The ecological effects of bioturbation on the eelgrass *Zostera capensis*: community interactions and the impacts on the biota of an intertidal sandflat.

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Declaration

This thesis documents original research carried out in the Department of Zoology, University of Cape Town. It has not been submitted in whole, or in part for any other degree at any other University. All of the work presented in this thesis is my own, except where otherwise stated in the text. Any other sources are fully acknowledged.

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Timony–Lee De Vos Siebert

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Date

This thesis is dedicated to my family:

Rob, Penny and Jamie.
You are my inspiration.

And, for Sarah,

Sisters we began,
Best friends we became
Forever two parts of the same whole.

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Abstract

Thalassinidean prawns in the genus *Callianassa* have been singled out as important bioturbators because of their size and activity, and because they often occur at high densities and burrow deep into the sediments. The ecological effects of bioturbation by *Callianassa kraussi* on the eelgrass *Zostera capensis*, and its indirect effects on the sedentary mudprawn *Upogebia africana* and the biota of an intertidal sandflat were assessed at Langebaan Lagoon, South Africa, through comparative surveys, observations and field experiments. I hypothesised that *C. kraussi* and *Z. capensis* have mutually detrimental effects on each other, with bioturbation by *C. kraussi* leading to smothering of *Z. capensis*, and stabilising of sediments by *Z. capensis* impeding burrowing of *C. kraussi*. I also hypothesised that *C. kraussi* would be negatively correlated with *U. africana* because the latter relies on semi–permanent U–tubes to filter–feed, and bioturbation is likely to disrupt these.

Surveys at several sites around the lagoon indicated that *Z. capensis* was negatively correlated with *C. kraussi*. *Z. capensis* was confined to a narrow band on the high shore, whereas *C. kraussi* dominated the intertidal sandflats immediately below the eelgrass beds. *U. africana* was absent or rare in the sandflats and its abundance and distribution closely mirrored those of *Z. capensis*. These patterns were consistent over time and were strongly suggestive of a negative amensal interaction between *C. kraussi* and *Z. capensis* (and *U. africana*). Sediment characteristics mediated the strength of this interaction. *Z. capensis* and *U. africana* were virtually absent at sites where currents and wind–driven distribution of particles led to coarse unstable sediment, and *C. kraussi* extended to the top of the shore under these conditions. Sediment penetrability in the bioturbated sandflats was significantly greater than in the seagrass beds. Cluster analysis of invertebrate communities revealed that sites vegetated by *Zostera capensis* were distinct from unvegetated *Callianassa*–dominated sandflats in terms of both community structure and composition. Contrary to previous research, species diversity and richness were higher in unvegetated sandflats, but the abundance of individuals was greater in the *Zostera* beds. Sandflat species were relatively small in size and most were burrowers. In contrast, *Zostera*–associated species were larger and relatively more were non–burrowing.

Experimental transplants of *Z. capensis* into intertidal sandflats supporting natural densities of *C. kraussi* produced a dramatic deterioration of the seagrass, but in areas where bioturbation was eliminated by defaunation, the seagrass increased in both cover and aerial extent. Densities of *C. kraussi* were initially reduced by the implantation of *Z. capensis*, but this effect was

short–lived. *U. africana* was consistently associated with *Z. capensis* and was common in areas lacking *C. kraussi* but virtually absent in the presence of *C. kraussi*.

The invertebrate assemblages that developed in the different treatments in the transplant experiment were divisible into four or five clusters by similarity analysis and multi–dimensional scaling, determined mainly by their association with seagrass beds or sandflats, and the size of the transplants. The 'indicator species' responsible for differences in community structure and composition were consistent with those identified during the field surveys. Species diversity and richness were not statistically different between *Callianassa*–dominated treatments and those containing *Zostera*, but the abundance of individuals was greater in the *Zostera* beds. The proportion of burrowing species recorded in treatments containing *C. kraussi* was greater than that expected by chance.

Both observational studies and field experiments thus support my primary hypotheses, as evidenced by the following results. (1) *Z. capensis* and *C. kraussi* generally had mutually exclusive zonation patterns. (2) In the absence of *Z. capensis*, *C. kraussi* achieved a larger maximum size and extended to cover the whole of the shore. (3) *U. africana* was consistently associated with *Z. capensis* and rare in areas where C. *kraussi* was dominant. (4) Penetrability of the sediment, sediment flux and suspension all increased in the presence of *C. kraussi* and decreased in the presence *Z. capensis*. (5) *Z. capensis* thrived if transplanted into areas in which bioturbation had been eliminated but diminished if *C. kraussi* was present. Faunal assemblages associated with seagrass beds were distinct from those in bioturbated sandflats. Seagrass beds supported higher densities but lower diversity than the sandflats. As predicted, burrowers were prevalent in sandbanks and non–burrowers in seagrass beds. However, contrary to predictions, hard–bodied large individuals and species were not more abundant in sandflats than in seagrass beds.

Chapter 1

General Introduction

Sheltered shallow-water lagoonal and estuarine soft-sediment communities are often densely populated by benthic fauna and flora. Generally, the distribution and abundance of benthic organisms in soft-bottom habitats are substantially determined by abiotic factors (Kerr & Corfield, 1998). However, more recently, interest has expanded to incorporate the influence of biological determinants (Peterson, 1977; Suchanek, 1983; Flint & Kalke, 1986, Posey, 1987). In particular, interactions among species in soft substrata often involve biological disturbance of the sediment, or bioturbation. Feeding and burrowing activities associated with a variety of bioturbators (e.g. fish, hemichordates, polychaetes, holothurians, crustaceans) can cause substantial sediment disturbance in intertidal habitats (e.g. Rhoads & Young, 1971, Grant, 1983, Berkenbusch *et al*, 2000), with either negative or positive effects on the abundance of associated organisms.

This thesis concerns such biotic interactions in Langebaan Lagoon (33°10'S: 18°5'E) on the West coast of South Africa (Figure 1.1). The lagoon is unusual in being the only one in South Africa that is entirely marine in origin. Having no riverine input except for small quantities of fresh water seepage from rain during the winter months, it consequently has a low silt load and a constant salinity approximating that of seawater (Mazure & Branch, 1979; Christie, 1981). Despite its unique character, however, Langebaan Lagoon has a rich fauna typical of most South African estuaries with open mouths (Day, 1959). The lagoon experiences minimal wave action apart from the channels near the mouth of the lagoon, where tidal movements can reach a velocity of 1m sec^{-1} during spring tides. Approximately half the volume of the lagoon passes though these channels into the bay during these tides, leaving vast areas of intertidal sandflats exposed at low water spring tides (Shannon & Stander, 1977). The intertidal sediments are composed principally of SiO_2 and range from coarse on the exposed beaches to fine, muddy sands at the head of the lagoon (Flemming, 1977 a, b). The mean monthly sea-surface temperatures vary between 19.5°C during the warmest summer months and 14°C during winter (Wynberg & Branch, 1991).

In recognition of its unique attributes, Langebaan Lagoon was proclaimed part of a national park in 1985 and, accordingly, was subdivided into three distinct zones, affording varying degrees of protection for its natural resources. Zone A is a multi-purpose recreational area, in which the use of motorboats, sailboats and windsurfers is permitted, as well as activities such

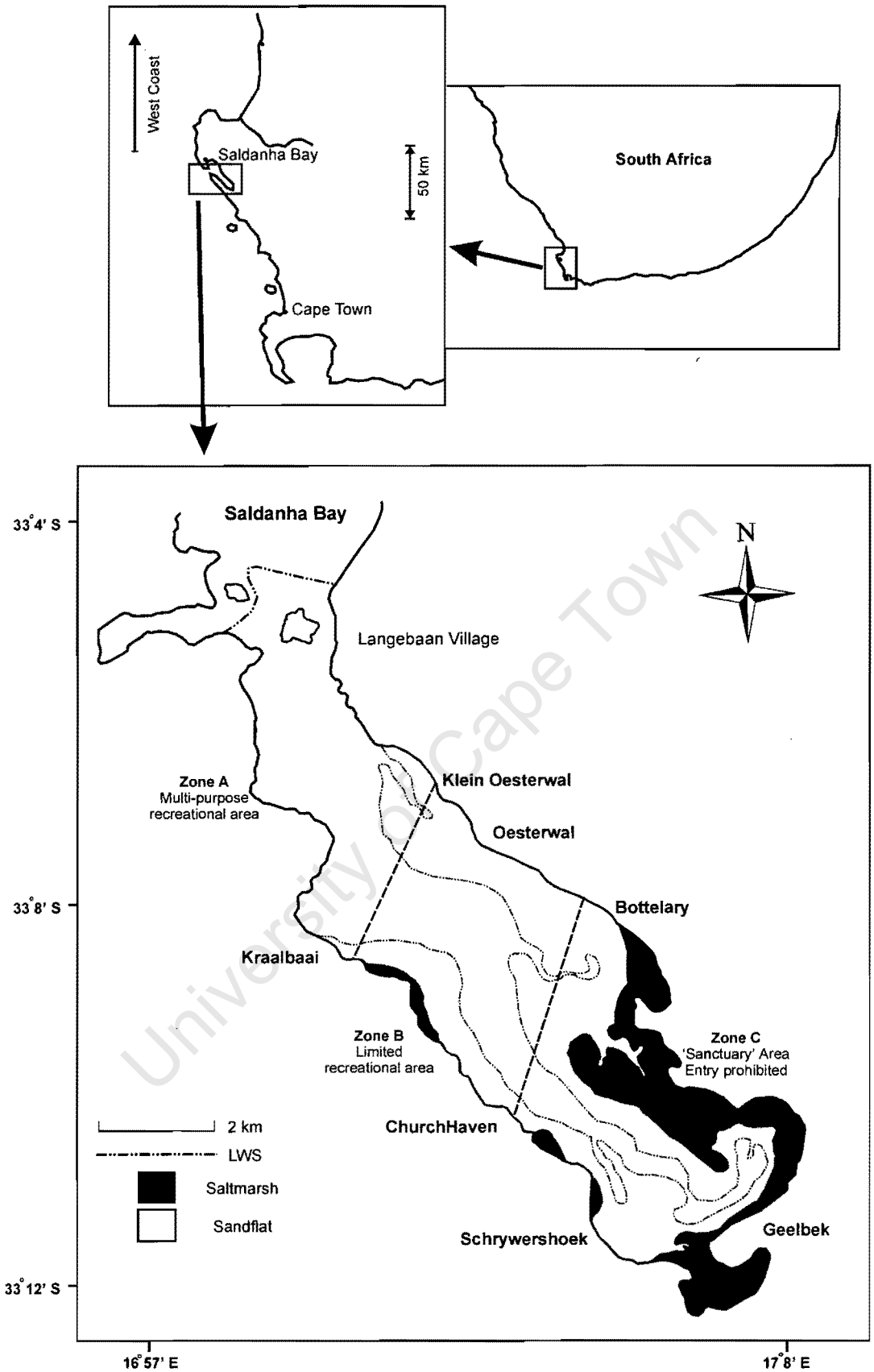


Figure 1.1: Map of Langebaan Lagoon showing park boundaries and sample sites. All seven sites were sampled in 1999. In 2000, surveys were restricted to sites located on the eastern shore of the lagoon but were extended to include stations immediately north and south of two of these of these sites, i.e. Klein Oesterwal and Bottelary.

as water-skiing, rowing, diving, swimming, bait-collecting and angling. Zone B is a limited recreational area, zoned solely for the use of sailboats and windsurfers and excludes extractive harvesting, whereas Zone C is a 'wilderness' area in which entry is prohibited without a permit. In addition to providing sanctuary for the myriad of fauna and flora that inhabits its shores, the lagoon is of international importance as a vital migration route for arctic migrants and, because of this, has been declared a RAMSAR site (sites deemed to be of global significance for wetland bird species). Considering both the uniqueness of this environment and the importance of protecting and preserving marine resources, detecting and understanding patterns in these communities and relating them to ecosystem function is critical, particularly if we are to develop an understanding of changes in community composition due to human influences and rationally plan resource use and conservation (Sink, 2001).

More specifically, this research focused on the interactions between eelgrass *Zostera capensis* Setchell and two species of thalassinidean prawns, the sand prawn *Callianassa kraussi* Stebbing and the mud prawn *Upogebia africana* (Ortmann). All three species are dominant elements within the lagoon, with the thalassinideans alone constituting approximately 48% of the total benthic biomass (Christie & Moldan, 1977). This pattern is not uncommon in other South African estuaries, where the two prawns often form dense beds of over 350 individuals m^{-2} (Hanekom, 1980). Of the burrowing decapod crustaceans, thalassinideans are reported to be among the most extraordinary and proficient diggers (Rodrigues & Hodl, 1990 in Coelho *et al.*, 2000). Aside from a brief pelagic larval stage, most species reside within burrows for the duration of their lives (Griffis & Chavez, 1988) and depend on them for shelter, protection from predators, feeding and reproduction (Coelho *et al.*, 2000). *C. kraussi* is however unusual, in that it lacks a pelagic larval stage (Forbes, 1973).

Among thalassinidean prawns, feeding mechanisms involve either suspension/filter–feeding or deposit/detritus-feeding. Most species specialize in one of these mechanisms, but some utilize both (MacGinitie, 1930; Scott *et al.*, 1988; Rodrigues & Hodl, 1990; Nickel & Atkinson, 1995 in Coelho *et al.*, 2000). Generally, callianassids are primarily deposit-feeders, while upogebiids are filter-feeders. Such differences in feeding habits are commonly related to burrow architecture and burrowing behaviour (Stamhuis *et al.*, 1997 and references therein). Characteristically, deposit-feeders are active burrowers with an architecturally complex burrow system that changes continuously as the sediment is harvested for food. As callianassids burrow, sediment is funnelled into sub–surface galleries, gleaned for organic material and sorted. Grains finer than approximately 1 mm in diameter are then pumped back up to the surface where they are deposited as mounds, while coarser grains are stored in deep chambers >1.5 m below the sediment surface (Suchanek, 1983; Suchanek *et al.*, 1996). In contrast, filter-

feeding *Upogebia* species usually have a simple permanent U-shaped burrow with two surface openings through which they circulate water, filtering out particles in the process (Hill, 1971; Schaefer, 1970; Branch & Branch, 1981; Wynberg & Branch, 1991, 1994). These fundamental differences in feeding methods are reflected in differences in the sedimentary characteristics favoured by the two species, with *C. kraussi* being more common in sandy areas, and *U. africana* favouring finer, muddier sediment (Wynberg & Branch, 1991, 1994 and references therein).

Zostera capensis occurs in the majority of South African estuaries from the Mozambique border in the East to Saldanha Bay in the South West (Edgcumbe, 1980), and fulfils several important functional roles. In addition to their high primary production (McRoy & McMillan, 1977), *Z. capensis* beds provide shelter for a variety of organisms, act as nursery grounds for larval and juvenile fish, are a source of food, either directly for grazers or indirectly for detritus–feeders, and are fundamental in stabilising sediments (Hanekom & Baird, 1988). Furthermore, *Z. capensis* beds may modify hydrodynamics by reducing current flow. Coupled with their complex root-rhizome system, they alter the sedimentary characteristics of the substratum by increasing the proportion of fine-grained particles and thus stabilise the sediment.

Given that Z. *capensis*, *C. kraussi* and *U. africana* all commonly occur in intertidal and shallow subtidal soft substrata and are dominant inhabitants of sheltered lagoonal sandflats and estuarine embayments (Edgcumbe, 1980; Day, 1981a; Wynberg & Branch, 1991, 1994), interactions among them are a likely scenario (Branch, 1984). The central theme of the thesis proposes that the abundance and local distributions of *Z. capensis* and *C. kraussi* will differ due to fundamental differences in their life activities and the way in which they modify their habitats. This follows previous observations that have drawn attention to the incompatibility between sediment stabilisers and destabilisers (e.g. Brenchley, 1982; Suchanek, 1983; Murphy, 1985; Harrison, 1987; Posey, 1987). Whereas *Z. capensis* functions as a sediment stabiliser, *C. kraussi* excavation maintains a soft, unstable substratum. Furthermore, the interaction between these two species is likely to promote or inhibit other species. For example, as a filter-feeder that requires stable U-shaped tubes for filtration, *U. africana* is likely to be favoured by *Z. capensis* but inhibited by *C. kraussi*. Within the lagoon itself, *Z. capensis* tends be prevalent in the upper tidal flats (Flemming, 1977; Day, 1981a) whereas *C. kraussi* dominates the mid-to-low shore, an area characterised by sandy sediment. *U. africana* on the other hand, prefers more muddy situations and occurs in increasing abundance toward the sheltered head of the lagoon.

Apart from interactions between these three central players, *Zostera capensis* and *Callianassa kraussi* are likely to have profound effects on other components of the fauna. It has been well

documented that relative to surrounding unvegetated soft-sediment habitats, seagrass habitats are areas of high productivity and biodiversity (Stoner, 1980; Bostrom & Bonsdorff, 1997). This is predominantly due to the contrast between the structural complexity afforded by eelgrass compared to bare sediments. In addition to a host of other benefits (see Heck & Wetstone, 1977; Fonseca *et al.*, 1983; Lewis, 1984; Orth, 1992; Bowden *et al.*, 2001; Edgar & Barrett, 2002) seagrass beds may indirectly favour species that are detrimentally affected or inhibited by *C. kraussi* bioturbation. Consequently, it can be expected that the macrofaunal assemblages associated with *Z. capensis* will differ markedly in species composition and abundance from those dominated by the deposit-feeding sandprawn *C. kraussi.*

Previous work on sandprawns and mudprawns has highlighted their extensive utilisation for bait (Wynberg & Branch, 1991, 1994). *C. kraussi* is a popular bait organism and is intensely exploited within the lagoon. Harvesting, which is restricted to the outer one-third of the lagoon (Zone A), not only removes prawns but also profoundly disturbs the sediment. In view of this, my research has practical implications. Damage inflicted by bait-collecting is, however, not limited to the extraction of prawns, but causes sedimentary instability and results in burial and consequent suffocation of trapped organisms, and may reduce the density of *Z. capensis* (Wynberg & Branch, 1991, 1994). Given the importance of eelgrass to ecosystem functioning and the diversity of its associated fauna, its depletion could have a multitude of ripple effects. Understanding the patterns underlying *Z. capensis* and *C. kraussi* distributions and how they influence associated faunal assemblages are therefore critical for the management of Langebaan Lagoon as part of the West Coast National Park.

The starting point for understanding the functioning of intertidal ecosystems is the quantitative description of natural patterns. Following this introduction, Chapter 2 uses correlative data to explore the distribution patterns of *C. kraussi*, *U. africana* and *Z. capensis* in Langebaan Lagoon. By the nature of its aims, this chapter is observational and pragmatic and tests the hypotheses that there should be negative associations between *C. kraussi* and *Z. capensis*, and between *C. kraussi* and *U. africana*, but that a positive association should exist between *Z. capensis* and *U. africana.*

Chapter 3 also employs an observational approach, and examines the degree to which macrofaunal community structure differs between areas dominated by *C. kraussi* and *Z. capensis* respectively. More specifically, it tests hypotheses originally advanced by Brenchley (1982). She argued that areas dominated by eelgrass are likely to support species that are small, flexible and non-burrowing, compared to those in bioturbated areas where most species can be expected to be larger, relatively inflexible and mostly burrowers.

Chapter 4 is a departure of approach, and adopts experimental manipulations to more precisely test hypotheses advanced in Chapters 2 and 3. It involves an experiment in which *Z. capensis* was transplanted into areas dominated by *C. kraussi*. In some of these areas, bioturbation was allowed to continue unchecked, but in others it was terminated by removing the infauna. In this way, the survival and development of *Z. capensis* was tested in the presence or absence of bioturbation. In Chapter 5, this same experiment was used to examine the types of faunal communities that develop under these conditions, and whether they conform to Brenchley's hypotheses.

Finally, Chapter 6 consolidates the above aspects and concludes with a brief synthesis that overviews the thesis and its findings.

Chapter 2

Field surveys of the distribution patterns of *Zostera capensis, Upogebia africana* and *Callianassa kraussi.*

2.1 Introduction

Detection of patterns in community organisation, the identification of dominant forces that underlie these patterns, and the application of theories developed from these studies are often major goals in the study of an ecological community (Flint & Kalke, 1986). Given the complexity of most ecological systems, however, the identification of causative mechanisms influencing community organisation is extremely difficult. Often, community patterns are the result of a variety of responses to spatial or temporal physical changes in the environment (e.g. hydrodynamics, sedimentation, erosion), biological processes (e.g. recruitment, predation, bioturbation) or the interactions of such processes (Dahlgren *et al.*, 1999).

