 3.3). Most of these correlations were with swash components, or with the overall beach indices or parameters, such as BSI or vertical displacement.

Both the abundance and biomass of crustaceans, the nemertean *Cerebratulus fuscus*, and *Bullia digitalis* were generally related to swash upwash distance and speed, and swash backwash distance and speed. These correlations were all positive, i.e. both the biotic factors (abundance and biomass) increased with an increase in these physical parameters (Table 3.3). Abundance and biomass of the polychaetes, *Sciolelepis squamata* and *Nephtys capensis*, displayed few significant correlations, while those of the filter-feeding bivalve (*D. serra*) were related solely to wave or compound beach parameters, and not swash variables. The negative correlation of *D. serra* abundance and biomass to RTR seems counter-intuitive. Increased RTR values lead to more dissipative states and generally greater abundance. However, *D. serra* seems to be stronger related to exposure and wave action than to 'dissipativeness'. Generally, the swash parameters appear to be important to species that venture into the swash on a tidal basis, e.g. *Bullia* and the cirolandid isopods, which are swash riders; whereas, species such as *D. serra* only venture into the swash to migrate on a semilunar rhythm. Moreover, *D. serra* is a filter feeder depending on waves and tides to bring food, while many of the other species are scavengers that must move into the swash to obtain food. Attributes such as swash speed could therefore be expected to have a direct influence on their success.

Table 3.3 Swash factors that could structure individual beach macrofaunal populations. P-levels are presented, and negative P-values indicate a negative correlation.

		Crustaceans				Nemer- tea	Polychaetes		Molluscs		
Abundance (Log ₁₀ No.m ⁻¹)	Var.	³ Ekens	Enat	Plat	Gpsa	Cfus	Ssqu	Ncap	Bdigi	Dser	
	N=	25	22	20	24	20	13	11	10	12	
	Wave	SURFZW	0.0083	0.037	0.0035		0.0005				
		WAVE H		0.019	0.0099						0.0028
	Swash	SUD	0.0016	0.0072	0.0001		0.0069			0.0015	
		SUT			0.041			0.0357			
		SUV	0.0278	0.0013	0.0009		0.0004			0.0052	
		SBD	0.033	0.0063	0.0019		0.0060		0.0437		
		SBT			0.036						
		SBV		0.0028	0.0042	0.0032	0.0020		0.026	0.0081	
		MEANST			0.036						
		Beach	BWIDTH						0.047		
	VERTDISP							0.0075		0.0058	0.019
	RTR			-0.042							-0.005
	BSI				0.028		0.049				0.001
	EXP			0.039							0.032
	⁴ TOTAL		4	8	10	1	6	3	2	4	4
Biomass (Log ₁₀ g.m ⁻¹)	Wave	SURFZW	0.012		0.0069		0.0017				
		WAVE H			0.010				0.035		0.016
	Swash	SUD	0.0047	0.0085	0.0001	0.024	0.0049			0.034	
		SUT						0.028			
		SUV	0.019	0.0013	0.0002	0.0035	0.0002				
		SBD	0.041	0.0013	0.0018	0.036	0.0088			0.025	
		SBT									
		SBV	0.043	0.0013	0.0013	0.0099	0.0034			0.035	
	Beach	VERTDSP					0.032	0.0103	0.0032	0.005	0.0058
		Water									0.025
		Table									
		Slope									-0.046
		Grain size									0.007
		RTR							-0.008		-0.015
		EXP									0.011
	TOTAL		5	4	6	4	6	2	3	4	4

³ Eken = *Eurydice kensleyi*; Enat = *Excirolana natalensis*; Plat = *Pontogeloides latipes*; Gpsa = *Gastrosaccus psammodytes*; Cfus = *Cerebratulus fuscus*; Ssqu = *Scolecopsis squamata*; Ncap = *Nephtys capensis*; Bdigi = *Bullia digitalis* and Dser = *Donax serra*.

⁴ Total = sum of the number of physical factors having a significant influence on either the abundance or biomass per species.

The physical factors, to which the community is related to, are therefore very different to those of individual taxa. Each of these taxa was related to a unique suite of physical parameters, depending on the lifestyle and adaptations of that particular species. Attempting to extrapolate community responses from those of individual species is thus unlikely to be successful, as indeed are attempts to infer the responses of individual species from those of the community as a whole.

3.4 DISCUSSION

There are three levels of analysis involved in this study, all highlighting very specific factors to which the beach community is related. On the most basic level, the investigation focussed on single species correlations to wave, swash and beach parameters. It is interesting to note the lack of correlation between either abundance or biomass of the individual species with either grain size or slope. The community as a whole responded significantly to these factors (in Chapter 2; Fig. 2.3). Both species richness and abundance were correlated to grain size (in ϕ -units) and slope. Yet the only population that was significantly correlated with slope and grain size, was *D. serra*. It is therefore suggested that each of these species responded to factors influencing their lifestyles directly. It seems that if it is possible for a species to survive and establish a population on a beach, parameters such as grain size and slope (unless extreme) are already acceptable/tolerable.

Species with similar lifestyles such as *Bullia* and *Cerebratulus* or the cirolanid isopods, which are all carnivorous scavengers, were all related to the same factors, whereas few of the other species seem to be influenced by the same variables. The isopods were strongly related to the swash parameters (SUD, SUV, SBD and SBV), while *D. serra* abundance was not correlated to any of these factors. *D. serra* in turn was correlated with all the factors determined by wave energy, such as WAVEH, RTR and EXP (Table 3.2). The community 'response' is thus

not merely a sum of the population 'responses', but rather a complex assemblage of effects. Larger, less mobile species abundance and biomass values are best explained by wave and overall beach parameters, whereas mobile species seem to be correlated with the speed, time and distance that swashes wash up and down the shore.

The second level of investigation analysed the community in terms of the number of species present, the total abundance and total biomass for a beach with respect to 26 single wave and swash variables (*Appendix 2*). It became apparent that there is no simple outcome and it is virtually impossible to identify a single superparameter controlling all aspects of the community. The analysis was further complicated by the amount of confoundness of the physical environment, but this is also an inherent characteristic of the beach environment. A change in wave height experienced on a rocky shore does not alter the gradient or the substratum of the intertidal, but it may cause a change in both grain size composition and slope of the intertidal on a sandy beach. A change in slope may in turn alter swash upwash and backwash processes, or the number of effluent line crossings. Organisms, such as *Bullia*, may then respond directly to the altered swash conditions, and not necessarily to the different wave conditions. It is for this reason that the analysis was conducted including all 26 physical variables (even if they are co-varying with other parameters) to elucidate which of these parameters the community as a whole responds to. Peres-Neto (1999) has warned against the approach of multiple statistical tests because of an increased change of committing TYPE I errors⁵. With a database of approximately twice the current size, Peres-Neto (1990) indicated that the number of 'significant' values due to random correlations would be ~ 5% for all correlations. Bearing this in mind, the analysis was conducted to identify suites of significant parameters, rather than concentrating on the actual physical factors and their effects on species richness, abundance and biomass. To determine the

⁵ **Type I error:** is committed if the null hypothesis is rejected when it is actually true. In other words significant differences are obtained due to chance and not because of real differences (Zar, 1984; Peres-Neto, 1999).

importance of actual single variables, much more rigorous procedures are required, in both experimental design and statistical testing. Correlative techniques need to be substituted with manipulative experiments.

Correlative results from the present study indicated that the number of species is related to the beach width and the swash frequency. The influence of beach width may be either direct or indirect. The direct importance has two possible mechanisms. Firstly, the increase in species may be caused by an increased amount of space (even though this might suggest competitive interaction/exclusion for space among animals, which seems unlikely). McLachlan (1988) stated that community and population patterns on exposed sandy beaches are the consequence of individual responses to the swash climate, sand movement and liquefaction on the beach face and not greatly controlled by biological interactions. Secondly, and perhaps more likely, increasing beach width may result in an increase in the number of niches. McLachlan and Jaramillo (1995) described a general zonation scheme (Fig. 1.4), where the number of faunal zones increases depending on the beach state. Dissipative beaches, which are generally very wide, contain four physical zones as described by Salvat (1964 cited by Wendt and McLachlan, 1985). If all these physical zones are found on narrow, reflective beaches they are generally very compressed, not allowing much latitude for migrating or swash-riding species to move according to changing conditions. It is therefore predicted that niches may be vacant on reflective beaches, but that most niches will be occupied on wide dissipative beaches.

Alternatively, the correlation between species richness and beach width may be an artefact of being correlated to the physical beach state. Beach width is strongly correlated to Ω (McLachlan, pers. com.). Thus, the wider the beach, the greater the area over which swash energy is spread. Species richness seems to increase with an increase in Ω -values, and a decrease in the energy reaching the beach. Either of the latter two explanations seems plausible.

Beach width is not the only factor correlated with beach macrofaunal diversity. Swash frequency has a negative influence on the number of species. A high frequency of coverage therefore could be a disturbance factor. Such a mechanism is probably not because of submersion *per se*. The simple regressions indicated that species richness is strongly related to swash upwash time (and total swash time), with an increase in the number of species corresponding to an increase in swash time. But the number of species decreases with an increase in effluent line crossings. An increase in the time that the intertidal is covered by swashes at low tide, thus favours the animals, but an increase in the frequency of swash covering does not necessarily result an increase in the total time covered. A few long swashes, as opposed to many quick swashes, therefore seem to favour more species.

Swash climate also seems to influence the overall abundance and biomass of the fauna on beaches, which conforms to the findings of McLachlan (1988). The ways in which these two biotic factors respond to the swash are different though. The control of abundance is similar to control of species diversity. Beach width is very important (whether it is expressed m^{-1} or m^{-2}). The importance of beach width in determining faunal abundance is also probably a function of either/both the influence of beach state, the number of available niches, or an increased amount of resources i.e. space. But the validity of each potential mechanism remains to be tested. Assuming that the same niches favour individuals of the same species, an increase in the number of niches (because on an increase in beach width) should lead to higher abundance. A larger number of individuals can also be accommodated without interfering with each other if more space is available.

An increase in swash period, which is the inverse of swash frequency, gave a better fit to (log) abundance than to the number of species. The disturbance mechanism of frequency and period is assumed to be the same in magnitude (although inverted). An increase in the swash frequency leads to a decrease in species number, whereas a decrease in swash

period, causes an increase in water/wave disturbance (probably as turbulence) and leads to a decrease in abundance per beach.

The third community parameter, i.e. biomass, 'reacted' slightly differently to the swash parameters. Although beach width seems important when correlated with biomass expressed per running meter, the correlation is not strong. Biomass was not significantly related to beach width when expressed per meter square. Swash period had a significantly positive influence on biomass (Table 3.1). It was interesting to note the relationship of the wave parameters, wave frequency/period, as well as surf zone width, with biomass. The influence of the wave parameters on biomass seems largely manifested in the presence on adult beach clams, *D.serra*, even though only a fraction of this population was sampled. This species generally occurs in the subtidal of west coast beaches (De Villiers, 1975a; Donn *et al.*, 1986; Donn, 1990a), and can make up over 90% of the biomass of beach macrofauna communities (Bally, 1983b; McLachlan 1983b; Wendt and McLachlan, 1985). Generally, *D. serra* are most abundant on exposed beaches comprised of sand that is not too coarse, where they subsist mainly on surf phytoplankton blooms and organic froth resulting from high wave action (McLachlan and Hanekom, 1979; Lastra and McLachlan, 1996). It is therefore likely that both swash and wave parameters would have an influence on the biomass of this species and therefore the biomass of communities on beaches.

The general trend obtained from the simple regressions of the biotic features of the communities against 26 wave and swash parameters is as follows: an increase in beach width and swash period (with a resultant increase in swash upwash time and distance), is correlated with an increase in the number of species, abundance and biomass of beach macrofauna communities.

The third level of investigation evaluated the wave, swash and compound beach indices (of Chapter 2) in concert. It also tried to establish whether the single swash and wave

parameters, or the all-encompassing beach parameters, explained the community structure better. The number of species was related specifically to grain size. This confirmed the results obtained by Stephenson and McLachlan (in press). They suggested that grain size is the most important parameter determining the number of species that can survive on a beach, with the percentage of unsaturated upwash⁶, and the number of effluent line crossings⁷ and swash period to be important. The reason for the absence of effluent line crossings as a significant factor in the present study is assumed to be a result of the limited time for which this parameter was measured. Only five minutes of measurements of this particular parameter were used in this study as opposed to the 15 min/hour used over both high and low tide by Stephenson and McLachlan (in press).

Macrofaunal abundance was strongly influenced by beach width. The secondary factors (in the absence of beach width) were swash period and slope. Stephenson and McLachlan (in press) on the other hand, found the percentage unsaturated upwash, number of effluent line crossings and also swash period to be important physical factors. The present study indicated a correlation between abundance and particularly biomass with swash upwash and backwash time and distance. Even though these two studies did not find correlations with identical factors, the suites of parameters are not contradictory. The factors seem related in a predictive fashion. It is predicted that swash time and distance in turn will have a direct influence on the effluent line crossings (either as a percentage or numbers as measured by McLachlan and co-workers; McArdle and McLachlan, 1991; Stephenson and McLachlan, in press). The importance of unsaturated upwash/effluent line crossings is therefore accepted (rather than disputed). Swash upwash time and distance can be obtained with relative ease around low tide, as opposed to the percentage unsaturated upwash or effluent line crossings as measured by Stephenson and McLachlan (in press). Factors such as swash period can

⁶ **% of unsaturated upwash:** which is the total upwash crossing the unsaturated sand i.e. above the effluent line, as a percentage of the intertidal (Grant, 1983; McArdle and McLachlan, 1991).

⁷ **Number of effluent line crossings:** number of times the swash crosses the effluent line per unit time.

be obtained in conjunction with transect sampling and many of the other low tide swash parameters. Moreover, the macrofauna community is sampled around low tide, and may not respond entirely in the same way, to the physical factors, as during high tide (Hacking, 1996).

The results of this study generally support to the *swash exclusion hypothesis* (SEH), i.e. the swash experienced in the intertidal towards the dissipative extreme is more conducive to macroscopic life, providing near optimum conditions for filter feeders, and aiding surfing movements of macrobenthos. Steep reflective beaches with rapid pulsing swashes, even where wave energy is relatively low, provide harsh conditions that few organisms can survive (McLachlan, 1988).

The SEH, however, outlines the importance of swash, but has no reference to specific factors that control the biota. It is now possible to redefine the SEH using the findings of this study in conjunction with the study of Stephenson and McLachlan (in press) which stated the SEH as follows: *“that the decrease in the number of species from dissipative to reflective conditions was the result of physical exclusion of species by coarse sand, turbulent swash and low effluent lines”*. It is possible to be more specific. This study redefines the SEH as *the exclusion of species from reflective beaches because of coarse sand and short swash periods, whereas abundance is specifically limited by space (and possibly niche availability), and biomass by swash upwash distance (or the % and number of effluent line crossings)*. The validity of these ideas remains to be tested experimentally.

It is also important to mention that the effect of turbulence⁸ has not been investigated. The effect of turbulence is in itself extremely complicated and worth of an independent, in-depth study. It is predicted though that an increase in the chaotic eddies, and hence an increase in

⁸ **Turbulence:** is defined as the chaotic distribution of flow speeds and direction (Denny, 1988).

turbulence, will probably act as an inhibiting force (also mentioned by Stephenson and McLachlan, in press). Turbulence, which is related to surface roughness, water speed and depth, will probably be the greatest on reflective beaches. This is because the greatest change in all three of these parameters seem to occur over a short distance on reflective beaches, right at the edge of the intertidal, close to the swash line. Dissipative beaches seem to experience turbulent wave action mostly in the surf zone, often driving phytoplankton blooms, while the intertidal seems to experience more laminar flow. This also remains to be tested.



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CHAPTER 4

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4.1 INTRODUCTION

The beach clam *Donax serra* Röding is the largest species in the genus (Ansell, 1983), and is phenotypically and behaviorally adapted for a dynamic lifestyle on sandy beaches (Ansell, 1981; Donn *et al.*, 1986; McLachlan *et al.*, 1995; Soares *et al.*, 1998). *D. serra*, colloquially known as the 'white mussel'¹, occurs along the southern and western shores of southern Africa, from East London (in the Eastern Cape) to the Cunene River, in northern Namibia (Donn 1990a; Branch *et al.*, 1994).

The mesoscale zonation of *D. serra* displays contradictory patterns. This species has adapted, through microevolutionary changes, to occupy different tidal zones on the different coasts (Soares *et al.*, 1998). The across-shore zonation pattern for animals on the west coast is such that large adults are generally restricted to the subtidal, while juveniles occupy the high shore (De Villiers, 1975a; Bally, 1983b). Adults and juvenile *D. serra* of the southern Cape coast are mixed in the intertidal, with adults occurring well up into the intertidal zone and recruitment taking place in the surf zone (Donn *et al.*, 1986; Lastra and McLachlan, 1996; Schoeman, 1997). In contrast to *Donax variabilis*, which displays active tidal migration, *D. serra* migrates according to a semi-lunar cycle, a feature which can probably be attributed to its large size (McLachlan and Hanekom, 1979; Ansell, 1983; Donn *et al.*, 1986; Ellers, 1995a). Large adults from the west coast do not appear to migrate at all since they occur in the shallow subtidal (Ansell, 1983; Brown *et al.*, 1989). White mussels therefore maintain a relatively stable position on the shore, apart from their spring tide circa-semilunar migratory

¹ **White mussel:** is the common name of this wedge shell or beach clam and will be referred to as 'white mussel' in the text.

activity and the seaward (or shoreward) movement (depending on the region) of the animals as they grow.

Gimenez and Yannicelli (1997) commented on mesoscale community structures (i.e. within beach faunal patterns). They reported that spatial variability, and therefore zonation of fauna within a beach, was related to the position of the swash zone, which in turn depends on beach slope and width. However, this does not explain why the same species would occupy different levels on similar beach types in different biogeographical provinces. The main reasons for the geographic change in zonation of *Donax serra*, as proposed in the literature, include lowered temperatures on the west coast (Donn and Els, 1990), change of predation pressures (Bally, 1983b) or the presence of kelp (Soares *et al.*, 1996). However, few of these ideas have been tested and it is thus still unclear whether it is an active or passive process which determines the intertidal distribution of *D. serra*.

Since *D. serra* appears to be so well adapted to the beach environment, it is expected to inhabit a wide range of beach types. Attempts have been made to correlate several physical factors with the distribution and abundance these beach clams, as well as other beach macrofauna (Brown, *et al.*, 1989). These factors include sand particle size (Bally, 1981; Brown *et al.*, 1989; Nel, 1995; Lastra and McLachlan, 1996), wave action (Corfield and Alexander, 1995; Farquhar, 1997) beach slope, sand moisture and food in the surf zone (McLachlan and Hanekom, 1979; McLachlan *et al.*, 1981; McLachlan, 1983a; 1990; Brown and McLachlan, 1990). Previous studies summarized these influences on the macrofauna community structure as either direct or indirect reactions to swash climate (McArdle and McLachlan, 1991; 1992; Brazeiro and Defeo, 1996). The general response is that: as conditions change from dissipative to reflective beach states, molluscs and polychaetes tend to disappear from the characteristic faunal assemblage, followed by small crustaceans, until only large robust crustaceans are found on fully reflective beaches (McLachlan, 1988; Brown and McLachlan, 1990). The longshore distribution of *D. serra* appears to follow this trend.

McLachlan (1990) first stated this general tendency as the *swash exclusion hypothesis* (SEH).

The aim of this chapter is to test whether the longshore distribution of *D. serra* follows this general trend, as formulated in the *redefined swash exclusion hypothesis* (RSEH of Chapter 3), which suggests that:

“the exclusion of species from reflective beaches is caused by coarse sand and short swash periods, whereas abundance is specifically limited by space (and possibly niche availability), and biomass by swash upwash distance (or the percentage and number of effluent line crossings)”.

The objective is to determine which swash or beach factors have the strongest effect in structuring *D. serra* distribution, across the shore. The null-hypothesis is therefore that the number of *D. serra* that remain on any beach (or that manage to escape stranding on the driftline) is independent of beach state. The prediction is that on reflective beaches more *D. serra* will remain above the effluent line (because they cannot burrow into coarse sand), or more are displaced to the subtidal (because they can not burrow between swashes due to short swash periods). The physical factors predicted by the *redefined swash exclusion hypotheses* (as stated in this study and by Stephenson and McLachlan, in press) that should be of significant importance are: sand grain size, effluent line crossings and swash period. (Swash turbulence and competition for space will not be addressed here).

The experimental procedure was also expanded to test whether the occurrence of adults in the subtidal on the west coast is an active or passive process. In order to do this, a comparison was made between the number of live (i.e. active burrowers) or dead (i.e. passive) *D. serra* that remained on the driftline of a west coast beach, as opposed to those that managed to burrow between swashes, or those that were dragged down to the subtidal.

If the same number of live and dead clams end in subtidal, it would suggest that live *D. serra* are probably passively dragged down to subtidal, rather than actively selecting the subtidal.

4.2 METHODS

4.2.1 General

Even though adult clams from the west coast are quite stagnant in their distribution and migratory patterns, these animals were used because of their large size and hence the feasibility of tracking them in the swash (Brown *et al.*, 1989). The experiment was conducted on three beaches, and compared the displacement of live and dead animals over a series of beach slopes within each beach.

4.2.2 Preparation

Fresh *D. serra* were collected and killed by taping them shut and then either freezing them for 12 hours, or heating them in hot sea water for a few minutes (< 4 minutes). The method depended on the facilities available in the field. Either way, care was taken not to let the animals dry out and thereby change their density. Fresh, live animals, collected during low tide, were stored in seawater until the commencement of the experiment. Each replicate of live and dead *D. serra* was marked by spray painting the shell lightly prior to the experiment.

4.2.3 Experimental procedure

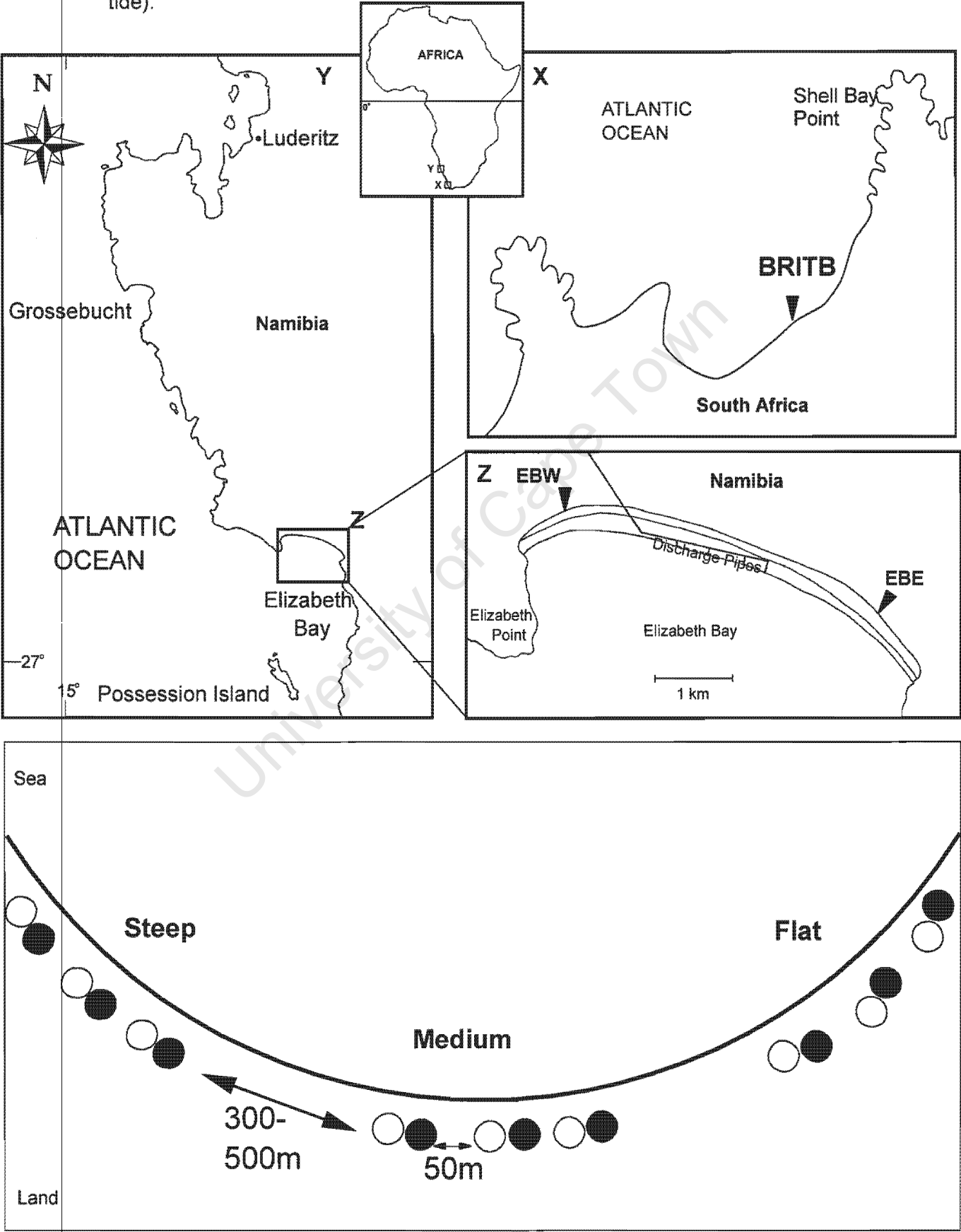
This experiment was conducted on three west coast beaches situated in log-spiral bays (with an east-west stretching shore line; Fig. 4.1), with varying beach slopes and exposures. The beaches were Britannia Bay, Elizabeth Bay East and Elizabeth Bay West (Fig. 4.1). Britannia Bay is a relatively sheltered beach with wave heights rarely exceeding 1 m. Since it is located in a bay, the western, less exposed side, has fine sand with a flat gradient, while the eastern

side has coarser sand and a steeper gradient. Elizabeth Bay East and West occur along a single stretch of sandy beach, with an artificial break in the *D. serra* population as well as many other beach species. The artificial separation has been created by mine tailings (constituting very coarse sand of about 1 mm) being dumped on the central part of the beach, resulting in beach accretion (McLachlan *et al.*, 1994). Possession Island, a few kilometers offshore shelters the eastern part of this bay. This results in two stretches of beach (each about 2.0 km long), with the one relatively sheltered from the west coast swell, and the other, western side, dynamic and exposed (Fig. 4.1). A range of gradients and exposures was available in Elizabeth Bay (Table 4.1). The experiment was therefore treated as if conducted on three beaches with three sites per beach of varying intertidal gradients.

Generally the experimental sites were 300 to 500 meters apart. On each of the three sites, additional 'replicates' were set up, 50 meters apart. The experiment was thus simultaneously repeated (in triplicate, 50 m apart) on three sites (300 - 500 m apart) with different beach gradients (Fig. 4.1). Each site was selected *a priori* on slope, to represent gentle, moderate and steep beach faces. This was in order to replicate the experiment in possibly all three beach morphodynamic states (i.e. dissipative, intermediate and reflective as defined by equation 1, Chapter 1).

Each experiment constituted placing 50 live and 50 dead *D. serra* on the effluent line on the incoming tide, two hours before high tide. This was to ensure that the animals will be covered by the wave-runup for the entire experimental time, as opposed to animals being stranded because of a receding tide. The white mussels were observed for a two-hour period, until high tide. This included counting the number of white mussels that are displaced into the subtidal, those that were taken by sea gulls, or (on 2 beaches = 6 sites x 3 'replicates') determining the number that managed to burrow successfully into the substrate between swashes.

Fig. 4.1 Experimental areas and design illustrating the procedure for one single beach, taking place on a single day. (Each open circle represents 50 live *D. serra*, and each filled circle 50 dead *D. serra*, that were placed on the effluent line, two hours before high tide).



A series of physical factors was measured around the time of high tide. These measurements included, wave height and period, swash frequency, effluent line crossings, swash upwash distance and time, swash backwash distance and time. Each of the swash factors was measured as in Chapter 3.

The slope of the beach was determined and surface sediment samples were taken on the effluent line at the beginning of the experiment. In the laboratory, sediment samples were sieved through a series of sieves and the mean grain size obtained graphically (Folk, 1966; Brown and McLachlan, 1990). The dimensionless fall velocity (or Ω -value) was calculated per sample. For the sake of this experiment, mean spring tide range was obtained from the theoretically predicted tide tables as calculated by South African Navy (Anonymous, 1998). The Beach State Index (BSI) and Exposure ratings (EXP) were estimated as described in Chapter 1.

Analysis constituted finding correlations, using single and multiple linear regressions, between the physical parameters and the number/proportions of clams that remained above the high tide mark. Additionally, the animals that buried successfully per experiment were recorded as far as possible. Hence, the number of live animals that were displaced to the subtidal was calculated as: $50 - (\text{live clams that remained on the beach} + \text{the clams that burrowed})$. The relationship between the number of animals displaced to the subtidal and various factors was also investigated using single and multiple regression analysis (Zar, 1984). On successive iterations, the largest non-significant physical parameter was eliminated until only factors that significantly explained the distribution were involved in the analysis (i.e. Step-down method, Zar 1984). However, only simple regressions that explained distribution significantly (at $\alpha=0.05$) were entered in the multiple regression.

The number of live and dead *D. serra* were also investigated independently from the beach state, to ascertain whether the displacement was active or a passive response. Chi-square analysis were used to compare the number of live and dead clams that remained on the driftline, and those that 'escaped' by burrowing in the intertidal or being displaced to the subtidal. And finally, the difference in the number of live vs dead individuals that were displaced to the subtidal, as opposed to those staying the intertidal, was investigated also using a Chi-square (Zar, 1984).

4.3 RESULTS

4.3.1 Physical parameters

The mean values of the physical factors describing the beach state are summarized in Table 4.1. All the beaches used in the experiments can be classified as exposed (i.e. $EXP > 10$), with a small tide range. The relative tide range values are less than 3, which confirms the wave dominated rather than tide dominated attributes of microtidal beaches (Masselink and Short 1993). According to the BSI, the first set of experiments (on Britannia Bay, BRITB) was conducted on relatively low energy reflective states (BSI generally < 0.5). Elizabeth Bay West (EBW) is in a medium energy, intermediate beach state (BSI between 0.5 and 1.0) and Elizabeth Bay East (EBE) a high energy intermediate/dissipative beach (BSI between 1 and 1.5). A range of beach conditions was therefore used during this experiment, with the beach morphodynamic state values (as per equation 1), ranging between 1.5 and 15. And the beach gradient ranging from $1/12$ - $1/60$ (Table 4.1).

Table 4.1 Physical factors as well as the *Donax serra* distribution as measured on Britannia Bay (BRITB), Elizabeth Bay East (EBE) and Elizabeth Bay West (EBW) beaches. (1, 2, and 3 refer to the three gradients/replicates that were investigated, and () indicate 'outliers/extremes').

	BRITB 1	BRITB 2	BRITB 3	EBE 1	EBE 2	EBE 3	EBW 1	EBW 2	EBW 3
Slope (1/H)	34-39	40-50	14-18	27-38	14-19	12-14	38-56	36-60	12-14
Grain size (μm)	177	220	233	183	234	368	228	192	223
Wave H (m)	0.51	1.0	0.4	1.16	1.16	1.11	2.01	2.36	2.15
WaveT (s)	6.8	9.1	7.4	11.1	8.5	10.0	14.8	10.1	11.5
Deans (Ω)	3.2-5.5	3.2-7.1	1.5-2.6	3.5-7.8	4.7-7.1	1.7-3.6	3.2-9.6	8.0-15	6.4-9.2
RTR	1.57	0.89	2.0	1.41	1.27	1.3	0.83	0.73	0.78
BSI	0.36	0.52	0.23	0.94	0.75	0.57	1.25	1.24	1.15
EXP	12	12	11	11	11	15	14	15	13
No of Live <i>Donax</i>	3-8	1	0-5	0-1	0-3	0-3	0-1	1-2(10)	0-2
No of Dead <i>Donax</i>	20-49	22-44	0-3	1(33)	0(18)	0(14)	12-31	8-32	0-5
Burrowed				16-18	1-2	0	20	9	8-11
Displaced				32-48	45-48	47-50	30	40	37-42

Even though the experimental replicates were at a set distance (spaced 50 m apart) which was decided on *a priori*, the experiment is pseudoreplicated. A variance test (Zar, 1984) measuring variance between 'replicates' against i) the variance among beaches of the same state, or ii) against variance within the same beach across different states, confirmed the interdependence of 'replicates' (Table 4.2). In most cases the variance in the number of live or dead animals that remained on the shore (among replicates) was less than the variance in the number between beaches (of the same state) or of different states on the same beach (Table 4.2). The replicates were therefore pooled and a mean number of animals that remained on the shore (per beach state) was calculated and used in further analysis.