One important mechanism that has been frequently implicated in maintaining the structural complexity of soft-bottom communities is biological disturbance (e.g. Thistle, 1981; Woodin, 1981). Probert (1984) maintains that wherever physical processes such as wave action or tidal currents are not too rigorous or are intermittent, biologically–induced modifications to the sediment-water interface assume considerable importance. Under these conditions, the structure of the benthic communities is often defined by the dynamic inter-relationships between the sedimentary requirements of some species and the changes to the sediment effected by others.

The biological implications of sediment disturbance by bioturbation have been well documented and include both negative and positive effects on the abundance of associated organisms (Peterson, 1977; Suchanek, 1983; De Witt & Levinton, 1985; Townsend & Fonseca, 1998; Berkenbusch *et al.*, 2000). Amongst other effects, bioturbation may exclude certain groups of organisms (Rhoads & Young, 1970), modify the transport of sediment (Jumars & Nowell, 1985), alter its geochemistry (Aller *et al.*, 1983) and increase mineralization and oxygenation (Kristensen *et al.*, 1985). It also has diverse effects on microalgae, microfauna and meiofauna (Koike & Mukai, 1983; Bell & Woodin, 1984; Probert, 1984; Alongi, 1985, Branch & Pringle, 1987). Further research into bioturbation has shown that it may exclude seagrasses and algae or reduce their productivity (Brenchley, 1981; Suchanek, 1983; Posey, 1986) as well as severely affecting the complex assemblage of species that depends either directly or indirectly on seagrass (Suchanek, 1983).

The intertidal sand flats of Langebaan Lagoon are dominated by two thalassinidean prawns, *Callianassa kraussi* and *Upogebia africana*, together constituting approximately 48 % of the total benthic biomass of the lagoon (Christie & Moldan, 1977). Both species have been recognized as 'pioneer' species, which are described by Virnstein (1977) as species that are much more important than others in their ability to control and structure the community (Wynberg & Branch, 1991, 1994). Due to their high population densities and relatively deep burrows, callianassid prawns have been identified as important infaunal bioturbators probably having greater effects over a larger depth range than any other species (Berkenbusch *et al.*, 2000). Rates of sediment reworking for *C. kraussi* have been estimated at 12.14 $kg.m^{-2}.day^{-1}$ (Branch & Pringle, 1987), a figure considerably higher than that proposed for other *Callianassa* species (Aller & Dodge, 1974; Suchanek, 1983). *C. kraussi* burrows continuously, digging deep burrows down to ~1 m, deposit-feeding on the sediment and thus effecting constant turnover of the sediment. *U. africana* on the other hand, creates shallower (~30 cm) U-shaped burrows that are semi-permanent and through which it circulates water to filter–feed. Consequently, *C. kraussi* is responsible for massive bioturbation and requires loose sediments for its burrows, whereas *U. africana* requires stable sediments and probably causes little bioturbation (Wynberg & Branch, 1994).

Given these differences in behaviour and feeding mode of *C. kraussi* and *U. africana*, rates of sediment reworking should be notably higher for *C. kraussi* than for *U. africana*. Although there has been no conclusive work conducted on the bioturbating effects of *U. africana*, logic dictates that sediment processing by this prawn will be minimal, and any associated effects considerably less than those of *C. kraussi* (Wynberg & Branch, 1991). Indeed, as the burrows of species such as *U. africana* function as semi-permanent dwelling structures, they probably promote sediment stability rather than disturb it (Probert, 1984). In addition, bioturbation by deposit-feeding macrofauna is commonly reported to have an inhibitory effect on suspension feeders by disrupting their burrows or smothering their filtration apparatus (Rhoads & Young, 1970; Aller & Dodge, 1974). As such, *C. kraussi* may restrict or even exclude *U. africana* altogether.

In Langebaan Lagoon, *U. africana* co-exists with the eelgrass *Zostera capensis*. Day (1959) describes how *Z. capensis* beds are frequently colonized by *U. africana* and that *U. africana* seems to have a negligible effect and influence on the condition of the eelgrass and its associated fauna, unlike *C. kraussi*. Indeed, the stability offered by *Z. capensis* may enhance the burrowing and feeding activities of *U. africana* by affording the prawn protection against structural damage of its burrows by *C. kraussi* bioturbation. *Z. capensis* is prevalent in the sheltered intertidal flats of the lagoon in situations characterised by weaker tidal exchange, low wave action and a

substratum of fine sand mixed with varying quantities of silt. Under these conditions, the impact of *C. kraussi* bioturbation may be exaggerated and may even compel the cohabitation of *U. africana* with *Z. capensis*.

With reference to the detrimental effect of bioturbation on seagrasses (Brenchley, 1981; Suchanek, 1983; Posey, 1986) it is likely that *C. kraussi* bioturbation may influence the distribution of *Z. capensis*. Consequently, the stage is set for a dynamic interplay between various ecological processes within the soft-bottom environment of Langebaan Lagoon, and presents an opportunity to test the effect of biological disturbance by *C. kraussi* and stabilisation by Z. *capensis* on intertidal community structure.

The objective of this part of my study was to use correlative data to determine the patterns of distribution and abundance of *C. kraussi*, *U. africana* and *Z. capensis* in Langebaan Lagoon. Specifically, surveys were undertaken to test following hypotheses:

1. *Z. capensis* is positively correlated with *U. africana*
2. *Z. capensis* is negatively correlated with *C. kraussi*
3. *C. kraussi* is negatively correlated with *U. africana*

Experimental manipulations to investigate underlying causes of the observed patterns are described in later chapters.

2.2 Methods

2.2.1 *Intertidal Transects*

Quantitative sampling of the density and distribution of *Callianassa kraussi*, *Upogebia africana* and *Zostera capensis* was undertaken at seven sites spanning both the eastern and western banks of the lagoon, namely Klein Oesterwal, Oesterwal, Bottelary, Geelbek, ChurchHaven, Schrywershoek and Kraalbaai (Figure 1.1). Samples were taken in April 1999 and traversed the entire intertidal range of each species.

Estimates of prawn densities were determined from counts of the holes created by *C. kraussi* and *U. africana*. At each site, holes were counted in triplicate 0.25m^2 quadrats at 10-m intervals between the levels of high water spring tides and low water spring tides along transects perpendicular to the shore. The triplicate samples were taken on the transect line and five meters on either side of it, resulting in three independent replicates along the transect line. Transects varied from 70-440 m in length depending on the slope of the shore. Prawn holes

were considered to represent 1:1 holes per adult *C. kraussi* and 2:1 holes per adult *U. africana* (Forbes, 1973 and Wynberg, 1991). Identity of the species creating the holes was confirmed by digging. *Z. capensis* abundance was assessed by estimations of percentage cover in all quadrats.

2.2.2 *Prawn sizes*

Two samples of 25 X 25 cm X 30 cm deep were taken in both eelgrass beds and outside the beds at each site that harboured *Z. capensis*. These were sieved through 1-mm mesh sieves and the total body lengths of all prawns measured to the nearest mm. Sizes were compared between sites and habitats by analysing the maximum size in each sample.

2.2.3 *Frontier Zone Transects*

Following initial observations based on the above sampling techniques, it became evident that a zone existed immediately below the *Z. capensis* bed where above-ground seagrass was absent, but below-ground rhizomes appeared to have an effect on the abundance of the two prawns. I termed this the 'frontier zone'. This appears to be a transitional zone between the *Z. capensis-U. africana* domination in the high shore and *C. kraussi* domination lower down. I hypothesised that an approximately 1-m wide area below the *Z. capensis* bed contains a high residual below-ground root-rhizome network. This may provide an obstruction to bioturbation by *C. kraussi* and, if it excludes *C. kraussi*, may constitute a buffer zone between the dense high–shore *Z. capensis* beds and the sandflats occupied by high densities of *C. kraussi*. More detailed examination of this zone was undertaken during low spring tides in April 2000, and was limited to five sites on the eastern bank of the lagoon where all three species were present: Klein-Oesterwal South, Klein-Oesterwal North, Oesterwal, Bottelary South and Bottelary North (Figure 1.1).

For this purpose, prawn densities were again determined through hole counts. Holes were counted in triplicate 0.1m^2 quadrats at 1-m intervals beginning 3 m above the *Z. capensis* bed on the high shore and ending 10 m below the *Z. capensis* bed, along linear transects at each of five sampling sites. Three replicate samples were taken approximately 5 m apart. Transects varied from 16-30 m in length depending on the width of the *Z. capensis* bed and the slope of the shore. In quadrats containing high *Z. capensis* cover, a spade was used to lift the *Z. capensis* to expose prawn holes to facilitate counting. This allowed more accurate hole counts as dense *Z. capensis* beds obscure holes, making surface counts difficult. Species identification of the prawns in the quadrats was verified by sucking up five 10-cm diameter sediment cores with a prawn pump and sieving them through a 2–mm sieve. Prawn sucks occurred at 2-m intervals along the transect.

Z. capensis distribution and biomass were determined by scoring the percentage cover and measuring the wet weight of the above-ground and below-ground plant biomass. Above-ground *Z. capensis* biomass was sampled by cutting surface shoots at ground level, rinsing, blotting and wet-weighing them to 0.01g accuracy. Once the above-ground biomass had been collected, the sediment below was removed using a 10 X 20 cm sediment corer dug down to 30 cm depth. The sediment core was sieved through a 2 mm sieve and all below-ground *Z. capensis* root-rhizome biomass and debris retained and wet weighed. The percentage cover and above-ground *Z. capensis* biomass were tightly correlated ($r > 0.9$, $p < 0.001$) for all sites except Bottelary North ($r = 0.64$, $p < 0.001$). In view of this close correlation, the data are presented as biomass values rather than percentage cover so that above and below-ground values can be compared.

2.2.4 *Statistical Analysis*

Levene's test and Kolmogorov-Smirnov one sample test were employed to test data for normality and homogeneity of variances (alpha set at 0.05). When possible, heteroscedastic data were transformed to achieve equality of variance. When this could not be achieved, nonparametric statistical tests were applied. Differences in the densities of *C. kraussi* and *U. africana* between samples that possessed or lacked *Z. capensis* were assessed using a Mann Whitney U test (Zar, 1984); for cases where $n > 2$, a Kruskal-Wallis ANOVA by ranks was applied. Sizes of prawns were compared by Two-Way ANOVA with sites as a random factor and habitat (*Zostera vs.* Non-*Zostera)* as a fixed factor. Relationships among *Z. capensis*, *C. kraussi* and *U. africana* were examined through regression analyses. When relationships were non-linear and included zero values, a constant value of 1 was added to all values to establish the regression equations and coefficients of determination. For all analyses, the replicate samples from each transect were pooled. This was necessary as *Z. capensis* is patchily distributed and occurs in narrow bands around the lagoon, resulting in an unbalanced and diminutive sample size in some cases. Statistical analyses were conducted using StatSoft, Inc. (2000) STATISTICA version 6 for Windows.

2.3 Results

The densities and distributions of *C. kraussi*, *U. africana* and *Z. capensis* on the transects covering the whole of the intertidal zone are presented in Figure 2.1. At sites lacking *Z. capensis*, *U. africana* was absent or very scarce, and *C. kraussi* extended throughout the intertidal zone. Where all three species were present, their abundances were clearly inter-related. Cover of *Z. capensis* and densities of *U. africana* were greater in the high shore, with high densities of *U. africana* confined to the *Z. capensis* beds or immediately below them.

Conversely, *C. kraussi* was present in highest densities, and largely confined to, the open sandflat of the low shore below the *Z. capensis* bed.

2.3.1 *Relationships between Z. capensis and U. africana*

A comparison of the mean densities of *U. africana* at all seven sites is given in Figure 2.2 A. Higher densities of *U. africana* were found within the *Z. capensis* bed vs. outside at Klein Oesterwal, Oesterwal and Bottelary. At Geelbek, noticeably higher densities of the prawn were found outside the *Z. capensis* bed. Schrywershoek, ChurchHaven and Kraalbaai were characterised by very low densities of *U. africana* (0.47 per $0.25m^2$ ± 0.26 SE). Comparisons between the densities of *U. africana* revealed significant differences within the *Z. capensis* bed versus outside at Klein Oesterwal, Oesterwal, Bottelary and Geelbek (Mann-Whitney U tests; Table 2.1). No such comparisons could be made at Schrywershoek, ChurchHaven and Kraalbaai because *Z. capensis* did not occur at there.

Table 2.1: Mann-Whitney U tests comparing *C. kraussi* and *U. africana* densities within and outside *Z. capensis* beds at each site that possessed seagrass beds. The U-statistic is accompanied by a Z value (normal distribution variate value) because when n>20, the sampling distribution of the U-statistic approaches the normal distribution (see Siegel, 1956).

	Mann- Whitney U			
Upogebia africana	**U**	**Z**	**p-level**	
Klein Oesterwal	0	-5.592	<0.0001	Significant
Oesterwal	0	-4.076	<0.0001	Significant
Bottelary	95.5	-3.446	0.0006	Significant
Geelbek	155.5	-4.84	<0.0001	Significant
Callianassa kraussi	**U**	**Z**	**p-level**	
Klein Oesterwal	259.5	2.499	0.01	Significant
Oesterwal	75.5	3.239	0.001	Significant
Bottelary	67.5	3.737	0.0002	Significant
Geelbek	46	-6. 223	<0.0001	Significant

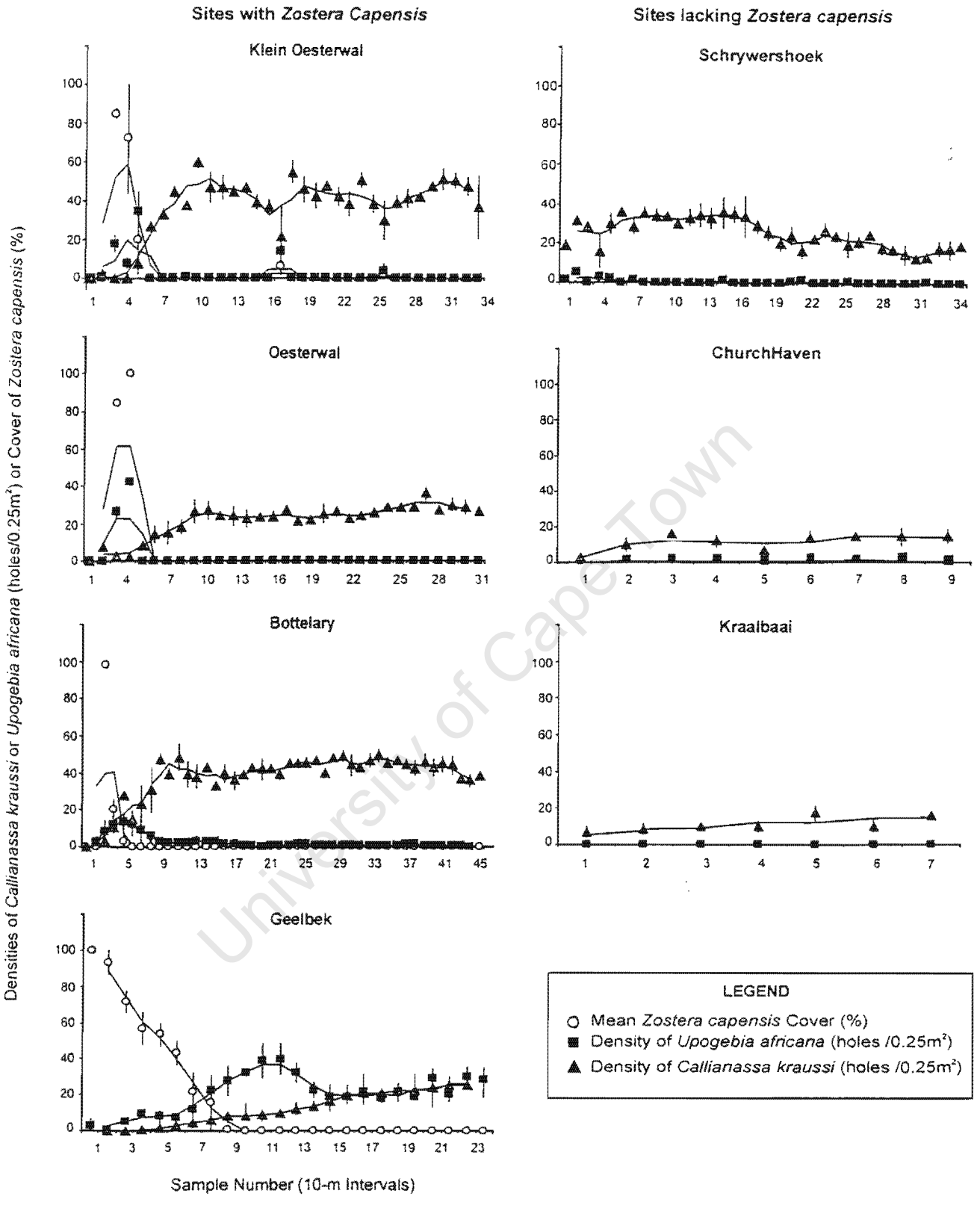


Figure 2.1: Densities (± SE) of *Callianassa kraussi*, *Upogebia africana* and *Zostera capensis* at seven sites in Langebaan Lagoon. Sites are representative of four areas where *Z. capensis* was present and three where it was absent. The running means show the trends and the individual data points were recorded at 10-m intervals.

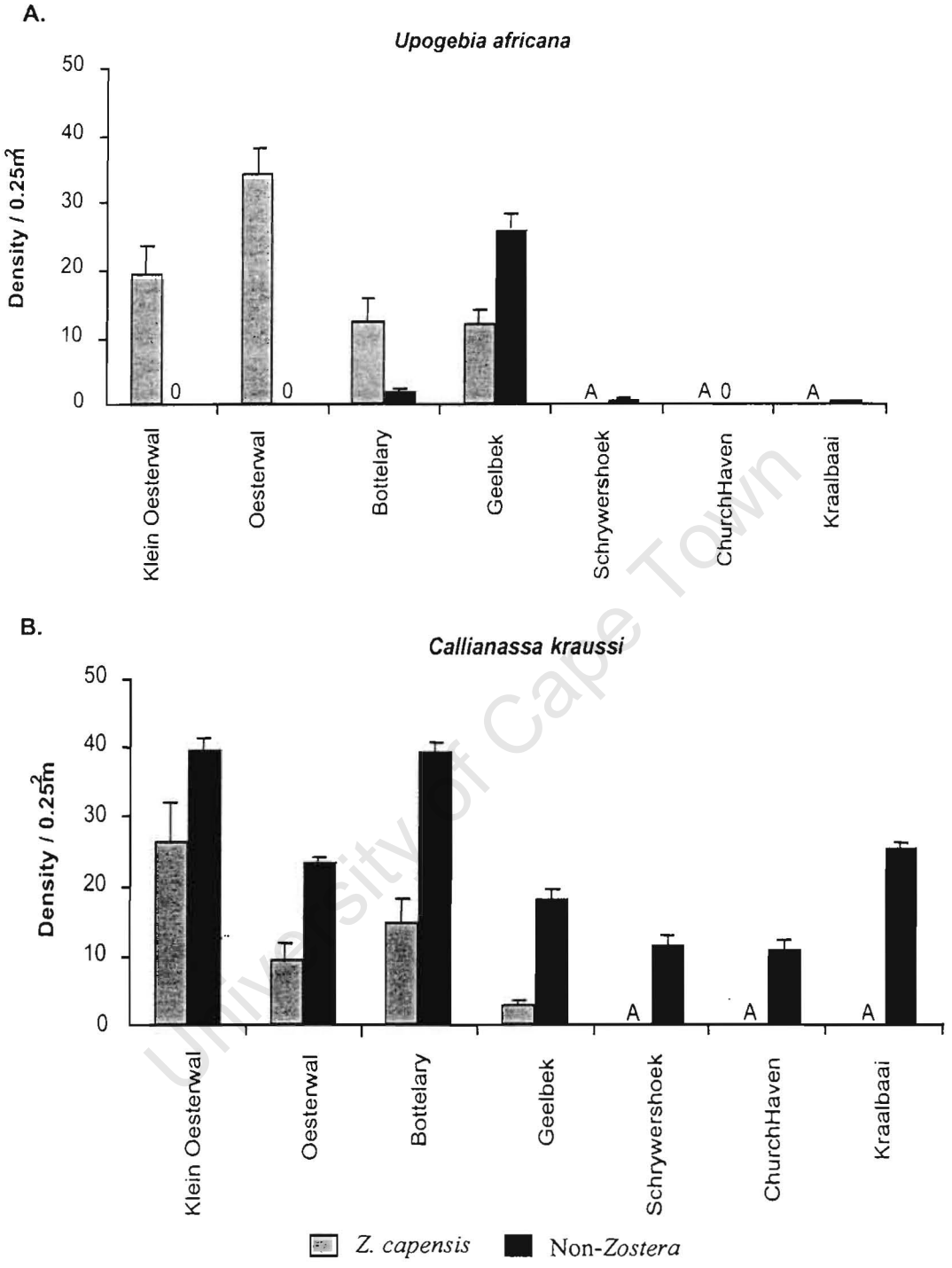


Figure 2.2: Comparison of the densities of *Upogebia africana* (A) and *Callianassa kraussi* (B) within and outside *Zostera capensis*. *U. africana* occurs in higher densities within the *Z. capensis* bed whereas the reverse is true of *C. kraussi*. 0= absence of species from a particular habitat; A= absence of *Z. capensis* beds at the last three sites.