Table 4.2 Results from variance tests comparing the number of live and dead *D. serra* that were collected from the 'replicates' against (i) the number of animals collected from beaches of the same type or (ii) against those from the same beach across beach states. (Values in **Bold** indicate a greater variance between replicates than within beach type or beach).

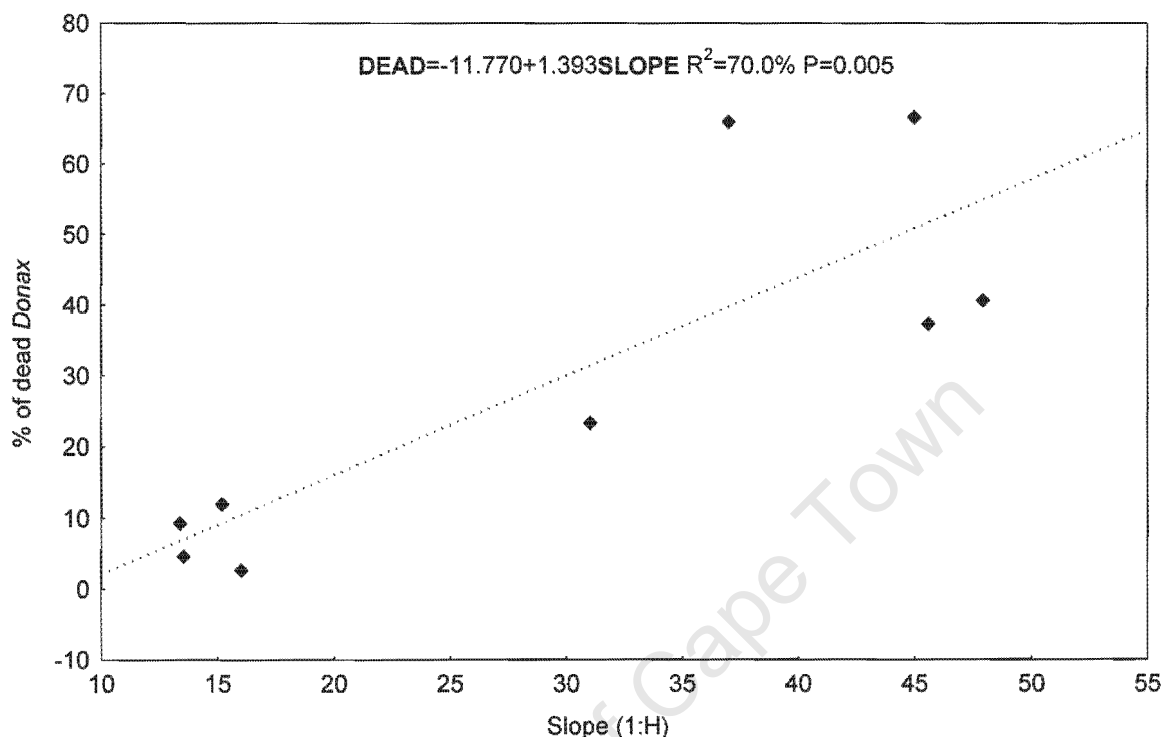
Sample	Live		Dead	
	(i) Beach type	(ii) Beach	(i) Beach type	(ii) Beach
	$\chi^2_{0.05,1}$	$\chi^2_{0.05,1}$	$\chi^2_{0.05,1}$	$\chi^2_{0.05,1}$
BRITB1	0.198	0.231	0.217	0.163
BRITB2	0	0	1.102	0.076
BRITB3	0.198	0.231	0.002	0.001
EBE1	0.010	0.012	0.342	0.256
EBE2	0.094	0.109	0.108	0.081
EBE3	0.094	0.109	0.065	0.049
EBW1	0.010	0.012	0.094	0.071
EBW2	0.760	0.886	0.150	0.112
EBW3	0.042	0.049	0.006	0.005

4.3.2 Swash exclusion

The mean proportion of dead animals (expressed as a %) that were dragged down into the subtidal was well correlated with one physical parameter, namely slope. More animals remained in the intertidal with flat gradients (1/35 – 1/45), than with steep gradients (1/15), which is probably reducing the force necessary to drag shells down by the swash (Chadwick and Morfett, 1998).

The mean proportion of live *D. serra* that were recovered from the effluent line after the two hours experimental time did not have any correlation with any of the physical parameters. This component of the animals that were neither displaced to the subtidal, nor managed to burrow, was however small (3.6% of total number of live animals), and was probably the result of them being unresponsive due to some stress or injuries sustained. This is expected to be unrelated to the physical environment.

Fig. 4.2 The physical factor that is significantly correlated with the mean fraction of dead *D. serra* recovered after high tide.



The effect of the physical parameters on the fraction of live *D. serra* displaced to the subtidal was investigated by correlating the fraction of displaced animals with the swash and beach morphodynamic factors. The fraction of *D. serra* that escaped being dragged down by burrowing, or remained on the effluent line was excluded for this analysis. The number of live, displaced *D. serra* was influenced by four beach characteristics. Negative regressions were obtained with swash upwash distance, swash backwash time and slope and a positive relationship with effluent line crossings (Fig 4.3). This suggests that animals having the ability to resist displacement to the subtidal (i.e. by being alive), are unsuccessful in maintaining their position in the intertidal under short, fast swashes and steep slopes (Fig 4.3).

Conversely, the number of animals that were successful in escaping the physical environment and therefore burrowed into the substrate between swashes, was highest under long, slow swashes with slow backwash times, few effluent line crossings, and on beaches

with flat gradients (Fig. 4.4). Multiple regression analysis was performed using these parameters to determine which of these factors (in combination) best relates to the experimental distribution.

No multiple regression could be performed on the mean fraction of dead *D. serra* that remained on the shore since this was only correlated to slope (Fig. 4.2). Multiple regression identified the fraction of live *D. serra* that was displaced from the intertidal to be significantly correlated to only one factor, and this was slope (Table 4.3). It therefore seems like an interplay of physical forces (such as upwash/downwash forces against frictional forces) that determines whether the shells remain on the effluent line or whether they are dragged down to the subtidal.

A multiple regression incorporating the swash climate factors that determines burrowing success indicated that (the number of live animals that managed to escape desiccation or being dragged down to the subtidal by digging into the intertidal sand) was also best correlated with only a single factor. This factor was effluent line crossings (Table 4.3).

Table 4.3 Physical factors influencing the fraction of dead *D. serra* left on the effluent line, the fraction of live clams displaced to the intertidal and the fraction of *D. serra* that burrowed between swashes.

<i>Donax</i> condition (Y)	Equation	F	P	R ²
Dead	Y=-11.7+1.4SLOPE	*		
Displaced	Y=102.2-0.9SLOPE	F _{1,4} =20.67	0.01	0.837
Burrowed	Y=43.9-20.9EFFCROS	F _{1,4} =84.22	<0.001	0.955

*No multiple regression performed since only one factor was significant (Fig. 4.2).

Fig. 4.3 Physical factors that are correlated with the mean fraction of live *D. serra* that were displaced below the intertidal.

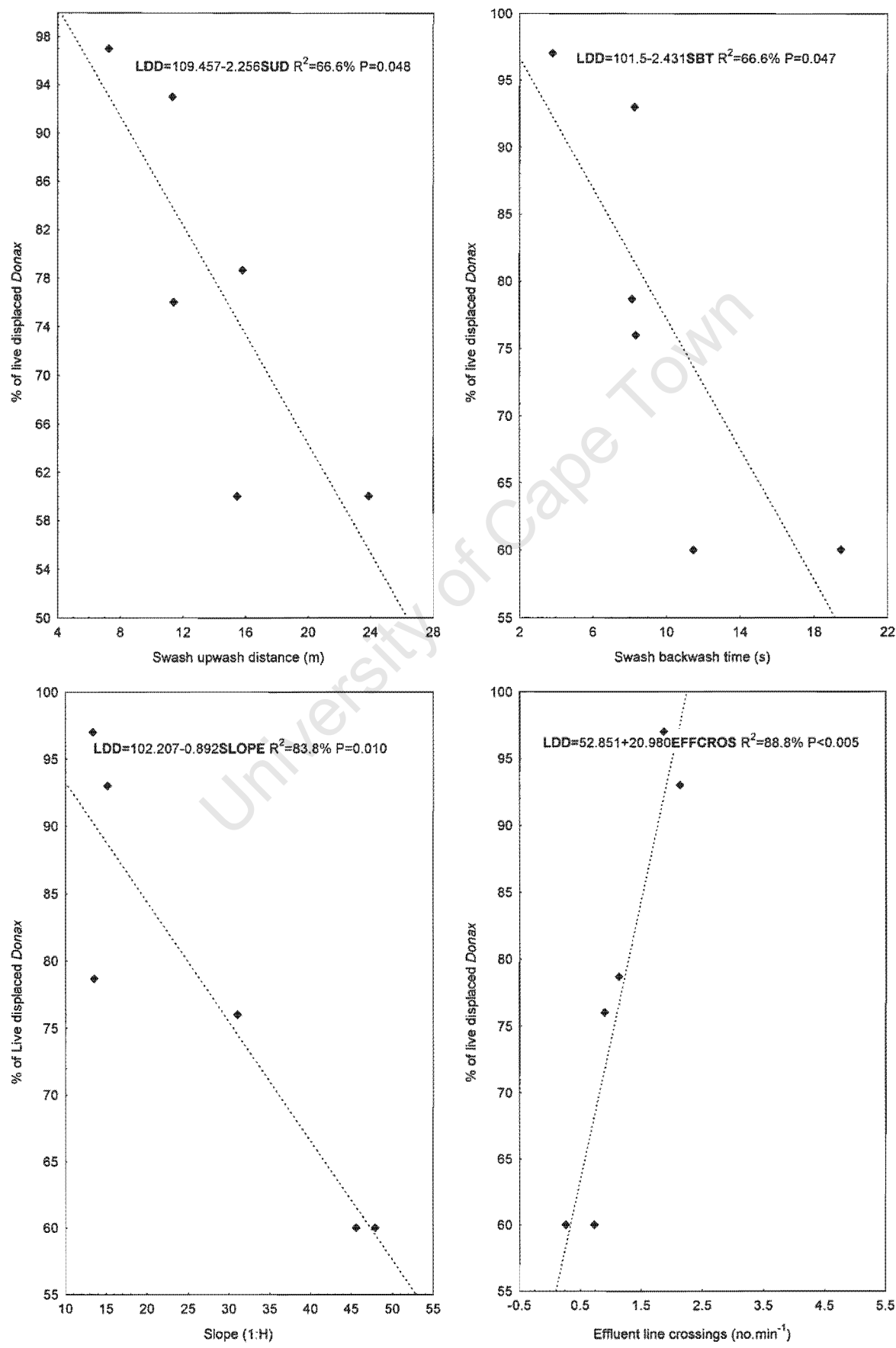


Fig. 4.4 Physical factors that are correlated with the mean fraction of live *D. serra* that managed to burrow into the intertidal.

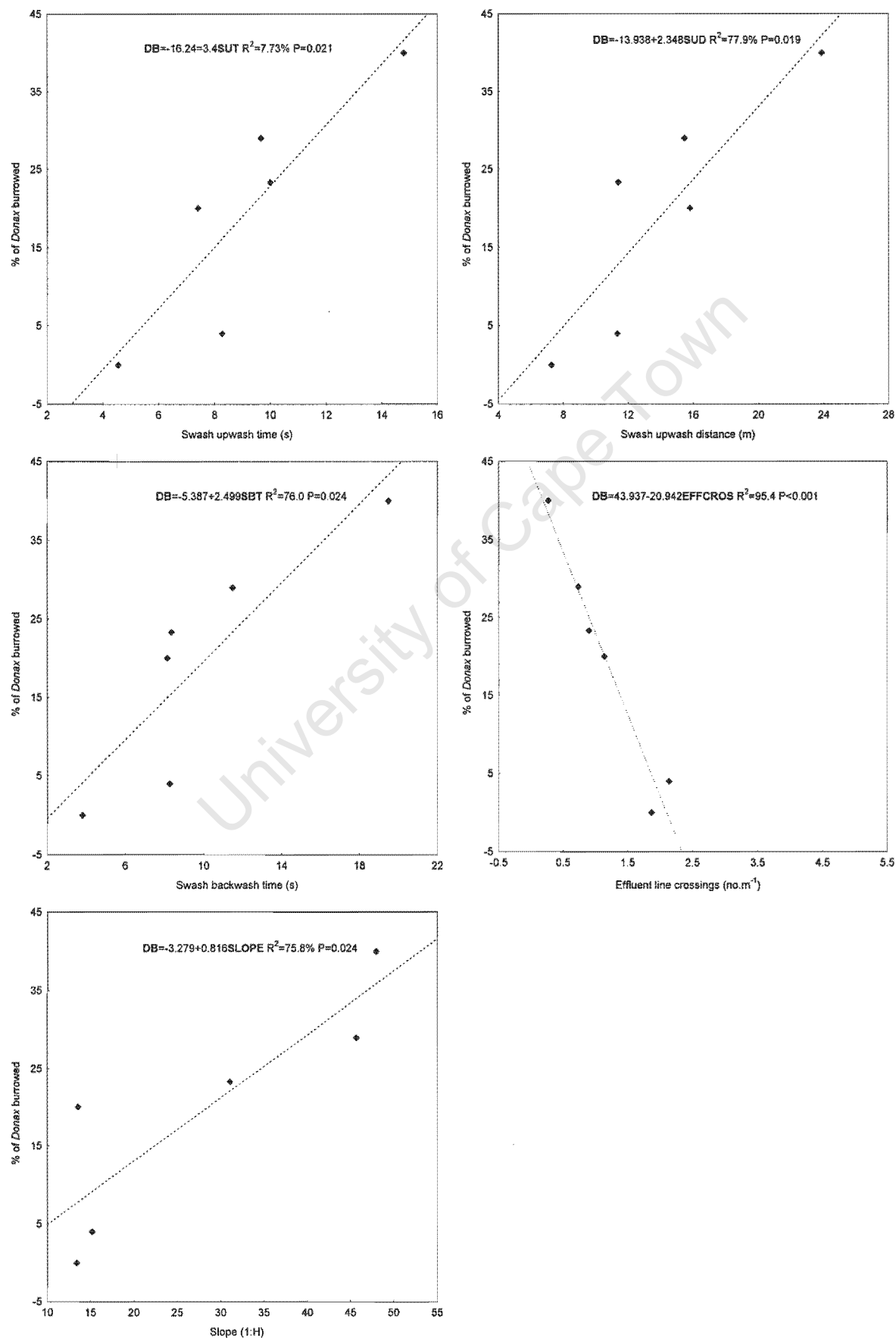
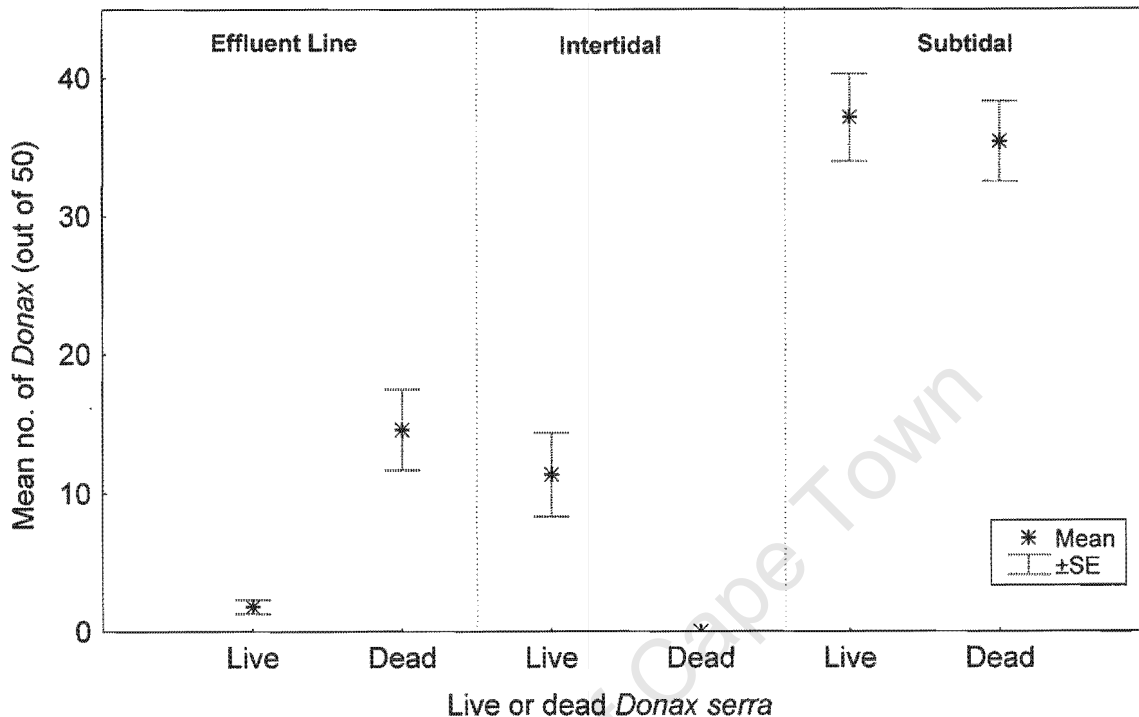


Fig. 4.5 The relative distribution of *D. serra* (as a mean out of 50) across the shore. These are the clams from the effluent line, intertidal and subtidal, at the end of the experiment after being exposed to different beach conditions for two hours on the incoming tide.



4.3.3 Active versus Passive displacement

A comparison of the total number of live or dead clams that remained on the driftline and the number of live and dead *D. serra* that escaped stranding (irrespective of beach state), indicated a significant difference ($\chi^2_{(0.05,1)}=98.3$ $P<0.05$) in the 'response' of live and dead animals. The mean percentage of white mussels that was obtained from the effluent line at high tide was about 29.1% of dead animals as opposed to 3.6% of live animals. Live animals actively avoid being stranded on the driftline. Fig. 4.5 indicates the mean number of live and dead animals that remained in the respective zones after the two-hour experimental period. A comparison of the total number of live animals vs the dead animals that remained in the intertidal (=burrowed + driftline clams), or those that were displaced to the subtidal, indicated no significant difference between the 'response' of live and dead animals ($\chi^2_{0.05,1}=0.012$ $P>0.05$). The number of live or dead animals that ended in the subtidal was, therefore, similar i.e. 74.3% and 70.8%, respectively (Fig. 4.5).

4.4 DISCUSSION

The results of this study partly agreed with the *redefined swash exclusion hypothesis*. It also confirmed that live and dead, i.e. active and passive, *D. serra* 'respond' to different swash factors. The distribution of dead animals was best correlated to slope. More dead animals ended in the subtidal on steep beaches than on beaches with a flat gradient. Live *D. serra* responded to swash upwash and backwash parameters, effluent line crossings and slope. The largest number of clams burrowed under conditions of long, slow swashes, seldomly crossing the effluent line, and preferably on flat beaches. Since this experiment was conducted over only a two-hour period around high tide, it is uncertain whether the *D. serra* that managed to burrow into the intertidal were able to maintain their position for a longer time. It is, however, assumed that if they can manage to burrow under the experimental condition, they should be able to do so most of the time (if the physical conditions on the beach do not change) since they have the ability. Furthermore, the experimental conditions were not particularly calm.

Following the results from the single and multiple regressions it is concluded that the white mussel distribution followed the trend as predicted by the SEH (McLachlan, 1990): more live animals were displaced to subtidal, as the beach morphodynamics tended towards more reflective conditions. The trend as predicted by the RSEH, i.e. being correlated long swash periods, few effluent line crossings and coarse sand was not directly followed. The number of animals that burrowed into the intertidal was related to the effluent line crossings, and the time or frequency factors, such as swash upwash distance swash backwash time had a significant influence (at $\alpha=0.05$) on the *D. serra* distribution. However, grain size seemed unimportant as a causative factor in clam distribution. This may be an artefact of the sampling design since the grain size range encountered varied only between 177 μm and 368 μm . It was therefore only in the medium and fine grain size range (according to the

Wentworth size scale; see Brown and McLachlan, 1990). The experimental design did not address the limitations of space and will therefore not be discussed. The reason for this was that the number of individuals would have had to increase dramatically, or the area limited, which in this case was not practical. This experiment therefore identified some swash factors (swash time and distance; slope and effluent line crossings) instrumental in controlling *D. serra* distribution.

Another factor that should be considered to explain white mussel distribution is that *D. serra* is the largest species in the genus, and probably the largest beach animal in South Africa (with the exception of some crabs, which are either limited to the high shore or the subtidal). Compared to most other beach animals, adult *D. serra* are particularly immobile. Adult white mussels on the west coast seem to have developed an exclusively subtidal lifestyle, unless disrupted by storm events (Soares *et al.*, 1998). Even adult *D. serra*, which inhabit the intertidal on the east coast, are at most semi-lunar migrators (Donn *et al.*, 1986; Brown *et al.*, 1989). Other beach faunal species, including the relatively large gastropod *Bullia digitalis* (which reaches a maximum length of 60 mm; Brown *et al.*, 1989) swash ride, exhibiting a tidal migratory pattern; so do other members of the genus *Donax*, such as *D. variabilis* and *D. sordidus* (Ansell, 1983; Ellers, 1995c). The coquena clam *D. variabilis*, is a discriminating swash rider being more active around the time of mid-tide. It emerges to drift with long, favourable swashes to avoid being stranded on the drifline (Ellers, 1995a; 1995b). It is predicted that the distribution of such highly mobile/active species may have a much stronger correlation with swash factors (as indicated in Table 3.3). *D. serra* are assumed to be the exception in terms of their inactivity in responding to swash parameters.

It also predicted that suites of animals (and possibly the majority), either defined by taxa or lifestyle (but probably both), respond to different swash factors, and that there is probably no single swash parameter that best describes swash climate. However, the prediction is that swash riders such as the cirralid isopod species, *D. sordidus* or *Bullia* species, should also

follow the RSEH (at least to some extent) and respond to swash parameters such as upwash and backwash time and distance, effluent line crossings and slope.

This study further determined that a fraction (22%) of adult *D. serra* has the ability to burrow into the substrate between swashes. The question is then that if a fraction of the animals can burrow into the substrate, why is there not a larger proportion of *D. serra* in the intertidal or specifically, why is the bulk of the adult population on the west coast in the subtidal?

Ending in the subtidal (as opposed to the intertidal or driftline) seems to be a passive result rather than an active selection. This is concluded since both live and dead animals are equally 'unsuccessful' in maintaining position in the intertidal. Predictive statements about the population structure (~80% subtidally and ~20% intertidally), because of the effect of this passive migration, is difficult and can be interpreted in two directions. Firstly, one could argue that the burrowing success on subsequent tides should also be only about 20% which would cause the whole population to be displaced to the subtidal on a few subsequent tides. Or secondly, unless reburial during following tides is less efficient than under the experimental conditions, subsequent burrowing sessions should not render animals (that were initially successful in burrowing) to be displaced to the subtidal. Therefore, if burrowing success was a measure of population distribution, approximately 22% of the adults should be found in the intertidal. Accurate estimates of adult distribution have not been done, but according to De Villiers, (1975a) and Farquhar (1997) only a small proportion of the adults occur in the intertidal zone. When clams reach the age of sexual maturity (at 55 mm) they are generally distributed around the SLWM or lower (De Villiers, 1975b; Farquhar, 1997). Since it seems to be a passive process by which the animals get displaced to the subtidal, it is possible that it is morphologically pre-selected (by shell evolution) that 70 – 74% end in the subtidal.

Soares *et al.* (1998) studied the morphology of *D. serra* from both coasts and concluded that the shell dimensions of white mussels from the west coast were better adapted for a subtidal

life style. This means that *D. serra* with higher, denser shells are less suitable to continuous reburrowing and swash travelling and therefore more successful subtidally. There is however no evidence whether this is the cause or the effect of a subtidal lifestyle.

Predation and temperature are factors that could have caused the change in the morphology and hence the across-shore distribution of *D. serra* (Soares *et al.*, 1998). Bally (1983b) speculated that bird predation is higher on the west coast, while fish predation was dominant on the east coast. Current densities of avi- and ichthyofauna seem to support the predation hypotheses; a dramatic difference exists in the abundance of birds (both species number and diversity), as well as a difference in predatory fish species and numbers, present between the coasts (Hockey *et al.*, 1983; Lasiak, 1983; Clark, 1997; Clark *et al.*, 1998). It was therefore argued that *D. serra*, with shells suitable to an intertidal life style, have been preyed upon by birds on the west coast, whereas east coast animals maintained an intertidal lifestyle as a result of continuous fish predation pressure on subtidal animals. It is, however, uncertain whether these densities existed 100 years ago let alone for evolutionary time (Hockey pers. com.).

The influence of temperature on the intertidal existence of *Donax serra* was evaluated by Donn and Els (1990). They measured slower burrowing rates for west coast clams and therefore concluded that these adult clams are rather displaced to the subtidal because they can not burrow between swashes. Less dense, east coast animals managed to burrow successfully between swashes.

Both the predation and temperature hypotheses could potentially result in altered clam morphologies (Soares *et al.*, 1998). The across-shore distribution of *D. serra* on the west coast is probably due to a combination of both these factors. This study also gives confirmation to some of the ideas of Soares *et al.* (1998), in that the displacement to the subtidal is the same for active or passive animals. It is thus possible that the adults on the

west coast that have been able to burrow into the intertidal between swashes, might have been more susceptible to bird predation, whereas the ones that were displaced to the subtidal escaped predation due to the lack of predatory fish. The lowered sea temperatures on the west coast and therefore slower burrowing times will augment this interaction. The opposite is true for the east coast.

Over time, the animals with denser, higher shells were therefore 'selected' to make up the bulk of the population in the subtidal on the west coast. It is thus assumed that the displacement to the subtidal is a passive process, very likely a result of shell morphology. In addition, a fraction of the animals managed to burrow successfully into the intertidal, which could indicate a previously intertidal life style, in both juvenile and adult form. However, both these hypotheses failed to explain why juveniles on either coast would assume positions opposite from the adults, and the reason for size segregation is still uncertain. Defeo (1996) and Schoeman (1997) have however added that the reason for the adult–juvenile clam segregation may be a density-dependent response of recruits to adults (see also Soares *et al.*, 1998; for discussion). As *D. serra* recruits grow, they could become more effective in 'competing' with adults, and move up/down the shore to the 'pre-selected' habitat (according to the morphology). However, this assumes competitive interactions between individuals. Only a few studies have speculated about the possibility of adult–juvenile or other biological interactions on sand beaches. The next question is therefore: do biological interactions exist on sandy beaches?



CHAPTER 5

University of Cape Town

5.1 INTRODUCTION

In contrast to physical determination of species distribution, where individuals are limited by their tolerance to environmental factors, biological interactions constitute the effect that organisms have on each other. These interactions can either be in the form of competition, predation or long-term symbiotic relationships between species, such as parasitism (Menge and Branch, in press). Biological interactions are often responsible for the modification of various aspects of the life-histories, size-structures, reproductive outputs, or spatial distributions of populations, and are hence major processes in shaping diversity and composition of natural assemblages (Underwood, 1988).

Understanding about the importance of biological interactions on sandy beaches has been slow to develop since the popular approach has been to relate community structure to fluctuations in the physical environment (Menge and Branch, in press). This is because the physical effects are mostly direct, which makes interpretation of results easier. Manipulative experiments investigating physical tolerances can also be less complicated than trying to 'prove' inter- and intraspecific processes, especially if one attempts to follow the rigorous experimental approach outlined by Underwood (1988).

The focus of this chapter is to evaluate the importance of biological interactions in shaping soft sediment benthic communities, particularly the macrofauna inhabiting open ocean beaches. Little work has been done on biological interactions on beaches (see McLachlan, 1988 for a review; Defeo, 1996), and this study aims to establish a relevant starting point and the direction in which future investigations should be aimed. Since many of the principles

involved in the study of the effects of biotic interactions on population dynamics are generated from studies conducted on rocky shores (Barnes and Hughes, 1982; Menge and Branch, in press), it is imperative to include some aspects of these works in this review.

5.2 TYPES OF INTERACTIONS

Biological interactions can take the form of competition, predation or a suite of symbiotic relationships, such as mutualism and parasitism (McLachlan, 1988; Begon *et al.*, 1990). This study, however, concentrates on population and community ecology of macrofauna and will therefore deal with competition and predation only. Symbiotic relationships most frequently occur between micro-organisms and macrofaunal individuals, such as *Bullia digitalis* and *Donax serra*, which may suffer degraded reproductive abilities or respiratory failure because of parasite infestation (Webb 1991; Tharme, *et al.*, 1996). The possibility of symbiotic relationships on beaches that affect species distribution patterns is accepted, even though evidence of symbioses is sparse for beaches. Symbiosis in itself is a very specialised topic and hence considered outside the scope of this study.

Branch (1984) has warned against reducing community ecology to 'either/or' situations by either considering only competition or predation, or focusing on the importance of physical processes alone, instead of considering these forces as acting in concert. Branch (1984) wrote that "*ecological theory is more likely to be enriched by discovering what circumstances lead to a dominance of each of these structuring forces than by denying that one or more of them plays any role*". Competition and predation will, however, be considered separately in this study since it is the least complicated way of reviewing the structuring mechanisms of each theory, but their relative contribution to community ecology will be addressed.

5.2.1 Competition

Competition has often been assumed to exist (or have existed in the past), simply because of differences between organisms (Branch, 1984), and this argument is often applied to explain ecological patterns without sufficient testing (Connell, 1980; Peterson, 1982; Branch, 1984; Underwood, 1988). Competition theory explains ecological phenomena in terms of biological interactions between individuals of the same species (or different species), which have similar requirements for survival, growth and reproduction (Underwood, 1988; Begon *et al.*, 1990). The combined requirements for a resource may then exceed the immediate supply. These limitations may not be direct or immediate, but may influence subsequent generations (Begon *et al.*, 1990). Competitive interactions can therefore be defined as the impact of individuals on each other, brought about by shared requirements for a resource in limited supply, leading to a reduction in survivorship, growth and/or reproduction of the competing individuals.

Two types of competition have been identified. Firstly, **direct interference competition** prevents an individual from occupying a portion of the habitat, so that it cannot exploit the resources in that area (Begon *et al.*, 1990). Secondly, **indirect competition by exploitation** occurs when a resource is in limited supply (Begon *et al.*, 1990). Broadly put, interference competition is denying access to the resource, often by some damaging activity, whereas competition by exploitation is generally a scramble for a common resource (McLachlan, 1988). The resources in question are frequently food and space.

The consequences of competition are likely to vary with the nature of the species involved, the means of competition, the kind of resource competed for and the amount of overlap in niches of the species. Competition always occurs between individuals, either of the same species (intraspecific) or of different species (interspecific) and is often most fierce between conspecifics (Branch, 1984).