2.3.2 *Relationships between Z. capensis and C. kraussi*

Figure 2.2 B shows that *C. kraussi* occurred at all seven sites and that its densities at the three sites lacking *Z. capensis* were substantially higher than those of *U. africana*. At the remaining sites, densities of *C. kraussi* were always significantly higher outside the eelgrass beds than inside.

2.3.3 *Relationships among species*

Regressions between *U. africana* and *C. kraussi*, *C. kraussi* and *Z. capensis,* and *U. africana* and *Z. capensis* were limited to the sites at which all three species co-occurred and showed consistent patterns between the species at all sites except Geelbek (Figure 2.3). At Klein Oesterwal, Oesterwal and Bottelary there were negative relationships between *U. africana* and *C. kraussi* and between *C. kraussi* and *Z. capensis,* whereas *U. africana* and *Z. capensis* were positively or parabolically related, thus supporting my hypotheses. In contrast, Geelbek revealed a parabolic relationship between *U. africana* and *C. kraussi,* and both *C. kraussi* and *U. africana* were negatively related to *Z. capensis*. Although the negative relationship between *C. kraussi* and *Z. capensis* at Geelbek was consistent with the pattern at the other sampling sites, *U. africana* was not limited in its distribution to *Z. capensis* or restricted by *C. kraussi* at this site.

2.3.4 *Prawn Size*

The maximum lengths of *C. kraussi* and *U. africana* sampled within and outside the *Z. capensis* bed at Klein Oesterwal, Oesterwal, Bottelary and Geelbek were compared among sites and between habitats. Geelbek was eliminated from the statistical analysis due to an incomplete data set. Figure 2.4 illustrates the clear differences in the mean maximum lengths of both *C. kraussi* and *U. africana* between habitats. *C. kraussi* was significantly smaller within the *Z. capensis* bed than in the sandflats, whereas the reverse was true for *U. africana* (Table 2.2). There was no significant effect of site, or the interaction between site and habitat.

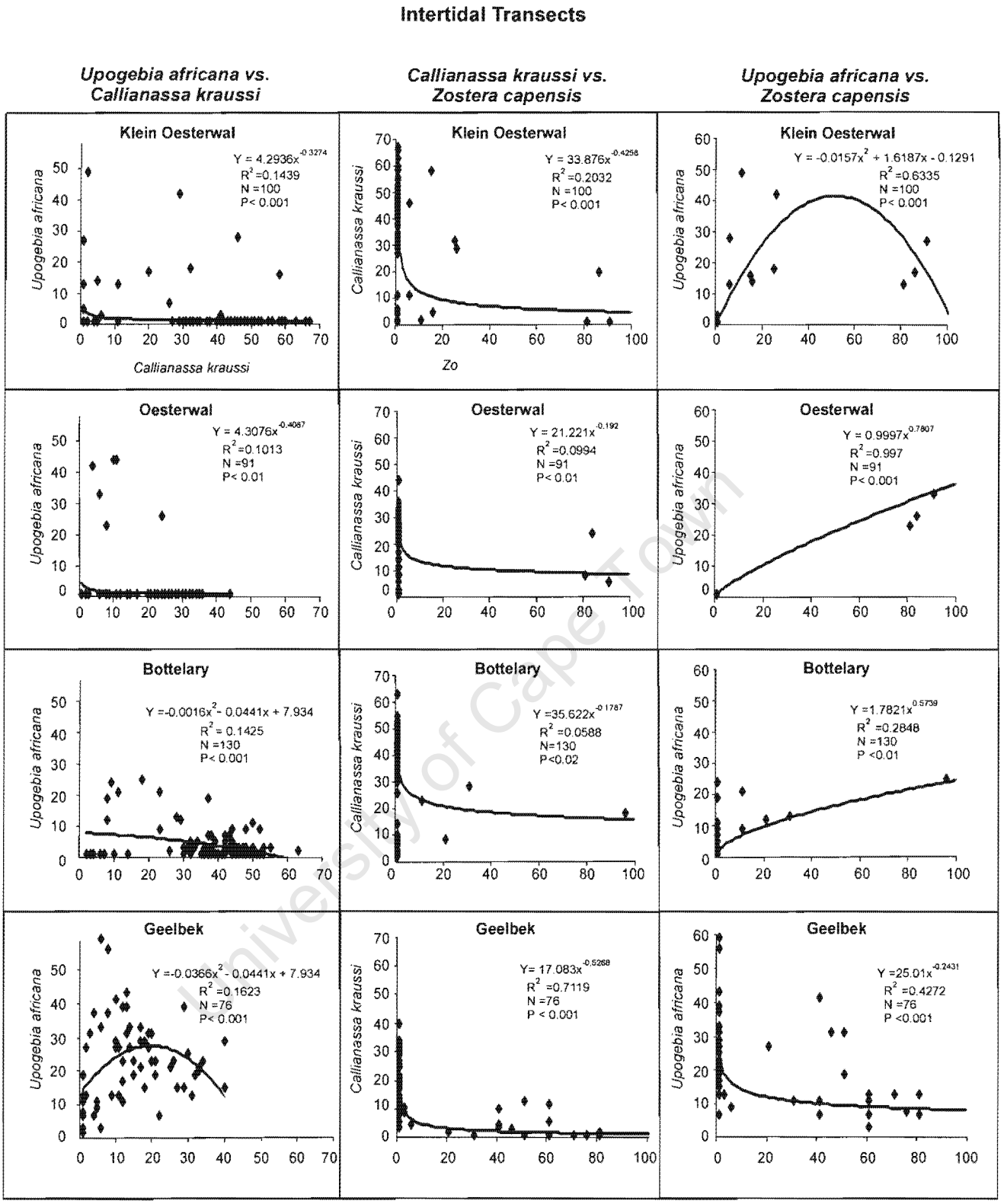


Figure 2.3: Regression analyses performed on the relationships between the abundance of *Upogebia africana* and *Callianassa kraussi* (densities of holes per 0.25m^2) and *Zostera capensis* (percentage cover), as evident from intertidal transect data obtained in April 1999.

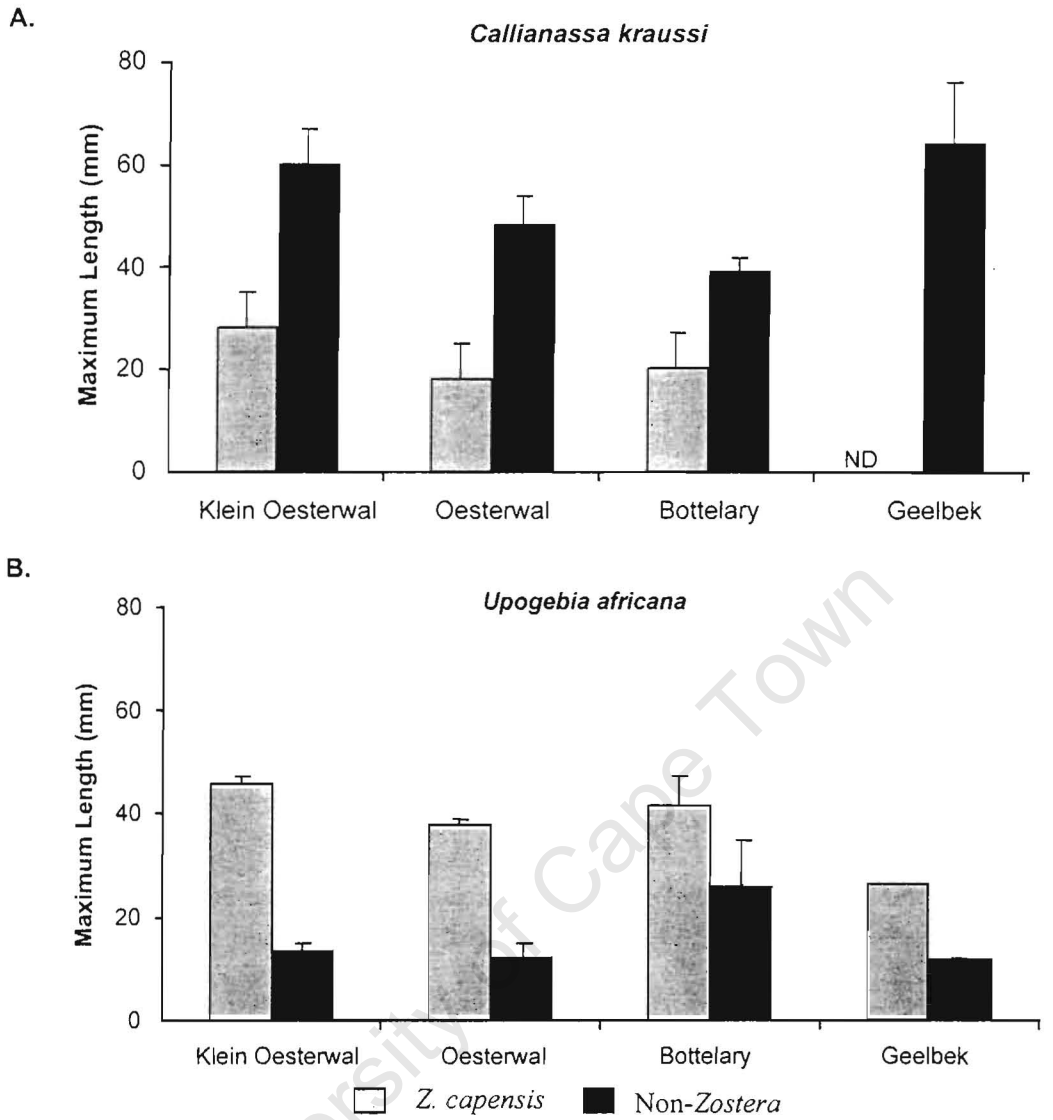


Figure 2.4: Differences in maximum sizes (+ SE) of *Callianassa kraussi* (A) and *Upogebia africana* (B) within and outside *Zostera capensis*. ND indicates no data.

Table 2.2: Results of a two-way ANOVA testing for differences in sizes of prawns among sites (n=3) and habitats (n=2).

		Two-Way ANOVA			
Upogebia africana	**df effect**	**MS effect**	**F**	**p- level**	
Site	2	76.58	1.97	0.219	Not Significant
Habitat	1	1825.33	47.00	0.0004	Significant
Site x Habitat	2	68.58	1.76	0.249	Not Significant
Callianassa kraussi	**df effect**	**MS effect**	**F**	**p- level**	
Site	2	229.0	3.34	0.105	Not Significant
Habitat	1	2187.00	31.92	0.001	Significant
Site x Habitat	2	49	0.71	0.526	Not Significant

2.3.5 *Frontier Zone*

A more detailed analysis of the relationships between *C. kraussi*, *U. africana* and *Z. capensis* including the 'frontier' zone was undertaken using transects that covered the eelgrass bed at 1-m intervals and extended 10–m below them (Figure 2.5). The samples were divided into four categories based on habitat: above the *Z. capensis* bed, within *Z. capensis*, within the frontier zone and below the frontier zone.

2.3.6 *Relationships between Z. capensis and U. africana*

The abundance of *Z. capensis* (represented by above-ground and below-ground biomass) and the densities of *U. africana* were closely associated at all sites (Figure 2.5). In the extreme high-shore, both species were either absent or scarce. High densities of *U. africana* coincided with high biomass of *Z. capensis*, creating a clearly delineated zone along the transects. *U. africana* was most abundant in the 'within *Z. capensis*' zone, extending downwards into the 'frontier zone'. Above-ground *Z. capensis* biomass was limited to the 'within *Z. capensis*' zone but below-ground biomass extended below the lower edge of the *Z. capensis* bed into the 'frontier zone'. A Kruskal-Wallis ANOVA by ranks showed significant differences when comparing *U. africana* densities between zones ($H = 140.104$, $df = 3$, $n = 307$, $p < 0.001$), and post-hoc Tukey-type tests (Zar, 1984) confirmed that the frequency of distribution of *U. africana* was significantly different between all four habitats (Table 2.3).

Table 2.3: Results of a post-hoc Tukey-type test for Kruskal-Wallis ANOVA by Ranks (Zar, 1984) comparing *U. africana* and *C. kraussi* densities between zones.

Post-Hoc Tukey Type Test for Kruskal-Wallis ANOVA by Ranks					
***U. africana* Comparisons**	**SE**	**Difference In Mean Ranks**	**Q**	**Qstat p= 0.05**	
Above *Z. capensis vs.* Within Z. capensis	7.726	142.425	18.434	2.639	Significant
Above *Z. capensis vs.* Within Frontier	5.178	171.352	33.091	2.639	Significant
Above *Z. capensis vs.* Below Frontier	8.761	45.147	5.153	2.639	Significant
Within *Z. capensis vs.* Frontier	8.458	28.927	3.420	2.639	Significant
Within *Z. capensis vs.* Below Frontier	8.943	- 97.278	- 10.878	2.639	Significant
Frontier *vs.* Below Frontier	9.967	- 126.204	- 136.171	2.639	Significant
***C. kraussi* Comparisons**	**SE**	**Difference In Mean Ranks**	**Q**	**Qstat p= 0.05**	
Above *Z. capensis vs.* Within Z. capensis	7.687	- 15.248	- 1.984	2.639	Not Significant
Above *Z. capensis vs.* Within Frontier	5.178	82.453	15.923	2.639	Significant
Above *Z. capensis vs.* Below Frontier	8.802	139.413	15.839	2.639	Significant
Within *Z. capensis vs.* Frontier	8.400	97.700	11.631	2.639	Significant
Within *Z. capensis vs.* Below Frontier	8.951	154.661	17.278	2.639	Significant
Frontier *vs.* Below Frontier	10.025	56.960	5.682	2.639	Significant

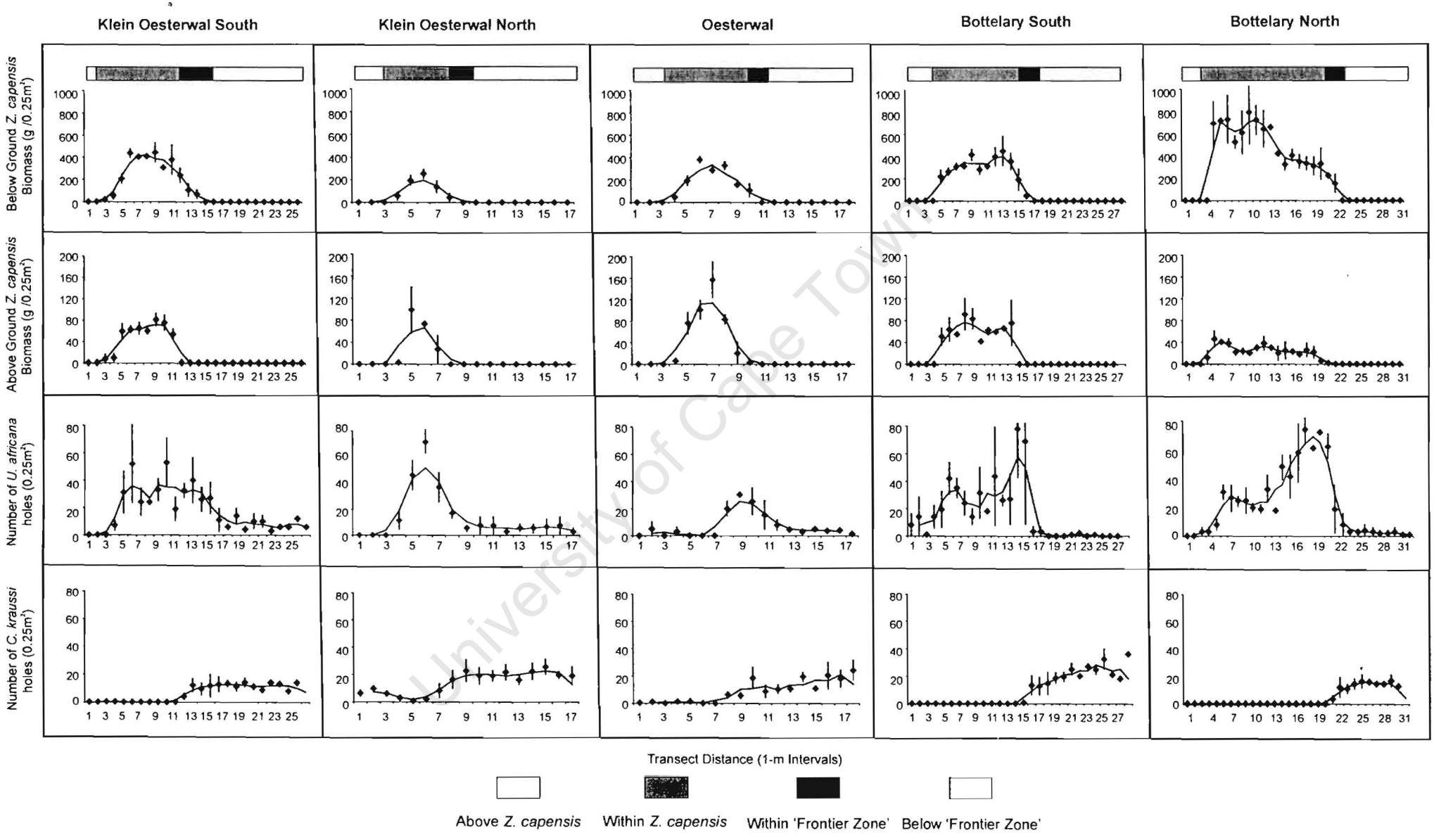


Figure 2.5: Mean densities of *C. kraussi*, *U. africana* and biomass of *Z. capensis* (± SE) along intertidal transects obtained at five sites. Samples were taken at 1-m intervals. The shaded bands delineate the four identified zones.

2.3.7 *Relationships between Z. capensis and C. kraussi*

C. kraussi was more abundant in the low shore, with a sudden increase in density from the lower edge of the frontier zone downwards (Figure 2.5). Highest densities were associated with an absence of above or below-ground *Z. capensis*. Low densities occurred in the 'frontier zone' but *C. kraussi* was even less abundant or absent from the 'within *Z. capensis*' zone and above the *Z. capensis* bed. A Kruskal Wallis ANOVA by ranks showed a significant difference in the density of *C. kraussi* between the four identified zones ($H = 220.1$, $df = 3$, $n = 3$, $p < 0.001$); post-hoc Tukey-type analyses (Zar, 1984) showed that only the 'above *Z. capensis*' versus 'within *Z. capensis*' habitats were not significantly different (Table 2.3).

2.3.8 *Relationships among Species*

Densities of *C. kraussi* and *U. africana* were regressed against above-ground *Z. capensis* biomass, below-ground *Z. capensis* biomass and against each other. Two general trends emerged. First, there was a positive association between *Z. capensis* and *U. africana.* Second, both species were negatively associated with *C. kraussi.* These relationships were consistent over all sites (Figure 2.6). Regressions of *U. africana* against *Z. capensis* (both above and below-ground biomass) depicted a positive and strongly significant relationship at all sites ($p < 0.001$) except for Oesterwal, where the relationship between *U. africana* and above-ground *Z. capensis* biomass was still positive but less significant ($p < 0.05$). The inverse occurred with the regression of *C. kraussi* densities and *Z. capensis* biomass. For both above-ground and below-ground *Z. capensis* biomass, *C. kraussi* showed a significant negative relationship at all sites ($p < 0.05$ in all cases). The regression analyses between *U. africana* densities and *C. kraussi* revealed significant negative relationships ($p < 0.01$) at all sites except Oesterwal.