The effects of competition are often difficult to detect. However, where two conspecifics/generics coexist they often differ more from each other, than where they occur allopatrically (Fenchel *et al.*, 1975; Begon *et al.*, 1990). The change in morphology, reproductive strategies, behaviour or physiology, as a result of competition, is termed 'competitive character displacement' (Fenchel *et al.*, 1975). Character displacement suggests differential resource utilisation¹ or habitat differentiation, which also implies that coexistence is possible through resource partitioning. However, few cases exist where character displacement has been unequivocally demonstrated in the marine environment. Fenchel *et al.* (1977) reported of two mud snail species (*Hydrobia ulvae* and *H. ventrosa*) which are similar in size in separated populations but display a marked difference in body size where they co-occur. Additionally, the diet particle size selection of *Hydrobia* was also amended in allopatric situations. Furthermore, reproductive character displacement was suggested between two species of *Sphaeroma* isopod species (Fenchel *et al.*, 1977). However, subsequent studies indicated that the sympatric and allopatric conditions used to test for character differences between the *Hydrobia* species were different, and that morphological differences are rather related to the physical environment (Begon *et al.*, 1990). The effects of competition are therefore even more difficult to verify, than detecting them.

Competition is often assumed to exist (or the *ghost of a competition past*²) because of differences between populations (i.e. character displacement), or because of niche separation that seems to allow co-existence of species (Branch, 1984). Connell (1980) and

¹ **Differential resource utilisation** / resource partitioning / niche differentiation or niche apportionment are interchangeably used in the literature as differential use of resources such as food and space or the tendency for coexisting species to differ in their niche requirements (to allow for coexistence; Begon *et al.*, 1990).

² **'Ghost of a competition past'**: is a term criticised by Connell (1980) because interspecific competition is often assumed to have acted as an evolutionary force in the past, and resulted in character displacement and therefore the absence of present-day competition between species.

Branch (1984) criticised this approach³ because it is often circular and untestable, and relies to a large degree on circumstantial evidence. Branch (1984) has suggested that in marine systems *exclusion* by interference would be a more likely consequence of competition, rather than niche differentiation. Exclusion seems to be a more potent evolutionary force (Branch, 1984). It is suspected that if competition is at all present on open ocean beaches, it would rather be in the form of niche reduction or a reduction of reproductive potential rather than complete exclusion. Predictable exclusion generally depends on two important factors. These are the existence of at least one strong competitor and unbalanced initial densities (as outlined by Lotka-Volterra models; see Begon *et al.*, 1990). Interspecific competition, and therefore exclusion, may also be controlled by intraspecific competition (Connell, 1983).

No evidence (to my knowledge) has been found of any 'strong competitors' on beaches. Moreover, the beach environment is highly dynamic with erratic fluctuations in 'population' abundance, and unbalanced initial densities may be reversed over a short term. Reduced resource utilisation seems very likely on beaches, but to 'prove' that this is a result of competition rather than physical determination, is difficult.

Interspecific competition

The essence of interspecific competition is that individuals of one species suffer a reduction in fitness as a result of resource exploitation, disturbance or interference by individuals of another species (Begon *et al.*, 1990). Connell (1961) conducted a classic study indicating interspecific competition between two species of barnacles. He showed that the survival (as well as growth and fecundity) of young *Chthamalus stellatus* (now *montagui*; Barnes and Hughes, 1982) was reduced by the presence of *Semibalanus balanoides*. This demonstrated

³ Approach of **Niche differentiation** has been criticised by Branch (1984) since it suggests that apportioning has been undertaken by a species with the *purpose* of reducing competition and has been driven by competition in order to *allow* co-existence.

how across-shore distribution patterns of barnacles on the rocky intertidal shores are regulated by interference competition rather than physical tolerance alone.

i. Exploitation

In all habitats where there is a finite amount of food or space, and as populations increase in density, competition for these resources may occur (Branch, 1984). Exploitation competition causes adverse effects that are brought about by the reduction in resource levels caused by competing individuals. It is therefore an indirect interaction.

Tilman *et al.* (1981) illustrated an indirect interaction between two fresh water diatom species, which competed for silica in the laboratory. In the marine environment, however, and especially the shallow subtidal zone, water movement continuously replenishes nutrient levels for many species. Local depletion is therefore unlikely to be a significant cause of exploitation competition in the infratidal zone. However, exceptions to the rule always exist. Some filter feeders (e.g. some sponges) can be sufficiently efficient to eliminate food from water and hence from competitors (Reiswig, 1971). Branch and Branch (1980) again indicated that while absolute amounts of food may not be in short supply, especially for deposit feeders, the food is often inadequate because of very low nitrogen content.

Space (to feed from) is sometimes limited, especially on hard substrata, as is evident from the large amount of crowding and overgrowth. Organisms thrive best if they occupy the 'ideal' space which provides protection against predators, physical space where feeding can take place, and an optimal position for reproduction (Branch, 1984). However, even if competition for space does occur, it is often difficult to determine whether it is by means of exploitation or interference competition, or both.

ii. Interference

Some species practice not only exploitative competition by having similar requirements, but attack their competitors to reduce their acquisition of resources. Menge (1974) reported how exploitation competition was enhanced between two species of starfishes by one of them *Pisaster*, attacking the other, *Lepasterias*, with its pedicellaria, causing a reduction of feeding rate of *Lepasterias*. This is a clear example of interference competition. Other examples of undercutting, fouling, overgrowing is common on hard substrata.

Disturbance is a likely process in stable soft sediments, where animals with different feeding modes modify the substratum and make it uninhabitable for other species (or conspecifics). These processes include bioturbation by some polychaetes and other deposit feeders, constant reburial by molluscs, or tube building by fauna such as amphipods, polychaetes, prawns, as well as the production of faecal pellets which change the sediment properties (Barnes and Hughes, 1982). The phenomenon of interspecific asymmetry⁴ could also be evident under disturbance conditions and can probably be extrapolated to intraspecific competitors of different sizes. Levinton (1977 cited by Branch, 1984) has successfully demonstrated competition between three bivalve species. At least two of the bivalves were in direct (interference) competition with each other because of sediment reworking, but also as a result of competition for food.

Intraspecific competition

Intraspecific competition is a consequence of individuals of the same species depleting shared resources to limiting levels. This may lead to an expansion of the range of the species, for when competition is intense it could 'pay' individuals to occupy marginal parts of

⁴ 'Interspecific asymmetry' states that the effect that species A has on species B is not equal to the effect of B on A (Underwood, 1988).

the habitat, where competition is less severe (Connell, 1983; Begon *et al.*, 1990). This is the converse of interspecific competition, which usually results in a contraction of the species to the most favourable portion of the range (Connell, 1983; Branch, 1984; Begon *et al.*, 1990). Inter- and intraspecific competition often act simultaneously in a faunal assemblage. Conspecifics in such an assemblage may be evenly matched competitors while individuals of different species can be ill-matched (Branch, 1984).

It is often difficult to determine whether interactions within species are by means of a direct exploitative mechanism or an indirect interference process, but an important consequence of intraspecific competition is that at high densities the reproductive output per individual animal may decrease. This can even result in a reduction in the total reproductive output of the population per unit biomass. There is often an initial rise in reproductive output with increasing density, but this then declines if the population density becomes too high, as demonstrated for *Patella cochlear* by Branch (1975). Based on these results, it was concluded that a population can be self regulating, provided that adults and juveniles are affected in the same way by an increase of either adult or juvenile numbers (Branch, 1975).

Different sized animals can also have unequal competitive abilities (i.e. competitive dominance), especially in terms of physical interference, and this is evident in adult-juvenile interactions. It seems likely that adults generally have a stronger competitive influence on juveniles than the reverse.

In some cases juveniles settle in a particular habitat and progressive migration occurs away from the settlement site as the individuals age (Defeo, 1996; Lastra and McLachlan, 1996; Schoeman, 1997). This is possibly the effect of intraspecific competition. Examples on rocky shores include *Littorina unifasciata* (Branch and Branch, 1981) and *Patella granularis* (Branch, 1975), which shows a size gradient along an environmental gradient. However,

without sufficient testing, it cannot be assumed that competition is reduced by adult-juvenile segregation, or is the cause of it.

5.2.2 Examples of competition in beaches and soft sediments

Competitive interactions in soft sediments seem to be largely limited to sheltered environments with stable communities (Defeo, 1996). Such interactions are likely on sand-flats and other stable, soft-sediment environments, especially those dominated by deposit feeders, where permanent structures can be formed. Food is often more constant for deposit feeders than for filter feeders, but not as restricted as it is for grazers, which may completely exclude one another (Branch, 1984).

Competition remains broadly untested for open ocean beaches (Defeo, 1996). Some studies have produced limited evidence for competitive interactions, but the mechanism is generally uncertain, i.e. whether it is competition by means of interference, or of exploitation and whether it is for food or space. It is very difficult to determine which of these parameters are responsible for specific distribution patterns of organisms, because they often act in concert. Direct and indirect mechanisms for competition will therefore be treated at the same time.

The general understanding is that exposed soft-sediment habitats, such as open ocean beaches, have no apparent shortage of food and space, and the extra depth dimension (compared to hard-substrata) favours habitat partitioning both vertically and horizontally (Branch, 1984; Defeo, 1996). This may be oversimplified. On open ocean beaches food may not be a restricted resource (at least not during high tide) and the substratum appears to be three-dimensional. However, feeding space for macrofaunal species is probably two-dimensional. Species can be buried to different depths (i.e. space partitioning) during low tide, but most need access to surface resources (i.e. 'fresh' seawater and food) at least at

high tide. Filter-feeding species such as *Donax serra* (especially juveniles) and *Donax sordidus* have the potential to compete on the east coast beaches of South Africa. These species occur in the same 'zone' on the shore, and when submerged they appear to depend on the same swashes to bring food to the same place. But competition is not yet 'proven' on exposed beaches.

Competition has been illustrated in stable soft sediments (such as tidal flats and subtidal communities) for several taxa, with a variety of effects (Peterson and Andre, 1980; Peterson, 1982; Grant, 1981; Grant, 1983; Hunt *et al.*, 1987; Marelli, 1990; Lee, 1996). Competition for space is visible as vertical stratification of species, whereas competition for food (or some other resources such as sediments of particular grain sizes) leads to resource partitioning. Both these competitive interactions can lead to spatial segregation of individuals, which are frequently displayed as adult-juvenile interactions in the case of within-species interactions.

As the tide recedes, beach animals burrow into the sand to various depths, to escape from the low tide exposure. These burrowing processes could affect substratum conditions. The importance of bioturbation lies in how burrowing, irrigation, pelletization, tube structures, mucus or other modifications affect near-bed water flow and the penetrability or erodibility of the surface sediments (Thrush *et al.*, 1992). Woodin (1976) predicted faunal associations as follows: no specific species associated with suspension feeders, burrowing polychaetes to occur with deposit feeders, whereas epifaunal bivalves that brood their young should be co-occur with tube builders. An important factor is the rate at which animals work through deposits whilst feeding and burrowing. Grant (1983) reported that the sediment reworking of an haustoriid amphipod has detectable effects in sediment reworking, but their influence

was still less than 1% of the overall bed form migration⁵. By contrast, an infaunal polychaete could cause sediment reworking of about 33% of that assigned to tidal action. Grant (1983) concluded that most of the reworking by larger animals (such as feeding pits created by rays) is 'noise' compared to the tidal influence, but that smaller animals, such as the amphipods and polychaetes, may be very important in structuring the interstitial environment.

Peterson and Andre (1980) implicated competition for space, but probably also for food, among three bivalve populations in Mugu Lagoon. They showed that the growth rate of *Sanguinolaria nuttallii* was depressed by the presence of *Tresus nuttallii* and *Saxidomus nuttallii* (even in the presence of unoccupied shells). These three species of bivalves occurred at the same depth in the substratum. Peterson and Andre (1980) further illustrated strong intraspecific interactions for *Protothaca staminea*, but could not, even with long term experiments (Peterson, 1982), find any evidence of interspecific interactions affecting growth rate or reproductive effort between *P. staminea* and the bivalve *Chione undatella*. These two species (*P. staminea* and *C. undatella*) occur at the same depth (Peterson, 1982). The shallower species, *P. staminea*, was unaffected by the three deeper occurring species, *Tresus nuttallii*, *Saxidomus nuttallii* and *Sanguinolaria nuttallii* (Peterson and Andre, 1980). Peterson (1977) concluded that competition was an important factor structuring the community and that it resulted in **vertical stratification** within the sand column. This is a common phenomenon between co-occurring species, but it is not clear whether it is caused by competition.

Peterson (1977) demonstrated in the sediments of a sandy lagoon that species with different life styles which overlap vertically in the sand column can also have an adverse effect on

⁵ **Bed form migration:** is the amount of sand that is moving as a result of water movement over the boundary layer.

each other. The prawn *Callinassa* and the bivalve *Sanguinolaria* had a negative effect on one another, suggesting competition for space. Moreover, when *Callinassa* was removed, *Tagelus* and *Sanguinolaria* increased in abundance and hence filled the vacant 'niche'.

Space and suitable space are not necessarily the same thing. Nevertheless, the three-dimensional environment of soft sand is expected to minimise competition (Branch, 1984). It is, however, important to remember that beach macrofaunal communities are largely made up of scavengers and filter feeders, for which food only comes with the tides (McLachlan, 1983b). Space is then probably occupied on a two-dimensional basis, rather than a three-dimensional scale, because food is brought in along the beach face. It is thus uncertain whether the three-dimensional nature of the substratum will be of any advantage. Competition would, however, be entirely dependent on abundance (of both macrofauna and food). Most sandy beach animals are opportunistic (probably with broad niches), hence intraspecific competition seems more likely than interspecific competition, but remains to be tested (McLachlan, 1988).

It is generally understood that **exploitative competition for food** is unimportant in sessile filter feeders. Their food is unpredictable, highly variable in time and space, and is predominantly a function of water movement (Branch, 1984). This generally leads to intense competition for space (on hard substrata) to optimise access to the food supply. It was commented that even if interference competition for space does not ordinarily exist in infaunal communities, the potential for such interactions exists at elevated densities (Peterson and Andre, 1980). One of the few studies that investigated direct interference competition within and between two species of bivalves (*Donax serra* and *D. sordidus*) on Eastern Cape beaches, could not demonstrate any interaction between bivalves except in extreme densities, and even then, only within the larger *D. serra* (McLachlan, 1998). No between-species interaction was obtained for these bivalves.

Rees (1975) described how two intertidal isopods, *Gnorimosphaera oregonesis* and *Exosphaeroma amplicauda* had very similar substratum preferences (in terms of boulder and gravel particle size) when they were separated from one another, but that the preferences changed when the animals occurred together in the field. It is uncertain whether this is behavioural character displacement to allow for co-existence, or whether it reflects exclusion of one species by the other, from a preferred habitat. Nel (1995) found some evidence of a similar change in particle size preferences amongst three species of cirrolanid isopods occupying open ocean beaches. Defeo *et al.* (1997) reported spatial segregation on a meso- and macroscale between *Excirolana armata* and *E. brasiliensis* probably as a result of competitive interactions.

Adult-juvenile interactions are rarely discussed in the context of sandy beach ecology, but it is accepted that competitive interactions possibly exist at relatively high densities of macrofauna, particularly under more sheltered conditions (McLachlan, 1988). Adult-recruit interactions also seem more likely on sheltered shores, where many species are more specialised and less opportunistic than on exposed sandy beaches (Branch, 1984; McLachlan, 1988).

Even though adult-juvenile interactions have been a topic of discussion, especially for benthic communities of subtidal soft sediments and intertidal sand flats, few generalities exist with respect to these interactions in soft sediments. It has been reported that size interactions in soft environments are strongly linked to feeding mode (Hewitt *et al.*, 1997). Juvenile suspension feeders are less likely to be inhibited by adults than deposit feeders (Olafsson, 1989; Thrush *et al.*, 1992; Hewitt *et al.*, 1997). Experiments on interactions in soft sediments generally fail to indicate consistent trends and are often modified and complicated by other factors such as habitat characteristics, or the physical environment (Thrush *et al.*, 1996; Olafsson, 1989).

Adult-juvenile interactions have also been demonstrated for psammophylic amphipods. High densities of adult *Corophium volutator* consistently depressed the abundance of small conspecifics, although the mechanism of the interaction has not been identified (Limia and Raffaelli, 1997). Wilson (1989 cited by Limia and Raffaelli, 1997) suggested that either interference competition or disturbance occurs, preventing smaller individuals from establishing burrows amongst adults at high densities. Crocker (1967) described the distribution patterns of five haustoriid amphipod species occurring on Georgia beaches (which ranged from sheltered, low energy beaches to tidal flats). Two of these species (*Neohaustorius schmitzi* and *Haustorius canadensis*) occupy the high shore, while two other species (*Parahaustorius longimerus* and *Acanthohaustorius millisi*) frequent the low shore. The fifth species (*Lepidactylis dysticus*) occurs between these groups and can change its distribution, depending on the presence of the other species. In addition, vertical partitioning and staggered breeding exist between the co-occurring species, as well as other filter feeders. These strategies hint at mechanisms that reduce competition for both space and food (Crocker, 1967).

Vermeij (1972) concluded from studies on rocky shores that it is generally more advantageous for gastropod populations to have immature animals settling where mortality is lowest. High-shore species, which are presumed to suffer more physiological stress, should increase in size up the shore. This seems to be a plausible explanation for the differential size distribution in the bivalve *D. serra* on South African south coast beaches. However, another donacid, *Donax trunculus*, on the French Atlantic coast, exhibits the opposite distribution pattern, with the smallest individuals highest on the shore and the largest ones near LWST⁶ (McLachlan and Jaramillo, 1995). This pattern is also evident for *D. serra* on the west coast of South Africa. Vermeij (1972) concluded that predation or other biological

⁶ LWST: is low water spring tide.

interactions might shape this increase in size down the shore. The detailed distribution patterns of intertidal bivalves therefore seems to be much more complicated than just the settling of juveniles, especially when it comes to determining whether the patterns are due to the specific physical or biological parameters.

Haley (1982), however, illustrated from laboratory experiments that the distribution of juvenile mole crabs was modified by the presence of adults. On sandy beaches small *Hippa pacifica* frequent the top of the shore, while the supposed stronger competitors, i.e. the adults, frequent the lower shore (Haley, 1982).

Even where competition among individuals does occur, there may be no effect on the distribution of any of the species involved (Creese and Underwood, 1982). The importance of competition therefore cannot be demonstrated by the mere presence of zonation on the shore, nor can the existence of competition be inferred (unambiguously) by observation of distribution patterns, abundance and/or size-structures (Underwood, 1988).

It is evident from these studies that there may be problems in extrapolating from sand flats to beaches. Many of the interactions, such as those caused by the burrow-dwelling amphipod, *Corophium volutator*, change the sediment properties of intertidal flats by pelletization or other physio-chemical processes that may not exist on sandy beaches (Limia and Raffaelli, 1997). The influences that these animals have on invertebrate assemblages are thus often not direct, and are difficult to interpret (Limia and Raffaelli, 1997). Moreover, pelletization or the influence of a single species of amphipod on the physio-chemical properties will probably be undetectable on exposed sandy beaches, where tide-driven water filtration rates range over 3 - 91 m³ of sea water per running metre of beach, per day (McLachlan, 1982; 1989; McLachlan *et al.*, 1985). The interstitial environment on beaches is thus constantly modified by physical processes, which are largely a function of wave action (McLachlan, 1982; 1988).

It is evident from these studies that exposed sandy beaches are one of the areas in ecology where competition theory has largely been ignored (Defeo, 1996). Instead, community and population patterns on exposed beaches are explained as a consequence of individual responses to wave action (Ellers, 1995c), swash climate (McArdle and McLachlan, 1992; McLachlan *et al.*, 1995; Gimenez and Yannicelli, 1997), sand movement and liquefaction of the beach face, rather than biological interactions (Defeo, 1996; McLachlan, 1988). This is especially the case with respect to exposed reflective beaches which are amongst the harshest of marine environments (McLachlan, 1988). However, as environmental conditions approach the ultra-dissipative extreme, competitive interactions seem more likely. Although evidence points to both competition and predation on sandy beaches decreasing with increasing exposure, this is difficult to substantiate, as there have been few experiments on either, on high-energy beaches (McLachlan, 1988). The highly dynamic nature of such beaches precludes caging (McLachlan, 1988). In the absence of such experiments conclusions are largely speculative (McLachlan, 1988).

5.2.3 Predation

Predation is an important biological force on rocky shores, often limiting population levels to a point where *competition* does not become a major structuring factor. It has also been reported that predation can have the opposite effect, and increase competition (Sih, 1987). The tropics have many fast-moving species year-round, so more prey-species are competing for crevices and holes for shelter (Branch, 1984). The relative importance of predation and competition thus seems to depend on the type of prey species involved (i.e. sessile vs. mobile) or their relative size (small vs. large; Paine, 1981; Henry and Jenkins, 1995).

Peterson (1991) described the predation present on soft-sediment intertidal communities as 'top-down' predation from the land and 'bottom-up' predation from the sea. These

communities are vulnerable on the incoming tide when swimming crabs and schools of predatory fishes follow the tide up to feed in the submerged intertidal. Similarly, the topography makes intertidal zones of beaches accessible to shore birds at low tide (Peterson, 1991). In all cases where predators have been excluded from soft substrata, diversity has increased (McLachlan, 1988). This also supports the impression that competition in sediments is far less important than on rocky shores (Branch, 1984; Brown and McLachlan, 1990), probably since 'niches' or parts of the habitat are still available to new species. It also suggests that predation may be a very important biotic factor influencing the community structure of soft sediment benthos. Limia and Raffaelli (1997) reported that the size structure of amphipods is different in the absence of vertebrate predators since these predators selected larger prey species.

Studies on tidal flats have focussed on how predator densities change with changes in prey density, and *vice versa*. Examples include the effect of an artificial increase in bivalve prey species on the density of waders (Cummings *et al.*, 1997), or the foraging response of eagle rays (Hines *et al.*, 1997). On a low-energy sandy beach, experiencing a semi-lunar tidal cycle, predation by the polychaete, *Nephtys cirrosa*, was shown to be important enough to cause recruitment failure of other infaunal species (Bamber, 1993). Adult abundance of other species was also negatively correlated with *Nephtys* abundance (if the effect of the physical environment was eliminated). It was concluded that predation is the most important biological interaction on tidal flats (McLachlan, 1988).

The effects of predation are generally assumed to be most severe in benign habitats and to decrease with increasing harshness (Connell, 1975 cited by McLachlan, 1988). It is thus predicted that predation will be least important on reflective beaches, which generally have very low diversities, but may be important as conditions approach that of dissipative and ultra-dissipative beaches. Beach predators that could suppress diversity, include various

species of elasmobranchs (e.g. *Rhinobatus*, *Myliobatus*; Lasiak, 1983; Lasiak and McLachlan, 1987; Du Preez *et al.*, 1990), various flatfishes, birds (oystercatchers, sanderlings, terns and plovers, Hockey, *et al.*, 1983; Van der Merwe *et al.*, 1994) and other invertebrates such as crabs (*Ocypode* or *Ovalipes*; Du Preez, 1984; McLachlan, 1983a; 1988; Brown and McLachlan, 1990). McLachlan (1983a) made a thorough study of predators acting on open ocean beaches throughout the world. Little evidence was, however, obtained for diversity or abundance of prey species on beaches being affected by predators.

5.4 DISCUSSION

Underwood and Denley (1984) formulated some ideas on biological interactions from lessons learned on rocky shores. They concluded that predation was most severe in benign environments, competition more important in harsher environments and physical stress the most important in the harshest environments. The Noy-Meir autecological hypothesis stated similar ideas, suggesting that populations are limited by abiotic factors in deserts (Noy-Meir, 1979). Exposed sandy beaches clearly fall into the category of physically stressed environments (McLachlan, 1988).

Whitlatch (1980) argued that as habitat diversity increases, faunal diversity increases, but this also leads to a concurrent increase in the average niche overlap between species. In order to reduce competition, species utilise different niche dimensions. A community of nine different species of surface-feeding polychaetes 'have to' utilise a variety of food particle sizes, whereas 17 co-occurring, burrowing polychaete species partitioned *both* vertical space and food sources in order to co-occur (Whitlatch, 1980). This is in direct contrast to the idea that as communities become more diverse so the mean overlap between species will reduce (Branch, 1984). Whitlatch (1980) came to his conclusion by ranking the species in the polychaete community in order of abundance. He concluded that it is the rarer species that have the greatest overlap with other species and will be eliminated first if food levels decline.

It is also no particular species that is responsible for the exclusion of rarer species, but rather an overall reduction of carrying capacity or food availability. This is termed diffuse competition⁷. Whitlatch (1980) recognised the controversy regarding the generality of the pattern. The reason for dispute, however, may be in the differences in the stability of different systems and the communities occupying them. It is suspected that diffuse competition may be more probable in less stable environments with varying community structures. A valid question would thus be to ask if this is a possibility on beaches?

A frequent assumption is that beach fauna generally comprises opportunists, which have wide niches that overlap easily. Diffuse competition thus seems plausible. Whitlatch (1980) commented that if diffuse competition is common in soft sediments it may explain why it is so difficult to understand community organisation in soft sediment benthos. However, since little information is available on the niche widths and resource utilisation on beaches, it is difficult to apply the principals of this (or any other) competition model. Diffuse competition does, however, seem like a biological analogy of the general *swash exclusion hypothesis*, i.e. that more benign dissipative beaches seem to have a greater variety of niches and higher carrying capacity, and therefore can support more diverse communities. As conditions approach that of intermediate and more reflective beach states, 'rarer' species disappear, until the extreme reflective condition is reached where only a small number of very robust species survive. (This approach is, however, highly dependent on the definitions of 'carrying capacity' and 'rarity' of species).

Reasons why predation pressure does not lead to an increase in diversity in soft sediments include the fact that animals cannot undercut/crush each other in soft sediments, overgrowth

⁷ **Diffuse competition:** is the cumulative effect of several species that are collectively responsible for exclusion of rarer animals as environmental conditions become less favourable.

is unlikely because animals are generally free to move, and habitat partitioning can take place into a third dimension (Branch, 1984, Peterson, 1991). Adult-juvenile interactions tend to maintain populations at low levels. Moreover, most invertebrates are plastic in their growth, meaning that they can survive even if food is limiting. Competition in soft sediments therefore leads to coexistence under sub-optimal conditions, rather than to competitive exclusion. Indirect competition by means of modification of the sediment and adult-larval interaction may be of greater importance in these communities, than the forms of competition conventional for hard substrata, i.e. for food and space (Branch, 1984).

The extent of competition on exposed sandy beaches is still uncertain. It seems likely though that competitive interactions may be present, particularly at high tide when the whole intertidal faunal assemblage would scramble to obtain food brought in by the tide. Food may not be limited for these opportunists or filter feeders, but feeding space may. Intraspecific interactions may lead to adult-juvenile segregation or zonation patterns. Furthermore, interference competition may be more important than previously realised. Even though beach species cannot overgrow or undercut others (due of the three-dimensional environment), the highly mobile lifestyle of many species, and the frequent reburial as a response to the dynamic environment, suggest that infauna are likely to disturb each other. Moreover, opportunistic, scavenging predators such as cirrolanid isopods are likely to influence other species when they are swimming in the water column at high tide. These interactions may take the form of either interference or predation. However, the existence of such interactions should be tested experimentally.

Even though experimental techniques to examine biological interactions in such dynamic environments as sandy beaches are still lacking (McLachlan, 1998), a starting point seems to be evident. An investigation can be approached in two ways. Firstly, experiments (similar to those done on rocky shores) should be conducted to quantify interactions directly. These

experiments should focus on (i) interference competition, where the sediments are modified by co-occurring species such as burrowing molluscs, (ii) exploitation competition in terms of feeding space for filter feeders; or (iii) investigate adult-larval or adult-juvenile interactions that structure across-shore distribution patterns (Defeo, 1996). These interactions potentially exist on exposed sandy beaches. A second and more complicated approach should define the niche widths and overlap of sympatric beach species, and hence the possibility of competitive avoidance and overlap. McLachlan (1978) successfully applied this approach for mysticocarids on a high-energy beach, and showed vertical stratification. Such an approach is possible if a limited number of species are involved, but may be difficult for diverse communities. The first approach is what I have applied to the rest of this study.

Chapter 6 evaluates intraspecific competition for space between adult and juvenile clams, by investigating the effect of infaunal clam densities on burial time. Chapter 7 aims to elucidate whether intraspecific interactions exist *in situ* (for the clam *D. serra*) and whether such interactions are strong enough to explain adult-juvenile segregation across the shore. Chapter 8 investigates the possibility of interspecific interference competition using three species of cirrolanid isopods.



CHAPTER 6

University of Cape Town

6.1 INTRODUCTION

The settlement of *Donax serra* spat on the south eastern coast of South Africa occurs in the surf zone. This settlement is strongly affected by physical parameters such as their affinity for fine sand and high organic content in the surf zone (Lastra and McLachlan, 1996). Initial growth is rapid, and juvenile clams are settled by the time they reach ~ 8 mm shell length (Schoeman, 1997). At this size, clams start to migrate into the intertidal. *D. serra* reach sizes of 32 mm in the first year, and up to 42 mm in the second year (Schoeman, 1997). During this time of growth, their affinity for fine sand weakens (Lastra and McLachlan, 1996), and as they leave the subtidal the pressures to survive change. The ability to burrow rapidly is a critical adaptation of bivalves to the dynamic intertidal beach environment (McLachlan, 1998). Tropical donacids tend to migrate actively with the tides, whereas the temperate *D. serra* migrates on a semi-lunar cycle (Ansell and Trueman, 1973; McLachlan *et al.*, 1979; Donn *et al.*, 1986; Ellers, 1995c). Either way migration requires constant reburial to move or maintain position. These animals use this burrowing ability to avoid desiccation and to escape from predation or being transported to unfavourable environments (McLachlan, 1988; 1998).

Various factors influence bivalve burial. These factors include shell shape and ornamentation (Trueman *et al.*, 1966; Stanley, 1969; 1970), burrowing mechanisms and energy costs (Trueman and Ansell, 1969; Ansell and Trueman, 1973), grain size, sorting and the penetrability of the substratum (Brown and Trueman, 1991; Alexander *et al.*, 1993; Nel, 1995), temperature (McLachlan and Young, 1982; Donn and Els, 1990) and swash climate (McLachlan *et al.*, 1995; Ellers, 1995a; 1995c). Only one study, however, has investigated intra- and interspecific interference competition causing changes in burial time. This study concluded that competition for space between *D. serra* and *D. sordidus* is highly unlikely

because these clams differ in size (McLachlan, 1998). Competition seems possible between conspecifics although under exceptionally high densities, i.e. 600 adult *D. serra* per m² (McLachlan, 1998). No study has investigated *their situ* effect of bivalves of different size classes on the burial time of conspecifics.

This chapter investigates competition (either by interference or exploitation) in terms of changes in burial times of *D. serra* because of the presence of other individuals buried in the substratum. The null hypothesis for the study is that: there are no changes in burial times of *D. serra* individuals in the presence of other individuals at **different densities** *in situ*. If the hypothesis is rejected, then biological interactions may occur in *D. serra* populations (and it is assumed that interference may exist or space may be a limited resource under these circumstances on sandy beaches).

6.2 METHODS

Beach clams were collected during low tides at Britannia Bay (17°50'40"E, 32°42'30"S). This is a low-energy intermediate beach on the west coast of South Africa (see BBE; Chapters 2 and 4 for physical description), having a large population of adult *D. serra* (Farquhar, 1997). The bivalves were kept in 5-litre buckets, filled with native sand and fresh seawater. The clams were allowed to burrow into the sand in the holding containers to identify individuals showing signs of injury sustained during collection. Individuals that did not manage to burrow into the sediment in the holding tanks were discarded. All animals were used on the day of collection.

The experimental container was a 25-litre bucket with a diameter of 30 cm and a depth of 37 cm. The experimental surface area was approximately 0.1 m². It was half-filled with saturated sand collected from Britannia Bay, and covered by 10 cm of water. Water was replaced regularly to keep the temperature between 15 °C and 17 °C.

Burrowing time was defined as the time from initiation of burrowing with the foot, until the posterior end of the valves was level with the sand surface. A prerequisite for the valid measurement of burial time was continuous burial by the individual, without resting. Each animal was only allowed to burrow once. Clams were measured and fitted into size classes, which were defined as small (< 25 mm), medium (25 – 55 mm) and large (> 55 mm). No recruits < 10 mm or exceptionally large adults were used. Fifteen animals were tested to obtain a mean burrowing time per size group, per treatment density.

Different densities of clams were placed in the experimental container to form a background density. The animals forming the background densities were allowed to burrow in a haphazard distribution pattern. The background densities in the substrate were either zero animals, which served as control, 15 or 30 individuals. The specific densities were derived from the abundance values obtained for BBE and other west coast beaches (as sampled in Chapter 2, *Appendix 1*). Adult densities on the low shore were frequently 10 m⁻², whereas juvenile densities reached 90 m⁻² on the high shore. McLachlan (1998) reported densities of 400 m⁻² on other beaches. The same experimental densities were repeated for all size classes. The experimental design was thus as follows (Table 6.1):

Table 6.1 Experimental design indicating three size classes of *D. serra* burrowing into sand containing different clam background densities.

<u>Background <i>D. serra</i> size and densities</u>							
	Control	Small		Medium		Large	
Small <i>D. serra</i> burrowing (n=15):	0	15	30	15	30	15	30
Medium <i>D. serra</i> burrowing (n=15):	0	15	30	15	30	15	30
Large <i>D. serra</i> burrowing (n=15):	0	15	30	15	30	15	30

Care was taken not to create excessive water movement, which could influence the burrowing process. Substrate compactness, which is inversely related to penetrability, was kept constant between experiments by tapping the experimental container at a constant frequency and force, a fixed number of times. Penetrability was measured between

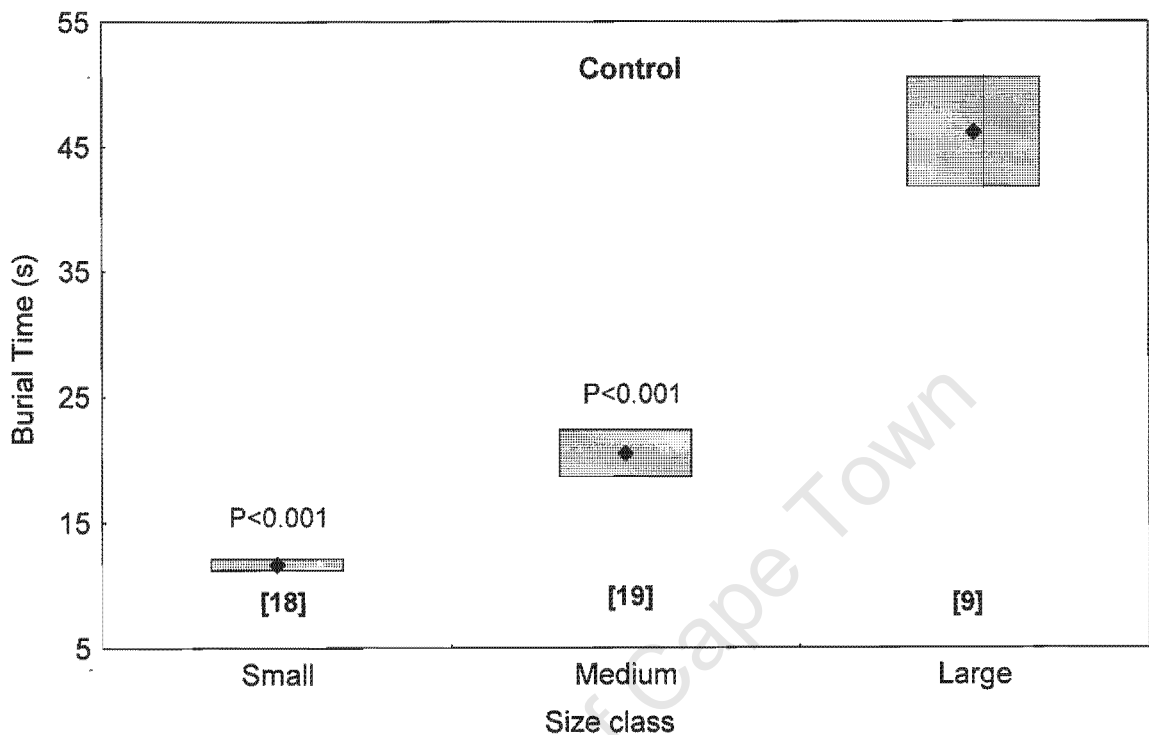
experiments by dropping a pointed metal rod from a constant height (18 cm) onto the sediment. This was replicated five times and measurements were recorded as distance of penetration (in mm). Granulometric analysis was performed by dry-sieving the sand using a series of sieves (graded in 0.5 ϕ intervals). The mean grain size, sorting and skewness were estimated graphically (as described by Brown and McLachlan, 1990).

Single-factor ANOVA and Tukey HSD multiple contrasts (STATISTICA '99) were firstly employed to determine if the size classes differed in terms of burial times. A Two-factor ANOVA and Tukey post hoc (HSD) multiple comparisons (at $\alpha=0.05$) were the employed (using STATISTICA '99) to test the effects of the treatment and size on burial time, simultaneously. Due to interactions between factors, and the complexity of interpreting multi-way ANOVA's further analyses were conducted to separate the different treatment effects. This was conducted using 3-way ANOVA and Tukey post hoc (HSD) multiple comparisons, but excluding the 'controls' to obtain a balanced design. The analysis entailed comparing the effect of (i) size classes against (ii) background densities of 15 or 30 animals, against (iii) different background size classes. Regression analysis was used to determine whether there was any correlation between compaction and burial time per size group (Zar, 1984).

6.3 RESULTS

An investigation into the burial times of small (mean length $\pm$ SD =12.7 $\pm$ 3.0 mm, n=20), medium (36.2 $\pm$ 3.9 mm, n=18) and large clams (68.5 $\pm$ 6.1 mm, n=13) in the absence of any treatments indicated that the burial times of these size classes differ (Fig. 6.1). Large animals burrowed in ~46 s, whereas juveniles achieved complete burial in ~11 s, and medium-sized individuals in ~20 s. A single-factor ANOVA confirmed these burial times to be significantly different ($F_{2,42}=41.85$, $p<0.001$). Since burial times for the three size classes were obtained in a single container this could not be an effect of sediment grain size, which was moderately sorted, with a mean particle diameter of 233 μ m (Inclusive Graphic Standard

Fig. 6.1 Mean burial times($\pm$ SE) of three different size classes of *D. serra*. P-values indicate the difference of the burial time per size group (small or medium) with that of the burial time for large animals. Penetrability values are presented in [mm].



Deviation; $sl = 0.502$; see Brown and McLachlan, 1990). It appears as if an exponential curve could be fitted though the burial time values for the three sizes (Fig. 6.1). This is probably an artefact arising from the use of size classes instead of linear measurements of shell length. *Post hoc* tests (Tukey HSD multiple contrast) confirmed that the control burial times of small and medium animals were not significantly different but the burial times of both these size classes differed significantly from that of adult clams (see Fig. 6.1 for P-values).

Penetrability values (presented in [mm] in Figs 6.1 & 6.2) indicate the compactness of the sediments. Elevated penetrability values therefore indicate less compact sediments, and bivalves should manage to burrow more easily in these sediments. Penetrability, however, seems to have a minor influence on burial times. Mean penetrability values ranged between 8.2 mm and 29 mm for all the experiments; and no correlation was found between the burial

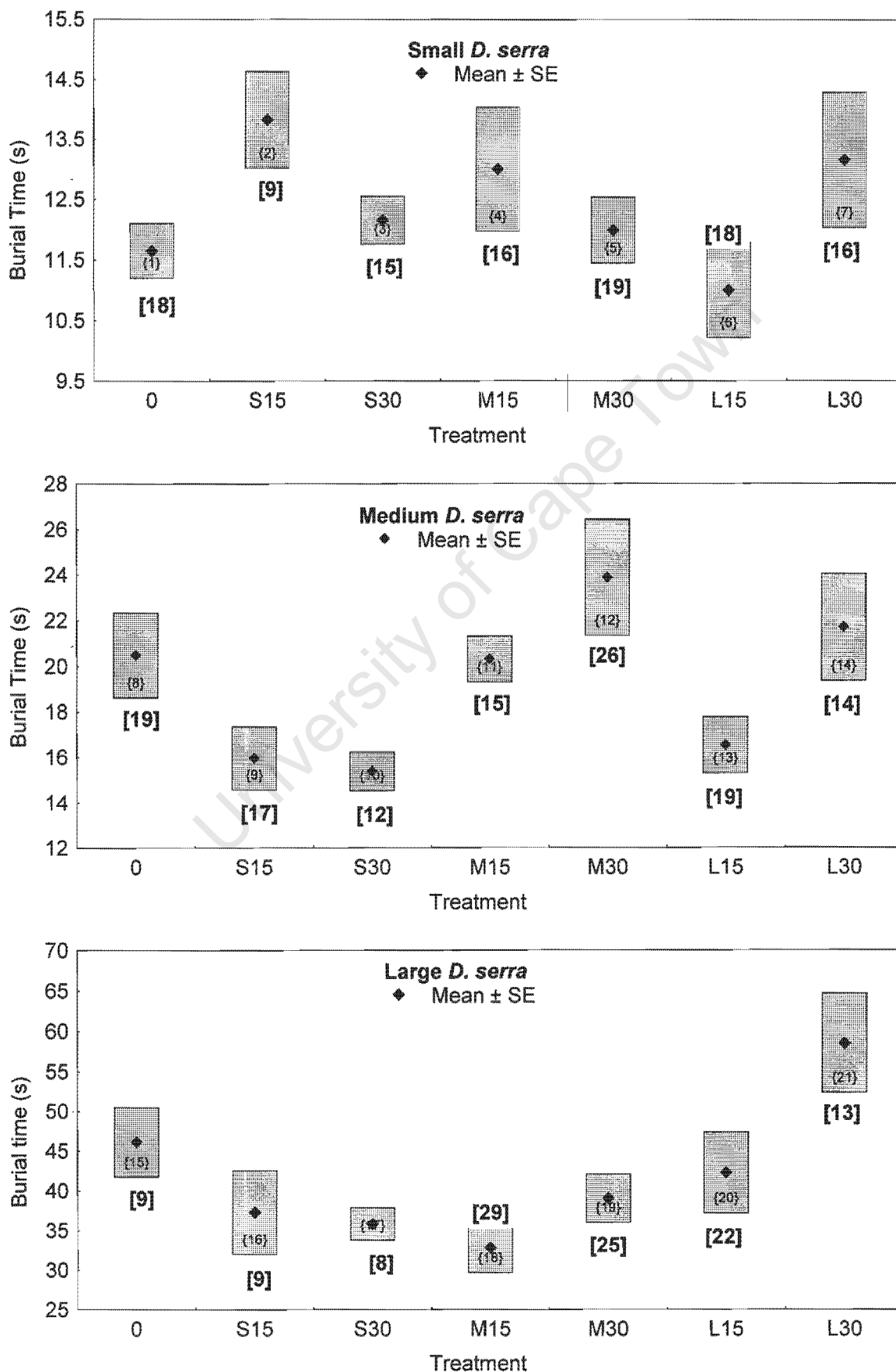
times and compaction for any size class (all $R^2 < 0.074$ & $P > 0.11$). Only the burial times of juvenile *D. serra* seemed to follow the changes in compaction slightly. The burial times of especially medium and large animals are unaffected by sediment composition or compactness (Fig. 6.1).

An investigation into the burrowing times of the three size classes in sand with different background densities did not indicate a consistent trend for all size classes. Burial responses seemed specific to the experimental size category, and treatment. Mean burial times for small animals in all treatments ranged 10.9 – 13.8 s (Fig. 6.2), and seemed unaffected by the presence of any other animals (Fig. 6.2). The mean burial times of medium sized animals ranged 16 – 24 s, which was faster than the burial times obtained for large clams under all treatment conditions (Fig. 6.2). However, burial times obtained for medium animals burrowing into sand containing 30 medium clams was the slowest for this size class, which seems to indicate the more severe treatment. Burial times for large individuals were more than 10 s slower with 30 adults in the sand when compared with the burial times when either zero or 15 adults were buried in the sand (Fig. 6.2). A Two-factor ANOVA confirmed significant responses to both treatment and size (Table 6.2). There was, however, also a significant interaction between the two factors (Table 6.2).

Table 6.2 Results from the Two-factor ANOVA investigating differences in burial times of *D. serra* belonging to different size classes (i.e. size) or burrowing into sediments containing background animals of varying densities (i.e. control, 15 or 30 animals of different sizes).

Experiment	$F_{k-1,df}$	P
1. Effect of <i>size</i> on burial time	$F_{2,294}=215.31$	$P<0.01$
2. Effect of <i>treatment</i> (including controls) on burial time	$F_{6,294}=4.57$	$P<0.001$
1vs2. The <i>interaction</i> of size and treatment	$F_{12,294}=3.27$	$P<0.001$

Fig. 6.2 Burial times of small, medium and large *D. serra* into sediments containing background densities of either zero, 15 or 30 clams of small (S), medium (M) or large (L) animals. Penetrability values are presented in [mm]. Values in {}-brackets refer to the treatment conditions as tabulated in Table 6.3.



The Tukey *post hoc* HSD test confirmed the interaction between size and treatment, and indicated that it is probably due to the overwhelmingly slower burial times of adult clams. Under almost all treatment conditions, the adult burial times differed significantly from that obtained for medium and small clams (Table 6.3). Moreover, the mean burial time for adult clams with 30 adult clams in the sediment differed significantly from all other treatments (but the adult control; Fig. 6.2 & Table 6.3). The burial times of all other treatments did not indicate any significant differences. It is interesting to note that the burial times of the control as obtained for the small, medium and large size classes were in the middle of the range of burial times obtained for all the treatment, and none of the treatments differed significantly from the control (Fig. 6.2). This begs the question whether there is any interaction/queue among animals to trigger, or stimulate burial?

The analysis was continued in order to separate the effects of background size and background density. This was investigated by using a 3-way ANOVA but eliminating the control values to obtain a balanced design. The three factors investigated were *size X background density X background size*. In isolation, all three these factors have a significant influence on burial time, but not combined (Table 6.4). The burial time per size category is independent of background density, but there is an interaction between size category and background size, and background density and background size. The critical parameter therefore seems to be the background size of animals and not the density *per se*.

A Tukey *Post hoc* multiple comparison again confirmed that the burial times for adults in almost all instances differed from medium and small animals. Burial times of adults under high densities of adults differed significantly from all other burial times (Table 6.5 & Fig. 6.3). Furthermore, burial times were always slower (with the exception of juveniles onto 30 adults *in situ*) when burrowing was measured into sand containing individuals of the same size class, at similar densities to other size classes. For example: burial time was slower for small animals burrowing into sand containing 15 small individuals rather than sand containing 15

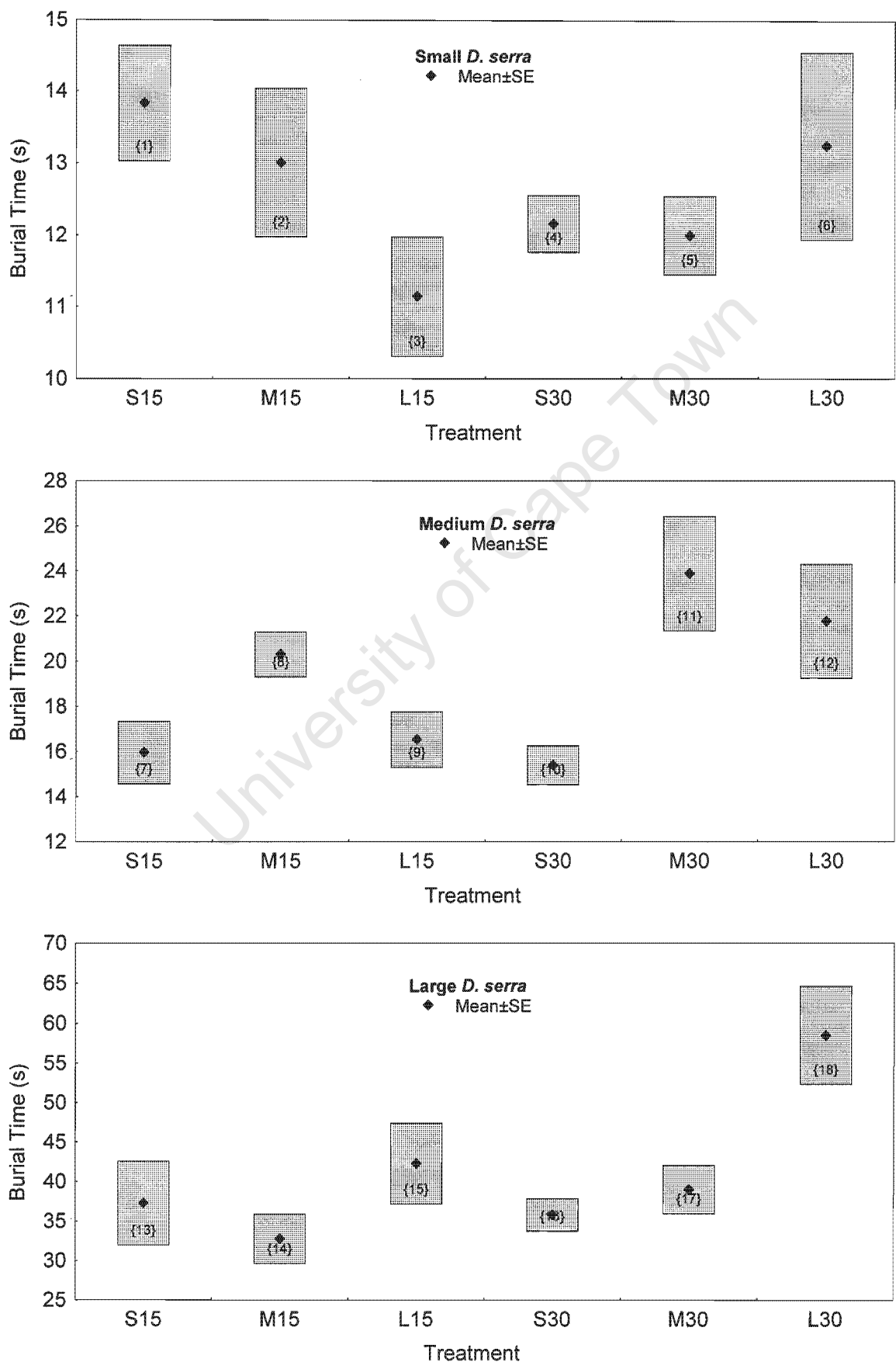
medium or 15 large clams; or burrowing was slowest for medium animals burrowing into sand containing 30 medium animals, rather than for sand containing 30 small or 30 large animals. Although these differences were not significant, the trend was consistent.

Table 6.4 Results obtained from a 3-way ANOVA performed, to evaluate the effects of background density and background size on the burial times per size class. (P-values in **Bold** indicate significant values).

Experiment	$F_{k-1,df}$	P
The effect of size	$F_{2,252}=174.45$	<<0.001
The effect of background density	$F_{1,252}=5.93$	0.015
The effect of background size	$F_{2,252}=6.05$	0.003
Size X background density	$F_{2,252}=2.54$	0.081
Size X background size	$F_{4,252}=7.06$	<0.001
Background density X background size	$F_{2,252}=4.06$	0.018
Size X background density X background size	$F_{4,252}=0.966$	0.426

In comparing the effect of background density on burial time, it was concluded that there was a progressive delay in burial time with an increase in density (and size). Burial times obtained per size category appeared to be slower at the higher densities, although this trend was not very strong. This effect was most pronounced with large animals burrowing into the sand. Mean burial times ranged ~32 – 42 s with 15 animals *in situ*, whereas it ranged ~35 – 58 s with 30 clams *in situ* (Fig. 6.3 & Table 6.5). Under all the conditions the only significant difference was obtained when background densities approached 30 *D. serra* per 0.1m². It is therefore concluded that this is the only density under which competition/interference competition can be concluded.

Fig. 6.3 Comparison of all treatments excluding the controls, to evaluate the effects of size, background density and background size. Values in {}-brackets indicate the treatment combination as per Table 6.5.



6.4 DISCUSSION

Previous studies indicated that the burial time of *D. serra* is linearly related to shell length, with larger animals burrowing slower than small ones (McLachlan and Young, 1982; Donn and Els, 1990; McLachlan *et al.*, 1995; Nel, 1995). The burial times obtained for the three size classes in this study compare well with the burrowing times obtained by Donn and Els (1990) for west coast *D. serra* burrowing into sediments at 15 °C. These authors did not specify the grain size but stated that the sediments were obtained from Maitlands River Beach. This beach is an intermediate - dissipative beach (McLachlan *et al.*, 1995), with medium grained sediments. (The present study measured the mean grain size value on Maitlands River Beach to be 268 µm; Table 2.1). The particle diameters recorded in these two studies should therefore be very similar.

It appears as if a slight exponential function could be fitted through the mean burial times observed in the controls for the present study. Since size classes were used rather than exact shell length values, the relationship is assumed to be linear, as was the case, for all the previous studies (McLachlan and Young, 1982; Donn and Els, 1990; McLachlan *et al.*, 1995; Nel, 1995).

Penetrability for all the treatment experiments was measured with the background animals already buried. Changes in penetrability could therefore be a result of the bivalves in the sand. It is thus difficult to ascribe changes in the burial times of animals to changes in an effect of the treatment on penetrability, or an effect of the treatment itself. However, since no correlation was obtained between burial times and penetrability per size class, it is assumed to be unimportant in this experimental procedure and is probably unimportant as an interference agent. The possible interference caused by animals *in situ* is thus suspected to be caused by a mechanism other than changing the physical properties of the substrate.

D. serra seems well adapted to the dynamic beach environment, having a strong burrowing ability. However, factors that affect burrowing ability may have important implications in terms of their success on the beach. Bivalves burrow into the substrate to avoid predation, desiccation or swash displacement (McLachlan, 1983a; Brown *et al.*, 1989). A burial time lasting a sixth longer due to the presence of other adults in the sediment may be to the detriment of the individual. It would, however, be unrealistic to extrapolate simply between swash parameters such as swash period, upwash time etc. and the success of *D. serra* on the beach. But, as discussed in Chapter 4, good correlations were obtained between the number of *D. serra* that managed to burrow into the sand between swashes and, swash upwash distance and backwash time, slope and effluent line crossings. Nel (1995) also partially attributed the success of *D. serra* on intermediate and dissipative beaches to the grain size characteristics of these beaches. Fine and medium sediments allow for the fastest burial (Nel, 1995). An increase in the burial time could eliminate this species from beaches with coarser grains (Stanley, 1969; McLachlan *et al.*, 1995; Nel, 1995). An increase in burial time, whether it is due to an increase in grain size or the presence of other individuals, should therefore cause the displacement of some animals. If burial time is thus sufficiently increased, not allowing bivalves enough time to burrow between swashes, it could be expected to have a significant influence on the population structure over time.

The burial time was always slowest (except for small animals burrowing onto 30 adults) for animals burrowing onto their own size class for both densities, e.g. medium sized individuals burrowed slower into sand containing 15 medium sized *D. serra* than sand containing either 15 small or 15 large *D. serra* (Fig. 6.2). The same was true for medium sized animals in the experiment containing 30 medium clams (Fig. 6.2). It is therefore suggested that animals of a similar size interfere more (even at lower densities) with each other, than animals of a different size, at the same density. This is probably a response to similar burrowing depths and burrowing frequencies/cycles because of similar physiological requirements and abilities. This could indicate resource partitioning. However, the only significant difference

was obtained with large adults burrowing into sand containing extreme densities (30 indiv. 0.1 m^{-1}) of their own size.

Competition for space seems to be a likely possibility among large adults at high densities. The burial time of adult *D. serra* was significantly slower (Fig. 6.2) when they were burrowing into sand containing 30 large clams when compared with sediments containing medium or small clams. This could have a dual cause, i.e. interference from similar sized individuals (interference competition) or simple lack of physical space (exploitation competition). Burial times for adult clams were also slower at lower densities where more space is available, but was not significantly different from any other adult/large burrowing times. Furthermore, an observation was made of an adult clam that was forced out of the sand by the burrowing process of its conspecifics. Another individual was observed to attempt burrowing, and because of the space occupied by a specific individual already in the sand where it attempted to burrow, it extended the foot further until it was possible to anchor the foot sufficiently. It then dragged its shell along the sediment surface to a point where it was possible to burrow without any obstructions. Bivalve densities ranging 10 - 40 *D. serra* per 0.1 m^2 have been measured in the field (Farquhar, 1997; McLachlan, 1998). The densities used during these experiments are thus not unrealistically high.

McLachlan and Young (1982) investigated the effect of temperature on the burrowing success of different beach macrofaunal species. They also recorded some swash parameters, including the number of effluent line crossings. They calculated that an adult *D. serra* requires between 32 s and 48 s to burrow successfully between swashes, due to the rate of effluent line crossings (see McLachlan and Young, 1982; for complete description). An increase of burial time well above 50 s could therefore cause adult *D. serra* to be displaced to the subtidal or stranded above the driftline under conditions described by these authors. It thus seems unlikely that competition would occur between individuals, unless when population densities of adult *D. serra* greatly exceed 30 or 40 individual per 0.1 m^2 . On

benign dissipative beaches where *D. serra* densities tend to be high, exploitation competition in terms of space, seems a likely mechanism.

The question whether competition exists between white sand mussel individuals of different sizes and whether this can be interpreted as an adult-juvenile interaction, seems unanswered. This study shows little evidence of such an interaction. In almost all instances, burial times were slowest when individuals had to compete for space with individuals of their own size, rather than smaller or larger ones in the sediment. Differences were strongest in the case of medium sized individuals. This is (presumably) because different sized clams occupy different depths in the sediments, and are therefore more likely to encounter animals of their own size. Medium and large animals can apparently burrow through the layer containing small individuals without being affected. But small individuals have few competitive abilities, especially at these densities. These results therefore suggest that resource partitioning could occur and that competition for space will be reduced between different size classes (since they occupy different depths), especially over the short term. However, the background densities will have to exceed 30 clams 0.1m^{-2} , especially for the small and medium clams.

Across-shore segregation by size therefore does not seem to be a function of a change in burial time because of competition for space. If adult-juvenile competition exists, it either operates over a longer period than tested here or has a completely different cause (such as competition for food). The behavioural response of some of the juveniles suggests a plausible mechanism (in terms of interference competition). Two of the juveniles 'jumped' out of the sand shortly after burrowing was completed. These juveniles probably continued their burrowing process until they encountered adults buried in the sand. It seems unlikely that the juveniles would simply avoid adults by 'jumping' out of the sand, since they again would be susceptible to all the dangers that they were trying to escape from. It is therefore suspected that it was the adults that 'forced' these juveniles out of the sand. This mechanism could either be by siphon action or the adult burrowing/emergence action.

The behaviour of these clams indicates a possible interference interaction between clams of different sizes, but it is unclear whether this is a likely process in the field. It is, however, expected that the ratio of juveniles that are displaced out of the sand may be increased at higher background densities of adults, such as those reported by McLachlan (1998). The experimental procedure also only allowed for one clam to burrow at a time (otherwise the background density would have been increased). It is probable that the interference effect of adults may be stronger in the field if a larger number of juveniles are trying to establish themselves in the sediment at the same time. Juveniles could then interfere with each other, as well as being affected by adults. Furthermore, all the experiments were conducted in isolation from wave action. In the field, juveniles that are 'ejected' out of the sand would be displaced by the waves, resulting in an adult-juvenile distribution. Moreover, Ellers (1995c) reported that the swash riding and burrowing behaviour of *D. variabilis* is governed by waves. It is therefore expected that the activity patterns (such as siphon actions and burrowing/emergence activities) of adult *D. serra* will be increased where they are exposed to constant wave action.

In conclusion, biological interactions among *D. serra* individuals in terms of competition for space are probable at high densities, especially for larger-sized individuals. It may also include medium-sized individuals if the densities exceed 30 clams 0.1 m^{-2} . This interference is expected to have the greatest ecological importance in the case of adult populations exceeding *in situ* densities of 30 adults per 0.1 m^{-2} , since these conditions are likely to occur. The experimental procedure found little 'proof' of adult-juvenile interactions, but observed a possible interference mechanism that may be important once juveniles are buried in the sand. It is therefore necessary to test whether adult and juvenile clams interfere with each other in the field, as they did in the laboratory.



CHAPTER 7

University of Cape Town

7.1 INTRODUCTION

Although not always obvious, zonation patterns are very typical of beach macrofaunal communities (Dahl, 1952; McLachlan *et al.*, 1984; Jaramillo *et al.*, 1993; McLachlan and Jaramillo, 1995; McLachlan *et al.*, 1996a; Gimenez and Yannicelli, 1997). Soares *et al.* (1998) defended the interspecific zonation scheme approach by recognising that biological zones are not static. This, however, does not imply that they do not exist, as has been claimed in recent studies by Hayes and Quin (1995), and Brazeiro and Defeo (1996). The primary causes of zonation are summarised as responses to exposure, changing wave energy levels and sediment water content and stability (Brown and McLachlan, 1990). A factor that complicates zonation schemes is the motility of fauna which do not occupy fixed levels on the beach, and that the zones are therefore constantly changing (Jaramillo and McLachlan, 1993; McLachlan and Jaramillo, 1995; McLachlan *et al.*, 1996a). Macrofaunal zones can generally be identified by a characteristic species or species typical of a specific physical level on the shore. Whether a universal zonation scheme will ever be defined remains uncertain, but definitions of zonation schemes should also include intraspecific zones.

Many authors have recorded spatial separation of individuals of the same species of different sizes, occupying the same physical zone or spanning more physical zones. Examples include the well-documented across-shore distribution patterns of *D. serra*, which are reversed on the south-east and west coast of South Africa (De Villiers, 1975a; Donn *et al.*, 1986; Donn, 1990a; Schoeman, 1997) and seasonally segregated size classes of *Mesodesma mactroides* (Defeo, 1992 cited by Schoeman 1997; McLachlan *et al.*, 1996b).

Donax trunculus on the French Atlantic coast also exhibits differential distribution by size, with the smallest individuals highest on the shore and the largest near LWST¹ (McLachlan and Jaramillo, 1995). *Bullia rhodostoma* and *B. digitalis* adults co-occur in the swash and juveniles of these species occur respectively higher and lower on the shore (Brown, 1982; McGwynne and McLachlan, 1985). Similarly, adult and juvenile crustaceans such as *Talorchestia saltator* (Fallaci *et al.*, 1999), *Gastrosaccus psammodytes* (Wooldridge, 1983) and cirolanid isopods (Jaramillo, 1987; Bally, 1987; De Ruyck *et al.*, 1991; de Alava and Defeo, 1991; Defeo *et al.*, 1997) occupy different levels of the intertidal and subtidal areas.

Unlike individuals of different species, conspecifics generally have the same physiological requirements and use the same mechanisms to interact with their abiotic environment. So, as discussed in previous chapters, the reasons for the spatial separation between recruit and adult *D. serra* is not clear. Some studies suggest that adult molluscs choose a position in the intertidal area and that juveniles are displaced because of either interference by adults, or by physical sorting of waves (Defeo, 1993a, cited by McLachlan *et al.*, 1996b; McLachlan *et al.*, 1996a; Schoeman, 1997). If the separation between adults and recruits is a result of some form of interference, it is probably a density-dependent response by recruits to adults (Schoeman, 1997; Soares *et al.*, 1998). Three possible mechanisms have been proposed: adult-larval predation (Schoeman, 1997), competition for food (Soares *et al.*, 1996; Soares *et al.*, 1998) or sediment disturbance by adults (Schoeman, 1997; Soares *et al.*, 1998). However, none of these mechanisms have been investigated for *D. serra*.

The aim of this chapter is not to investigate a possible mechanism for biological interaction but rather to test if density-dependent interference between adult and juvenile *D. serra* exists at all. More specifically, it attempted to establish whether adult *D. serra* are responsible for displacing juvenile clams from a specific level in the intertidal band. The null-hypothesis is

¹ LWST: is defined as the Low Water Spring Tide level.

thus that juvenile white mussel² recovery³ after 24 hours is independent of adult white mussel densities.