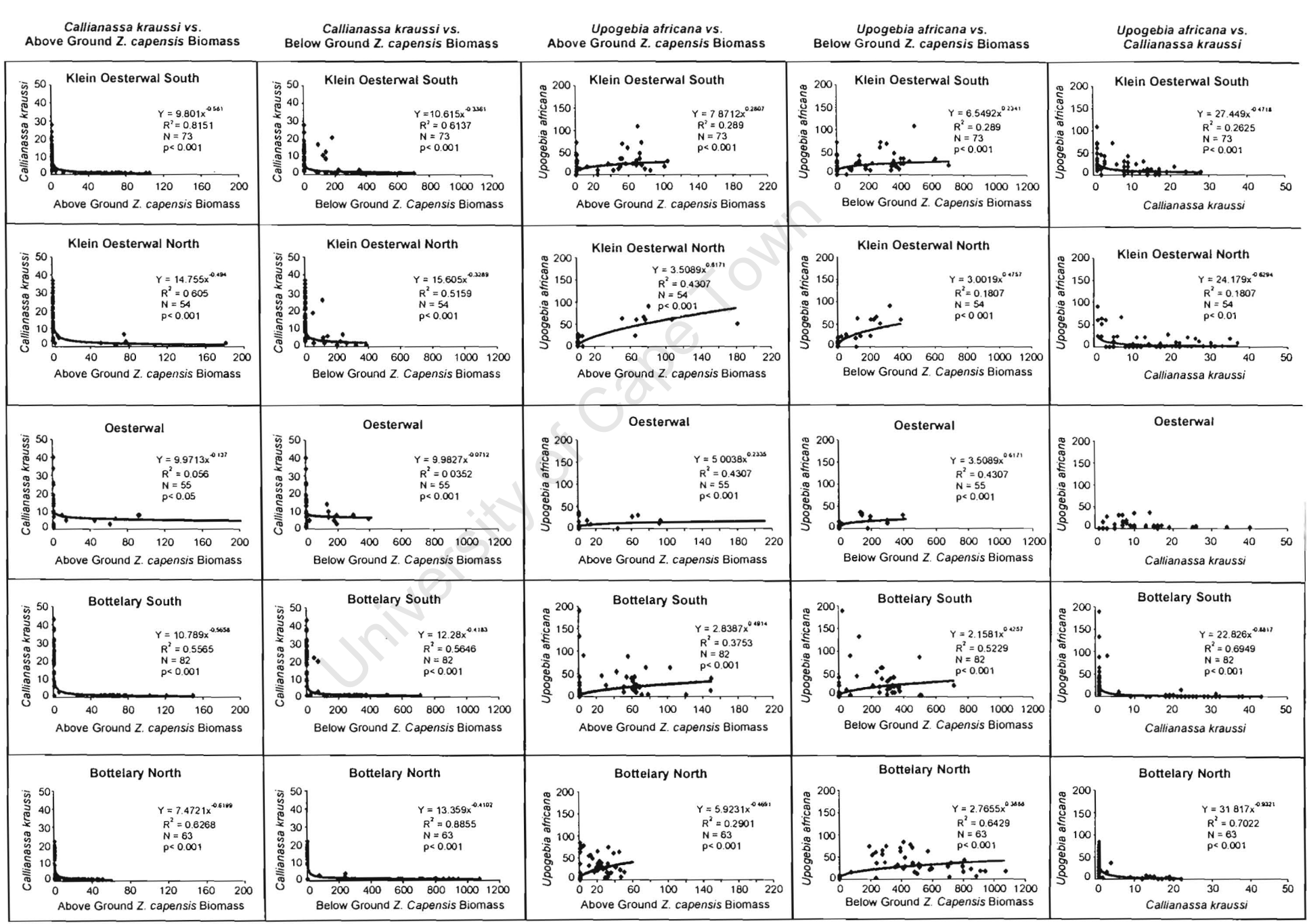


Figure 2.6: Regression analyses performed on the relationships between the abundance of *Upogebia africana* and *Callianassa kraussi* (densities of holes per 0.25m^2) and *Zostera capensis* (above and below ground biomass per 0.25m^2), as evident from intertidal transect data obtained in April 2000.

2.4 Discussion

A primary concern of ecology is to determine why different areas support different densities of species (Heck & Wetstone, 1977). The distribution, zonation and abundance of species are most often influenced by a complex web of interactions between physical environmental forces and biological interactions. *Z. capensis*, *U. africana* and *C. kraussi* are certainly influenced by a suite of abiotic factors, including vertical height on the shore and particle size, but bioturbation and sediment stabilisation appear to be important structuring forces that have resulted in a dynamic inter-relationship between these species.

Z. capensis is patchily distributed within the lagoon, reaching its greatest abundances high on the shore in sheltered areas where relative energy levels are low and fine sediments accumulate (Flemming, 1977; Day, 1981a). Consequently, *Z. capensis* predominates along the south-eastern shore (Klein Oesterwal to Geelbek) and is absent along the western shore and around the mouth of the lagoon where tidal velocities are high, generating current ripples and coarse-grained sediment (Flemming, 1977). The eelgrass is limited to narrow bands in the upper intertidal flats, at about the high neap tidal level. The upper limit of the *Z. capensis* bed is probably determined by desiccation, as evidenced by stunted leaf growth (Talbot & Bate, 1987), whereas the lower limit of its distribution seems to be influenced by disturbances resulting from the activities of *C. kraussi*, which occurs at high densities from immediately below the eelgrass beds, extending downwards to a depth of at least 2–m into the subtidal zone.

In close association with *Z. capensis*, *U. africana* exhibits a similar distribution pattern to the eelgrass. It is common in areas in the lagoon characterised by fine, stable sediment and occurs in higher abundances in areas colonised by *Z. capensis*. Although maximum densities occur between high neap and high spring tide it less commonly occurs far below the *Z. capensis* bed, down to about mid-tide (Day, 1981a). This is substantiated by the transect data, as very low densities of *U. africana* (0.47 ± 0.26 SE) were recorded at Schrywershoek, ChurchHaven and Kraalbaai, sites characterised by a lack of *Z. capensis* and by coarse-grained sediment (Flemming, 1977). At most of the sites that possessed *Z. capensis*, *U. africana* was largely confined to the eelgrass beds. The exception was Geelbek, where *U. africana* extended throughout the intertidal zone and reached highest densities below the eelgrass bed, where it co-existed with *C. kraussi*. This is probably attributable to the nature of the sediment at Geelbek, which is finer than anywhere else in the lagoon, with a high mud and clay content (Flemming, 1977). This may provide the cohesive sedimentary fabric required by *U. africana* for its semi–permanent burrows. Under these conditions, the root-rhizome network of *Z. capensis* may

be redundant or even a hindrance to *U. africana*, unlike other parts of the lagoon where it appears to provide stability and protection from *C. kraussi*.

One focus of this study was to establish the existence of a hypothesised 'frontier zone'- an approximate meter–wide area below the *Z. capensis* bed in which *U. africana* is abundant, and below which densities of the mud prawn decrease in association with the onset of *C. kraussi* populations. It is apparent from the transect data (Figure 2.5) that a transition zone does exist between the distributional ranges of *Z. capensis* and *C. kraussi*. The origin of this zone may stem from seasonal 'die-back' of *Z. capensis* aerial shoots after flowering, so that only rhizomes remain buried in the substratum (Edgcumbe, 1980). Alternatively, the zone may represent an area in which the rhizomes can penetrate down-shore, but where the adjacent activities of *C. kraussi* may suspend sufficient sediment to smother the above-ground blades of eelgrass. The below-ground rhizomes will stabilise the sediment, providing a favourable environment for the permanent burrows of *U. africana* while impeding the excavation of *C. kraussi* burrows, thus creating an exclusion area. This pattern was consistent for all sites where *Z. capensis* and *U. africana* co-occurred, with the exception of Geelbek. As previously mentioned, Geelbek is unique in that it supports large amounts of all three species, with *U. africana* more abundant outside the *Z. capensis* bed than in it.

The lower intertidal sand flats of Langebaan Lagoon are dominated by *C. kraussi*, in a distributional pattern that is opposite to that of *Z. capensis* and *U. africana*. Although the distributional patterns of all three species are certainly influenced by abiotic factors, there is sizeable circumstantial evidence from the data that *C. kraussi* bioturbation has a dramatically negative effect on *Z. capensis* distribution and abundance. Experimental transplants of *Thalassia testudinum* by Suchanek (1983) revealed that *Callianassa rathbunae* had a negative influence on its productivity, and excluded or inhibited the seagrass by smothering or by reducing the penetration of light as a result of suspension of particles. Bioturbation by *C. kraussi* is similarly likely to restrict the abundance and distribution of *U. africana*. The modification of the benthic environment by deposit feeders is known to prohibit suspension feeders because turnover and suspension of sediment particles either smothers or clogs filtering structures (Rhoads & Young, 1970; Aller & Dodge, 1974), as well as causing the collapse of the semi-permanent, dwelling–burrows of organisms such as *U. africana*, resulting in suffocation.

Z. capensis may, in turn, have a limiting effect on *C. kraussi*. The root-rhizome system forms a dense matrix that is known to restrict the movement of burrowing organisms. Brenchley (1982) demonstrated that *Callianassa californiensis* was unable to penetrate dense root-mats and that this restriction of mobility increased disproportionately for larger individuals of burrowing

organisms. On average, the size of *C. kraussi* found within *Z. capensis* was smaller than that of individuals sampled outside the eelgrass beds (Figure 2.4) suggesting that established *Z. capensis* beds with dense root assemblages either completely exclude large individuals of *C. kraussi*, or impose energetic demands that stunt those individuals of *C. kraussi* that live in the eelgrass beds. Taken in conjunction with the dramatic reductions of *C. kraussi* densities in eelgrass beds, it seems likely that sedimentary stabilisation by the eelgrass contributes to the exclusion of *C. kraussi*, enforcing a reversed distribution to that of *Z. capensis*. Interestingly, although Brenchley (1982) hypothesised that eelgrass should restrict the movement of larger individuals within the bed, *U. africana* was generally larger within *Z. capensis* beds than outside. This could be because *U. africana* is less mobile than *C. kraussi*. Although initially its burrowing may be restricted, once a permanent burrow structure has been established, a tight sedimentary fabric may facilitate the sedentary lifestyle and filtering mode of feeding of the prawn.

The results of this chapter are largely correlative and the patterns described can be interpreted as a result of multiple factors that structure soft-bottom communities (Brenchley, 1982). The distributions and densities of *Z. capensis*, *U. africana* and *C. kraussi* are most probably attributable to changes in the physical factors as one moves upshore (increased desiccation, reduced opportunities to circulate water through burrows or to filter–feed), in combination with biogenic stabilisation of the sediments by *Z. capensis* and antagonistic bioturbation by *C. kraussi*. Understanding the observed patterns of distribution and abundance of organisms must involve an evaluation of the relationships between these organisms and the structure of the habitat (Woodin, 1981). It is clear that *Z. capensis* and *U. africana* share distributions, apparently based on mutual needs for a stable substratum. In contrast *C. kraussi* and *Z. capensis* (and, in most cases, *C. kraussi* and *U. africana*) are mutually exclusive of each other, and this is reflected in their converse distributional relationships, creating two distinct biotic assemblages. Despite the difficulty in confidently attributing direct causality for the distribution patterns described, the results infer that the most likely agents responsible are physical disturbance caused by *C. kraussi* bioturbation, versus stabilisation caused by eelgrass root-rhizomes. The detrimental effects that bioturbation by *Callianassa* spp. have on corals, suspension-feeders and seagrasses has been well documented (Rhoads, 1974; Aller & Dodge, 1974, Rhoads *et al.*, 1977; Day, 1981a; Suchanek, 1983; Branch and Pringle, 1987; Wynberg and Branch, 1994). Given that the intertidal benthic biomass in the sandbanks of Langebaan Lagoon is largely dominated by *C. kraussi* (Wynberg & Branch, 1991, 1994), it can be deduced that *C. kraussi* plays a powerful role in structuring soft sediment communities within Langebaan Lagoon.

In summary, this chapter has produced several lines of circumstantial evidence that *Z. capensis* and *C. kraussi* have negative effects on each other. These include: (1) their almost mutually exclusive distribution patterns, (2) the smaller size of *C. kraussi* inside eelgrass beds versus outside, and (3) the existence of a 'frontier zone' at the bottom of the eelgrass beds, where above-ground growth of *Z. capensis* may be stunted by suspension of particles in the adjacent *Callianassa* dominated sandbanks, but below-ground rhizomes and roots of *Z. capensis* may hinder up-shore penetration by *C. kraussi.* There is similar circumstantial evidence from the data for a positive effect of *Z. capensis* on *U. africana* because of (1) their shared distribution patterns, (2) the observation that *U. africana* was virtually absent from sites lacking eelgrass, and (3) the fact that *U. africana* achieved largest sizes in the eelgrass beds. This may be due to the direct effect *Z. capensis* has on stabilising the sediment and/or the indirect effects of excluding *C. kraussi,* with which *U. africana* is negatively correlated.

Three situations seem to exist in Langebaan Lagoon. At sites such as Schrywershoek, ChurchHaven and Kraalbaai on the western bank, currents and wind-driven distribution of particles lead to coarse unstable sediments (Flemming, 1977). There, *Z. capensis* and *U. africana* are virtually absent because of this physically-driven instability, and *C. kraussi* extends to the top of the shore. A second condition exists on most of the eastern bank where there is less water movement and wind deposits finer particles (Flemming, 1977). *Z. capensis* forms high-shore beds, excluding *C. kraussi* from the high shore and supporting *U. africana.* Lower on the shore, bioturbation by *C. kraussi* excludes *Z. capensis.* Finally, at Geelbek, particle size is extremely fine. *Z. capensis* and *C. kraussi* are still negatively correlated, but *U. africana* now expands below the eelgrass beds to co-exist with low densities of *C. kraussi.* However, as *C. kraussi* numbers increase down the shore the effects of *C. kraussi* bioturbation may supersede the mediating effect that the cohesive sedimentary fabric has on the stabilisation of *U. africana* burrows at Geelbek, resulting in a negative correlation between *U. africana* at high densities of *C. kraussi.* Thus, the correlative data support all three hypotheses advanced in the introduction. They also allow plausible causative explanations for these patterns. Confirmation of the causality of these relationships requires experimental manipulations and these are the subjects of Chapter 4 and 5.

Models of soft-bottom community structure have emphasized the importance of disturbance in producing a mosaic of habitats (Wynberg & Branch, 1994), which in turn supports a mosaic of benthic groups. The division of *Z. capensis* and *U. africana* versus *C. kraussi* into two distinct distributional communities due to *C. kraussi* bioturbation and *Z. capensis* stabilisation of sediments is likely to be reflected in the composition of the benthic assemblages associated with

each community. Differences in the composition of the biological communities correlated with each habitat are examined in Chapter 3.

Chapter 3

Influence of biological interactions on community structure within *Zostera capensis* and adjacent sandprawn-dominated sandflats.

3.1 Introduction

Concepts of 'patch' dynamics and the relationships between habitat heterogeneity, disturbance and biodiversity have received recent attention in both terrestrial and marine ecology (e.g. Shaffer, 1994; Hanski, 1994; Robins & Bell, 1994 in Bowden *et al.*, 2001) and attempt to explain distributions of organisms as a mosaic of heterogeneous units between which individuals can migrate and within which community interactions occur (Bowden *et al.*, 2001). Physical disturbance has long been recognized as one factor that is important in determining the distribution and abundances of organisms (Bell & Woodin, 1984), as well as influencing patterns of habitat heterogeneity (Woodin, 1981). In addition, biological disturbance plays a major role in influencing the establishment, maintenance and turnover of biotic assemblages (e.g. Orth, 1977; Sousa, 1979; Paine & Levine, 1981; Woodin, 1981; Suchanek, 1981; Bell & Woodin, 1984).

In Chapter 2 it was established that two distinct habitats exist in Langebaan Lagoon: one comprising beds of the eelgrass *Zostera capensis*, and the other sandflats dominated by the sandprawn *Callianassa kraussi*. These may be manifested as two divergent biotic communities (*Zostera*-associated *versus* Sandflat-associated), as a result of sediment binding by the eelgrass on one hand, and biogenic reworking (bioturbation) of the sediment by *C. kraussi* on the other. The effects of such processes on community and trophic structure have been well documented in seagrass beds from a variety of geographic locations (see review by Short & Wyllie-Echeverria, 1995), revealing that bioturbation strongly influences the size and patchiness of seagrass meadows (Townsend & Fonseca, 1998) and may retard the spread or colonisation of seagrass cover. Much attention has been placed on seagrass as a 'structural species' and its influence on habitat heterogeneity and the structure of marine communities (Webster *et al.*, 1998).

In particular, it is a widely reported characteristic of macrophyte beds that species richness, diversity, abundance and biomass of animals associated with vegetated habitats are much higher than those in adjacent unvegetated habitats (e.g. Sand-Jensen, 1975; Stoner, 1980; Homziak *et al.*, 1982; Fitzhardinge, 1983; Suchanek, 1983; Lewis, 1984; Heck *et al.*, 1989; Edgar, 1990; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1997; Lee *et al.*, 2001). The leaves and root–rhizome system of seagrass create habitats of relatively high structural complexity which, by contrast to

The analysis of spatial and temporal patterns in soft-bottom communities is inherently difficult, particularly because of the variety of interactions and their modification by abiotic conditions (Thrush, 1991). Consequently, though physical factors may be directly responsible for infaunal distribution patterns (Edgar & Robertson, 1992), indirect effects among macrofaunal species may be even more important in influencing the composition of biological communities (Widdicombe & Austen, 1999; Strauss, 1991). These biotic interactions may be complex because they relate to differences among species in size, feeding mode, burrowing activity and mobility.

I examined species composition and abundance of the benthic fauna of *Zostera*-dominated versus *Callianassa*-dominated areas in Langebaan Lagoon, to determine the extent to which each houses distinctive communities. I also used this analysis to test hypotheses advanced by Brenchley (1981, 1982) who argued that because eelgrass stabilises sediment, the fauna of eelgrass beds should comprise species characterised by small size, flexible bodies and non-burrowing habit. Conversely, sandprawn-dominated areas, which will be experience substantial bioturbation, will house species that are relatively larger, inflexible and burrowing. Specifically, I tested the following hypotheses.

1. Differentiation in intertidal biological community structure within Langebaan Lagoon will exist between sediments disturbed by *C. kraussi* and those stabilised by *Z. capensis* (following Suchanek, 1982 and others).
2. Sediment penetrability will be greater in unvegetated *Callianassa*-dominated sandflats than in *Zostera* beds.
3. Differences in the composition of each habitat's associated faunal assemblage will be explained by Brenchley's (1982) hypothesis, which distinguishes taxa according to mobility, morphology and size, and argues that *Zostera*-associated fauna will be disproportionately represented by smaller, non-burrowing, soft-bodied species and those in unvegetated bioturbated sandflats by large, burrowing, hard-bodied species.

3.2 Methods

Sampling undertaken to identify differences in community composition of invertebrates living within and outside beds of *Z. capensis* was based at the same sites used for analyses of biological associations in Chapter 2.

3.2.1 *Biological Communities*

Surveys of community composition were conducted at all of the transect sites sampled during 1999 and 2000 field surveys (see Chapter 2). In 1999, four sites on the eastern and three on the western shores of the lagoon were surveyed, but because *Zostera* beds were absent from the western bank, surveys in 2000 were confined to the eastern bank and expanded to include five sites: Klein Oesterwal South, Klein Oesterwal North, Bottelary North, Bottelary South and Oesterwal (see Figure 1.1 for localities). At each site two randomly selected replicate $0.1m^2$ samples were taken, one pair within the *Z. capensis* bed and the other in the open sandflat. All samples were taken within a 10-cm height range at each locality. Sediment was dug down to a depth of 30 cm and sieved through a 1–mm mesh sieve. All living macrofauna retained by the sieve was collected and identified to species level using the classification of Branch *et al* (1994), Day (1981b), Griffiths (1976), Kensley (1972) and Kilburn & Rippey (1981), and then preserved in 10% formalin. Species were further categorised according to whether they were 'hard–bodied' or 'soft–bodied', and 'burrowing' or 'non-burrowing', following categories of relative mobility and functional morphology identified by Brenchley (1981).

3.2.2 *Invertebrate Size*

Macrofaunal sizes were measured to determine whether differences exist between seagrass beds and sandflat areas. Total body lengths or maximum shell dimensions were measured to the nearest mm from samples collected during the surveys in 2000. With one exception, no species were present in both habitats in sufficient numbers to allow intraspecific comparisons between the two habitats. Instead, species were pooled into three functional groups (Polychaeta, Thalassinidea and Brachyura). The selection of species in each group was based on their identification as indicator species by Simper analyses. In the case of Brachyura, only one species, *Cleistostoma edwardsii*, was included in the analysis, so in that instance the comparison between habitats was intraspecific. Subsamples of 20 individuals per species per sample were measured. Many of the polychaetes were too fragmented to record accurate body lengths. Consequently, all polychaete measurements were standardised as the width of the 4^{th} segment, measured to an accuracy of 0.1 mm under a microscope using an ocular micrometer.

3.2.3 *Sediment Penetrability*

Penetrability of the sediment within *Z. capensis* beds and in open sandflats was measured in both 1999 and 2000. Ten random penetrability measurements were taken in each habitat at each locality by dropping a standardized steel rod 1 m long and 8 mm in diameter from a height of 1

m above the substratum. The distance of penetration into the substratum was used as an index of penetrability.

3.2.4 *Statistical Analysis*

Data were tested for normality and homogeneity of variance by means of Kolmogorov-Smirnov test and Levene's test respectively (alpha set at 0.05). If necessary, data were transformed to meet the assumptions of parametric tests; when this failed, equivalent nonparametric statistical tests were applied. Differences in the densities of macrofaunal species within either seagrass beds or the sandflats were assessed by Mann-Whitney U tests. A Kruskal-Wallis ANOVA by Ranks tested for site effects (n> 2) on the densities of macrofauna, followed by Tukey-type post-hoc tests (Zar, 1984). Comparisons of species diversity and species richness between habitats and between sites were assessed by ANOVA. Some of the sites examined contained both eelgrass beds and sandprawn-dominated sandflats. Others contained only the latter. Consequently it was impossible to develop a fully balanced sampling design for all sites. To overcome this, two types of analyses were undertaken. At sites where both habitats were present, a two-way ANOVA was conducted, with site as a random factor and habitat as a fixed factor. Separately, a one-way ANOVA was run for all sites, with site as a random factor, comparing only the sand-prawn dominated samples. When appropriate, ANOVAs were followed by multiple comparison Tukey tests. This procedure was also applied to comparisons of sediment penetrability between habitats and sites. The Shannon diversity index ($H' = -\sum (Pi * \text{Log}(Pi)$, where Pi is the proportion of the total count arising from the *i*th species) was used to establish species diversity, and Margalef's richness index ($d' = (S-1)/\text{Log}(N)$, where S is the total number of species and N the total number of individuals) determined species richness. Differences in relative mobility and functional morphology (hard–bodied *vs.* soft–bodied and burrowing *vs.* non–burrowing) of macrofaunal assemblages between habitats were assessed by Chi–square analyses. Statistical analyses were conducted using StatSoft, Inc. (2000) STATISTICA version 6 for Windows.

PRIMER (Plymouth Routines in Multivariate Ecological Research, version 5, 2001) was used for analysis of species composition and abundance (Clarke & Warrick, 1994). Biological data were fourth-root transformed to weight the contribution of less abundant species. Hierarchical cluster analysis using Bray-Curtis similarity and multidimensional scaling (MDS) were used to compare community composition between habitats and sites. Similarity percentage breakdown analysis (SIMPER) was used to identify characteristic and distinguishing species accountable for significant differences in community structure between '*Zostera*-associated' and 'sandflat-associated' habitats. Species were only considered if they cumulatively accounted for at least

80% of the overall similarity or dissimilarity within or between habitats. Comparisons between the sizes of macrofauna within *Z. capensis* habitats and sandprawn-dominated habitats were assessed by Mann Whitney-U tests. Replicate samples at each locality were pooled and analysis was limited to comparisons between three functional groups only (polychaetes, thalassinideans and crustaceans) due to low sample numbers in most other groups.

3.3 Results

3.3.1 *Community Structure*

Abundance estimates of 33 macrofaunal species were used to compare community structure within *Z. capensis* with that of the adjacent sandflat in 1999 and 2000 respectively. Species that were clearly more abundant within *Z. capensis* were categorised as '*Zostera*-associated'. Similarly, species that were more abundant in the open sandflat were categorised as 'sandflat-associated'. The remaining species that showed no discernable habitat preference (or were too scarce to draw statistical conclusions) were categorised as 'neutral' species.

Mean densities (±SE) of macrofauna recorded within each habitat in 1999 are given in Table 3.1. Of the species recorded, 15.2% were considered to be *Zostera*-associated, 27.3% were sandflat-associated and the remaining 57.6% were neutral. Comparisons of densities within *Z. capensis* and the adjacent sandflat revealed significant differences for all species classified as either *Zostera*-associated or sandflat-associated, whereas no significant habitat differences were evident for the neutral species (Mann-Whitney U tests, Table 3.1). No site effects on the abundance of species were apparent, except for densities of *Cleistostoma edwardsii* and *Eurydice longicornis* (Kruskal-Wallis tests, Table 3.1). Results of post-hoc Tukey type tests for Kruskal-Wallis ANOVA by Ranks showed significant differences between all sites in the case of *Cleistostoma edwardsii*, with higher densities occurring at most sites on the Eastern shore of the lagoon (Klein Oesterwal, Bottelary and Geelbek) compared to those on the western shore (Schrywershoek, ChurchHaven and Kraalbaai). *E. longicornis* occurred at Kraalbaai only, and even there its densities were low.

In 2000, surveys were limited to the eastern bank of the lagoon, where both eelgrass and sandflat habitats were present. Mean densities (±SE) of macrofauna within each habitat are given in Table 3.2. Of the 33 species recorded, 30.3% were classified as *Zostera*-associated, 12.2% were sandflat-associated and the remaining 57.6% were categorised as neutral.

Table 3.1:Mean densities per $0.1m^2$ (±SE) of macrofauna sampled within *Z. capensis* or the adjacent sandflat in 1999, categorised according to habitat preference. Mann-Whitney U test results show significant differences in species density between habitats. Kruskal-Wallis test results indicate significant differences between sites ($p < 0.05$).

1999		HABITAT				STATISTICS						
		Zostera		Sandflat		Habitat Difference (Mann Whitney-U)				Site Difference (Kruskal-Wallis: 6, n=22)		
	Species	Mean	SE	Mean	SE	U	Z	P		H	P	
***Zostera*-Associated**	*Upogebia africana*	10.75	3.98	0.07	0.07	0.0	3.822	0.000	Significant	6.015	0.422	Not Significant
	Perinereis nuntia vallata	51.38	9.00	0.00	0.00	0.0	3.822	0.000	Significant	4.699	0.583	Not Significant
	Assiminea globulus	35.63	11.76	0.00	0.00	7.0	3.344	0.001	Significant	5.193	0.519	Not Significant
	Cleistostoma edwardsii	19.25	5.24	2.50	0.84	9.0	3.207	0.001	Significant	14.715	0.022	Significant
	Patiriella exigua	0.50	0.27	0.00	0.00	35.0	1.433	0.016	Significant	6.975	0.323	Not Significant
Sandflat-Associated	*Orbinia angrapequensis*	2.00	1.31	16.07	4.31	6.50	-3.378	0.001	Significant	2.336	0.886	Not Significant
	Urothoe grimaldii	0.00	0.00	9.00	2.59	12.0	-3.003	0.002	Significant	5.848	0.440	Not Significant
	Scoloplos johnstonei	0.00	0.00	8.36	2.13	12.0	-3.003	0.002	Significant	2.852	0.827	Not Significant
	Callianassa kraussi	0.00	0.00	4.29	1.22	8.0	-3.276	0.001	Significant	2.674	0.848	Not Significant
	Hymenosoma orbiculare	0.00	0.00	0.86	0.18	16.0	-3.070	0.002	Significant	4.875	0.559	Not Significant
	Euclymene sp.	0.00	0.00	2.00	0.50	16.0	-2.730	0.003	Significant	8.137	0.228	Not Significant
	Glycera tridactyla	0.00	0.00	1.50	0.48	16.0	-2.740	0.006	Significant	9.767	0.135	Not Significant
	Notomastus latericeus	0.38	0.28	5.86	1.95	36.0	-1.365	0.098	Not Significant	9.358	0.154	Not Significant
Neutral spp	*Ampelisca palmata*	0.13	0.13	0.00	0.00	49.0	0.477	0.633	Not Significant	4.500	0.609	Not Significant
	Marphysa sanguinea	0.88	0.64	0.36	0.23	52.0	0.270	0.780	Not Significant	5.442	0.488	Not Significant
	Marphysa depressa	1.13	0.61	0.29	0.16	38.50	1.190	0.232	Not Significant	4.738	0.577	Not Significant
	Syllis sp.	0.13	0.13	0.00	0.00	49.0	0.470	0.632	Not Significant	4.500	0.609	Not Significant
	Betaeus jucundus	0.00	0.00	0.21	0.15	48.0	-0.546	0.585	Not Significant	9.428	0.151	Not Significant
	Diogenes brevirostris	0.25	0.16	0.07	0.07	46.0	0.682	0.494	Not Significant	6.815	0.338	Not Significant
	Protomella capensis	0.00	0.00	0.29	0.16	44.0	-0.819	0.412	Not Significant	8.812	0.184	Not Significant
	Fissurella mutabilis	0.13	0.13	0.00	0.00	49.0	0.470	0.632	Not Significant	4.500	0.609	Not Significant
	Volvarina capensis	0.00	0.00	0.14	0.10	48.0	-0.546	0.585	Not Significant	3.675	0.720	Not Significant
	Nassarius plicatellus	0.00	0.00	0.14	0.10	48.0	-0.546	0.585	Not Significant	9.450	0.149	Not Significant
	Lumbrineris tetraura	0.13	0.13	0.36	0.36	53.5	0.170	0.864	Not Significant	6.827	0.337	Not Significant
	Telothelepus capensis	0.25	0.25	0.00	0.00	49.0	0.477	0.632	Not Significant	4.500	0.609	Not Significant
	Cymadusa filosa	1.13	1.13	0.00	0.00	49.0	0.477	0.632	Not Significant	4.500	0.609	Not Significant
	Lysianassa ceratina	0.13	0.13	0.14	0.10	55.0	-0.060	0.945	Not Significant	4.789	0.571	Not Significant
	Thaumastoplax spiralis	0.00	0.00	0.14	0.10	48.0	-0.546	0.585	Not Significant	6.562	0.363	Not Significant
	Eurydice longicornis	0.00	0.00	0.50	0.34	48.0	-0.564	0.585	Not Significant	20.952	0.002	Significant
	Nassarius kraussianus	1.00	0.87	0.07	0.07	45.5	0.717	0.437	Not Significant	6.975	0.323	Not Significant
	Carditella rugosa	0.00	0.00	0.57	0.27	40.0	-1.092	0.104	Not Significant	8.134	0.228	Not Significant
	Ceratonereis erythraeensis	0.75	0.62	3.57	1.95	37.50	-1.262	0.206	Not Significant	1.047	0.983	Not Significant

Table 3.2: Mean densities per 0.1 m^2 (±SE) of macrofauna sampled within *Z. capensis* beds or sandflats in 2000. Species are categorised according to habitat preference. Mann-Whitney U test results indicate significant differences between species densities and habitat. Kruskal-Wallis tests show significant differences between sites ($p < 0.05$).

2000		HABITAT				STATISTICS						
		Zostera		Sandflat		Habitat Difference (Mann Whitney-U)				Site Difference (Kruskal-Wallis: 4, n=22)		
	Species.	Mean	SE	Mean	SE	U	Z	P		H	P	
***Zostera*-Associated**	*Lumbrineris tetraura*	1323	453.93	158.9	121.09	17.00	2.494	0.012	Significant	6.523	0.163	Not Significant
	Assiminea globulus	72.20	51.26	0.00	0.00	30.00	1.512	0.030	Significant	7.132	0.192	Not Significant
	Perinereis nuntia	57.50	13.02	3.70	3.48	3.00	3.552	0.000	Significant	1.449	0.836	Not Significant
	Cleistostoma edwardsii	38.00	8.59	5.40	1.32	3.00	3.553	0.001	Significant	1.917	0.751	Not Significant
	Upogebia africana	16.70	4.64	1.30	0.40	3.50	3.515	0.000	Significant	3.942	0.414	Not Significant
	Siphonaria compressa	16.10	10.66	0.00	0.00	30.00	2.162	0.030	Significant	4.772	0.312	Not Significant
	Anthothoe stimpsoni	4.50	1.56	0.50	0.50	23.50	2.003	0.018	Significant	7.622	0.106	Not Significant
	Isanthus	1.20	0.51	0.00	0.00	30.00	2.164	0.030	Significant	7.092	0.131	Not Significant
	Exosphaeroma truncatitelson	1.10	0.53	0.00	0.00	30.00	2.164	0.030	Significant	4.779	0.311	Not Significant
	Hydrobia sp.	3.10	1.94	0.40	0.22	31.00	1.582	0.114	Not Significant	10.180	0.037	Significant
Sandflat-Associated	*Orbinia angrapequensis*	5.50	1.97	39.80	17.05	24.50	-1.927	0.049	Significant	6.251	0.181	Not Significant
	Urothoe grimaldii	0.00	0.00	8.20	3.16	20.00	-2.267	0.023	Significant	3.228	0.520	Not Significant
	Callianassa kraussi	0.00	0.00	7.40	2.28	10.00	-3.024	0.002	Significant	3.384	0.496	Not Significant
	Marphysa depressa	0.40	0.16	3.90	1.57	20.00	-2.267	0.023	Significant	5.368	0.251	Not Significant
Neutral spp	*Tellimya trigona*	1.50	1.01	1.80	1.209	48.50	-0.113	0.910	Not Significant	9.954	0.041	Significant
	Euclymene sp.	0.00	0.00	0.10	0.10	45.00	0.378	0.705	Not Significant	4.000	0.406	Not Significant
	Glycera tridactyla	0.10	0.10	0.50	0.40	44.50	-0.416	0.677	Not Significant	2.250	0.670	Not Significant
	Notomastus latericeus	0.00	0.00	0.10	0.10	45.00	-0.378	0.705	Not Significant	4.000	0.406	Not Significant
	Timarete tentaculata	0.10	0.10	0.10	0.10	50.00	0.00	1.00	Not Significant	3.167	0.530	Not Significant
	Marphysa sanguinea	0.30	0.21	0.00	0.00	40.00	0.756	0.440	Not Significant	3.171	0.529	Not Significant
	Cirolana undulata	0.00	0.00	0.10	0.10	45.00	-0.377	0.705	Not Significant	4.000	0.406	Not Significant
	Exosphaeroma hylecoetes	0.30	0.30	0.00	0.00	45.00	0.377	0.705	Not Significant	4.000	0.406	Not Significant
	Betaeus jucundus	0.20	0.20	0.20	0.20	50.00	0.00	1.000	Not Significant	3.167	0.530	Not Significant
	Littorina	0.20	0.20	0.00	0.00	45.00	0.378	0.705	Not Significant	4.000	0.406	Not Significant
	Gastrosaccus psammodytes	0.40	0.40	0.20	0.63	49.50	0.038	0.970	Not Significant	8.421	0.077	Not Significant
	Dosinia lupinus orbignyi	0.10	0.10	0.00	0.00	45.00	0.378	0.705	Not Significant	4.000	0.406	Not Significant
	Volvarina capensis	0.90	0.90	0.60	0.27	37.00	-0.983	0.326	Not Significant	9.073	0.059	Not Significant
	Thaumastoplax spiralis	0.30	0.21	0.00	0.00	40.00	0.756	0.449	Not Significant	3.171	0.529	Not Significant
	Hymenosoma orbiculare	6.00	3.76	2.11	0.67	49.00	0.080	0.929	Not Significant	5.645	0.227	Not Significant
	Nephtys capensis	7.00	7.00	0.10	0.10	49.50	0.037	0.969	Not Significant	3.171	0.520	Not Significant
	Scoloplos johnstonei	2.30	2.08	1.40	1.09	49.50	-0.037	0.969	Not Significant	11.828	0.018	Significant
	Carditella rugosa	0.10	0.10	2.40	1.63	44.00	-0.729	0.466	Not Significant	6.321	0.176	Not Significant
	Patiriella exigua	1.10	0.59	0.00	0.00	35.00	1.180	0.067	Not Significant	6.120	0.190	Not Significant
	Nassarius kraussianus	1.80	1.69	0.20	0.13	49.00	0.108	0.917	Not Significant	10.302	0.036	Significant

Comparisons of macrofaunal densities within *Z. capensis* and the adjacent sandflat revealed significant differences for all species classified as either *Zostera*-associated or sandflat-associated, except *Hydrobia* sp. No significant habitat effect was evident for the neutral species (Mann-Whitney U tests, Table 3.2).

Although *Hydrobia* densities were low, resulting in no statistical difference in abundance between habitats, the species was approximately seven times more abundant within *Z. capensis* than in the adjacent sandflat, so I classed it as a *Zostera*-associated species (Table 3.2). Kruskal-Wallis analysis revealed that *Hydrobia* sp., *Tellimya trigona*, *Nassarius kraussianus* and *Scoloplos johnstonei* abundances differed between sites (Table 3.2), but apart from *Hydrobia*, these species were too scarce to show any observable habitat preference, or be recorded at all sites. Post–hoc Tukey type tests showed that *Hydrobia* was more abundant at Klein Oesterwal North and Bottelary South and North than at other sites.

The overall pattern was that a small group of species showed strong affinities with *Zostera* that were consistent between years: *U. africana*, *P. nuntia vallata*, *A. globulus* and *C. edwardsii*. A notable addition in 2000 was *L. tetraura*, which increased enormously in numbers in that year. Conversely, three species were consistently sandflat-associated in both years: O. *angrapequensis*, *U. grimaldii* and *C. kraussi*. Additional species that contributed to the sandflat-associated list in 1999 but not in 2000 were relatively scarce species. Although only these eight listed species consistently contributed to distinguishing the two habitats, they dominated the numbers of individuals, contributing >97% of the individuals identified.

Figures 3.1 and 3.2 show the results of the hierarchical cluster analyses and the two-dimensional MDS ordination plots for macrofaunal species sampled within either *Z. capensis* or sandflat habitats in 1999 and 2000 respectively. The dendrogram for 1999 (Figure 3.1 A) showed that both *Zostera*-associated and sandflat-associated samples formed discrete clusters with more than 80% dissimilarity between the two habitats. One site within the sandflat habitat (Kraalbaai) was an outlier with more than 60% dissimilarity to all other sites within the sandflat group. The MDS plot (Figure 3.1 B) also indicated that *Zostera*-associated and sandflat-associated groups differed in community structure and that Kraalbaai was distinct from all other sites.

The dendrogram for 2000 (Figure 3.2 A) showed more variability between *Zostera*-associated and sandflat-associated regions, but still clustered into discrete groups, more than 65% dissimilar. The exceptions were the two Oesterwal *Zostera*–bed samples, which clustered with the sandflat samples. Macrofauna samples from within *Z. capensis* at Klein Oesterwal South grouped with the other *Zostera*-associated sites, albeit as an outlier more than 60% dissimilar.

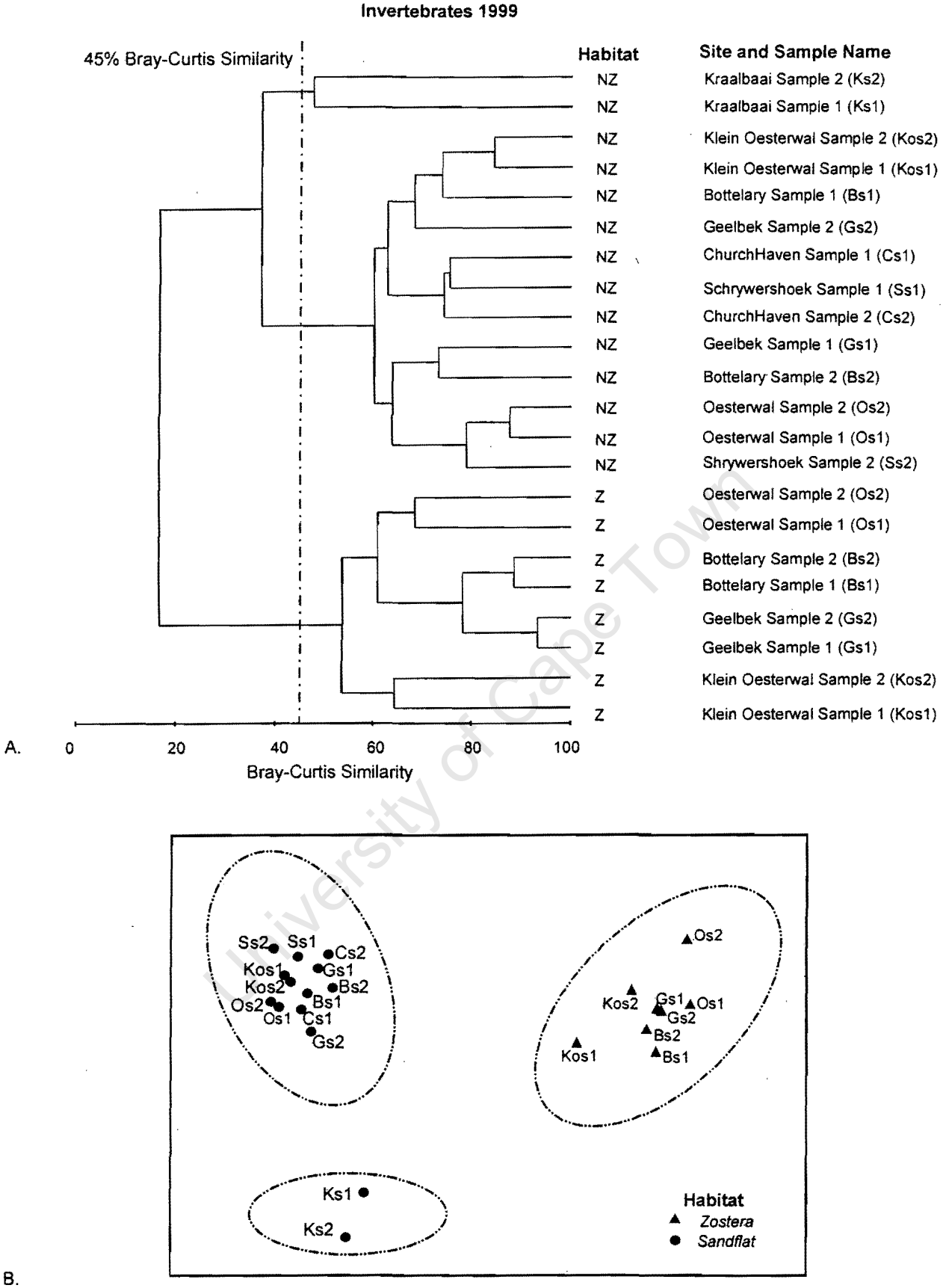


Figure 3.1: Dendrogram (A) showing results of the hierarchical cluster analysis and (B) MDS plot (stress=0.08) based on fourth-root transformed invertebrate data from *Zostera* (Z) and Sandflat (NZ) habitats at 7 sites around Langebaan Lagoon. Abbreviated site names are given with full names in (A).