7.2 METHODS

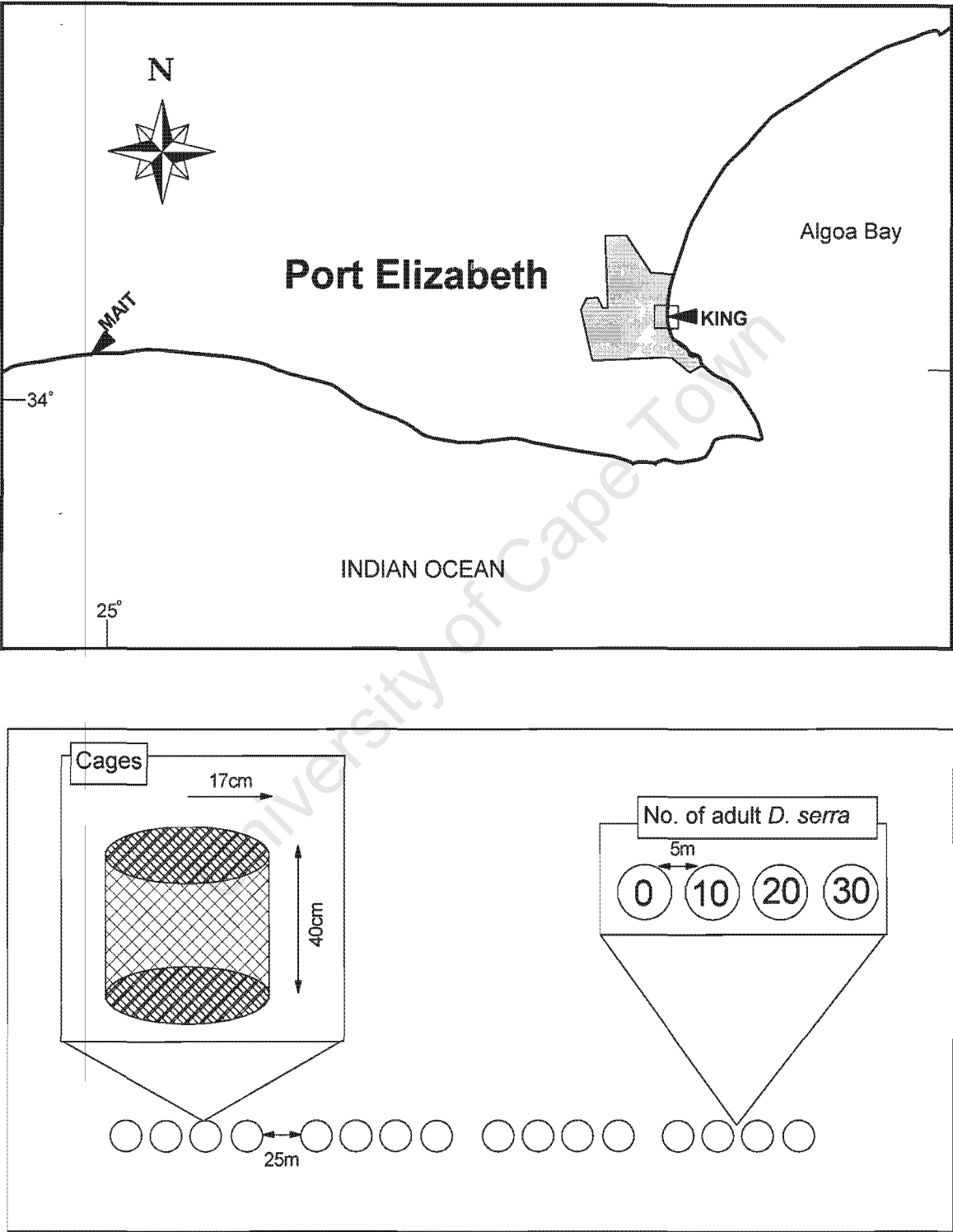
The beaches that were used for the experiments were chosen on the basis of three criteria. First, a large population of clams had to be easily obtained since each experiment required hundreds of clams daily. Second, the experimental area had to be devoid of juveniles as they could bias the experimental outcome by moving into the cages. Last, it should preferably have limited public access to avoid interference with the experiments.

The daily experimental procedure was preceded by collecting a large number of adult (> 55 mm) and juvenile (15 – 30 mm) *D. serra* from Maitlands River Beach (MAIT, Fig. 2.1), which harbours a large population of white mussels (Fig. 7.1). These animals were then transplanted to the experimental area, which was on Kings Beach (Fig. 7.1). The experimental area is a low energy intermediate beach with fine/medium sand with a low abundance of *D. serra* (McLachlan *et al.*, 1993; also see Chapter 2). Adult and juvenile clams were placed in cages with a mesh aperture of approximately 20 mm x 20 mm. This allowed juvenile clams to escape from the cages, but retained the adults. The number of adult clams was therefore fixed per cage, with the exception of one cage per treatment set. The cages were stocked with 30 juveniles per cage and either zero (= control), 10, or 20 adult white mussels. During the first three days of experimentation, fourth cage was not stocked with any animals (= empty). This was to monitor whether juveniles moved into the cages from the resident population. On the following two experimental days this cage was also used as a treatment and was stocked with 30 adults and 30 juveniles. This was done to strengthen possible interference effects. However, this yielded only a few replicates, which

² **White mussel:** is the colloquial name of the beach clam, *Donax serra*, and is interchangeably used with 'beach clam'.

³ **Recovery:** refers to the number of juvenile clams placed in the cages (containing adult clams at different densities) and then recapturing the same animals still in the cages, 24 hours later.

Fig. 7.1 Experimental placement of cages to determine the possible interference of adult *D. serra* with juvenile calms. (*The cage with 30 adults contained no clams for the first three days of the experimental period).



Cages were buried 5 m apart, and each replicate set was separated by 25 m along the shore (Fig 7.1). The cages were buried so that the base was at least 30 cm below the surface, which allowed sufficient space for adult *D. serra* to burrow comfortably (Nel, 1995). Depending on the tidal state, either four were subsequently pooled with the 'more severe treatment' of 20 adults per cage. The treatment densities are thus referred to as 10, and 20 (or more) adults, and the zero adult density is referred to as the control. Five sets of replicates were set daily, for five consecutive days. Mesh cages were sunk just below the effluent line on the low to mid shore where juvenile *D. serra* would usually be found. The cages were therefore submerged for at least half of the tidal cycle.

The caged animals were left overnight for two high tides and a low tide cycles. After 24 hours, the cages were dug out and lifted into mesh bags with the sand still in the cages. It was possible to transfer the cages with the content into sieve bags as a solid unit without losing sediments, due to the thixotropic properties of the beach sediments. The sand was then sieved out in the surf-zone and the number of juveniles retained per cage was counted. This was defined as juvenile recovery.

A preliminary study was conducted on Elizabeth Bay Beach (Namibia) to test the experimental procedure and the efficiency of the cages. During the preliminary experimental period the sampling area was hit by a winter storm, and the juvenile recovery values changed dramatically. This indicated the necessity for additional information, especially about the physical environment, in interpreting the results. A series of physical parameters was therefore measured simultaneously on a daily basis on Kings Beach. These measurements were obtained, after the cages were buried on the incoming tide, and were assumed to be representative of the physical conditions that prevailed for 24 hours before the excavation of the cages. These parameters include wave height (WAVEH), wave period (WAVET) or frequency (WAVEF), swash frequency (SWASHF) or period (SWASHT), swash

up and backwash time (SUT / SBT), distance (SUD / SBD) and speed (SUV / SBD), effluent line crossings (EFFCROS) and slope (SLOPE). These parameters were defined in Chapter 3.

Analyses of the experimental results were conducted using Multidimensional Contingency Tables (Zar, 1984; 1996), based on the frequency of recovered : unrecovered juveniles over time (10 days) for three treatments (i.e. a control, 10 and 20/more). Non-parametric Kruskal-Wallis rank test (STATISTICA '98) and Contingency Tables (Zar, 1984) were used to detect differences between treatments. Non-metric MDS (PRIMER ver. 3.1b) using the Bray-Curtis similarity index was conducted (on the number of juveniles recovered per day) after regression analysis proved unsuccessful in evaluating the effects of the physical environment on juvenile recovery.

7.3 RESULTS

7.3.1 Biological interactions

The empty cages indicated that resident juveniles did not move into any of the cages of their own accord. Thus all the juvenile white mussels recovered from the cages the next day were assumed to be experimental animals planted in the cages. The mean juvenile recovery ranged between 60 – 80%, but with a large amount of variance between replicates so it is difficult to detect any influence of treatments conclusively.

Juvenile recovery over time, per treatment, was evaluated simultaneously using a Contingency Table. This analysis indicated that there was a large effect of either treatment and/or time on the ratio of recovered : unrecovered clams ($\chi^2_{0.05,47}=983.7$ $P<0.01$). Partial interactions between factors (i.e. juveniles recovered : unrecovered, per treatment over time) indicated that there was a significant interaction among all three variables (Table 7.1).

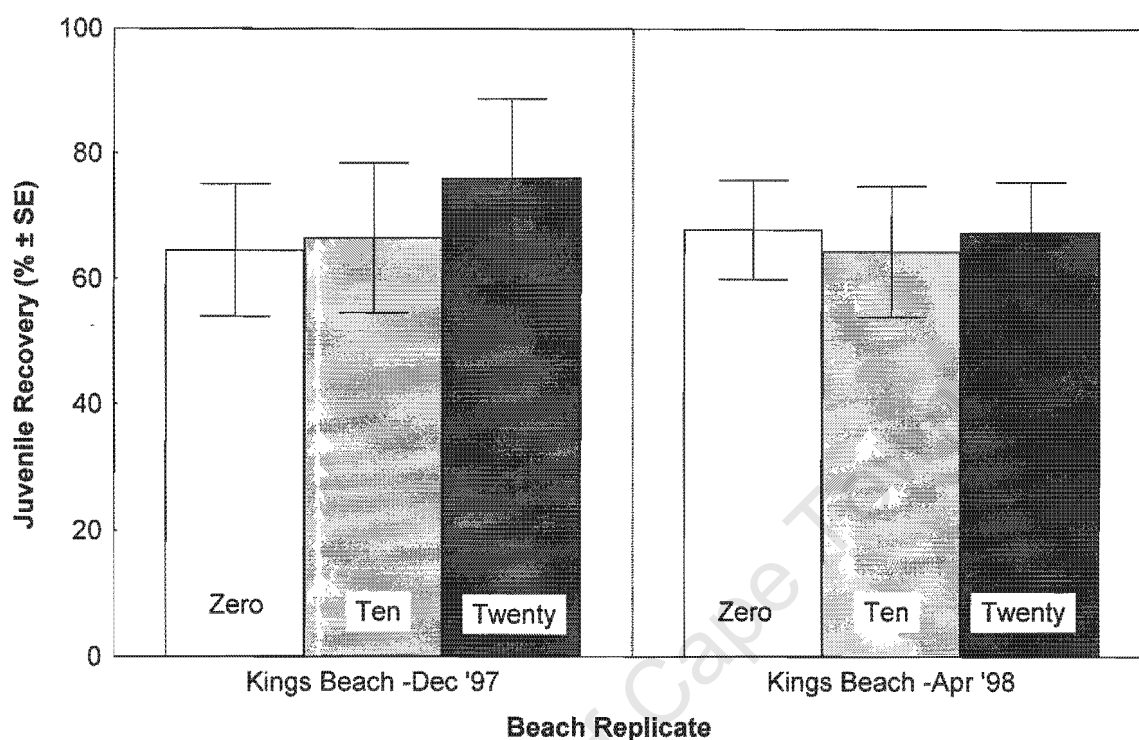
Table 7.1 Results from the (A) multi-dimensional Contingency Tables evaluating mutual and partial independence between the effects of treatment and time on the ratio of recovered : unrecovered *D. serra*. Then (B) evaluates the effects of only treatment on juvenile recovery over time (using Contingency Tables; with time replicates pooled).

A. Factors interacting	χ^2	df	P
Mutual independence (ratio X time X treatment)	983.7	47	<<0.001
Recovery ratio independent of time and treatment	983.7	29	<<0.001
Time independent of recovery ratio and treatment	837.7	45	<<0.001
Treatment independent of recovery ratio and time	239.3	38	<<0.001
B. Recovery per treatment (2 x 3 table)	178.42	2	<0.001
Zero vs. Ten (2 x 2 table)	0.086	1	>0.25 (NS)
Zero vs. Twenty (2 x 2 table)	120.29	1	<0.001

The multi-dimensional Contingency Tables (2 X 3 X 10) could not identify a single, important parameter determining juvenile recovery, because of the mutual and partial interdependence of the parameters (Table 7.1A). Inspection of the data indicated a large change in juvenile recovery for over time. Due to the interdependence and large variation with time, alternate routes of analysis were taken.

With the large variation in recovery over time, it was difficult to detect any significant influence that the treatments specifically could have on the distribution of the juveniles. Since the experiment was repeated over time (to incorporate the effect of a range of physical conditions) and the treatments were applied at the same time, it seemed appropriate to pool the time replicates. The data-set then constituted the ratio of recovered : unrecovered juveniles for three treatments, summed over 10 days. This was to done to evaluate the effect of the treatments only on juvenile recovery, independently of time. Initially a (2 X 3) Contingency Table was performed to determine if treatments have a significant influence on the juvenile recovery rate (Table 7.1B). With a significant difference detected, the treatments were separated and individually measured against the control (i.e. 2 X 2 Contingency Tables; Table 7.1B). There was no difference in the juvenile recovery between the control and 10 adult clams buried, but there was a highly significant influence with 20 adults in the

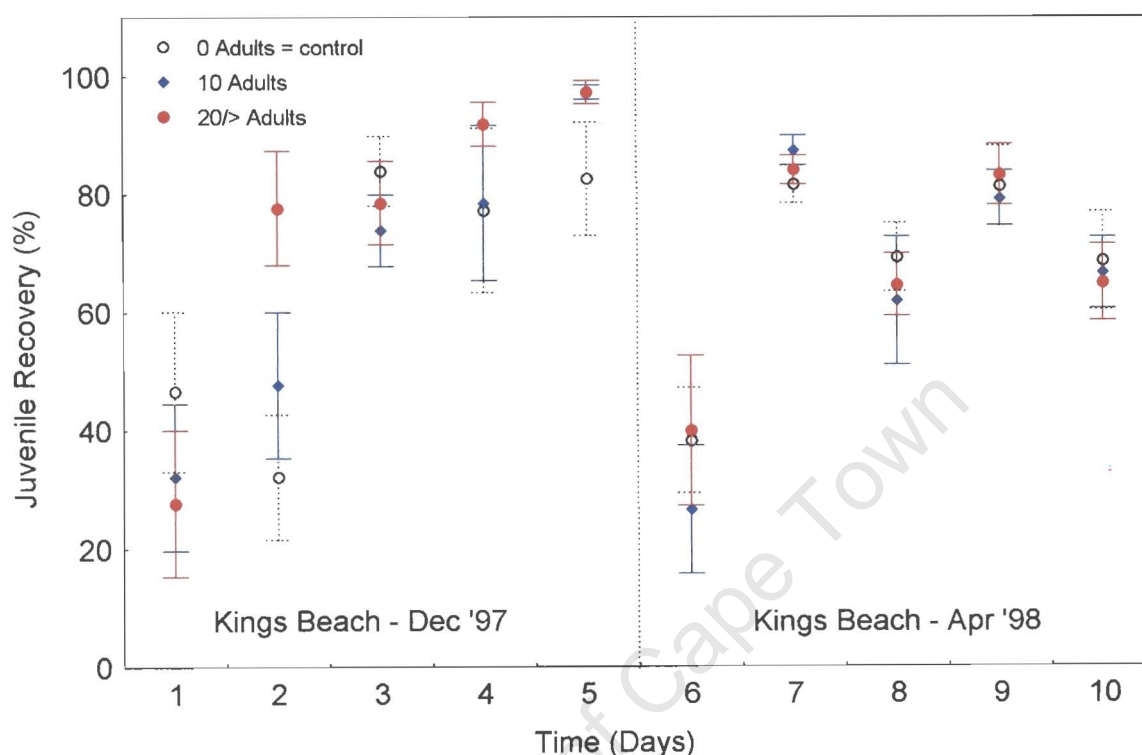
Fig. 7.2 Mean juvenile recovery ($\pm$ SE) for two sampling events (totalling 10 days) as obtained for two treatments (i.e. 10 or 20/> adults *in situ*) and the control.



sand (Table 7.1B). The highest number of juveniles recovered under the lowest densities of adults. The ratio of recovered : unrecovered clams in the control and intermediate adult density (10) was $\sim 68.1 : 31.9\%$, whereas the 20 adult clams resulted in a ratio of $\sim 50.3 : 49.6\%$ clams. It therefore seems as if adult clams at high densities in the sediment have a negative effect on juveniles.

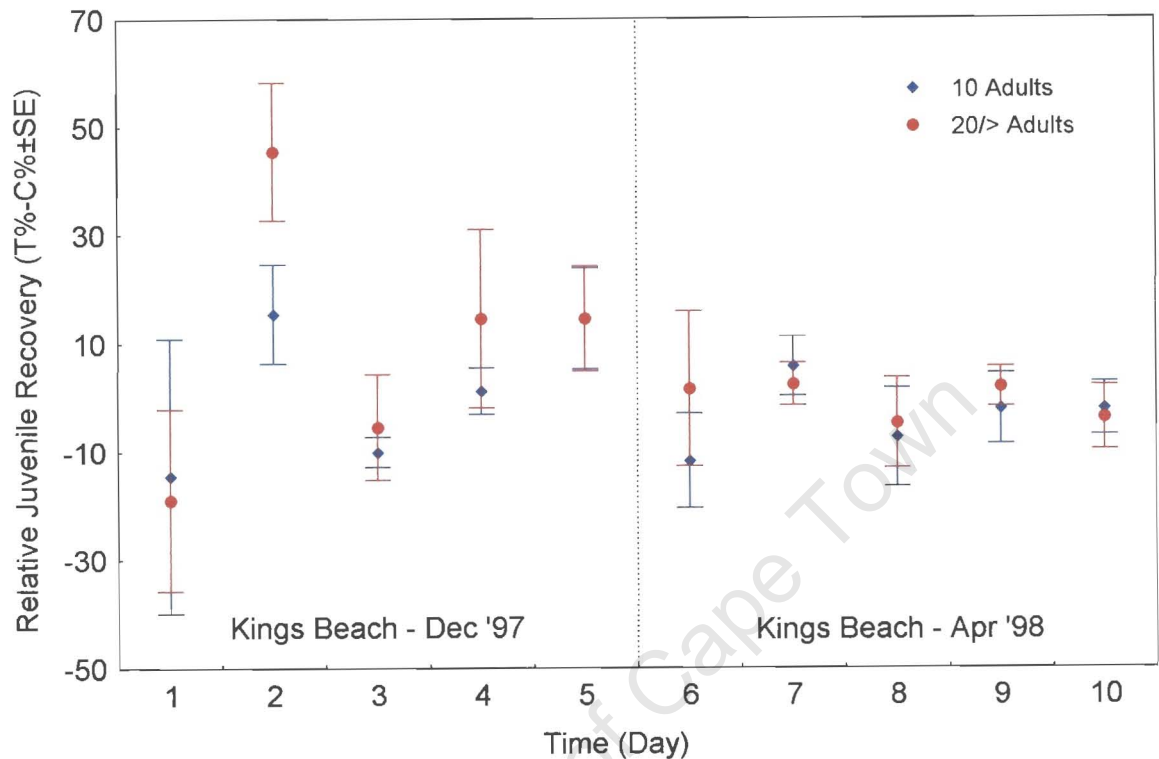
It is realised that pooling of the data may bias the frequency/consistency with which these results are obtained, since a strong 'interaction' on one day may augment the results from another day under different physical conditions. Moreover, a comparison of the % juvenile recovery over the two sampling events are conflicting with the trend that the lowest juvenile recovery is obtained at the highest adult densities (Fig. 7.2). The consistency/frequency of the effect of the treatments were then investigated. A Kruskal-Wallis test was

Fig 7.3 Change in juvenile recovery (between two treatments and a control) over 10 days on Kings Beach. Values are reported as mean % $\pm$ SE.



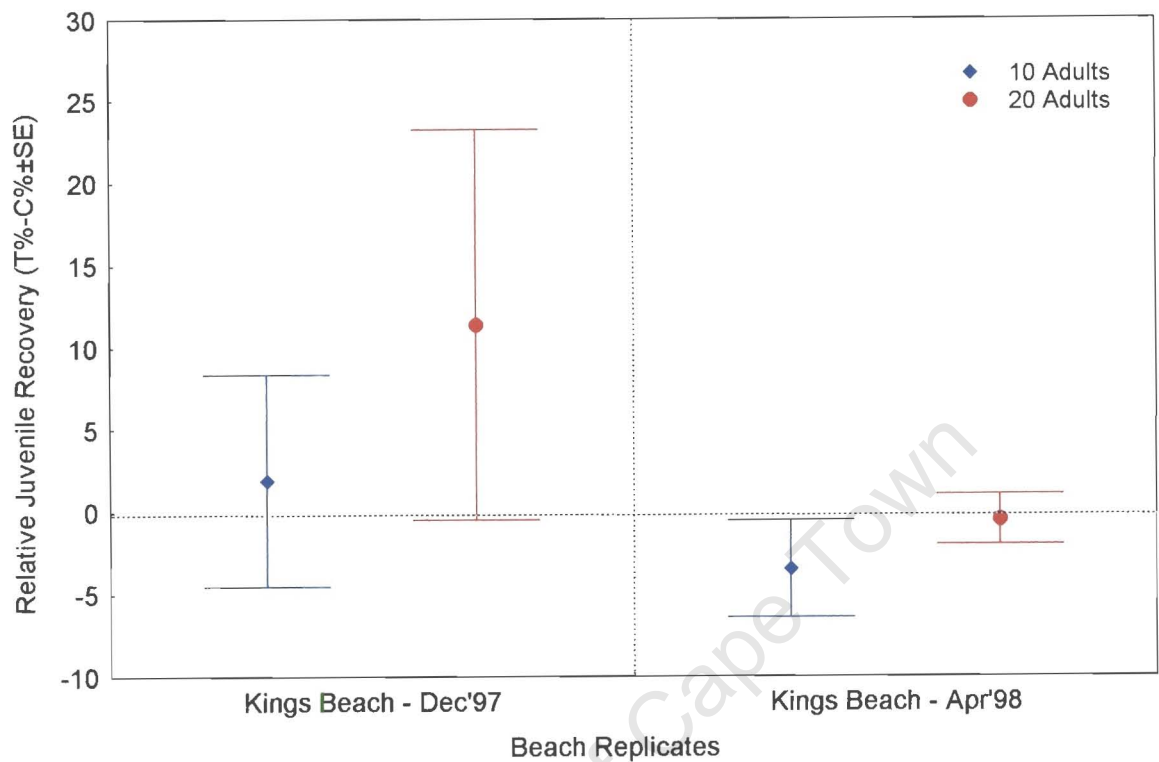
subsequently applied (which employs ranks and not the actual recorded values and is therefore able to accommodate heterogeneous samples) to evaluate the effect of *time* on the recovery ratio. This was to evaluate the frequency with which these ratios were recorded, treating the 10 sampling days as replicates. No significant difference could, however, be detected ($H_{0.05,30}=0.763$, $df=2$ $P=0.68$) in the juvenile recovery between the treatments. The effect of the treatments are therefore not very consistent, and seems to be greatly influenced by changes in physical conditions. An inspection of juvenile recovery on a daily basis indicated that there was indeed strong temporal variation, as indicated by the significant interactions in the contingency table analysis. (Table 7.1A). This variation is probably related to changes in swash and surf zone conditions (Fig. 7.3). The recovery of juveniles changed daily, and changed similarly for all treatments, i.e. if the recovery of juveniles increased in the control, the recovery in the treatments changed concurrently. The recovery values therefore suggest that the environmental factors experienced on the beach may exert a greater influence than the presence of adults.

Fig. 7.4 Relative juvenile recovery (i.e. treatment recovery – ‘control’ recovery $\pm$ SE) over a time period on two occasions on the same beach.



Recognising the complexities and the influence of the beach dynamics, an alternative approach was used to elucidate the effect of treatments on juvenile distribution. The effect of the adult densities on recovery rates was calculated using the control, i.e. zero adults, as a standardising factor. The relative juvenile recovery was subsequently calculated as the difference between the treatment and that of the control (Fig. 7.4). The trends are still not consistent, but there is a marginally higher recovery in both instances of juveniles from the more severe treatments (Fig 7.4). This was summarised in Fig. 7.5 by obtaining the 'mean difference' pooling the data over the 10 sampling days. It appears as if more juvenile *D. serra* individuals were recovered in the presence of 20 or more adults, than in the presence of 10 adults.

Fig 7.5 Mean juvenile recovery ($\pm$ SE) of *D. serra* from two different treatments (i.e. 10 and 20 adult white mussels per cage) on two occasions on Kings Beach.



The number of juveniles recovered seemed higher at higher adult densities. The presence of adults therefore seem to be more of a stabilising factor than a disturbance factor. During the preliminary experiments (in Elizabeth Bay) some cages were erected in the shallow subtidal. In these, juvenile recovery there was also higher at higher densities of adults ($45 \pm 12\%$ in 0 adult; and $63 \pm 8\%$ in 15 adults). However, since this trend was not consistent, meaning that the mean number of juveniles obtained was not always highest for 20 (or more) adults and not always lower for 10, it was accepted that the treatments do not have any effect on the juvenile recovery. Moreover, the results suggest that adult presence is probably not a strong influence in structuring the juvenile distribution, especially at the densities tested. It is therefore concluded that adult white mussels do not play a significant role in the distribution of juvenile white mussels in the intertidal at these given densities over a 24 hour time span. It seems necessary to investigate the effect of the abiotic environment on the juvenile recovery values obtained, since this seems to exert a stronger influence over buried clams.

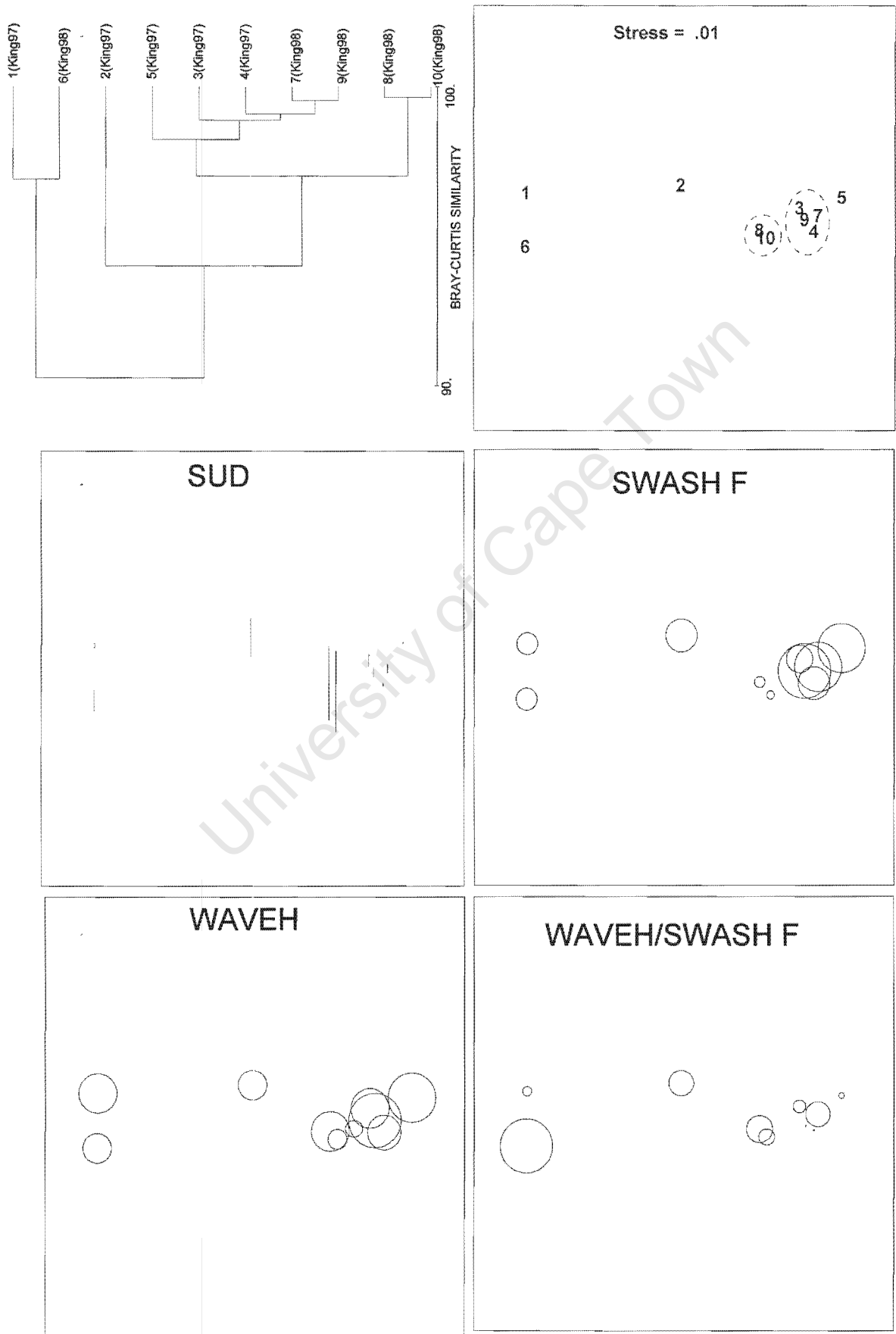
7.3.2 Physical environment

Regressions of single physical parameters against the mean juvenile recovery over 10 days were all insignificant. It is therefore possible that it was not only a single parameter that was responsible for variation in juvenile recovery obtained. Multivariate analysis was further employed to investigate correlations between the response of juveniles and the prevailing physical conditions.

The relative difference in the percentage juvenile recovery on different days, using the Bray-Curtis similarity measure as presented in the dendrogram (in Fig 7.6), is limited. All the values are more than 90% similar, which is probably an artefact of the small sample size (i.e. 3 'treatments' per day). However, this yields a relatively uncomplicated non-metric MDS-plot, with a stress level at 0.01 (Fig. 7.6). This graphic representation indicated that juvenile recovery does vary with changes in the physical environment but as discussed in Chapters 1 – 4, it is very difficult to isolate a single physical parameter that is responsible for macrofaunal distribution patterns. Factors (using the MDS) that seem to have an influence on the temporal variation in juvenile recovery are swash upwash distance, wave height and swash frequency (Fig 7.6). No single factor explains the whole MDS-plot, but it explains why certain groups are separated from others. Wave height and swash frequency indicate that juvenile recovery is generally highest (day 3, 4, 5, 7 and 9) when the wave height is smallest and swash frequency highest. Swash frequencies experienced on day 1 and 6 seem to be similar, hence the close grouping, while few other physical parameters for these days are similar.

When the wave height is divided by the swash frequency, this gives an indication of the relative amount of wave energy that is reaching the cages. The lowest juvenile recovery values were obtained on the sixth day (= Kings Beach Apr '98 day 6; Fig. 7.3), which appears to have received most wave energy, whereas the highest recovery was obtained on the fifth day (= Kings Beach Dec '97 day 5; Fig. 7.3); this is when the wave energy reaching the beach was lowest.

Fig 7.6 A dendrogram and MDS-plots indicating important physical parameters in determining the juvenile *D. serra* recovered on a daily basis.



Juvenile distribution thus seems to be highly variable on a short temporal scale, and seems to be strongly influenced by changes in the physical conditions experienced across the beach face. The probability of displacement by adults seems low, although it is difficult to make conclusive statements from results with so much variability.