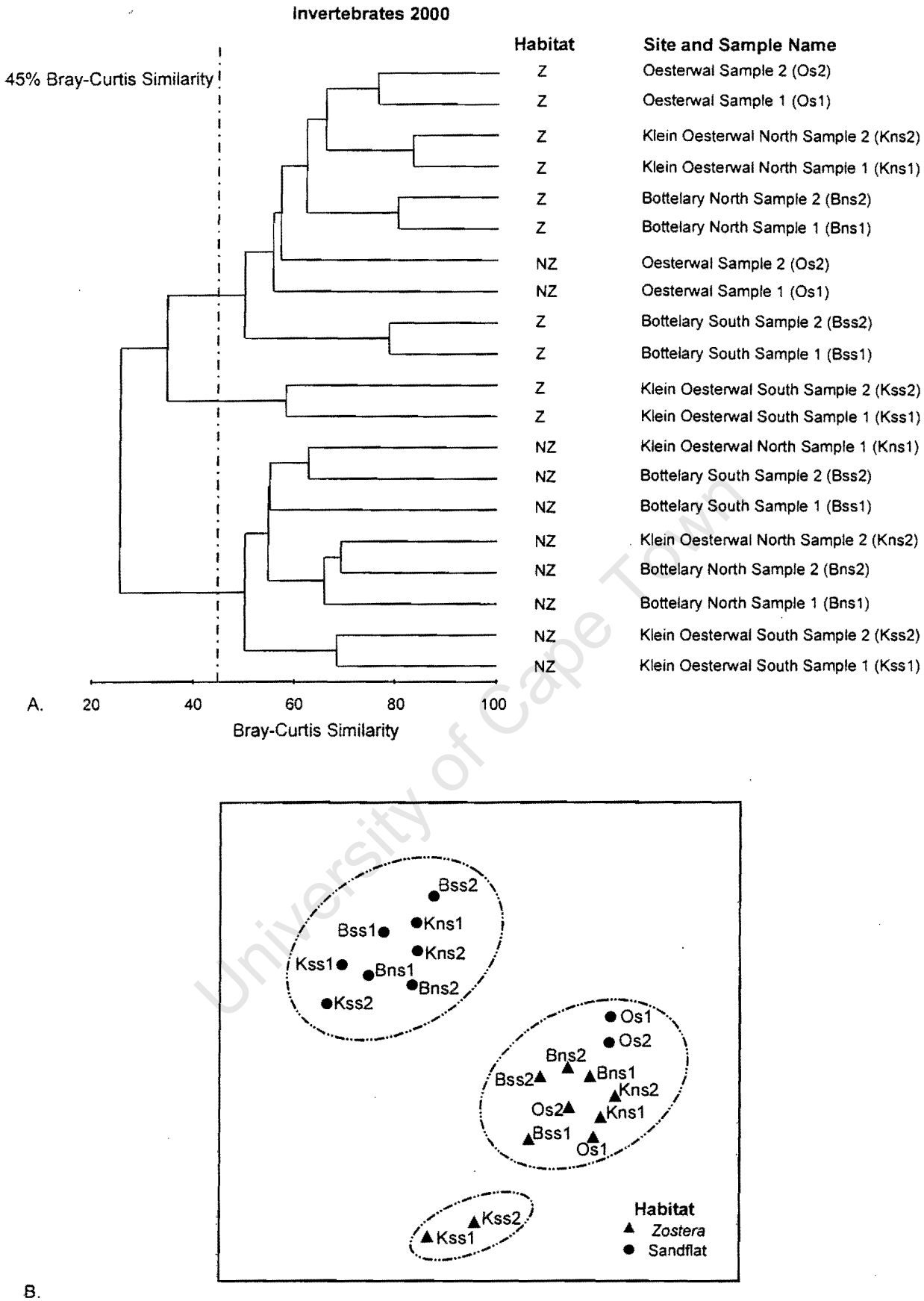


Figure 3.2: Dendrogram (A) showing results of the hierarchical cluster analysis and (B) MDS plot (stress=0.13) based on fourth-root transformed invertebrate data from *Zostera* (Z) and Sandflat (NZ) habitats at 5 sites around Langebaan Lagoon. Abbreviated site names are given in full in (A) names.

These results were reflected in the MDS plot (Figure 3.2 B), which generally separated *Zostera*-associated and sandflat-associated samples. Both Klein Oesterwal South and Oesterwal South were outliers, with the latter closely grouped with the *Zostera*-associated samples.

3.3.2 *Community Composition*

The differences between macrofaunal assemblages sampled within *Z. capensis* beds and in the adjacent sandflat indicate that two distinct assemblages exist. Table 3.3 shows the characteristic species principally responsible for determining this in 1999. Samples from *Zostera*-associated habitats were on average 63% similar (Table 3.3), and 90 % of the similarity was accounted for by four taxa (Table 3.3). The most characteristic species was the polychaete *Perinereis nuntia vallata*, accounting for almost 33 % of the similarity. *Cleistostoma edwardsii*, *Upogebia africana* and *Assiminea globulus* constituted the remainder. The average similarity for samples from sandflat-associated habitats was 57 %, with 90% of the group similarity explained by 10 taxa. The most important characteristic species was *Orbinia angrapequensis*, accounting for 20.84 % of the group similarity. Other important characteristic species were *Nephtys* spp, *Scoloplos johnstonei*, *Callianassa kraussi* and *Urothoe grimaldii*. There was high variability in abundance between samples as reflected by the low Si/SD(Si) ratios. *Orbinia angrapequensis*, *C. kraussi* and *Nephtys* spp were the most consistently characteristic species.

Table 3.4 shows the distinguishing species responsible for the divergence between faunal communities between *Zostera* and sandflat-associated habitats in 1999. *Zostera*-associated regions were on average 83.41% dissimilar to sandflat-associated regions. Fourteen taxa contributed to the overall dissimilarity. *Perinereis nuntia vallata* was the key distinguishing species, accounting for 12.26% of the dissimilarity and, together with *Assiminea globulus* and *Upogebia africana* was more abundant in *Zostera* beds than sandflats. Four species that were abundant in sandflats (*Scoloplos johnstonei*, *Urothoe grimaldii*, *Orbinia angrapequensis* and *Callianassa kraussi*) additionally contributed to the first 50 % of the dissimilarity. The variability of the remaining species abundance was high, and the above-mentioned species constituted the most consistent distinguishing species.

Table 3.3: Characteristic species for (A) *Zostera*-associated and (B) sandflat-associated habitats as determined by SIMPER analyses based on fourth-root transformed invertebrate densities sampled in 1999 and the Bray-Curtis measure of similarity. The ranking is determined by S_i, the average contribution of each species to the overall similarity of each habitat (S). AvD indicates the average density per 0.1 m^2 of each species from all sites within each habitat. $S_i/SD(S_i)$ is the ratio between S_i and $SD(S_i)$, the standard deviation of S_i. This ratio reflects how consistently the species abundance varied within each habitat. $\sum S_i\%$ is the cumulative percentage contribution of each species to the overall similarity, S. Only taxa accounting for the first 90% of the cumulative similarity are shown.

1999	Characteristic species			
***Zostera*-Associated**	**AvD**	**S_i**	**$S_i/SD(S_i)$**	**$\sum S_i\%$**
Perinereis nuntia vallata	51.38	20.27	3.81	32.24
Cleistostoma edwardsii	19.25	13.32	4.44	53.44
Upogebia africana	10.75	11.75	3.56	72.12
Assiminea globulus	35.63	11.47	1.53	90.36
Overall Similarity (%)				62.86
Sandflat-Associated	**AvD**	**S_i**	**$S_i/SD(S_i)$**	**$\sum S_i\%$**
Orbinia angrapequensis	16.05	11.81	5.86	20.84
Nephtys sp.	4.93	6.38	1.51	32.09
Scoloplos johnstonei	8.34	6.18	1.20	43.00
Callianassa kraussi	4.29	6.06	1.54	53.70
Urothoe grimaldii	9.00	5.62	1.15	63.61
Glycera tridactyla	1.50	3.91	0.94	70.50
Cleistostoma edwardsii	2.71	3.80	0.96	77.20
Euclymene sp.	2.00	3.72	0.94	83.77
Hymenosoma orbiculare	0.86	3.49	0.96	89.93
Ceratonereis erythraeensis	3.57	2.50	0.65	94.34
Overall Similarity (%)				56.68

Table 3.4: Major species distinguishing between *Zostera*-associated and sandflat-associated habitats, as determined by SIMPER analyses based on fourth-root transformed invertebrate densities sampled in 1999, and the Bray-Curtis measure of similarity. The ranking is determined by D_i, the average contribution of each species to the overall dissimilarity of each habitat (D). AvD indicates the average density per 0.1m^2 of each species from all sites within each habitat. $D_i/SD(D_i)$ is the ratio between D_i and $SD(D_i)$, the standard deviation of D_i. This ratio reflects how consistently the species abundance differed between habitats. $\sum D_i\%$ is the cumulative percentage contribution of each species to the overall dissimilarity, D. Only taxa accounting for the first 80% of the cumulative dissimilarity are shown.

1999: Distinguishing species	**AvD *Zostera***	**AvD Sandflat**	**D_i**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
Perinereis nuntia vallata	51.38	0.00	10.22	4.21	12.26
Assiminea globulus	35.63	0.00	7.73	2.08	21.52
Upogebia africana	10.75	0.07	6.30	2.61	29.07
Scoloplos johnstonei	0.00	8.34	5.00	1.76	35.07
Urothoe grimaldii	0.00	9.00	4.85	1.62	40.89
Orbinia angrapequensis	2.20	16.05	4.63	1.46	46.44
Callianassa kraussi	0.00	4.29	4.52	1.99	51.86
Cleistostoma edwardsii	19.25	2.71	4.25	1.44	56.96
Nephtys capensis.	0.25	4.93	4.20	1.57	62.0
Euclymene sp.	0.00	2.00	3.33	1.39	65.98
Glycera tridactyla	0.00	1.50	3.28	1.36	69.92
Ceratonereis erythraeensis	0.75	3.57	2.98	1.09	73.49
Hymenosoma orbiculare	0.00	0.86	2.83	1.46	76.89
Notomastus	0.38	3.67	2.65	0.88	80.07
Overall Dissimilarity (%)					83.41

In 2000, *Zostera* and sandflat-associated habitats had differences in community structure that corresponded closely to those recognized in 1999. Simper analyses revealed that *Zostera*-associated habitats were on average 52.59 % similar (Table 3.5). Of this similarity, 90% was accounted for by eight taxa; almost 80% was contributed by *Lumbrineris tetraura*, *Perinereis nuntia vallata*, *Cleistostoma edwardsii* and *Upogebia africana* (the latter three being consistently characteristic in 1999 as well). Variability among these four species was low compared to the remaining indicator species, signifying that they were the most consistent characteristic species among the group. The average similarity for species living within the sandflat-associated habitat was 45.60 %, with 90 % of the group similarity explained by seven taxa (Table 3.5). *Orbinia angrapequensis* accounted for 20.65% of the group similarity, similar to the situation in 1999. Other important characteristic species were *Cleistostoma edwardsii*, *Callianassa kraussi* and *Marphysa depressa*, cumulatively contributing 47.75% to the overall similarity. *Cleistostoma edwardsii* was the most consistently characteristic species, as reflected by its high $S_i/SD(S_i)$ ratio. However, *Orbinia angrapequensis* showed greatest temporal consistency, being top-ranking in terms of consistency in both 1990 and 2000.

Table 3.6 shows the major species contributing to the 70.63% average dissimilarity between *Zostera* and sandflat communities. Seventeen species contributed to 80% of the similarity. Unlike 1999, *Lumbrineris tetraura* was the most important distinguishing species (16.71%). Like *Perinereis nuntia vallata*, *Assiminea globulus* and *Upogebia africana*, it was more abundant in *Zostera* beds than in the sandflats. Conversely, *Orbinia angrapequensis*, *Callianassa kraussi* and *Urothoe grimaldii* were more abundant in sandflats. Collectively these species contributed >50% of the dissimilarity between habitats, repeating the pattern in 1999. The most consistently distinguishing species were *Perinereis nuntia vallata, Cleistostoma edwardsii*, *Callianassa kraussi* and *Upogebia africana*, all of which were consistent in 1999 as well. The variability in species abundance for the remaining species was high. Only 10 species contributed more than 3% each to the average dissimilarity between *Zostera* and sandflat-associated assemblages.

There was relatively little temporal difference between 1999 and 2000 when comparing the two habitats and the species identified as either characteristic of or distinguishing the habitats. There were greater differences between the two habitats in 1999 (D = 83.41%) than in 2000 (70.63%) as well as greater average similarities (S = 62.86% *vs.* 52.59% for *Zostera*-associated and S = 56.68% *vs.* 45.60% for sandflat-associated). SIMPER analyses identified twice the number of species in 2000 as characteristic of *Zostera*-associated habitats than in 1999, but the three

Table 3.5: Characteristic species for (A) *Zostera*-associated and (B) Sandflat-associated habitats as determined by SIMPER analyses based on fourth-root transformed invertebrate densities sampled in 2000 and the Bray-Curtis measure of similarity. The ranking is determined by S_i, the average contribution of each species to the overall similarity of each habitat (S). AvD indicates the average density of each species from all sites within each habitat. $S_i/SD(S_i)$ is the ratio between S_i and $SD(S_i)$, the standard deviation of S_i. This ratio reflects how consistently the species abundance varied within each habitat. $\sum S_i\%$ is the cumulative percentage contribution of each species to the overall similarity, S. Only taxa accounting for the first 90% of the cumulative similarity are shown.

2000	Characteristic species			
***Zostera*-Associated**	**AvD**	**S_i**	**$S_i/SD(S_i)$**	**$\sum S_i\%$**
Lumbrineris tetraura	1323.0	13.11	1.09	24.93
Perinereis nuntia vallata	57.50	10.76	4.25	45.39
Cleistostoma edwardsii	38.0	9.76	8.91	63.94
Upogebia africana	16.7	7.52	3.84	78.24
Anthothoe Stimpsoni	4.50	2.43	0.68	82.86
Orbinia angrapequensis	5.50	1.71	0.52	86.12
Hydrobia sp.	3.10	1.51	0.69	88.99
Assiminia globulus	72.20	1.28	0.35	91.42
Overall Similarity (%)				52.59
Sandflat-Associated	**AvD**	**S_i**	**$S_i/SD(S_i)$**	**$\sum S_i\%$**
Orbinia angrapequensis	39.80	10.70	1.69	23.47
Cleistostoma edwardsii	5.40	9.42	5.29	44.12
Callianassa kraussi	7.40	6.91	1.24	59.28
Marphysa depressa	3.90	5.44	1.22	71.22
Urothoe grimaldii	8.20	3.89	0.69	79.76
Upogebia africana	1.30	3.54	0.92	87.53
Hymenosoma orbiculare	1.30	1.17	0.38	90.10
Overall Similarity (%)				45.60

Table 3.6: Major species distinguishing between *Zostera*-associated and sandflat-associated habitats, as determined by SIMPER analyses based on fourth-root transformed invertebrate densities sampled in 2000 and the Bray-Curtis measure of similarity. The ranking is determined by D_i, the average contribution of each species to the overall dissimilarity of each habitat (D). AvD indicates the average density of each species from all sites within each habitat. $D_i/SD(D_i)$ is the ratio between D_i and $SD(D_i)$, the standard deviation of D_i. This ratio reflects how consistently the species abundance differed between habitats. $\sum D_i\%$ is the cumulative percentage contribution of each species to the overall dissimilarity, D. Only taxa accounting for first 80% of the cumulative similarity are shown.

2000: Distinguishing species	**AvD *Zostera***	**AvD Sandflat**	**D_i**	**$D_i/SD(D_i)$**	**$\sum D_i\%$**
Lumbrineris tetraura	1323.0	158.90	11.80	1.50	16.71
Perinereis nuntia vallata	57.50	3.70	6.55	2.41	25.98
Orbinia angrapequensis	5.50	39.80	4.03	1.29	31.68
Callianassa kraussi	0.00	7.40	3.83	1.81	37.10
Assiminea globulus	72.20	0.00	3.57	0.68	42.15
Upogebia africana	16.70	1.30	3.18	1.56	46.66
Urothoe grimaldii	0.00	8.20	3.12	1.17	51.07
Anthothoe stimpsoni	4.50	0.50	2.83	1.12	55.08
Cleistostoma edwardsii	38.00	5.40	2.67	1.96	58.86
Marphysa depressa	0.40	3.90	2.50	1.28	65.40
Hymenosoma orbiculare	6.00	1.30	2.30	1.01	65.66
Siphonaria compressa	16.10	0.0	2.20	0.72	68.77
Hydrobia sp.	3.10	0.40	2.05	1.13	71.67
Scoloplos johnstonei	2.30	1.40	1.70	0.86	74.07
Tellimya trigona	1.50	1.80	1.56	0.68	76.28
Volvarina capensis	0.90	0.60	1.46	0.86	78.35
Protomella capensis	0.10	2.20	1.44	0.71	80.39
Overall Dissimilarity (%)					70.63

most consistently characteristic species were common to both years. In the sandflats there was more variation in the species that most fundamentally influenced similarity within habitats and differences between habitats. Nevertheless, of the top seven species distinguishing habitats in 1999, all but one fell in the top nine in 2000. The only exceptions were *Lumbrineris tetraura* (rare in 1999, but the most important distinguishing species in 2000) and *Scoloplos johnstonei* (the 4th most important distinguishing species in 1999, but less so in 2000). The most consistently distinguishing species (as indicated by similarly high $D_i/SD(D_i)$) were *Perinereis nuntia vallata*, *Orbinia angrapequensis*, *Upogebia africana*, *Assiminea globulus*, *Callianassa kraussi*, *Urothoe grimaldii* and *Cleistostoma edwardsii*.

Patterns were thus remarkably consistent between 1999 and 2000 in terms of the indicator species distinguishing between macrofaunal assemblages in *Zostera* beds and sandflat-associated habitats (Figure 3.3). Most striking is that species indicative of each habitat were either absent or occurred in very low densities in the other habitat, reflecting the divergent macrofaunal communities that exist between the two habitats.

3.3.3 *Species Richness and Diversity*

A comparison was made of richness and diversity indices of species sampled within *Z. capensis* and the adjacent sandflats. In 1999, the total number of species averaged across all sites within sandflat areas was almost 34% greater than that of *Z. capensis* areas (Table 3.7). This was further confirmed by Margalef's richness index (d'), which established that species richness in the open sandflat was approximately 73% higher than that within the *Z. capensis* bed (Table 3.7). This pattern was also reflected in the Shannon index (53% higher in sandflat versus *Z. capensis*). Conversely, the total number of individuals was 109% greater in *Zostera* than in the sandflats. These patterns remained unchanged if the comparisons were made only for those sites at which both habitats were present. Analyses of the four indices comparing site and habitat by means of two-way factorial ANOVA for the sites that had both habitats are shown in Table 3.8. The number of individuals was affected only by the habitat effect. Species richness indices (both Total species and Margalef's Richness) showed highly significant results ($p < 0.001$) for both main effects (site and habitat), but no interaction between them (Table 3.8). Interpretation of the Shannon diversity index however was clouded by a significant interaction between site and habitat. However, post-hoc Tukey tests (Table 3.9) showed that diversity differed between habitats at all four sites and that the site effect was due only to Oesterwal having a lower value than the other sites for *Zostera* samples.

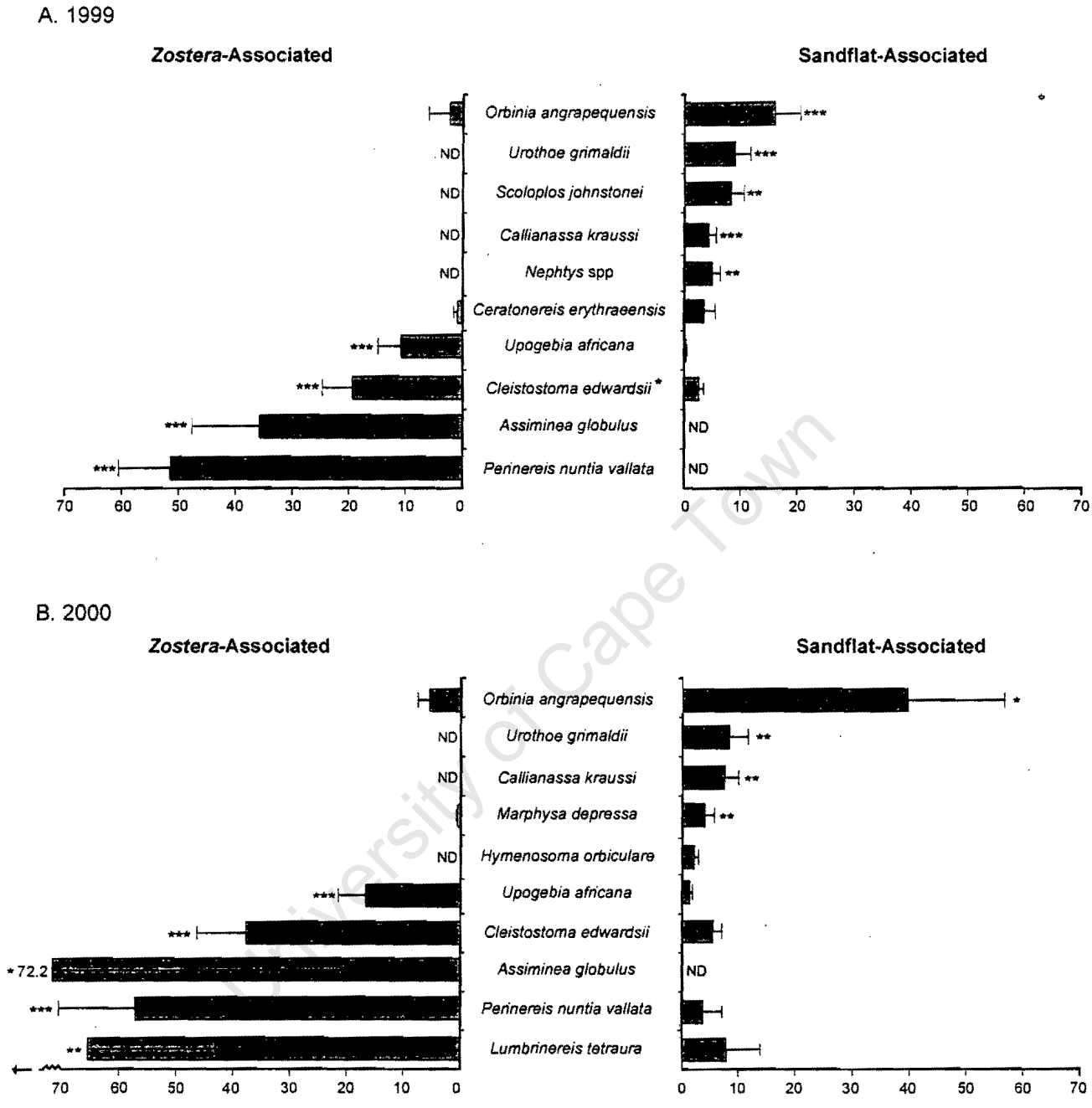


Figure 3.3: Mean density per $0.1m^2$ (+ or - SE) of indicator species sampled in (A) 1999 and (B) 2000 that consistently distinguished between *Zostera*-associated and sandflat-associated habitats, as determined by SIMPER analyses. Taxa accounting for 90 % of the cumulative similarity are shown: *, ** and *** denote significant differences between habitats at $p< 0.05$, $p< 0.01$ and $p< 0.001$ respectively, as determined by Mann-Whitney U tests. Significant differences between sites are indicated by * next to the species name. ND denotes absence of a species from a particular habitat. The data for *L. tetraura* are divided by 20 to scale them down.

Table 3.7: Indices of species richness, diversity and abundance for invertebrates sampled in 1999. Species richness is given as the Total Number of Species (S) and Margalef's richness index (d'). Shannon Diversity was determined by PRIMER analyses based on fourth-root transformed data. All of the data are mean (±SE) values per site and habitat. ND denotes absence of a particular habitat.

	Indices							
1999	**Total Species (S)**		**Margalef's Richness (d')**		**Total Individuals (N)**		**Shannon Diversity (H')**	
Site	***Zostera***	**Sandflat**	***Zostera***	**Sandflat**	***Zostera***	**Sandflat**	***Zostera***	**Sandflat**
Klein Oesterwal	12.5 (± 1.5)	14.0 (± 1.0)	2.3 (± 0.2)	3.1 (± 0.2)	135.0 (± 32.0)	70.0 (± 1.0)	1.5 (± 0.03)	2.0 (± 0.0)
Oesterwal	4.5 (± 0.5)	10.5 (± 0.5)	0.8 (± 0.04)	2.2 (± 0.1)	65.0 (± 23.0)	69.0 (± 1.0)	0.6 (± 0.02)	2.0 (± 0.0)
Bottelary	8.5 (± 0.5)	12.0 (± 0.0)	1.5 (± 0.04)	2.3 (± 0.1)	141.0 (± 25.0)	123.0 (± 35.0)	1.4 (± 0.1)	1.9 (± 0.06)
Geelbek	5.0 (± 0.0)	9.0 (± 1.0)	0.8 (± 0.04)	1.9 (± 0.05)	163.5 (± 3.5)	68.5 (± 25.6)	1.3 (± 0.03)	1.9 (± 0.08)
MEAN	7.6 (±1.2)	11.4 (± 0.7)	1.4 (± 0.2)	2.4 (±0.2)	126.1 (± 16.5)	82.6 (± 12.1)	1.2 (± 0.1)	1.9 (± 0.03)
Schrywershoek	ND	8.5 (± 0.5)	ND	1.9 (± 0.04)	ND	47.9 (± 15.6)	ND	1.4 (± 0.2)
ChurchHaven	ND	9.0 (± 1.0)	ND	2.6 (± 0.2)	ND	21.0 (± 2.0)	ND	1.8 (± 0.09)
Kraalbaai	ND	8.5 (± 0.5)	ND	2.4 (± 0.2)	ND	22.5 (± 1.5)	ND	1.9 (± 0.1)
TOTAL MEAN		10.2 (± 0.6)		2.4 (± 0.1)		60.3 (± 10.2)		1.8 (± 0.0)

Table 3.8: Results of Two-way ANOVA's on the effects of habitat and site on diversity indices sampled in 1999. Species Richness is represented by Total number of species (S) and Margalef's Richness (d'). Abundance is represented by Total number of individuals (N) and Species Diversity by the Shannon Diversity Index, as determined by PRIMER analyses based on fourth-root transformed data.

1999	**Two-Way ANOVA**				
Total Species (S)	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	3	33.17	26.53	<0.001	Significant
Habitat	1	56.25	45.0	<0.001	Significant
Site X Habitat	3	3.41	2.73	0.113	Not Significant
Margalef's Richness (d')	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	3	1.41	43.13	<0.001	Significant
Habitat	1	4.12	126.04	<0.001	Significant
Site X Habitat	3	0.10	2.97	0.096	Not Significant
Total Individuals (N)	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	3	3064.9	2.97	0.096	Not Significant
Habitat	1	7569.0	7.35	0.027	Significant
Site X Habitat	3	2007.0	1.95	0.200	Not Significant
Shannon Diversity (H')	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	3	0.18	34.43		
Habitat	1	2.25	437.40		
Site X Habitat	3	0.21	40.50	<0.001	Significant

Table 3.9: Results of post-hoc Tukey tests analysing the effects of the means of one factor separately at each level of the other factor and *vice versa*. ns= not significant ($p < 0.05$).

	TUKEY TESTS			
1999	Shannon Diversity (H')			
A: Effect of site at each habitat	***Zostera***		**Sandflat**	
Klein Oesterwal *vs.* Bottelary	ns		ns	
Klein Oesterwal *vs.* Oesterwal	<0.001		ns	
Klein Oesterwal *vs.* Geelbek	ns		ns	
Bottelary *vs.* Oesterwal	<0.001		ns	
Bottelary *vs.* Geelbek	ns		ns	
Oesterwal *vs.* Geelbek	<0.001		ns	
B: Effect of habitat at each site	**Klein Oesterwal**	**Oesterwal**	**Bottelary**	**Geelbek**
Zostera vs. Sandflat	0.001	0.001	<0.001	0.001

In 2000 the patterns were less clear-cut. Both total species and Margalef's richness index were not significantly different between habitats (Tables 3.10 & 3.11). The Shannon diversity index was greater on sandflats than in *Zostera* (Table 3.10) but ANOVA indicated a significant interaction between the main effects of site and habitat (Table 3.11). Post-hoc Tukey tests revealed that significant differences between habitats were limited to one site only (Bottelary North). The total number of individuals was also affected by an interaction between the main effects (Table 3.11). In this case, however, Tukey tests showed that numbers of individuals were significantly smaller in sandflats than in *Zostera* at three of the five sites. Considering the two years together, all three diversity and richness indices were greater in the sandflats than in *Z. capensis* in 1999 but statistically indistinguishable in 2000. Conversely, the total number of individuals was greater within *Z. capensis* than in the adjacent sandflats in both years.

Table 3.10: Indices of Species Richness, Diversity and abundance for invertebrates sampled in 2000. Species richness is given as the Total number of species (S) and by Margalef's richness index (d'). Shannon Diversity was determined by PRIMER analyses based on fourth-root transformed data. All the data are mean (±SE) values per site and habitat.

	Diversity Index							
2000	**Total Species (S)**		**Margalef's Richness (d')**		**Total Individuals (N)**		**Shannon Diversity (H')**	
Site	***Zostera***	**Sandflat**	***Zostera***	**Sandflat**	***Zostera***	**Sandflat**	***Zostera***	**Sandflat**
Klein Oesterwal South	10.0 (± 3.0)	9.5 (± 1.5)	1.5 (± 0.5)	2.1 (± 0.3)	549.0 (± 140.0)	58.5 (± 9.5)	1.2 (± 0.3)	1.9 (± 0.1)
Klein Oesterwal North	13.0 (± 1.0)	7.5 (± 0.5)	1.5 (± 0.1)	1.5 (± 0.1)	2291.0 (± 414.0)	96.0 (± 48.0)	0.4 (± 0.03)	1.2 (± 0.3)
Bottelary South	13.0 (± 0.0)	9.5 (±0.5)	2.1 (± 0.04)	1.7 (± 0.2)	264.5 (± 2.5)	160.5 (± 39.5)	1.8 (± 0.3)	1.1 (± 0.2)
Bottelary North	9.5 (± 1.5)	9.5 (± 0.5)	1.0 (± 0.1)	2.1 (± 0.3)	3579.0 (± 911.0)	59.0 (± 18.0)	0.3 (± 0.1)	1.8 (± 0.1)
Oesterwal	7.5 (± 1.5)	6.5 (± 0.5)	0.9 (± 0.2)	0.8 (± 0.01)	1129.5 (± 303.5)	830.0 (± 386.0)	0.4 (± 0.1)	0.3 (± 0.1)
MEAN	10.6 (± 0.9)	8.5 (± 0.6)	1.4 (± 0.2)	1.6 (± 0.2)	1562.6 (± 494.2)	240.8 (± 114.9)	0.8 (± 0.2)	1.7 (± 0.2)

Table 3.11: Results of Two-way ANOVA's on the effects of habitat and site on diversity indices sampled in 2000. Species Richness is represented by Total number of species (S) and Margalef's Richness (d'). Abundance is represented by Total number of individuals (N) and Species Diversity by the Shannon Diversity Index, as determined by PRIMER analyses based on root-transformed data.

2000	Two-Way ANOVA				
Total Species (S)	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	4	0.02	2.91	0.076	Not Significant
Habitat	1	0.03	4.87	0.052	Not Significant
Site X Habitat	4	0.01	1.33	0.325	Not Significant
Margalef's Richness (d')	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	4	0.63	5.34	0.01	Significant
Habitat	1	0.23	1.99	0.187	Not Significant
Site X Habitat	4	0.39	3.36	0.054	Not Significant
Total Individuals (N)	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	4	0.33	8.92		
Habitat	1	4.17	113.22		
Site X Habitat	4	0.51	13.85	<0.001	Significant
Shannon Diversity (H')	**df Effect**	**MS Effect**	**F**	**p-level**	
Site	4	0.99	11.31		
Habitat	1	0.95	10.72		
Site X Habitat	4	0.77	8.71	0.002	Significant

Table 3.12: Results of post-hoc Tukey tests analysing the effects of the means of one factor separately at each level of the other factor and *vice versa*. ns= not significant (p> 0.05).

	TUKEY TESTS				
2000	Total Individuals (N)				
A: Effect of site at each habitat		*Zostera*		Sandflat	
Klein Oesterwal South *vs.* Klein Oesterwal North		ns		ns	
Klein Oesterwal South *vs.* Bottelary South		ns		ns	
Klein Oesterwal South *vs.* Bottelary North		0.033		ns	
Klein Oesterwal South *vs.* Oesterwal		ns		0.004	
Klein Oesterwal North *vs.* Bottelary South		0.014		ns	
Klein Oesterwal North *vs.* Bottelary North		ns		ns	
Klein Oesterwal North *vs.* Oesterwal		0.003		0.013	
Bottelary South *vs.* Bottelary North		ns		ns	
Bottelary South *vs.* Oesterwal		ns		ns	
Bottelary North *vs.* Oesterwal		ns		0.004	
B: Effect of habitat at each site	**Klein Oesterwal South**	**Klein Oesterwal North**	**Bottelary South**	**Bottelary North**	**Oesterwal**
Zostera vs. Sandflat	0.011	<0.001	ns	<0.001	ns
	TUKEY TESTS				
	Shannon Diversity (H')				
A: Effect of site at each habitat		*Zostera*		Sandflat	
Klein Oesterwal South *vs.* Klein Oesterwal North		ns		ns	
Klein Oesterwal South *vs.* Bottelary South		ns		ns	
Klein Oesterwal South *vs.* Bottelary North		ns		ns	
Klein Oesterwal South *vs.* Oesterwal		ns		0.005	
Klein Oesterwal North *vs.* Bottelary South		0.017		ns	
Klein Oesterwal North *vs.* Bottelary North		ns		ns	
Klein Oesterwal North *vs.* Oesterwal		ns		ns	
Bottelary South *vs.* Bottelary North		0.008		ns	
Bottelary South *vs.* Oesterwal		0.014		ns	
Bottelary North *vs.* Oesterwal		ns		ns	
B: Effect of habitat at each site	**Klein Oesterwal South**	**Klein Oesterwal North**	**Bottelary South**	**Bottelary North**	**Oesterwal**
Zostera vs. Sandflat	ns	ns	ns	0.009	ns

3.3.4 *Sediment Penetrability*

The physical penetrability of the sediment within the intertidal sandflat was consistently higher than that within the *Z. capensis* bed (Figure 3.4), suggesting that both binding of the sediment by *Z. capensis* and mechanical disturbance via bioturbation have marked effects on the sediment stability within the corresponding habitats.

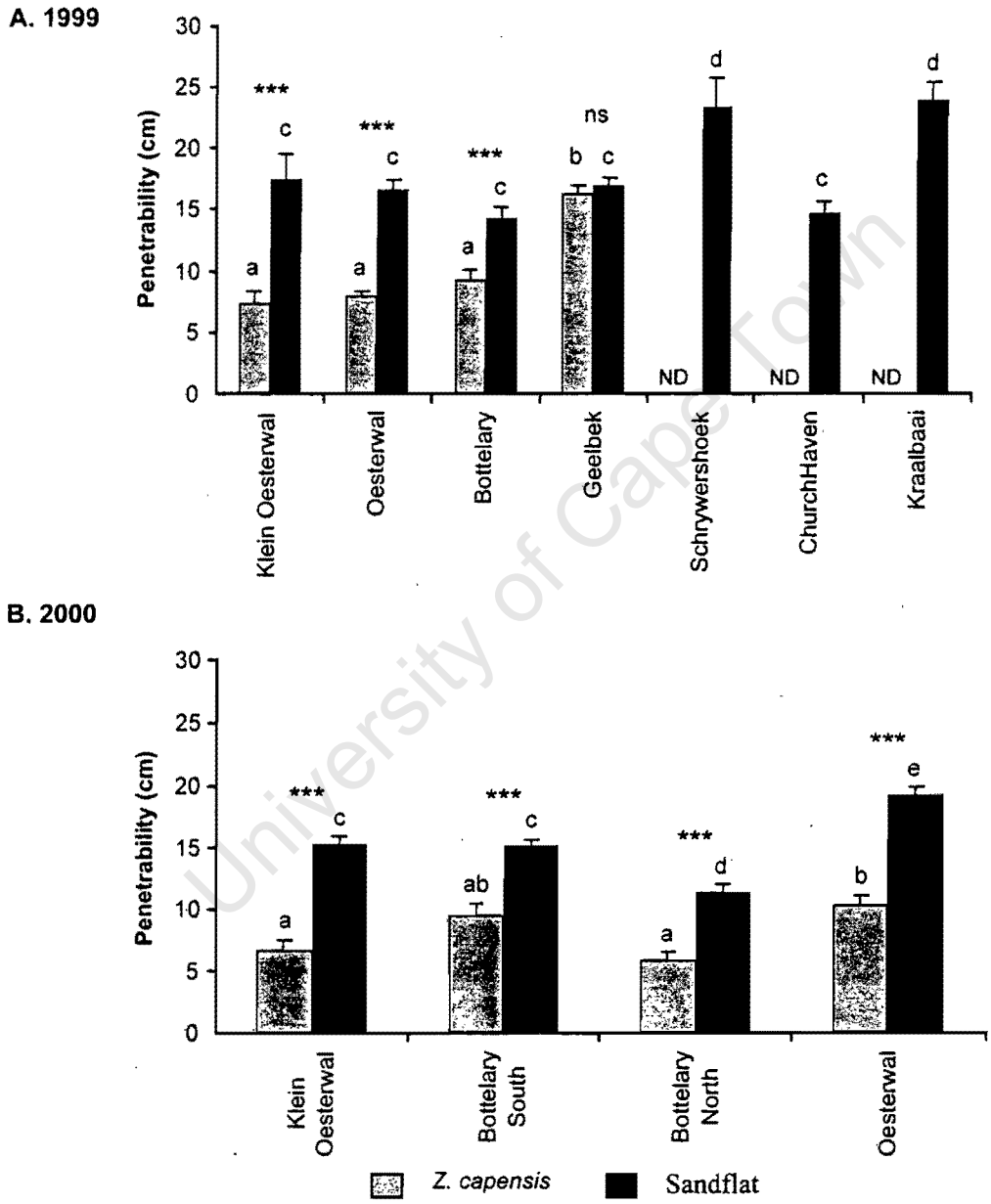


Figure 3.4: A comparison of the mean (+SE) penetrability (cm) of the sediment within *Z. capensis* beds and in the adjacent intertidal sandflat in (A) 1999 and (B) 2000. ND denotes no data due to the absence of eelgrass. *** indicates sites at which significant differences existed between habitats ($p < 0.001$), and samples that share letters indicate sites that were not significantly different within habitats.

Direct statistical comparisons of sedimentary character between habitats could only be made between the first four sites in 1999, as *Z. capensis* does not naturally occur at Schrywershoek, ChurchHaven and Kraalbaai. At Klein Oesterwal, Oesterwal and Bottelary the sediment penetrability was significantly greater within the intertidal sandflat compared to the *Z. capensis* bed. At Geelbek, penetrability was not significantly different in these two habitats, most likely a consequence of the finer sediments that exists there.

A two-way ANOVA comparing the effects of site and habitat on penetrability at these four sites produced a significant interaction between the main factors ($F_{3, 82} = 20.436$, $p < 0.001$). When this occurs, tests of the main effects are unreliable. As a result, the means of one factor were compared separately at each level of the other factor and *vice versa* by multiple comparison Tukey-tests. These indicated that for all sites except Geelbek, the penetrability within and outside *Z. capensis* beds was significantly different ($p < 0.001$). A one-way ANOVA testing the effects of site separately across sandflat samples at all seven sites showed highly significant differences between sites ($F_{6, 113} = 17.227$, $p < 0.001$). Post-hoc Tukey tests on site effects revealed significant differences in penetrability at Schrywershoek and Kraalbaai on the western shore of the lagoon where *Z. capensis* is absent, versus all other sites, most of which lay on the eastern shore where *Z. capensis* was present (Figure 3.4 A).