7.4 DISCUSSION

Does intraspecific interference take place on sandy beaches? This question has been addressed in different forms. Defeo (1992 cited by Schoeman, 1997) suggested that the size separation of recruits and adult *Mesodesma mactroides* individuals is either a result of pre-settlement mortality by accidental filtration, or because of settlement inhibition due to sediment disturbance by adults during routine feeding activity. Contrary to the suggestions of Defeo (1992; 1996; and those of Schoeman, 1997 for *D. serra*), the present study was unable to demonstrate (conclusively) interference by adults with juveniles over the short term in the field. The only significant difference was obtained between the control and 20/more adults *in situ*. However, in this experimental procedure, juveniles of between 15 and 30 mm shell length were used. They are past the recruitment stage and are approximately 0.5 to 1.5 years old (De Villiers, 1975a; Schoeman, 1997). Recruits are generally considered to be <15 mm in length, while juveniles range 15 – 50 mm and adults > 50 mm (De Villiers, 1975a; Farquhar, 1997; Schoeman, 1997). The methodology therefore relied on settled juveniles and placed them in the same intertidal zone as the adults. This should have demonstrated whether the change in the size structure across the beach face was a result of either/both the reburial action or siphon activity of adult clams, especially at high densities.

If any disturbance interaction exists between adult and juvenile white mussels it does not seem strong enough to have a significant influence on the presence of juveniles. However, there were indications that juvenile recovery might change marginally at higher densities of adults, but this was not consistent. Juvenile recovery was significantly lower with 20/more

adults in the sand. Neither of the possible methods of interference, i.e. displacement of juveniles by the adult reburial, nor siphon action while feeding, seem to interfere with juveniles in the field. In fact, the presence of adults may settle the substratum somewhat to keep the juveniles from being displaced. This does not mean that biological interactions are not possible. It is also possible that the effects of adults on juveniles in the sediment is different under different physical conditions, and the modal beach state (and therefore the modal interference state) should be considered. It rather highlights that adults do not displace already buried juvenile beach clams within a 24-hour period.

The overall temporal variation in juvenile recovery suggests that the physical environment or some other factor ignored by this experimental procedure is more critical in displacing juveniles from the cages. Zonation patterns from other studies were also reported to change when sea conditions were rough. For example, Soares *et al.*, (1998) reported that on Sundays River Beach, the juveniles and adults were mixed after a storm. It therefore appears that size separation persists only under calm conditions, but as conditions become more dynamic, the zonation patterns may be completely different. Farquhar (1997) also reported a seasonal shift in the adult population on the west coast. The resident intertidal adult population (on the west coast) seems to move offshore in the winter months, especially on exposed beaches. When calmer summer conditions return, the across-shore distribution returns to the modal state (Farquhar, 1997).

Intraspecific zonation is thus not static, and it seems likely that changes in distribution may be a result of wave sorting. It was indicated that the juvenile recovery might change with a change in wave energy reaching the beach. Since it was not the primary aim of the experiment to relate *D. serra* zonation to physical factors the analysis is superficial (see Chapters 2 - 4 for a more detailed discussion). However, it highlighted that physical factors could be important in the intraspecific zonation of *D. serra*. Wave height and swash frequency seem to coincide with the factors responsible for interspecific zonation patterns (Chapters 3 & 4). These results supports previous studies, which concluded, that beaches

are physically controlled environments (McLachlan, 1988; 1990; Brown and McLachlan, 1990; McArdle and McLachlan, 1992; McLachlan *et al.*, 1993).

An interesting question still remains to be answered in terms of the inverse size distribution on the shores east of Cape Point and west of Cape Point. Why does the size segregation persist, especially under calm conditions (Soares *et al.*, 1998; Farquhar, 1997; Schoeman, 1997)? If the physical environment is sorting the juveniles to a specific point in the intertidal, why don't the juveniles occur in similar zones on the two shores, or do they? According to a survey by Farquhar (1997), *D. serra* individuals of less than 30 mm are rarely found below the mid-intertidal mark on the west coast, while adults are predominantly found in the subtidal area. *D. serra* populations generally display a bimodal distribution with the bulk of the adults below LWST mark. Beach studies on the east coast indicated that adults on the east coast are centred in a narrow band in the mid to upper intertidal (during spring tides), while juveniles, which are sometimes mixed with the adults, are generally centred in the low intertidal (Donn, 1990a; Schoeman, 1997). Donn and co-workers (Donn *et al.*, 1986; Donn, 1987; 1990a; 1990b; Donn and Els, 1990) have also done extensive work on the long-shore and across-shore distribution patterns of *D. serra* along the coast. They found that juveniles occupy the intertidal zone on both shores, but on different levels. Ultimately, Donn (1990b) proposed the temperature hypothesis, which assumed that swash displacement is a passive process, and claims that all *D. serra* prefer to occupy the intertidal area because they can burrow between swashes, whereas adult *D. serra* on the west coast cannot burrow fast enough and are subsequently displaced to the subtidal.

Because of the motility of beach macrofauna, such as the swash riding beach clam, it is difficult to make rules about faunal assemblages, because they vary through space and time. It is possible that Donn's hypothesis (1990a; 1990b) is broadly true in explaining the relative distribution of *D. serra*. It does not address the problem though, as to why juveniles of similar sizes occupy different levels of the intertidal area on the two coasts. It fails to explain why the slower burrowing juveniles of the west coast occur higher on the shore.

Alternatively, the distribution has been described in terms of recruitment taking place in the surf zone on shores east of Cape Point, and as these individuals grow they move into the intertidal, while the opposite happens on west coast beaches (De Villiers 1975a; Farquhar, 1997; Schoeman, 1997). The possibility thus exists, that adult *D. serra* occur where it is most advantageous for them, and that there is a possible size-related interference pressure between adults and recruits (rather than juveniles). It seems that similar-sized individuals may still have a better chance of co-occurring than individuals of disparate sizes, especially at relatively low densities (< 30 clams 0.1m^{-2} ; see Chapter 6).

This experiment thus raised questions rather than provide answers. The reasons for the lack of trends in similar studies are generally twofold. Interactions, may either be absent or weak, or complicated and therefore masked by habitat variation and physical factors; or alternatively, trends may have been obscured by incorrect spatial investigation (Defeo, 1996). These observations are still considered as valuable though; Hewitt *et al.* (1997) stated that large-scale *in situ* experiments (although with a large amount of variability) are more appropriate than (adult-juvenile) interactions observed on a small scale or in the laboratory. These interactions are normally scale-dependent and larger scale processes contribute to variability, which makes it impossible for small-scale results to be scaled up. The present study, therefore, eliminates short-term adult-juvenile interactions as a structuring process over small spatial scales. It recognised that some larger scale processes (which vary in time and space), e.g. the likely influence of wave energy acting across the beach face, may play a significant role on biota, or that the biological interactions may be shaped by the physical environment. The across-shore distribution of juvenile *D. serra* seems to be strongly influenced by wave height and swash frequency (or some other physical parameter). It is also reconfirmed that most beach ecological problems cannot be explained in terms of a single variable such as temperature.

Spatial and temporal trends have been analysed separately, but a better experiment may be designed where both factors can be controlled, and therefore the relative importance of the

abiotic environment and biotic interference can be determined. For the current experiment, the conclusion has to be that intraspecific competition is absent or unimportant with respect to juvenile *D. serra* distribution.



University of Cape Town



CHAPTER 8

University of Cape Town

8.1 INTRODUCTION

The small aquatic crustaceans inhabiting intertidal sands form a very important component of the macrofauna community. Because of their relatively small size in comparison to gastropods or bivalves, and therefore their relatively small contribution to biomass, cirrolanid isopods are often considered unimportant in macrofaunal assemblages, especially in terms of nutrient recycling on more dissipative beaches. Moreover, the small size of cirrolanids makes it almost impossible to devise *in situ* manipulative experiments involving them. However, their exceptional abundance on a range of beach types (Jaramillo and McLachlan, 1993; Jaramillo, 1994), including the harsher reflective type beaches, render them ideal in defining across-shore zonation patterns (Dahl, 1952; McLachlan, 1980b; Jaramillo, 1987; Jaramillo *et al.*, 1993; Brazeiro and Defeo, 1996). Furthermore, because of their remarkable mobility and strong endogenous rhythms, experimental studies involving cirrolanid isopods have focused on their activity rhythms and migratory patterns (Bally, 1987; De Ruyck *et al.*, 1991) or grain size preferences and burrowing rates (Brown, 1973). Their relatively large numbers, wide distribution and mobility have attested them to be one of the (few) groups of beach animals where biological interactions have been suspected (Fenchel *et al.*, 1977; de Alava and Defeo, 1991; Nel, 1995).

Fenchel *et al.* (1977) investigated interspecific interactions between two species of isopods of the genus *Sphaeroma*. They showed possible character displacement in terms of the time of the release of juveniles by females between allopatric and sympatric species. Nel (1995) indicated an overlap in the grain size preferences of *Excirolana natalensis*, *Eurydice longicornis* and *Pontogeloides latipes* in the laboratory. It was suspected that this could be responsible for spatial segregation among these species on beaches where they co-occur

on southern African shores, and was therefore interpreted as a possible biological interaction (without defining the mechanism; Nel, 1995).

The taxonomic status of cirolanid isopods in southern Africa is currently in a state of flux since the species name '*Eurydice longicornis* (Stüder)' has been incorrectly applied for the last few decades (Bruce and Soares, 1996). More than one species of the genus *Eurydice* seems to be present on the southern African shores. *E. longicornis*, though, is absent from these beaches since it seems to be a subtidal species (Bruce and Soares, 1996). Interbreeding between cirolanid species has also been mentioned (by Bruce and Soares, 1996), complicating identification further. However, only three species of cirolanids seems to occur widely along southern African sandy shores, across a range on beach types (see Chapter 2 and Appendix 1).

The aim of the present study was to further investigate the possibility of interspecific competition on sandy beaches, and specifically among three species of isopods. This was done by investigating grain size preferences of three species in isolation (as allopatric species) or character displacement of species in combination (as sympatric species). The species used during this study are *Excirolana natalensis* Vanhöffen 1914, *Pontogeloides latipes* Barnard (= *Excirolana latipes*) and *Eurydice kensleyi* Bruce and Soares 1996.

8.2 METHODS

8.2.1 Field collection

The three species of cirolanid isopods were collected from a variety of beaches, depending on the relative abundance of the species per beach. The species were, however, primarily collected from Muizenberg beach, Bloubergstrand and Yzerfontein (see Table 2.1 for physical description of MUIZ and YZC). Bloubergstrand varies greatly along the shore in terms of

grain size composition, wave height and intertidal gradient. This seems to be due to severe periodic storms and shelter from Robben Island (pers. obs.) The central portion of this beach, where isopod collection took place, is a broad, intermediate/dissipative beach with a moderate gradient and medium grained sand. Wave height is generally about 1 m and there are no permanent burrows present in the intertidal. Isopods were collected from beaches where all three species co-occur, but on different levels of the beach. The isopods collected were kept in containers of fresh sea water and sediments from their beach of origin, until used in the laboratory experiments. Isopods were separated into species, and only one species was housed per holding container.

8.2.2 Grain size preference

Sediments that were offered to isopods were obtained from a variety of beaches and sieved through a series of sieves to obtain well-sorted sediment fractions. Seven different fractions were collected from 3.5 ϕ (90 μm) to 0.5 ϕ (710 μm) at $\frac{1}{2}$ ϕ -intervals. These grain size fractions were offered to isopods in a circular container (radius 15 cm), with an approximate total surface area of 0.1 m^2 (Fig. 8.1). Each of the wedges ($\pm$ 500 ml each) was half-filled with sand of a particular grain size. Grain sizes were assigned to the container in a haphazard¹ order, so that there was no gradient in the coarseness of the sediments. Because of the difficulty in obtaining large numbers of isopods, animals had to be reused. However, the animals were placed back in their holding containers with native sediments to mix into the 'population' and to rebury themselves in the 'normal' beach sand. The same isopods were never used on consecutive days, since the experimental animals were only returned to mix after the new experimental run was set up.

¹ **Haphazard order:** as opposed to random implies that no random table or any other specific method was used to allocate grain sizes to wedges.

Fig. 8.1 Design of the containers with seven wedges containing sediments of seven different particle diameters used for grain size preference experiments.

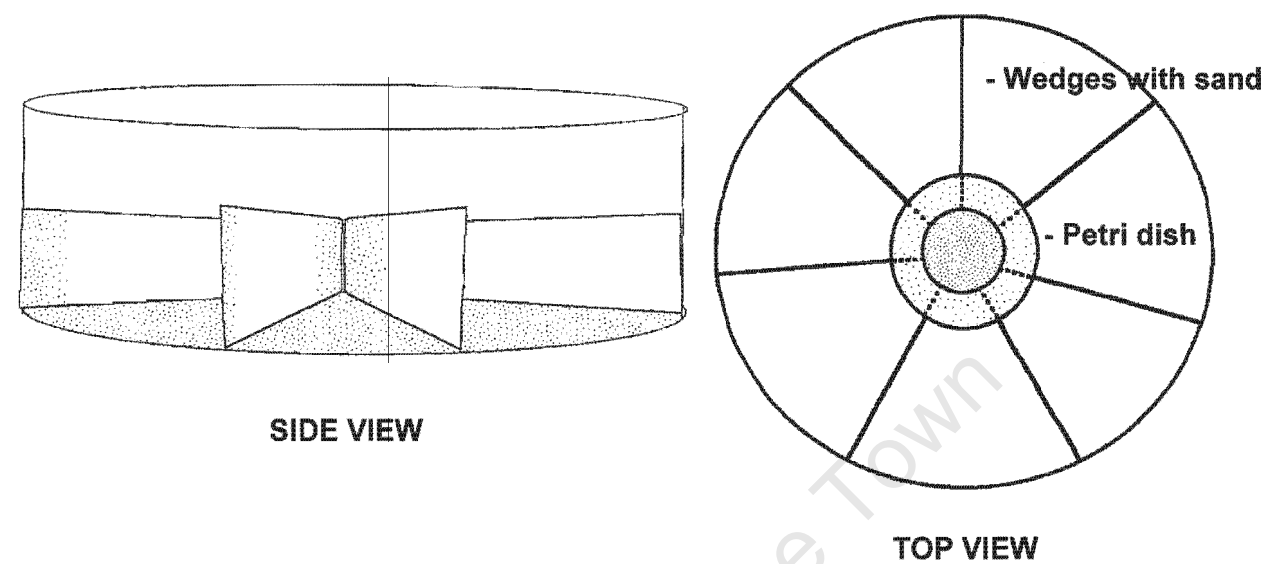


Table 8.1 The experimental design used to assess grain size preferences for three species of cirrolanid isopods. Each of the grain sizes was available in each experimental 'treatment'.

		Grain size fractions (in μm) offered						
Interactions	Species	90 – 125	125 – 180	180 – 250	250 – 355	355 – 500	500 – 710	710 – 1000
1 Species	• Controls (<i>Ek</i> , <i>En</i> , <i>Pl</i>)	N = 30 – 40 per replicate						
	• <i>Ek</i> vs <i>En</i>	N = ~ 15 per species, per replicate						
2 Species	• <i>Ek</i> vs <i>Pl</i>	N = ~ 15 per species, per replicate						
	• <i>En</i> vs <i>Pl</i>	N = ~ 15 per species, per replicate						
3 Species	• <i>Ek</i> vs <i>En</i> vs <i>PL</i>	N = ~ 15 per species, per replicate						

Ek = *Eurydice kensleyi*; *En* = *Excirolana natalensis*; *Pl* = *Pontogeloides latipes*.

Isopods were introduced into the experimental container (Fig 8.1), by placing the animals in a small petri dish at the centre of the container, and then siphoning water into the experimental container. This was continued until enough water was added so that the isopod could swim around freely out of the petri dish and over the separator walls. Each species was placed in a separate dish and stacked in the middle of the container. This was so that each individual had an equal chance to swim in any direction, and choose any of the grain sizes.

The control experiments were conducted by placing each species separately into the experimental containers to determine the grain size preference of each species in isolation. The treatment experiments were then conducted with a combination of either two or all three species at the same time. The total number of isopods was limited to 45 or less, at any time in the containers (Table 8.1). The isopods are highly active predators and even cannibalistic, the number of isopods was therefore limited to prevent mortality. When two species were tested together, 15 individuals per species were placed in the dishes. Species were introduced in combinations (as outlined in Table 8.1), so that all possible combinations of interactions were tested.

Once enough water was siphoned into the containers to allow free movement, air stones were placed in the central petri dish to aerate the water without causing excessive water movement or any directional currents. The containers were closed and covered with a thick cloth to eliminate visual cues/stimuli. The isopods were left over-night for ± 24 hours to allow for at least a low and high tide cycle to pass (although the water levels in the containers were not altered) and for a nocturnal peak activity of the isopods (De Ruyck *et al.*, 1991).

The following day, the water was siphoned out of the containers without disturbing the isopods. The isopods were all buried in the sand by the time of the analysis, but if the animals were not buried (which was exceptional) they were ignored during the analysis. The

sediments were carefully excavated and the number of isopods of each species per grain size counted. The experiment was repeated 8 times.

Statistical testing of the laboratory tests aimed to firstly, define a grain size preference distribution for each species and secondly, detect changes (if any) in the grain size preferences of each species due to the presence of other species. All analysis used contingency tables, since it dealt with frequency data (Zar, 1984).

Initially, the grain size distributions of each species were tested against the others to determine if they are different/unique. This was then followed by testing the frequency per grain size, against an expected value, which was calculated as the mean frequency for all grain sizes. Deviation from the mean frequency would indicate significant preferences or avoidance of a particular grain size.

After obtaining the grain size preference per species (in isolation), the frequencies obtained per grain size in combination with other species were then tested against the control distribution. This was performed by means of contingency tables. A *post hoc* χ^2 -analysis was performed to determine changes in the frequency per grain size (from the control frequency) when species were combined. This was conducted by subdividing the contingency table to test the ratio of control : treatment *per grain size* against the ratio of the control : treatment *for all other grain sizes* for a specific species combination. For example: the frequency of *E. kensleyi* in 90 μm sand for the control : frequency in 90 μm sand in the treatment (such as with *E. natalensis*), against the control in sand of 125 - 1000 μm : frequency in the treatment of sand from 125 – 1000 μm (Zar, 1984). Significant differences are recorded in Figs. 8.2 – 8.7, with the P-values indicated for each pair tested against the rest of the grain size fractions.

8.2.3 Field distribution

The longshore distribution of adult populations was investigated by scoring the grain sizes of 27 beaches (as sampled in Chapter 2), as well as the presence or absence of adult isopod populations for each beach. The frequency of each isopod species per grain size fraction was expressed as the percentage occurrence. This was done to determine if the laboratory grain size preference and the field distribution of the adult cirolanids coincided. The abundance of each species, per square meter, was also recorded for the 27 beaches and plotted against the grain size to determine which beaches had the highest abundance of each species. Furthermore, kite diagrams were constructed for three beaches with the highest abundance per species to qualitatively assess the across-shore zonation and overlap between species.

8.3 RESULTS

8.3.1 Grain size preference

The species tested during this study seemed relatively catholic in their particle preference, and were all capable of burrowing into the complete grain size range offered. No species overwhelmingly targeted a grain size fraction. Each species seemed to have a preferred grains size distribution.

Excirolana natalensis displayed a gradual increase in the grain size preference from fine to coarse sand. Only a small fraction of the *E. natalensis* individuals (i.e. < 3%) buried themselves into sand finer than 180 μm , while 10 – 20% buried into medium sand (180 – 7100 μm). The strongest preference (~ 36%) was, however, for the coarsest sediment fraction (710 – 1000 μm). The grain size preference for the coarsest sand fraction was significantly higher than the mean frequency, as well as the avoidance of the finer sand fractions (Fig. 8.2)

Eurydice kensleyi displayed a distribution pattern similar to that of *E. natalensis* by having the greatest, significant preference for coarse sand (~ 30% buried into 710 - 1000 μm sand), whereas the preference for the other particle diameters was relatively even (Fig. 8.2). It ranged 6 – 15% for all six other fractions of sand between 90 – 710 μm , although the frequency deviated significantly from the mean for the fine sand fractions (125 - 250 μm ; Fig. 8.2).

Pontogeloides latipes had weak particle diameter preferences (Fig. 8.2). No distinct selection was obtained for any of the fractions within the control, although the preference tended towards medium and coarse sand (Fig. 8.2). The percentage of individuals that preferred fine sand (i.e. < 180 μm) was less than 6% (which was significantly less than the mean), while 15 – 21% occupied sand between 180 – 1000 μm . The highest preference percentage (of 21%) was obtained in the medium fraction of 250 – 355 μm .

Comparing the preferences of the three species against each other, it became evident that the preferences differed significantly (Table 8.2 & Fig 8.2). The greatest difference in the overall distribution was between the mid-shore species *P. latipes*, and the other two cirrolanid isopods tested (Fig. 8.2). Both *E. natalensis* and *E. kensleyi* had the strongest preference for the coarsest sand, although *E. natalensis* seems to be more of a grain size specialist than *E. kensleyi*, which had a more catholic distribution (Table 8.2).

Fig. 8.2 The grain size preference of three species of cirrolanid isopods in isolation. Significant differences between a mean frequency (dotted line) and the frequencies obtained per grain size (for the species) are indicated by the P-values.

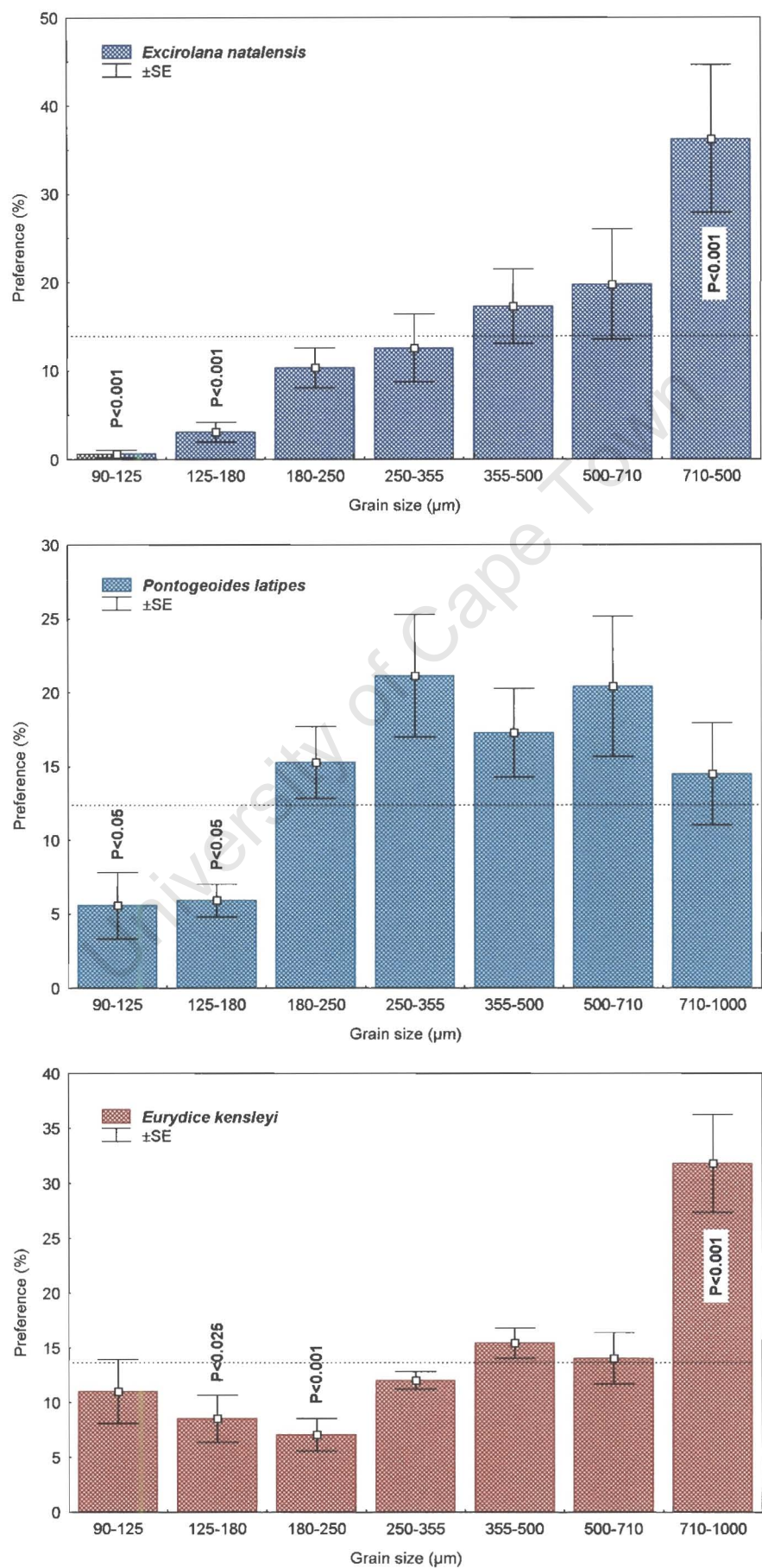


Table 8.2 Comparison of the grain size distributions in the control experiments of the three species against each other.

Species Combinations	χ^2	P	
<i>E. natalensis</i> vs <i>P. latipes</i> (df = 6)	41.46	P<0.001	REJECT
<i>E. natalensis</i> vs <i>E. kensleyi</i> (df = 6)	39.60	P<0.001	REJECT
<i>P. latipes</i> vs <i>E. kensleyi</i> (df = 6)	30.47	P<0.001	REJECT
<i>P. latipes</i> vs <i>E. kensleyi</i> vs <i>E. natalensis</i> (df = 12)	68.75	P<0.001	REJECT
REJECT = Reject the null hypothesis which assumes no difference in the frequencies per grain size, for the species tested.			

When these species were tested simultaneously their grain size preferences changed from that obtained in isolation (Table 8.3). In combination, both the high shore species (*E. natalensis*) and the low shore species (*E. kensleyi*) altered their preference for the extremely coarse sand fraction (Fig. 8.3 & Table 8.3). *E. kensleyi* executed no specific preference, and showed an almost even distribution throughout all the grades of sand in the presence of *E. natalensis*. The fine sediment fractions which were not popular in the control were (in the presence of *E. natalensis*) selected more frequently. *E. natalensis*'s individuals changed their distribution to a more symmetrical preference around the medium grades of sand (i.e. 355 – 500 μm ; Fig. 8.3), with a significant decrease in the preference for 710 - 1000 μm and an increase in the preference for 355 – 500 μm . This particular species again avoided fine sand.

A comparison of the relatively small *E. kensleyi* (0.019 $\pm$ 0.03 g wet mass) and the larger *P. latipes* (0.125 $\pm$ 0.01 g) yielded a similar change in grain size preference. *E. kensleyi* again abandoned the preference for coarse sand (and significantly so, using a 2 X 2 contingency table; see Fig 8.4 for P-values) while *P. latipes* changed from occupying medium sand to occupying primarily fine sand (Fig. 8.4). Values ranged 15 – 20% in sand finer than 250 μm , as opposed to 5 – 10% in 250 – 500 μm (Fig. 8.4). These changes were statistically significant, (Fig. 8.4) and the influence of *P. latipes* and *E. kensleyi* on each other was strong enough to alter their distribution across the gradient of grain size fractions (Table 8.3).

Table 8.3 Results from the Contingency Tables testing for differences in the distribution of three cirolanid isopod species, across seven grades of sand, as a result of species interacting. All distributions were tested against the control for the species.

Species Combinations	χ^2 , (df=6)	P	
<i>E. natalensis</i> vs <i>E. kensleyi</i>	28.12	P<0.01	REJECT
<i>E. kensleyi</i> vs <i>E. natalensis</i>	17.92	P<0.01	REJECT
<i>E. kensleyi</i> vs <i>P. latipes</i>	20.23	P<0.005	REJECT
<i>P. latipes</i> vs <i>E. kensleyi</i>	20.04	P<0.005	REJECT
<i>E. natalensis</i> vs <i>P. latipes</i>	18.40	P<0.01	REJECT
<i>P. latipes</i> vs <i>E. natalensis</i>	31.66	P<0.001	REJECT
<i>E. natalensis</i> vs <i>P. latipes</i> & <i>E. kensleyi</i>	19.77	P<0.005	REJECT
<i>P. latipes</i> vs <i>E. natalensis</i> & <i>E. kensleyi</i>	22.36	P<0.001	REJECT
<i>E. kensleyi</i> vs <i>E. natalensis</i> & <i>P. latipes</i>	19.48	P<0.005	REJECT

REJECT = Reject the null hypothesis

The third combination entailed testing the high-shore *E. natalensis*, which showed a preference for coarse sand in the control (Fig 8.2 and Fig. 8.5), in combination with the mid-shore species, *P. latipes*, which preferred medium to coarse sand in the control (Fig 8.2 and Fig 8.5). These species are similar in size (wet weight of *P. latipes* = 0.125 ± 0.01 g and *E. natalensis* = 0.106 ± 0.02 g). The relative distribution of *E. natalensis* changed in the presence of *P. latipes*, while *P. latipes* also displayed a significant alteration in their own distribution with *E. natalensis* present in the experimental container (Table 8.3 & Fig. 8.5). The grain size preference of *P. latipes* changed quite dramatically and there is almost an inverse relationship between the frequency per grain size of *P. latipes*, and that of *E. natalensis*. A significant number (see Fig. 8.5 for P-values) of *P. latipes* individuals occurred in the finest grain size offered (25% in 90 – 125 μm) which previously occupied coarser sand fractions. The finer sand also had the fewest *E. natalensis* individuals in this grain size (7%). Only 6% of the *P. latipes* individuals managed to burrow into the coarsest grain size, which was predominantly occupied by *E. natalensis* (35%; Fig. 8.5).

Fig. 8.3 A change in grain size preference (from the control – grey series) of *Eurydice kensleyi* (**Ek**) and *Excirolana natalensis* (**En**; as the treatments - coloured series), when tested in the presence of each other. Significant differences (using a subdivided 2 x 2 contingency table) between the control and treatment preferences for a specific grain size fraction is indicated by the P-level.

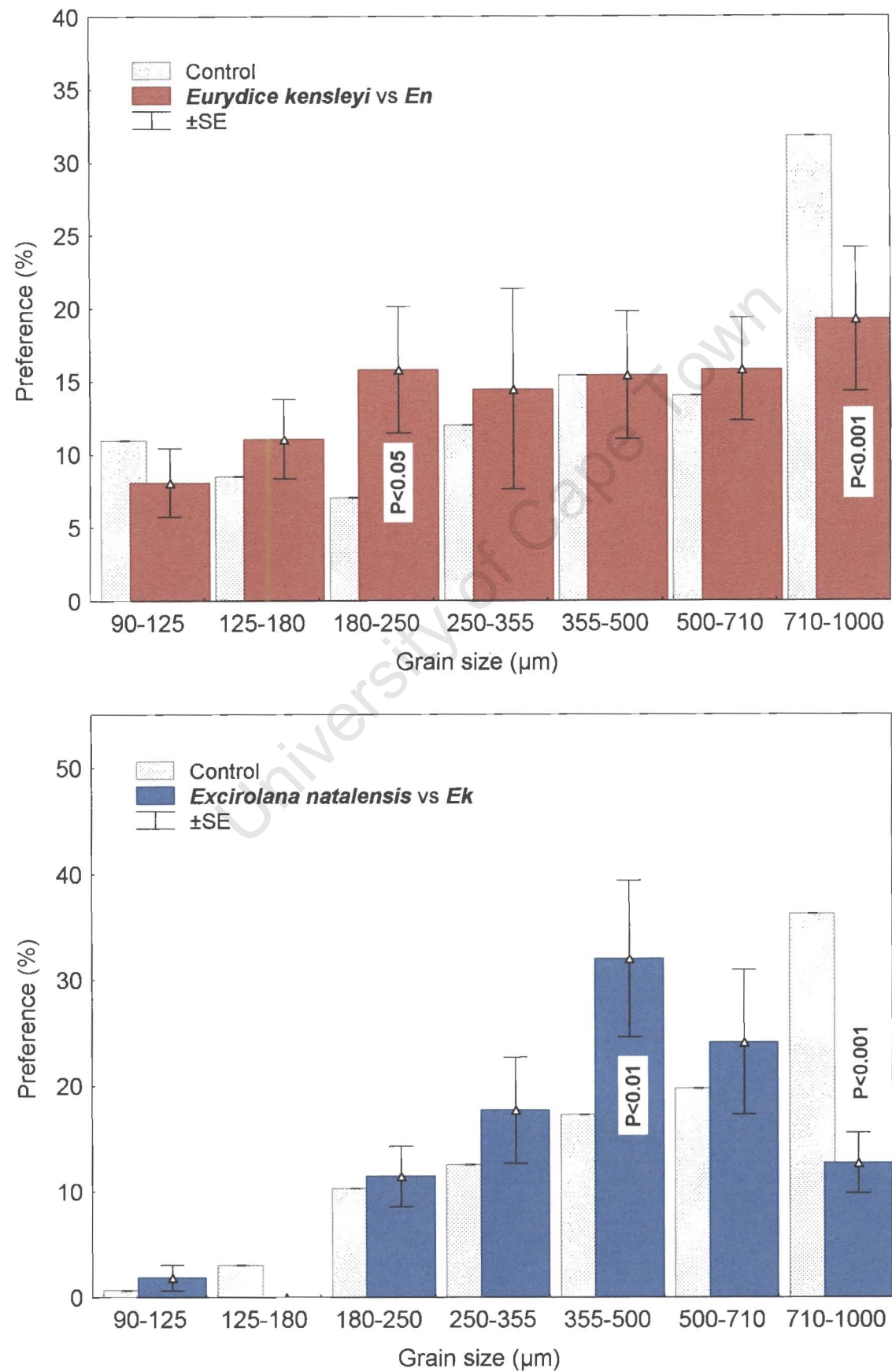


Fig. 8.4 A change in grain size preference (from the control – grey series) of *Eurydice kensleyi* (**Ek**) and *Pontogeloides latipes* (**Pl**); as the treatments – coloured series) when tested in the presence of each other. Significant differences (using a subdivided 2 x 2 contingency table) between the control and treatment preferences for a specific grain size fraction is indicated by the P-level.

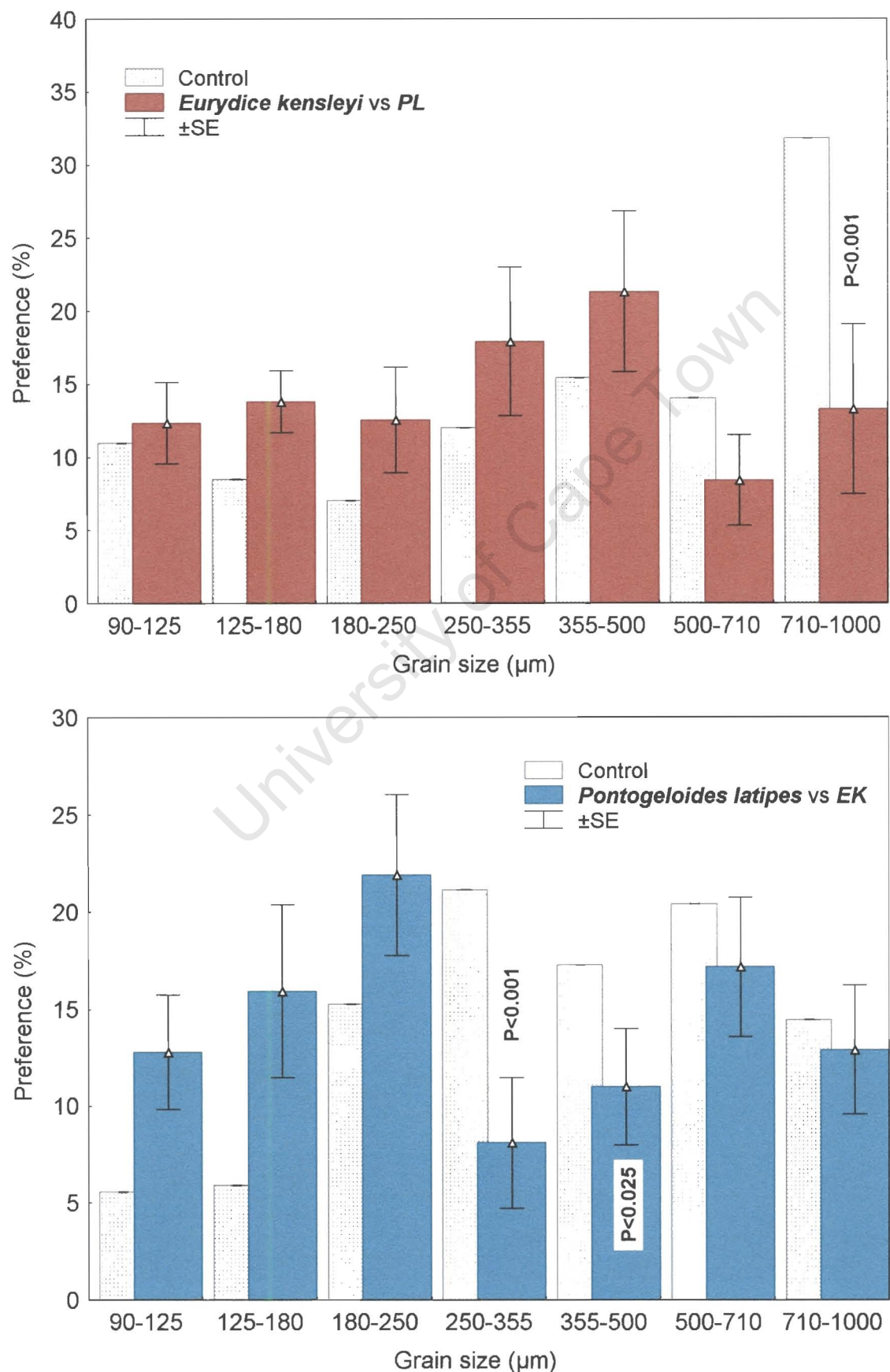
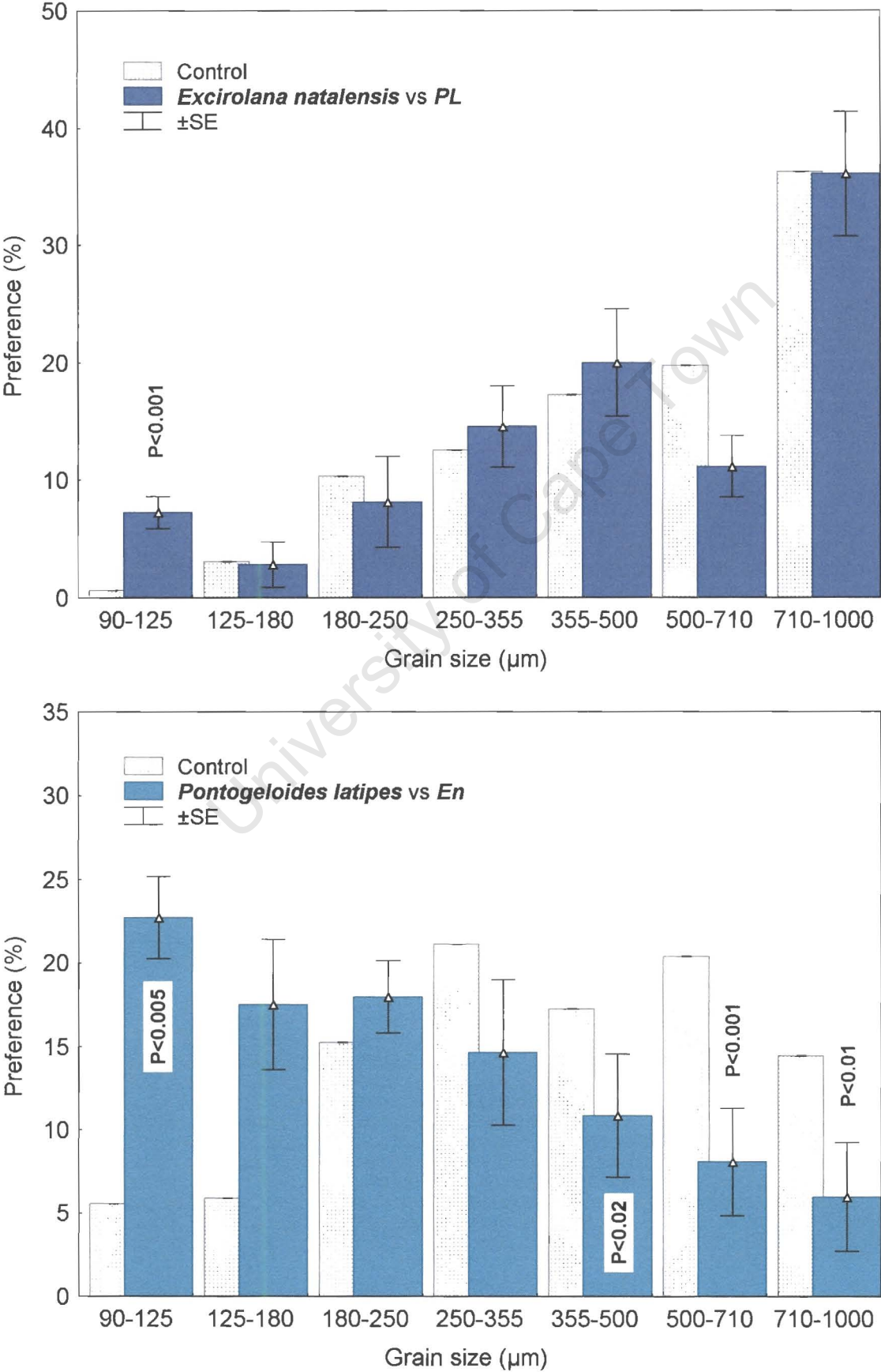


Fig. 8.5 A change in grain size preference (from the control – grey series) of *Excirolana natalensis* (**En**) and *Pontogeloides latipes* (**Pl**; as the treatments – coloured series) when tested in the presence of each other. Significant differences (using a subdivided 2 x 2 contingency table) between the control and treatment preferences for a specific grain size fraction, is indicated by the P-level.



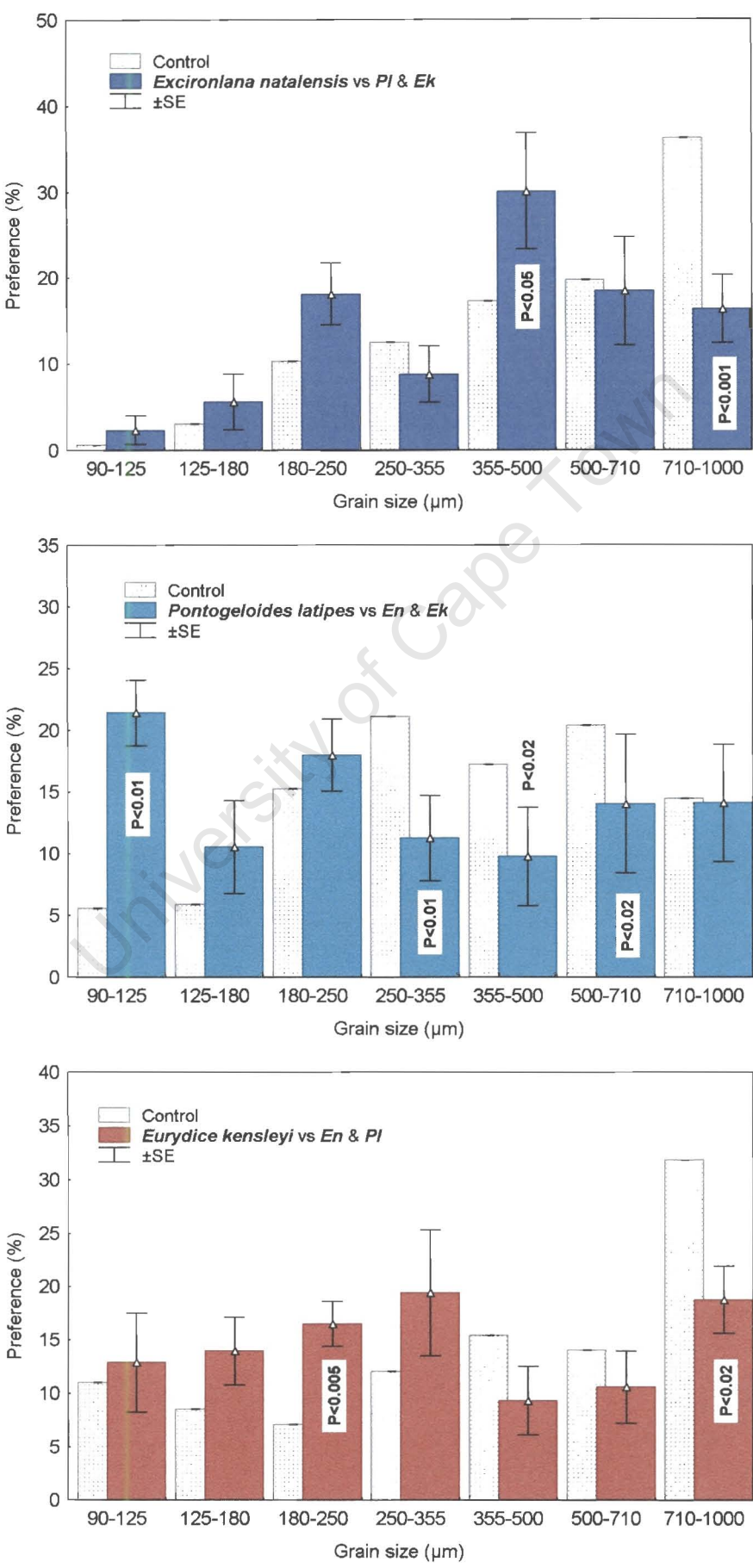
The three way interaction, with all three species present in the experimental chamber at a time, is more complicated but appears to display roughly the same trends but with the interactions superimposed on each other (Fig. 8.6). The interference between *E. kensleyi* and *E. natalensis* persisted, and both species altered their preference for coarse sand (Fig. 8.6 & Table 8.3). *E. kensleyi* changed preference (again) to an even distribution with no single grain size favoured. *E. natalensis* had the highest preference for the medium sand particle size (29% in 355 – 500 μm), while *P. latipes* altered the preference frequency for four grain sizes. This species changed from occupying medium to coarse sand to predominantly occupy the finest grain size. In a combination of three species, it therefore seems that *E. kensleyi* and *E. natalensis* are least effected by each other, but that *P. latipes* is dramatically influenced by *E. natalensis* whereas the converse interaction is not demonstrated.

8.3.2 Field Distribution

The longshore field distribution broadly reflects the above findings, even though only four of the particle size grades offered in the laboratory experiments were sampled in the field (Fig. 8.7). All three species were obtained in the grain size range (i.e. 125 – 500 μm) sampled, but *E. kensleyi* and *E. natalensis* occurred on most of the beaches. *E. kensleyi* occurred on 24 of the 27 beaches (~ 89%) and *E. natalensis* on 23 of the 27 beaches (~ 85%). These two species also obtained the highest abundance values on any the beaches sampled (Fig. 8.7). *P. latipes* frequented only 19 of these beaches (~ 70%).

A negative relationship was detected between *E. natalensis* and *E. kensleyi* in the field. The abundance values for *E. kensleyi* were highest where the abundance of *E. natalensis* was lowest. The same is true for the frequency of occurrence, meaning that *E. kensleyi* tended to

Fig. 8.6 Three-way interaction between three isopod species (as the treatment - coloured series) compared to the control grain size preference of each species (grey series). The species were *E. natalensis* (**En**), *P. latipes* (**Pl**) and *E. kensleyi* (**Ek**).



frequent beaches unoccupied by *E. natalensis* (Fig. 8.7). Furthermore, the catholic grain size preference of *E. kensleyi* seems to be altered in the field. It has the highest frequency of occurrence in fine sand (100%), and the lowest in medium sand (78 - 84%; Fig. 8.7). *P. latipes* had the lowest presence in the medium sand (250 – 355 μm) which is the grade preferred by this species when tested in isolation in the laboratory (Fig. 8.7). It also seems to frequent beaches most often unoccupied by *E. natalensis* (i.e. < 250 μm).

The across-shore distribution though, confirmed that there was an overlap in distribution among these species (Fig. 8.8), although peak abundances for the species (as seen on the kite diagrams) did not coincide. It also indicated that all three cirolanid isopod species were tolerant of conditions across the shore and capable of occupying more than one specific part of the beach. All three species have extended their distribution across the beach face in the absence of, or in the presence but relatively low abundance of, another species. It is, however, unclear whether this is the cause or effect of the absence of other species. The argument can be circular, but since all three species are capable of burrowing into all the grades obtained on the beaches, it must be some factor other than grain size preference, that governs their presence on beaches.

The extensive down-shore distribution of *E. natalensis*, on YZS, seems to a negative impact on the other cirolanid species (Fig. 8.8). *P. latipes* was completely absent from this particular beach, and *E. kensleyi* occupied zones above and below the centre of peak distribution of *E. natalensis*. The mean grain size of this particular beach is close to the grain size favoured by *E. natalensis* as well as *E. kensleyi*. The grain size of this particular beach is also in the grade of sand favoured by *P. latipes* in the laboratory (i.e. 250 – 355 μm). As the sand became finer on other beaches, more species were present even in the presence of *E. natalensis* (i.e. YZC and PB4).

Fig 8.7 Field distribution per grain size (or as % frequency of occurrence per grain size) as well as the abundance (no.m⁻¹) of *Excirolana natalensis*, *Pontogeloides latipes* and *Eurydice kensleyi* on 27 beaches sampled. (Laboratory studies investigated 90 – 1000 µm, but the beaches sampled fell into a grain size range of 125 – 500 µm).

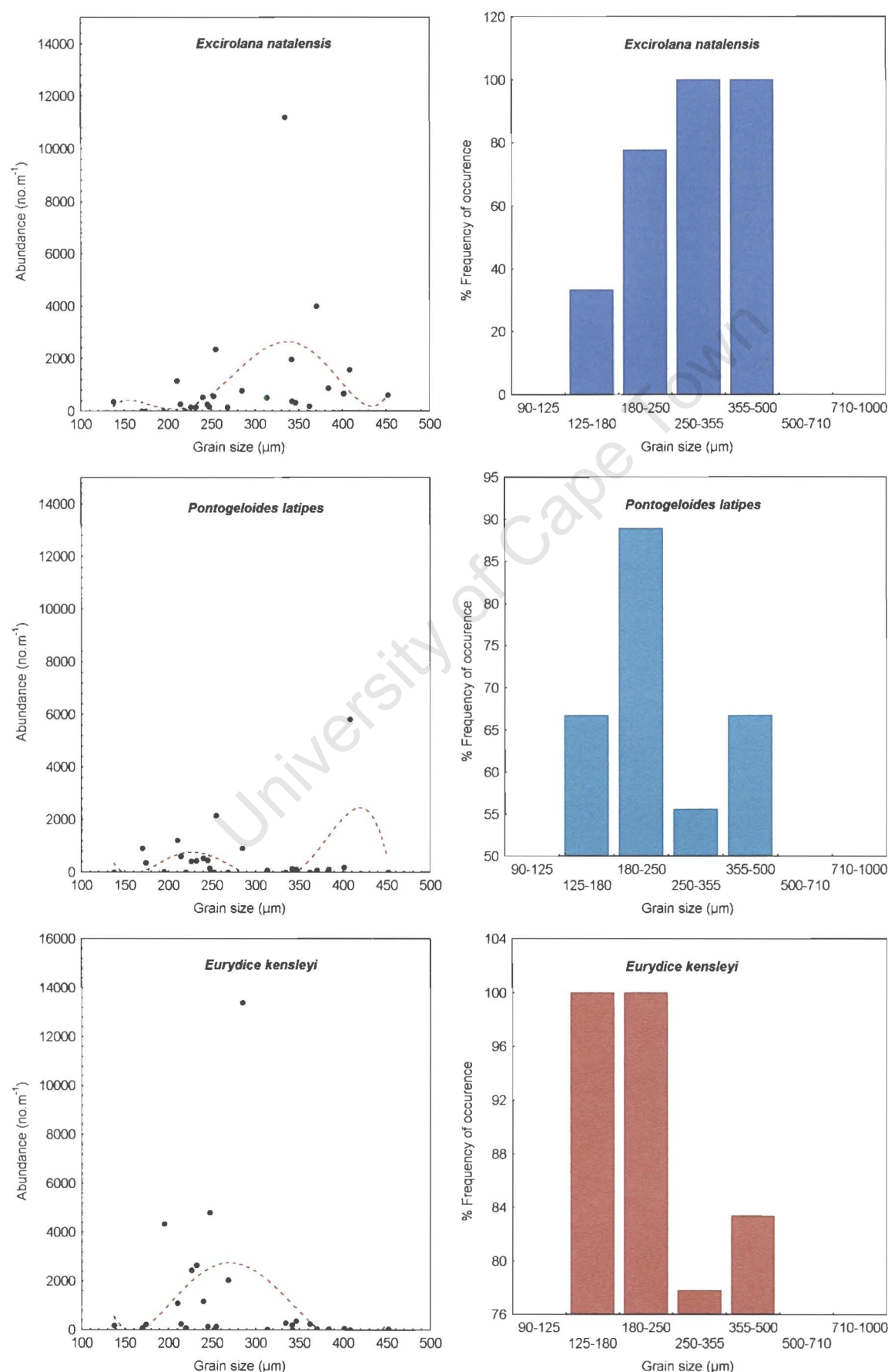
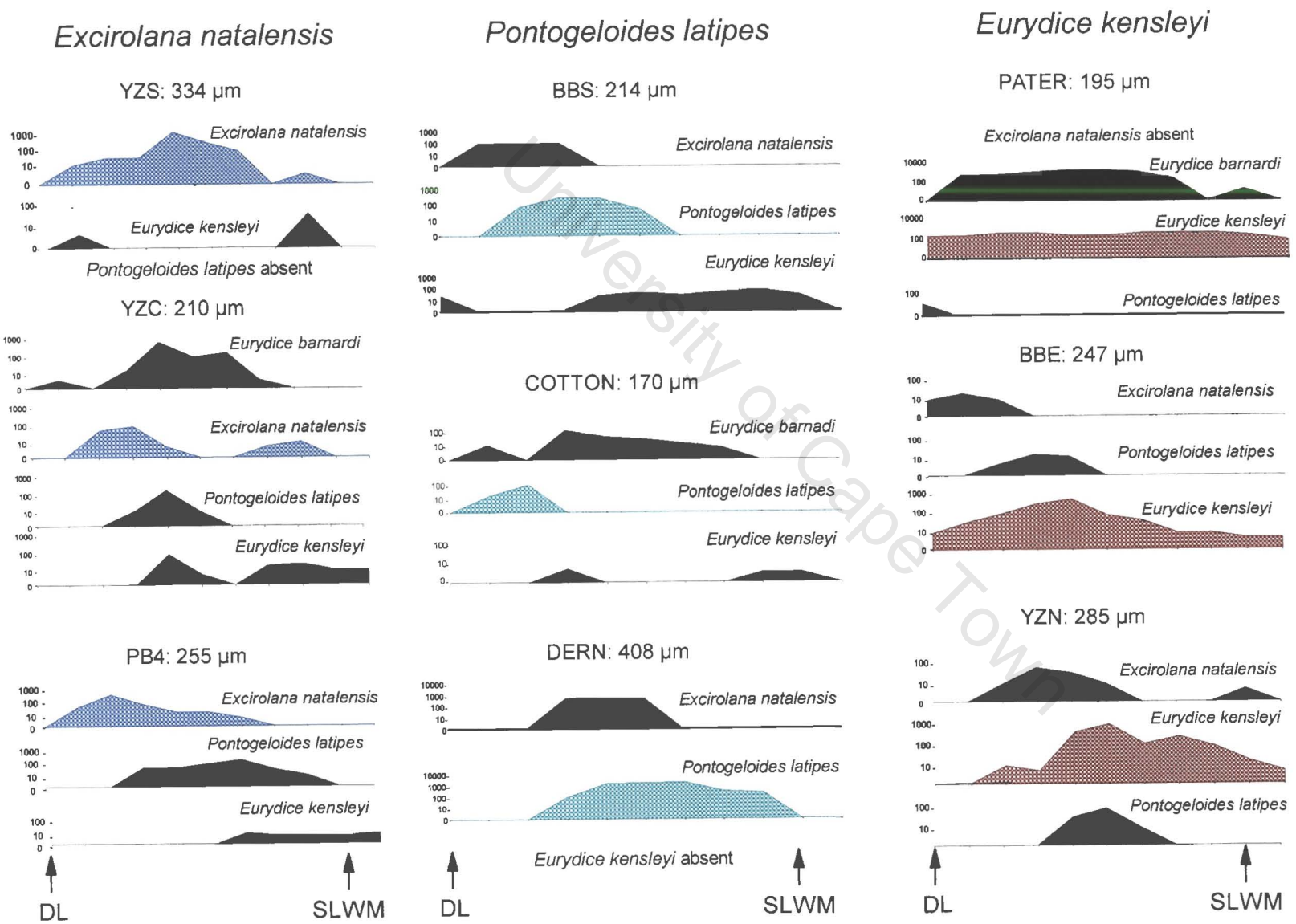


Fig 8.8 The grain size distribution of three species of cirrallid isopods across the shore from the driftline (DL) to the spring low water mark (SLWM). The kite diagrams of the three beaches (mean grain size given in μm) with the highest abundance values indicate the zones of peak abundance, and the relative change thereof in presence/absence of other cirrallid isopod species. (A description of the physical properties of the beaches can be obtained in Table 2.1). A forth species, *Eurydice barnardi* was sampled on three occasions.



On one particular beach (i.e. COTTON), *P. latipes* occupied the top of the shore, in the absence of *E. natalensis*. *E. kensleyi* displayed a bimodal distribution, minimising the overlap with *P. latipes*, but also with *Eurydice barnardi*, which was the most abundant isopod on this beach. *E. barnardi*, though, was absent from the level of the beach occupied by *P. latipes*. On Dernberg Bay Beach (DERN) *P. latipes* stretched almost across the entire beach in the absence of *E. kensleyi* (Fig. 8.8).

It appears as if *E. kensleyi* was unaffected by the other isopod species when physical conditions favoured *E. kensleyi*. On PATER, BBE and YZN, *E. kensleyi* occurred across the entire shore and overlapped widely with the other cirolanid species across the shore (Fig. 8.8). On five (of the 27) beaches sampled a fourth cirolanid species, *Eurydice barnardi*, was found. Because of the limited distribution of this species it has been ignored throughout this investigation. However, the across-shore distribution of this particular species seems to follow the trend that the zone of peak abundance does not coincide with that of any of the other species (Fig. 8.8). On three beaches (presented in Fig. 8.8) *E. barnardi* occupied the mid-shore with other species generally occurring above or below it. On Paternoster beach (PATER), the two congeners occupied all levels of the shore.

8.4 DISCUSSION

Bally (1987) reported that *Excirolana natalensis* occupies the uppermost zone of drying, whereas *Pontogeloides latipes* is found in the zones of retention and resurgence, while *Eurydice longicornis* was thought to occupy the zones of resurgence and saturation (Bally, 1987). It is evident from this study that these species are not restricted to these zones (Fig 8.8), and that these distribution patterns may not be governed by only physical conditions. Crocker (1967) reported that the ecological isolation (or niche differentiation) of some marine

animals is often apparent in terms of the zones that they occupy, the relation to the substratum or the kind of food consumed. The three cirolanid isopod species tested in this study could rather follow this trend, i.e. determining the zone that they occupy on the shore according to niche differentiation, or at least spatial segregation (Fig. 8.8).

A lack of spatial overlap between species has generally been attributed to ecophysiological or behavioural adaptations. Bally (1987) related the relative distribution of the three isopod species to the differences in their activity patterns and respiratory responses. The activity potential² of *E. natalensis*, which occurs at the top of the shore, is greatest, whereas *E. longicornis* which occupies the lower shore, had the lowest activity potential (Bally, 1987). *P. latipes* is a mid-shore species and the activity potential is intermediate between that of the other two species. Jones and Hobbins (1985) attributed the intertidal zonation of four European cirolanids to behaviour. These species displayed strong circa-tidal and circa-semilunar migratory patterns to avoid being stranded. De Ruyck *et al.*, (1991) found similar patterns for *Excirolana natalensis*, *Eurydice longicornis* and *Pontogeloides latipes*.

The results of the present study suggest that ecological segregation in terms of zonation of *E. natalensis*, *P. latipes* and *Eurydice kensleyi* is influenced by biological interactions. This is especially evident in the across-shore distribution of the species that rarely overlap, but also in the invasion of apparently 'unoccupied niches' in the absence of other cirolanid species.

The grain size preference experiments in the laboratory indicated differences in competitive abilities. All three species had some effect on one another, but it was most pronounced between the larger species. The largest of the species, *P. latipes*, seems to be negatively influenced by the presence of *E. natalensis*. On every occasion that these two species were under sympatric conditions (i.e. 2-way or 3-way interaction), *P. latipes* changed its grain size

preference (significantly). This suggest character displacement in terms of grain size preference. Both the larger species had a significant influence on *E. kensleyi*, although it was more pronounced for *E. natalensis*. *E. kensleyi* did not execute their strong preference for coarse sand in the presence of *E. natalensis*, which also preferred coarse sand. The latter species changed their distribution in the presence of the relatively small *E. kensleyi*. *E. natalensis* rather occupied medium sand in the presence of *E. kensleyi*. The reason for this behavioural change is unclear, although it is suspected that it may be a positive interaction. It is suspected that *E. kensleyi* avoid coarse sand because of the presence of *E. natalensis*, but that *E. natalensis* is attracted by *E. kensleyi*, since the former species is hunting for food and is preying on any free-swimming organisms. This suspicion needs to be tested though.

The longshore and across-shore distribution seems to occur as follows: on a macroscale, the distribution of isopods is determined by tolerance to physical parameters. Defeo *et al.*, (1997) related the longshore distribution of *Excirolana armata* and *Excirolana braziliensis* to parameters such as grain size, slope, sediment water content and penetrability. The present study found positive correlations of abundance and biomass (m^{-1}) with swash parameters (Table 3.3). If a species finds the physical conditions to be favourable it can occupy the area 'available' to it. The broad zones of occupation and specifically areas of peak abundance could be determined by ecophysiological tolerance and behaviour. These cirolanids seems to be able to survive across the entire shore on a range of beaches. However, in the presence of other species, the intertidal distribution is restricted and hence the niche width seems to be reduced. The grain size preference experiments in the laboratory and the across shore zonation patterns in the field suggest *E. natalensis* to be the strongest competitor, displacing both *E. kensleyi* and *P. latipes*. The interaction between *P. latipes* and *E. kensleyi* seems more conditional, depending on the relative abundance of each species.

² **Activity potential:** refers to the difference in the respiratory rates measured when isopods are active versus the rates measured when passive (Bally, 1987).

In the laboratory, where the abundances of the species were equal, no significant alteration was detected in the distribution per grain size of either. These species are thus equally strong competitors. Moreover, the across-shore kite diagrams seem to confirm that the species with the greatest abundance is the stronger competitor. The Lotka-Volterra model for competitive interaction suggests initial densities to be important in terms of equal competitors (Begon *et al.*, 1990). *P. latipes* is therefore influenced by both *E. natalensis* and *E. kensleyi* at high densities.

Furthermore, *E. natalensis* is probably the more tolerant (agreeing with the findings of Bally, 1987) and stronger competitor, and where physical conditions allow, this species occupies the high shore and extends down the shore. *E. kensleyi* seems to be least affected by other species of isopods in the laboratory, probably due to its size. It is small in comparison to the other species and can hide easily. This species also has a more catholic grain size preference. This species was generally buried just below the surface of the substratum. In the field this could be correlated with the relatively low activity potential as measured for *E. longicornis* (Bally, 1987). It seems to be functioning almost at optimum/maximum at most times, which seems to be a consequence of constant reburial low in the shore. The shallow burial may be indicative of resource partitioning. *P. latipes* seems to have similar abilities to *E. kensleyi*, but in the laboratory *P. latipes* frequently burrowed until the bottom of the container was reached and not only until flush with sand. This could be the result of either a good burrowing ability (but so does the other fossorial species; Nel, 1995), but even more likely, a strategy to avoid/reduce competition. It is difficult to indicate whether resource partitioning by vertical stratification is a possibility *in situ* since these species all occur in great numbers at a very shallow depth (< 10 cm; pers. obs.). No specific studies have been undertaken to determine vertical stratification for these species since biological interactions have rarely been considered and tested in beach ecology.

As found by Defeo *et al.* (1997) this study indicates that the mesoscale distribution of cirolanid isopods cannot be explained only by animal-sediment relationships. The longshore distribution of these three species of cirolanid isopods is related to physical conditions, whereas the across-shore distributions seem to be greatly influenced by competitive interactions. The mechanisms of interaction, viz. interference or exploitation, are unclear.

It is suspected that interference competition makes an important contribution to the community structure of these isopod species. Resources such as space and food should not be limited for these species while buried at low tide and therefore provide little opportunity for interference. Interference while buried can also be further reduced by vertical stratification (as is the case for fossorial, sympatric amphipods; Crocker, 1967). During high tides, especially at night, these cirolanid species venture into the water column to feed in the swash (De Ruyck *et al.*, 1991). This also provides for the greatest likelihood of encountering cannibalistic and carnivorous isopods, which seems to be the case for all species which have the lowest numbers where they overlap with other species.

It is therefore concluded that biological interactions, in the form of either exploitation or interference competition takes place among *E. natalensis*, *P. latipes* and *E. kensleyi*. The grain size preferences of these species in isolation (i.e. *E. kensleyi* and *E. natalensis* that preferred coarse sand and *P. latipes* that preferred medium sand) were altered when tested in combination. *E. kensleyi* seemed relatively unaffected by the larger species in the laboratory, but not in the field. *E. natalensis* reacted significantly to *E. kensleyi* but less so to *P. latipes*, whereas *P. latipes* was strongly (negatively) affected by *E. natalensis*. These interactions seemed to govern field distribution patterns of these populations, over and above the influence of physical parameters, since the across-shore distributions mirrored these interactions. Taking both the laboratory and field data into account, the species are ranked as *E. natalensis* being the strongest competitor, *E. kensleyi* the second strongest

competitor (or possibly the greatest generalist), especially if present at high densities, whereas *P. latipes* is ranked as the weakest competitor due to its inability to displace any of the other two species (unless abundant in the field). It is also suspected that *P. latipes* is restricted to the mid-shore (when present) to avoid competition with *E. kensleyi* and *E. natalensis*. Biological interactions therefore seem to occur on open ocean beaches and are strong enough to govern the distribution patterns of cirrolanid isopods.





CHAPTER 9

University of Cape Town

9.1 FINDINGS FROM THIS STUDY

9.1.1 Physical factors

Dimensionless fall velocity and other indices

Chapter 2 described a range of beaches of different morphodynamic types as defined by the dimensionless fall velocity (Ω), BSI, RTR and EXP. These indices highlighted the variation in the physical parameters over spatial and temporal scales, and also a concurrent change in the communities occupying these beaches. The most important physical conditions controlling beach communities on a macroscale include biogeographical province, grain size, slope and beach state. Species diversity is highest on fine, flat beaches in the warmer biogeographical province. Generally, the best correlations were obtained with more conservative physical parameters, such as slope, that varied little over time. Although the regressions were not always significant (as obtained by previous workers, who studied a smaller number of beaches in a single province only, or both microtidal and mesotidal ranges) it was considered a representative sample of a series of microtidal beaches with varying physical conditions. The zonation patterns indicated that the number of faunal zones is a function of species diversity, which in turn is a function of beach state/width. An increase in the number of species resulted in an increase in the number of biological zones. Conversely, larger numbers of unoccupied zones were identified on reflective beaches that harbour fewer species. A general increase in the number of zones was observed from reflective to dissipative beach states. It is concluded that more zones (and therefore niches) exist towards the dissipative extreme, and this leads to an increase in species diversity.

Defining swash climate and swash exclusion

The results from Chapter 2 broadly supported the *swash exclusion hypothesis* (by McLachlan, 1990), with an increase in the number of species, abundance and biomass from coarse grained reflective beaches to fine, flat dissipative beaches. These findings also support the notion that beach communities are primarily controlled by the physical environment. A further, in-depth investigation, in **Chapter 3**, into parameters controlling the swash climate and influencing macrofauna communities suggested the following: swash period, swash upwash distance or effluent line crossings were indicated as critical swash factors. However, no single swash parameter could be regarded as a superparameter. Furthermore, populations of different species react differently to the same swash parameters. Thus even though significant correlations were obtained between the biota and certain swash parameters, such as swash upwash time, species were not all equally affected by these parameters. Community responses therefore cannot be extrapolated from species responses to specific factors. The converse also holds; factors that influence the community as a whole may not have a controlling effect on particular populations. Each species has very specific ecophysiological and behavioural responses to the intertidal environment. Moreover, if community structure could be explained as the sum of the responses of the individual populations to physical parameters, then this could be used as evidence that biological interactions between organisms would be unimportant in beach communities.

Combining the important intertidal beach parameters and critical swash factors the *swash exclusion hypothesis* was redefined (i.e. RSEH). The hypothesis that now needs rigorous testing is: *species are excluded from reflective beaches because of coarse sand and short swash periods, whereas abundance is limited by space (or niche availability), and biomass by swash upwash distance (or the percentage and number of effluent line crossings)*. The importance of two factors, that vary greatly with beach state, that needs to be tested specifically is *space* and *turbulence*. It is possible that beach width, and therefore space, is

not limited but just an artefact of being a function of beach state. The influence of turbulence so far is unmeasured.

Intertidal distribution of west coast *Donax serra*

The RSEH was tested in **Chapter 4** using the beach clam *Donax serra*. The large size of this animal made it more tractable in the swash than any other species, but this size makes it relatively immobile. Comparing the response of passive clams (i.e. dead animals) to that of active clams (i.e. live animals), it was found that passive animals were more directly influenced by swash parameters than active ones. The distribution of dead clams was correlated with slope, whereas live clams reacted to swash upwash distance, backwash time, slope and effluent line crossings. It was concluded that this species generally conforms to the RSEH, although not completely. The across-shore distribution of this species on the west coast of southern Africa, as opposed to macrofaunal communities (that react strongly to grain size), is not exclusively governed by swash climate (as cautioned in Chapter 3). Possible reasons for this variation to the predictions made by the RSEH include (i) the large size and immobility of the animal, and (ii) the behavioural response of live animals to avoid stranding on the driftline. Displacement to the subtidal seems to be the result of long term microevolutionary changes in shell shape since equal fractions of live and dead clams got displaced to the subtidal. A fraction (~ 22%) of live clams avoided the risk of being stranded on the driftline or being preyed upon by birds, by burrowing into the substratum. The behavioural responses observed from this study seem to support the ideas of microevolutionary changes of shell shape proposed by Soares *et al.* (1998). Furthermore, it lends support to the predation and temperature hypotheses proposed by Bally (1983b) and Donn (1990a; 1990b), respectively. The longshore distribution of adult populations is still physically controlled, while spatial control of segregation between size classes within this species remains unclear.

9.1.2 Biological interactions on beaches

Underwood (1985) described the importance of physical environmental factors in modifying biological interactions, leading to different outcomes under different conditions. The opposite seems to be true for exposed open ocean beaches, although no thorough investigation has been conducted to quantify the contribution of biological interactions to community structures. **Chapter 5** concluded that few significant interactions are likely to occur on open ocean beaches. But interactions that are likely, are intraspecific competition either by means of exploitation or interference for physical/feeding space by bivalves, interspecific competition between sympatric populations of small mobile fauna such as cirrolanid isopods and amphipods, or predation (as discussed in Chapter 4). Some of these ideas were tested experimentally.

Intraspecific competition for space

Donax serra can occur in very high densities with a high biomass on particular exposed beaches. Adult and juvenile distributions along the coast are generally segregated with little overlap in peak abundance of size classes. This study (**Chapter 6**) could not demonstrate competition for space between *D. serra* individuals. However, medium- and large-sized individuals may compete with other individuals of the same size when present at high densities in the substratum (30 clams per 0.1 m²). It is expected that the effect of interference/exploitation would even be more pronounced at higher densities. Little evidence was obtained for competitive interaction between the smallest and largest size classes. It was interpreted that animals of different sizes burrow to different depths and this therefore results in vertical space partitioning. Competition may therefore be absent or reduced between different size classes. Burial time, however, is a very short-term measurement and no confident long-term predictions can be made, especially in the presence of wave action. Observations on the behaviour of these animals suggest that interference competition may occur, especially regarding the effect of adults on juveniles.

Intraspecific competition and zonation

The adult-juvenile experiments were expanded to longer-term studies, lasting 24 hours, in the field. The *in situ* experiments of **Chapter 7** found no evidence of competition between adults and juvenile *D. serra*. The juvenile recovery was unrelated to adult densities but strongly related to physical changes along the beach, over time. Experimental densities of adults appear to be below the critical density proposed by the burrowing rate experiments. Adult densities were moderate to high i.e. 30 or less per 0.1 m². It therefore has to be concluded that adult-juvenile interactions for *D. serra* are weak/absent from beaches (at least at moderate densities) and that the spatial segregation between these size classes seems to be the result of physical parameters such as wave sorting or some untested biological factor.

Interspecific competition between isopods

The investigation in **Chapter 8** agreed with the findings of Defeo *et al.*, (1997); macroscale distributions of cirolanid isopod species are largely physically controlled but the mesoscale distribution patterns of cirolanids (i.e. *Eurydice kensleyi*, *Pontogeloides latipes* and *Excirolana natalensis*) may be modified by competitive interactions. *E. natalensis* seems to be the more tolerant species and the strongest competitor. This species occurs at the top of the shore and prefers coarse sand beaches. As the numbers of this species decline on finer beaches, the relative abundance of *P. latipes* and *E. kensleyi* increases. These two species frequent the mid- and low-shore, respectively. These two species also appear to have similar competitive abilities but burrowed to different depths in the laboratory experiments. *E. kensleyi* displayed a very catholic grain size preference in the laboratory, but is displaced by *E. natalensis* in the field. *P. latipes* preferred medium to coarse sand but occurred most frequently on fine sand shores. Furthermore, *P. latipes* never occurred in extremely high densities on any of the beaches and had the highest densities where both the other two cirolanid species occurred in very low numbers. The across-shore distribution and relative abundance of *P. latipes* seems to be restricted to the zone between *E. natalensis* and *E.*

kensleyi. Biological interactions, probably in the form of interference competition, therefore seem to control across-shore distribution patterns of these three cirolanid populations.

9.1.3 The control of macrofauna community structures

Exposed, open ocean beaches should be compared to pelagic systems rather than rocky shores. As in pelagic systems, beaches are physically controlled environments, with absolute population numbers unstable and unpredictable in time and space (Branch *et al.*, 1987). Macrofaunal diversity is low compared to other marine systems. The Noy-Meir (1979) autecological hypothesis, that has been applied to deserts, can also be applied to beaches. This implies that beach animals broadly respond to physical parameters rather than to interactions between individuals. Keystone species are absent from beaches, and long term removal of a species may have little effect on the systems.

On a macroscale: dissipative beaches present the most benign beach conditions harbouring large communities of the major invertebrate taxa. Physical factors that favour a broad range of species include: slow, long, infrequent swashes, over a broad, flat beach face comprised on fine or medium sand, with a limited amount of wave energy and turbulence reaching the beach face. The fast swash speeds and periods, coarse sand, steep beach face, high levels of turbulence and filtration rates of reflective beaches limit the species that can survive here. Species diversities are therefore restricted on these beaches.

On a mesoscale: across-shore zonation patterns are governed by the number of species present and thus beach type (and niche availability). The level of the beach that a species occupies is primarily a result of ecophysiological tolerance and an optimal position to feed and breed, hence the migration with the rise and fall with the tide. The species are generally highly tolerant, but also highly mobile, which adds to the unpredictability of the system.

Because of the mobility of the animals and the three-dimensional substratum, species should rarely compete for space. This study found that molluscs, such as *D. serra*, certainly have the potential to compete but the physical instability probably limits abundance before it reaches the threshold density for competition. Biological interactions therefore are generally overridden by physical fluctuations. The across-shore distribution of cirratanid isopods, though, which can occur in extremely high numbers across the beach face, indicated biological interactions (probably by means of interference) to be present among these species, even on exposed beaches. The variability of predictive models/indices, such as Ω or swash on macrofaunal diversity, is often accepted (but not explained). This variability may be related to complex biotic relationships that exist but were previously disregarded. Our understanding of beach systems will only improve if we can clarify the importance of biological interactions on beach macrofauna assemblages.

9.2 WHAT NEEDS TO BE TESTED

Underwood (1985) gave guidelines for the valid investigation of ecological patterns. He made two important comments. Firstly, that untested models are not necessarily valid and are simply guesses with little status. Secondly, that any investigation into the validity of a particular model should include an alternative, and a plausible model explaining the original phenomena. The ecological investigation would further be improved if these ideas are contrasting so as to test conflicting ideas (Underwood, 1985). It was further advised that experiments should be conducted while never losing sight of the effect of the physical environment. Experiments should therefore be conducted through a range of physical conditions and not only extremes. It is therefore necessary to test the validity of the *redefined swash exclusion hypothesis*, i.e. the effects of grain size, swash period and effluent line crossings or swash frequency on species richness, abundance and biomass, across different biogeographical provinces and tide ranges. The effects of swash turbulence should also be

determined. Further work should also focus on hypotheses which include biological interactions and then experimentally test these within and between species over a range of beach morphodynamic states.

In the South African context specifically the following needs investigation:

- The importance of biological interactions on the across-shore zonation patterns and spatial segregation of size classes of *Donax serra*;
- The mechanisms driving the inverted distribution of adult clams on south and west coast beaches;
- The possibility that biological interactions may also be responsible for within- and between-species segregation of gastropods of the genus *Bullia*, that also display segregation by size (Brown, 1982; McGwynne and McLachlan, 1985);
- Burrowing rate experiments should be expanded to test the mechanism i.e. interference or exploitation competition within size classes of clams at high densities. This can be achieved by having background densities constituting live *versus* dead animals in the substratum.

9.3 WHERE TO FROM HERE IN BEACH ECOLOGY

Few of the effects of physical factors on the community structures of rocky shores are additive or linear (Underwood, 1985). This must also serve as an admonition to beach ecologists. Most of the responses are considered in terms of linear models (such as: McLachlan, 1990; McArdle and McLachlan, 1992; Jaramillo and McLachlan 1993; McLachlan *et al.*, 1993), with the exception of a few (e.g. Ellers, 1995a; 1995b; Hacking, 1996). It is only during spring low tides that beaches harbour exposed intertidal benthic communities. It may

be time to consider integrated 'three-dimensional' models as are used for prediction in pelagic systems. Multivariate statistics are often applied and found useful to describe zonation patterns, but the inter-relatedness of the variables make most statistical procedures inappropriate. Artificial Neural Networks may be applied with greater success, especially in trying to map the effects of co-varying physical parameters (such as turbulence, wave height and slope) determining swash climate. It is also necessary to expand the correlative type approach by follow-up work, testing the predictions from the correlations, with rigorous experimental designs.

Experimental techniques can easily include cages or burrowing time tests. It has been assumed that cages cannot be erected on beaches. The cages used during the caging experiments in this project worked exceptionally well on these microtidal beaches, and have been used in further studies. These cages were also used to test the effect of off-road vehicles on beach clams. The cages had a sufficiently coarse mesh not to interfere with sand and water movement, and were pliable since made of stiff nylon mesh. Further studies focusing on reproductive cycles and recruitment patterns, ecophysiological tolerances, dietary preferences and ultimately niche widths of these behaviourally plastic, mobile but cryptic creatures should continue if we wish to improve the all-round understanding of beach ecosystems.



CHAPTER 10

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Appendix 1

IX

Species diversity and abundance (as per running metre of beach) for the 27 beaches sampled along the

Namibian Beaches													
	PB1s1	PB1s2	PB2s1	PB2s2	PB3s1	PB3s2	DBs1	DBs2	BBs1	BBs2	DERN	PB4	PB1
	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13
<i>Abarenicola</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bullia digitalis</i>	0	0	0	0	0	0	0	0	32	0	0	0	0
<i>Bullia pura</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bullia rhodostoma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Callianassa kraussi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cerebratulus fuscus</i>	68	0	133	37	114	453	0	18	318	90	30	153	0
Coleoptera 1	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera 2	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera 3	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera 4	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera 5	0	0	0	0	0	0	0	0	0	0	0	22	0
Crab megalopa	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumaceae	0	0	0	0	0	0	0	0	32	0	0	0	0
<i>Donax serra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Donax sordidus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Euclymene</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eurydice bamardi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eurydice kensleyi</i>	17	64	50	50	205	1173	139	369	2450	247	0	153	33
<i>Eurydice</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Excirrolana natalensis</i>	509	658	4000	882	1977	533	263	316	159	269	1574	2356	611
<i>Gastrosaccus psammodytes</i>	170	145	417	3205	8500	1307	1916	88	6809	4575	1425	240	0
<i>Glycera</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hyale saldanha</i>	0	0	17	0	0	0	0	35	0	0	0	0	0
<i>Indischnopus capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Insecta	0	0	17	0	0	0	0	0	0	0	0	0	0
Larvae	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lumbrinereis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mandibilophoxus latipes</i>	0	0	0	50	23	453	216	53	5059	673	89	1331	0
Nemertean	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephtys capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Oligochaeta	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Periculodes longimanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoxocephalid	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaete 1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pontogeloides latipes</i>	85	193	83	124	136	533	464	123	414	605	5821	2160	0
<i>Scolecopsis squamata</i>	102	0	0	0	0	0	0	0	0	0	0	22	0
<i>Scoloplos</i> sp.	0	0	0	0	0	0	0	0	32	0	0	0	0
<i>Talorchestia australis</i>	0	0	0	0	0	0	0	0	0	0	0	458	0
<i>Talorchestia capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Talorchestia quadrispinosa</i>	221	225	183	944	182	613	170	158	255	359	2584	284	284
<i>Tylos capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tylos granulatus</i>	85	289	117	62	68	107	77	352	95	269	327	87	0
<i>Urothoe coxalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Urothoe pinnata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Abundance (no.m ⁻¹)	1256	1574	5017	5355	11205	5173	3245	1512	15655	7086	11849	7265	927
Total no. of species	8	6	9	8	8	8	7	9	11	8	7	11	3

south and west coasts of southern Africa.

West Coast Beaches						South Coast Beaches				False Bay Beaches				
YZN	YZC	YZS	BBE	PATER	VELD	SUND	VANS	MAIT	KING	STRAND	MACAS	COTTON	MUIZ	
#14	#15	#16	#17	#18	#19	#20	#21	#22	#23	#24	#25	#26	#27	
0	0	0	0	0	0	0	0	0	0	0	0	0	74	<i>Abarenicola</i> sp.
121	533	0	188	30	0	27	7980	40	25	0	0	20	74	<i>Bullia digitalis</i>
0	0	0	0	0	0	189	180	320	76	0	0	0	0	<i>Bullia pura</i>
0	0	0	0	0	0	405	1080	840	127	207	96	704	0	<i>Bullia rhodostoma</i>
0	0	0	0	0	0	0	0	0	0	0	0	0	25	<i>Callianassa kraussi</i>
242	67	0	0	30	0	54	180	80	51	0	0	0	0	<i>Cerebratulus fuscus</i>
61	100	27	0	0	0	0	0	0	0	0	24	20	0	Coleoptera 1
0	0	0	0	0	0	0	0	0	0	30	0	0	0	Coleoptera 2
0	0	0	0	0	0	0	0	0	0	59	0	0	0	Coleoptera 3
30	33	0	0	0	0	0	0	0	0	30	0	0	0	Coleoptera 4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	Coleoptera 5
0	0	0	0	30	0	0	0	0	0	0	0	0	0	Crab megalopa
0	0	0	0	61	0	0	0	0	0	0	169	0	0	Cumaceae
1455	833	0	902	2030	0	3078	0	12800	152	30	72	20	74	<i>Donax serra</i>
0	0	0	0	0	0	621	660	920	25	0	24	0	25	<i>Donax sordidus</i>
0	0	0	0	0	0	81	0	0	0	0	0	0	0	<i>Euclymene</i> sp.
0	7733	0	0	10485	0	0	0	0	0	57791	9275	2385	0	<i>Eurydice barnardi</i>
13394	1100	293	4810	4348	0	2646	0	2040	76	177	217	78	245	<i>Eurydice kensleyi</i>
0	0	0	0	0	0	81	6690	0	0	0	0	0	0	<i>Eurydice</i> sp.
788	1167	11200	169	0	373	162	570	160	0	355	0	0	196	<i>Excirolana natalensis</i>
636	1833	0	413	2030	0	135	420	240	25	798	1012	723	638	<i>G. psammodytes</i>
0	0	0	0	0	0	135	210	560	0	207	0	0	98	<i>Glycera</i> sp.
0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Hyale saldanha</i>
0	0	0	56	0	0	837	0	0	0	0	0	0	0	<i>I. capensis</i>
0	0	0	0	0	0	0	30	0	0	0	0	0	0	Insecta
61	0	27	0	0	0	0	60	0	0	59	24	20	491	Larvae
0	0	0	0	0	0	0	90	0	0	0	0	20	25	<i>Lumbrinereis</i> sp.
212	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>M. latipes</i>
0	0	0	0	0	0	0	0	0	25	295	24	20	0	Nemertean
30	1300	0	132	333	0	81	0	280	25	325	554	528	417	<i>Nephtys capensis</i>
0	0	0	0	0	0	0	0	0	0	0	0	20	0	Oligochaeta
0	0	0	376	0	0	54	210	0	481	0	72	137	785	<i>P. longimanus</i>
0	167	0	0	15	0	0	600	200	0	2630	1542	59	0	Phoxocephalid
0	0	0	0	0	0	0	0	0	0	266	217	20	0	Polycheate 1
909	1200	0	150	15	0	432	0	0	0	0	361	899	0	<i>Pontogeloides latipes</i>
91	100033	0	19	227	0	81	30	0	152	355	1253	391	49	<i>Scolecopsis squamata</i>
0	0	0	0	0	0	0	0	0	0	2098	5107	1759	491	<i>Scoloplos</i> sp.
0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Talorchestia australis</i>
0	0	0	0	0	0	0	30	0	0	148	120	0	0	<i>Talorchestia capensis</i>
545	400	2267	56	0	45	0	0	0	0	0	0	176	74	<i>T. quadrispinosa</i>
0	0	0	0	0	0	0	30	0	0	0	0	0	0	<i>Tylos capensis</i>
3879	1433	0	19	0	0	27	0	0	0	0	0	20	0	<i>Tylos granulatus</i>
0	0	0	0	0	0	1080	210	1920	0	0	0	0	0	<i>Urothoe coxalis</i>
0	0	0	0	0	0	0	0	0	0	9780	1686	2502	49	<i>Urothoe pinnata</i>
22455	117933	13813	7290	19636	418	10206	19260	20400	1241	75636	21850	10515	3829	Abundance (no.m ⁻¹)
15	15	5	12	12	2	19	18	13	12	19	20	21	17	Total no. of species

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APPENDIX 2

XI

Physical parameters measured on 27 beaches from two biogeographical provinces.

Date sampled	Namibian Beaches												
	PB1s1	PB1s2	PB2s1	PB2s2	PB3s1	PB3s2	DBs1	DBs2	BBs1	BBs2	DERN	PB4	PB1
	Feb'98	Feb'98	Feb'98	Feb'98	Feb'98	Feb'98	Feb'98	Feb'98	Feb'98	Feb'98	Aug'97	Aug'97	Aug'97
	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13
1. SURFZ (m)	150	120	70	50	90	180	50	80	20	60	100	200	100
2. WAVENO	6.6	5.4	4.6	6.2	5.6	7.2	3.4	4.4	3	5.2	5.4	7.8	4.75
3. WAVEH (m)	1.47	2.04	1.44	1.96	0.86	1.85	0.62	0.96	0.48	0.78	3.1	3.1	3
4. WAVEF (m ⁻¹)	6.5	4.8	6.4	4.4	5.6	6.4	5.2	6	4	9.2	6.2	6	6
5. WAVET (s)	9.23	12.50	9.38	13.64	10.71	9.38	11.54	10.00	15.00	6.52	9.68	10.00	10.00
6. SWASHF (m ⁻¹)	6.80	5.00	5.20	7.60	11.20	4.40	5.60	6.80	6.80	6.40	4.50	4.80	10.00
7. SWASHT (s)	0.15	0.20	0.19	0.13	0.09	0.23	0.18	0.15	0.15	0.16	0.22	0.21	0.10
8. SUT (s)	15.00	10.40	8.60	9.90	5.30	13.50	12.90	15.80	5.60	12.80	28.00	16.60	4.38
9. SUD (m)	9.02	7.23	6.51	7.28	5.11	13.05	10.26	10.91	7.69	9.40	15.78	11.99	2.95
10.SUV (m.s ⁻¹)	1.62	1.34	1.32	1.34	0.99	1.03	1.22	1.43	0.71	1.26	1.78	1.38	1.53
11.SBT (s)	9.00	15.60	11.60	11.00	5.20	11.40	9.80	7.80	11.40	10.00	26.00	12.80	5.40
12.SBD (m)	9.83	9.43	8.03	8.47	6.28	18.89	10.69	9.06	14.93	10.93	16.22	15.31	3.77
13.SBV (m.s ⁻¹)	0.91	1.58	1.43	1.30	0.82	0.56	0.85	0.90	0.77	0.94	1.59	0.97	1.56
14.TOTST (s)	18.85	16.66	14.54	15.75	11.39	31.94	20.95	19.97	22.62	20.33	31.99	27.29	6.71
15.TOTSD (m)	24.00	26.00	20.20	20.90	10.50	24.90	22.70	23.60	17.00	22.80	54.00	29.40	9.78
16.EFFCROS (m-1)	1.50	1.20	0.80	1.50	2.40	0.00	2.00	0.00	0.40	0.00			
17.VERTDIS (cm)	341	346	284	616	287	204	197	302	231	267	172	225	288
18.BWIDTH (m)	56	53	55	41	75	88	51	58	105	74	98	72	36
19.SLOPE (1:H)	16.4	15.3	19.4	18.1	26.1	43.1	25.9	19.2	45.5	27.7	57.0	32.0	12.5
20.WATERTABLE (cm)	87.4	15.76	87.4	15.76	87.4	15.76	87.4	15.76	87.4	15.76	13.3	24.2	10.4
21.GRAIN SIZE (µm)	313	401	370	384	342	240	245	346	226	214	408	255	452
22.GRAIN SIZE (phi)	1.68	1.32	1.44	1.38	1.55	2.06	2.03	1.53	2.15	2.22	1.29	1.97	1.15
23.GIBBS (cm.s ⁻¹)	4.0921	5.4806	4.7871	5.1342	4.4395	2.7179	2.7179	4.4395	2.3837	2.3837	5.4806	2.7179	6.1697
24.DEANS	3.90	2.98	3.21	2.80	1.81	7.26	1.98	2.16	1.34	5.02	5.84	11.41	4.86
25.RTR	0.55	0.73	1.17	0.91	0.90	0.89	2.31	0.68	2.40	1.12	0.27	0.45	0.37
26.BSI	0.69	0.81	0.89	0.86	0.44	1.20	0.66	0.44	0.47	0.81	0.85	1.32	0.89
27.TR	81	148	168	178	77	164	143	65	115	87	84	138	111
28.EXP	15	14	15	12	13	9	12	17	14	15	12	14	17

	West Coast Beaches						South Coast Beaches				False Bay Beaches			
Date sampled	YZN	YZC	YZS	BBE	PATER	VELD	SUND	VANS	MAIT	KING	STRAND	MACAS	COTTON	MUIZ
	Apr'98	Apr'98	Apr'98	Apr'98	Apr'98	Apr'98	May'98	May'98	May'98	May'98	Sept'98	Sept'98	Sept'98	Aug'98
	#14	#15	#16	#17	#18	#19	#20	#21	#22	#23	#24	#25	#26	#27
1. SURFZ (m)	300	80	200	15	70	12	200	150	150	40	120	100	80	200
2. WAVENO	3.4	7.2	3.8	1.4	3.6	0.4	7.2	6.4	6.8	3	6.5	7.8	5.25	5.8
3. WAVEH (m)	1.949	1.18	2.2	0.53	0.5	0.3	1.9	1.7	1.44	0.46	0.78	0.7	0.52	0.62
4. WAVEF (m ⁻¹)	3.8	6	4.4	4	3.8	5.8	3.6	5.2	5.2	4.8	6.4	3	5.8	5.2
5. WAVET (s)	15.79	10.00	13.64	15.00	15.79	10.34	16.67	11.54	11.54	12.50	9.38	20.00	10.34	11.54
6. SWASHF (m ⁻¹)	5.20	1.00	5.60	2.60	2.00	7.60	3.20	3.00	9.60	3.60	5.60	6.00	4.20	7.20
7. SWASHT (s)	0.19	1.00	0.18	0.38	0.50	0.13	0.31	0.33	0.10	0.28	0.18	0.17	0.24	0.14
8. SUT (s)	40.00	13.00	16.20	10.00	6.40	7.26	9.80	12.20	12.80	12.40	19.20	23.00	6.50	13.10
9. SUD (m)	12.40	16.60	13.32	9.25	9.60	4.40	11.51	10.97	11.68	13.99	14.90	16.35	9.54	12.97
10.SUV (m.s ⁻¹)	3.15	0.74	1.18	1.05	0.73	1.64	0.80	1.12	0.99	0.87	1.29	1.37	0.65	1.00
11.SBT (s)	41.00	15.30	19.20	8.60	3.20	9.80	8.20	8.60	11.00	6.50	36.00	15.20	11.00	13.20
12.SBD (m)	17.40	12.60	9.60	8.37	6.00	4.80	11.50	6.50	11.20	9.17	18.28	12.88	10.28	11.94
13.SBV (m.s ⁻¹)	2.51	0.91	2.00	1.03	0.60	2.07	0.72	1.29	1.03	0.54	1.96	1.11	1.12	1.10
14.TOTST (s)	27.60	29.20	22.92	17.62	15.60	9.20	23.01	17.47	22.88	23.16	33.18	29.22	19.82	24.91
15.TOTSD (m)	81.00	28.30	35.40	18.60	9.60	17.06	18.00	20.80	23.80	18.90	55.20	38.20	17.50	26.30
16.EFFCROS (m ⁻¹)	0.60	0.40	1.40	0.00	0.00	3.80	0.40	0.40	0.80	0.00	0.80	0.80	0.00	1.60
17.VERTDIS (cm)	409.5	367	191	223	279.5	297.5	227	263	297	251	202	244	249	243
18.BWIDTH (m)	100	110	88	62	50	30	81	90	120	76	130	106	86	81
19.SLOPE (1:H)	24.4	30.0	46.1	27.8	17.9	10.1	35.7	34.2	40.4	30.3	64.4	43.4	34.5	33.3
20.WATERTABLE (cm)	49.1	43.3	58.7	29.7	12.25	72.2	28.6	31.4	24.8	29.3	25.2	21.2	22	36.6
21.GRAIN SIZE (µm)	285	210	334	247	195	342	232	252	268	220	137	174	170	362
22.GRAIN SIZE (phi)	1.81	2.25	1.58	2.02	2.36	1.55	2.11	1.99	1.90	2.18	2.86	2.52	2.56	1.47
23.GIBBS (cm.s ⁻¹)	3.4001	2.0564	2.719	2.7179	1.4325	4.4395	3.0035	3.356	3.356	2.6538	1.3217	1.9693	1.6392	5.126
24.DEANS	3.63	5.74	5.93	1.74	2.21	0.65	3.80	4.39	3.72	1.39	6.29	3.55	3.07	1.05
25.RTR	0.70	1.14	0.59	1.89	2.58	4.50	0.80	0.89	1.08	3.00	1.90	2.00	2.90	2.35
26.BSI	0.86	1.03	1.02	0.59	0.66	0.32	0.91	0.97	0.92	0.53	1.10	0.61	0.83	0.46
27.TR	136	134	129	134	129	135	152	152	156	138	148	140	151	146
28.EXP	13	13	12	12	10	9	16	15	14	12	8	8	9	14