A similar pattern was evident from penetrability measurements taken in 2000 (Figure 3.4 B). Penetrability outside *Z. capensis* was between 1.5 and 2.3 times higher than inside *Z. capensis* at all of the sample sites. Once again, a two-way ANOVA comparing the effects of habitat and site on penetrability revealed a significant interaction between the main factors (two-way ANOVA $F_{3, 72} = 3.773$, $p = 0.014$). Post-hoc Tukey-test results showed that the comparison of sediment penetrability inside versus outside *Z. capensis* was consistently significantly different ($p < 0.001$) at all sites (Figure 3.4 B), but there were also significant differences between sites within the two habitats.

3.3.5 *Morphological Characteristics*

To test hypotheses advanced by Brenchley (1981, 1982), differences between macrofaunal assemblages sampled within *Z. capensis* beds and in sandflats were assessed according to their relative mobility and functional morphology (burrowing *vs.* non-burrowing; hard-bodied *vs.* soft-bodied). Eight sets of data were considered: three sites sampled in 1999, and five in 2000.

Brenchley's first hypothesis proposed that a disproportionately greater number of hard-bodied fauna should reside in bare, unvegetated sandflats whereas *Zostera* beds should sustain more

soft-bodied, flexible fauna. Two methods were employed to address this question. The first was to explore the proportions of species representative of different morphological categories that were found within *Z. capensis* beds versus the adjacent sandflats. Figure 3.5 presents the data collected in 1999 and 2000 respectively. In seven of the eight cases analysed, the data did not deviate from the expected chi-square values. The eighth case (Oesterwal) on the other hand, the data showed a significant difference from that expected by chance but exhibited a trend opposite to Brenchley's predictions, with fewer soft-bodied species and more hard-bodied species existing within the *Zostera* bed, and *vice versa* for the sandflat habitat. Examining the data in this way by using the proportion of species as the unit of analysis is, however, of questionable value in some instances, as the numbers of species sampled within each habitat were in some cases less than those recommended for valid Chi-square analyses (Zar, 1984; Garvin, 1986).

The same hypotheses can, however, be assessed in a different manner by examining the proportions of individuals representing the same morphological categories (Figure 3.6). This, too, revealed a similar pattern. Of these eight cases explored, one yielded a non-significant result; four showed support for the hypothesis while the remaining three opposed it. Consequently, support for Brenchley's first hypothesis is ambivalent, whether the results are considered in terms of the number of species or the number of individuals within each habitat.

Brenchley's second hypothesis proposed that burrowing fauna would be disproportionately more abundant within sandflats as opposed to *Z. capensis* beds, with the reverse trend among non-burrowing fauna. Again, the data can be explored in terms of the number of species or the number of individuals. With reference to the proportions of species representing either burrowing or non-burrowing taxa within each habitat, the data supported Brenchley's hypothesis in only two of the eight cases (Figure 3.7). The remaining six showed no significant differences in the frequency of burrowing *versus* non-burrowing species from those expected by chance. As noted above, however, these results should be interpreted with caution because of low sample numbers.

In contrast, analysis of the proportion of individuals from each category provided more convincing support for Brenchley's (1982) hypothesis, with five of the eight cases conforming to her predictions (Figure 3.8). Even though the remaining three yielded non-significant results, their trends were consistent with the hypothesis. Overall, there was modest support for the hypothesis when considering the number of species, but stronger support when analysing the number of individuals. None of the cases yielded results that were in opposition to Brenchley's expectation that *Zostera* beds should contain fewer burrowers and sandflats more burrowers than expected by chance.

HYPOTHESIS 1a:
Hard Bodied Species *vs.* Soft Bodied Species

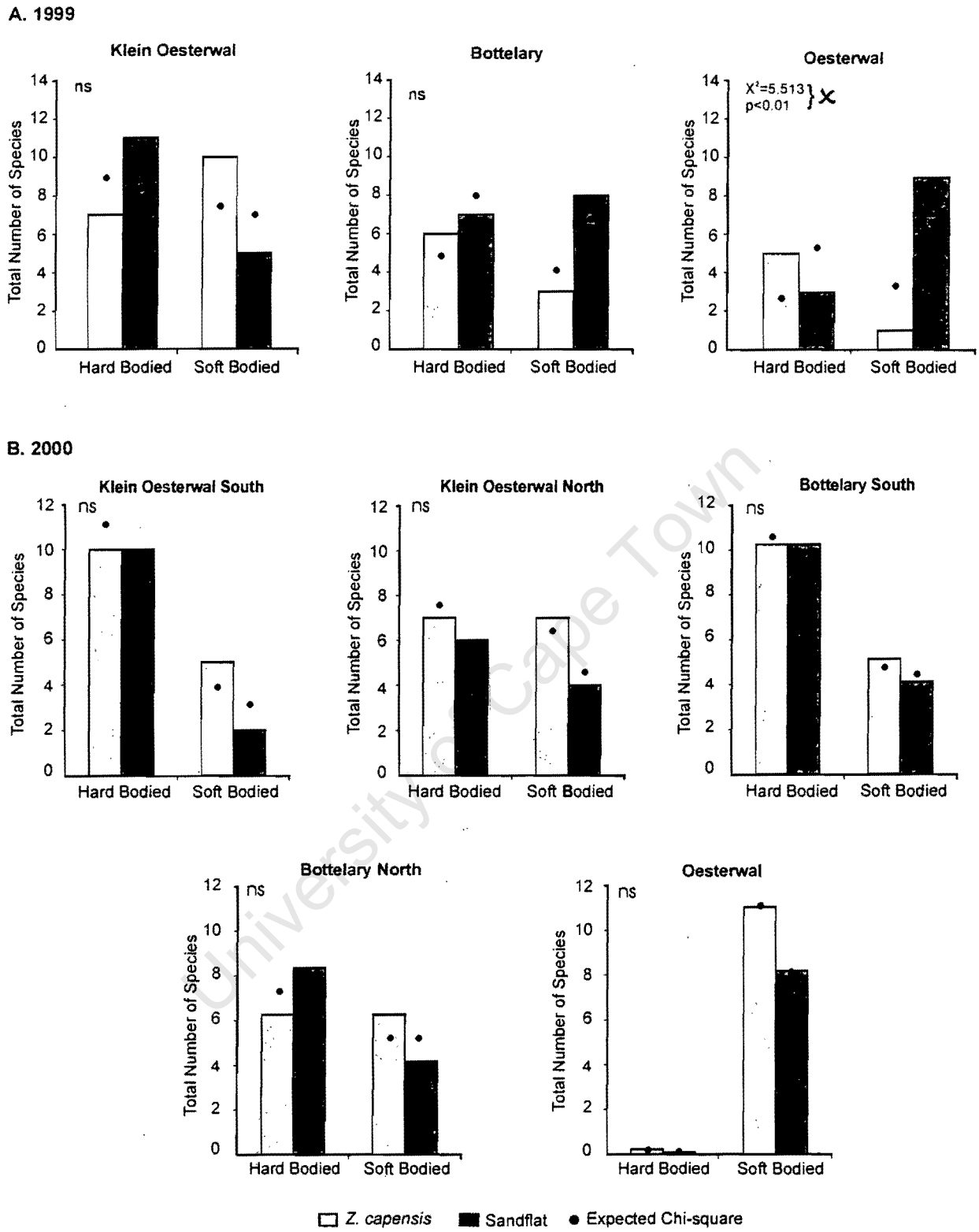


Figure 3.5: Histograms showing the total number of hard-bodied and soft-bodied species sampled within *Z. capensis* beds or in sandflats (A) at three sites in 1999 and (B) five sites in 2000. Dots indicate expected values. Chi-square analyses and corresponding p-values shows significant differences between expected and observed values for hard and soft-bodied species found within eelgrass compared to the sandflat; ns denotes absence of significance. In cases where there were significant departures from the expected values, tick or cross symbols show either support for or opposition to Brenchley's (1982) hypothesis.

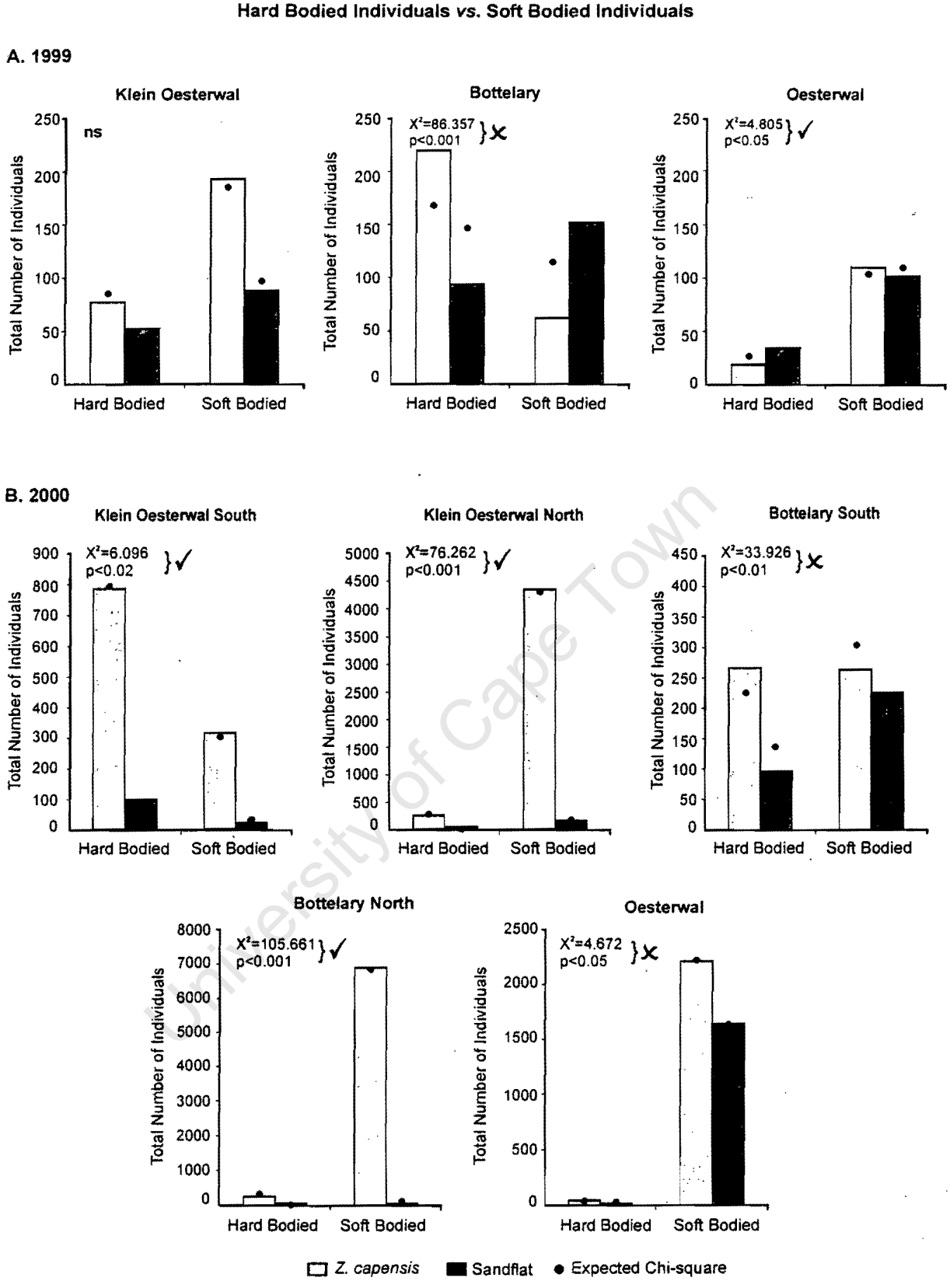


Figure 3.6: Histograms showing the total numbers of hard-bodied and soft-bodied Individuals sampled within *Z. capensis* beds or in the sandflats at three sites in (A) 1999 and five sites in (B) 2000. Dots indicate expected values. Chi-square analyses and corresponding p-values shows significant differences between expected and observed values for hard and soft-bodied individuals found within eelgrass compared to the sandflat; ns denotes absence of significance. In cases where there were significant departures from expected values, tick and cross symbols show either support for or opposition to Brenchley's (1982) hypothesis. Note the different scale of the ordination between sites and years.

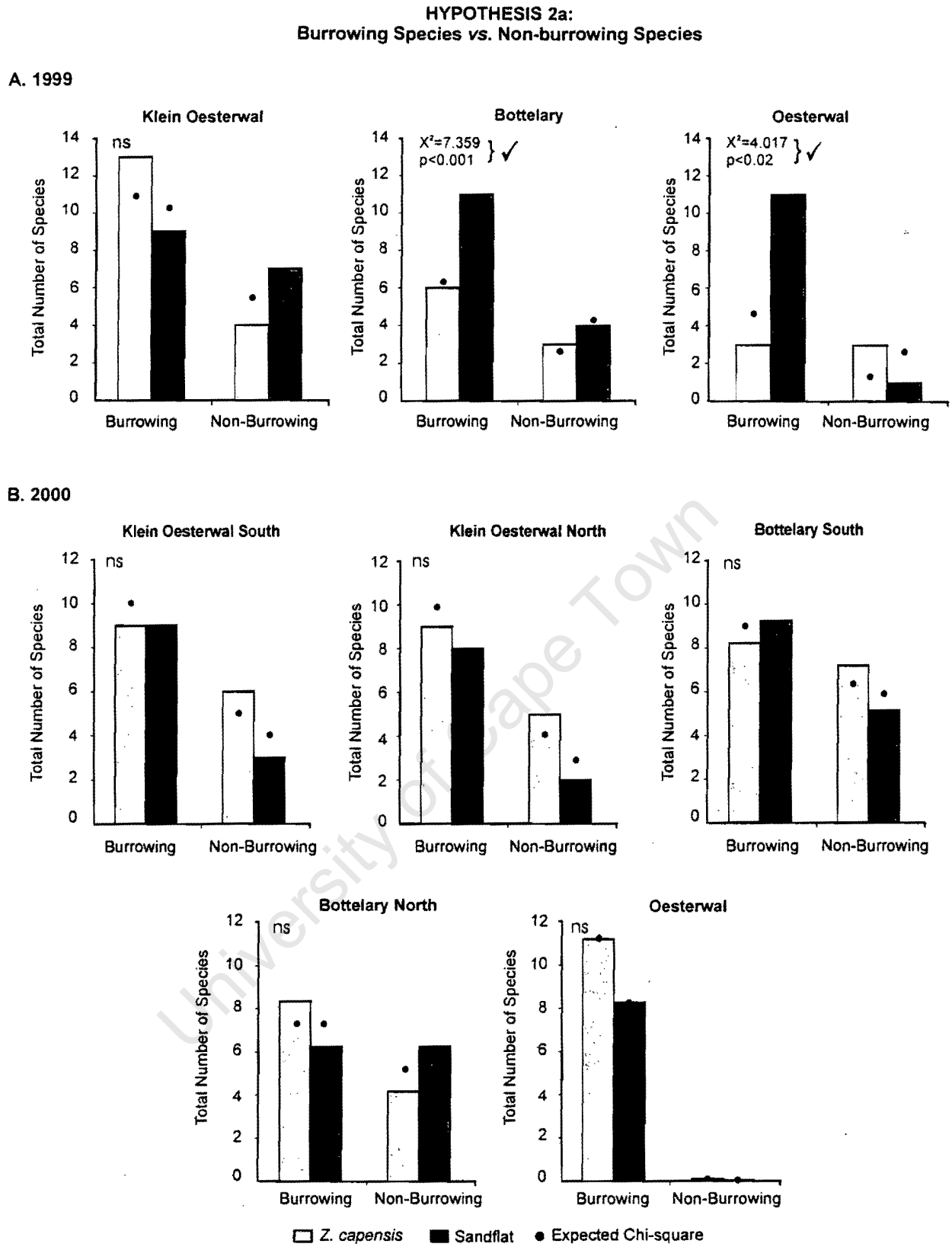


Figure 3.7: Histograms showing the total number of burrowing and non-burrowing species sampled within *Z. capensis* beds or in sandflats (A) at three sites in 1999 and (B) five sites in 2000. Dots indicate expected values. Chi-square analyses and corresponding p-values shows significant differences between expected and observed values for burrowing and non-burrowing species found within eelgrass compared to the sandflat; ns denotes absence of significance. In cases where there were significant departures from expected values, tick and cross symbols show either support for or opposition to Brenchley's (1982) hypothesis.

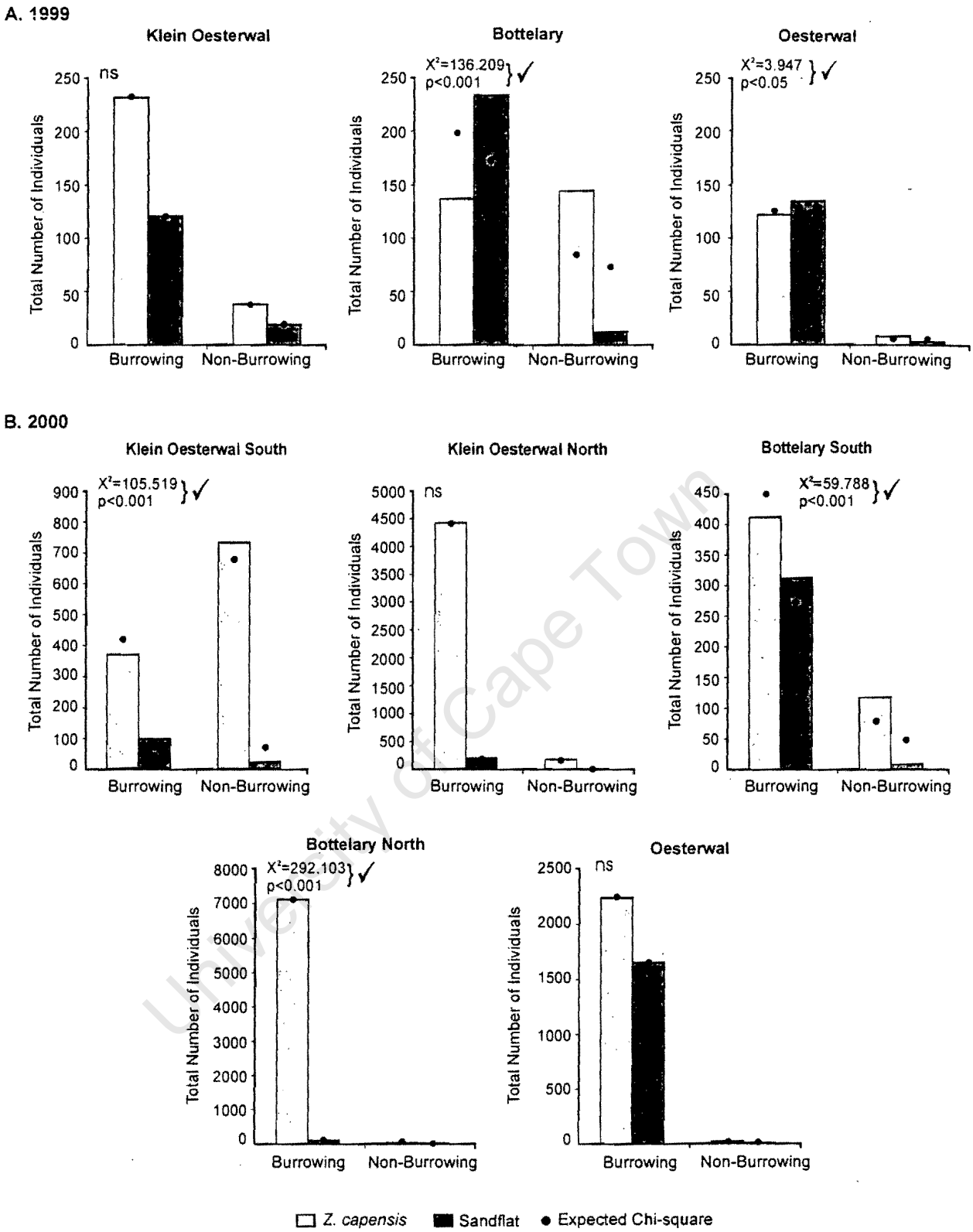


Figure 3.8: Histograms showing the total number of burrowing and non-burrowing individuals sampled within *Z. capensis* beds or in sandflats (A) at three sites in 1999 and (B) five sites in 2000. Dots indicate expected values. Chi-square analyses and corresponding p-values shows significant differences between expected and observed values for burrowing and non-burrowing individuals found within eelgrass compared to the sandflat; ns denotes absence of significance. In cases where there were significant departures from expected values, tick and cross symbols show either support for or opposition to Brenchley's (1982) hypothesis. Note the different scales of the ordination between sites and years.

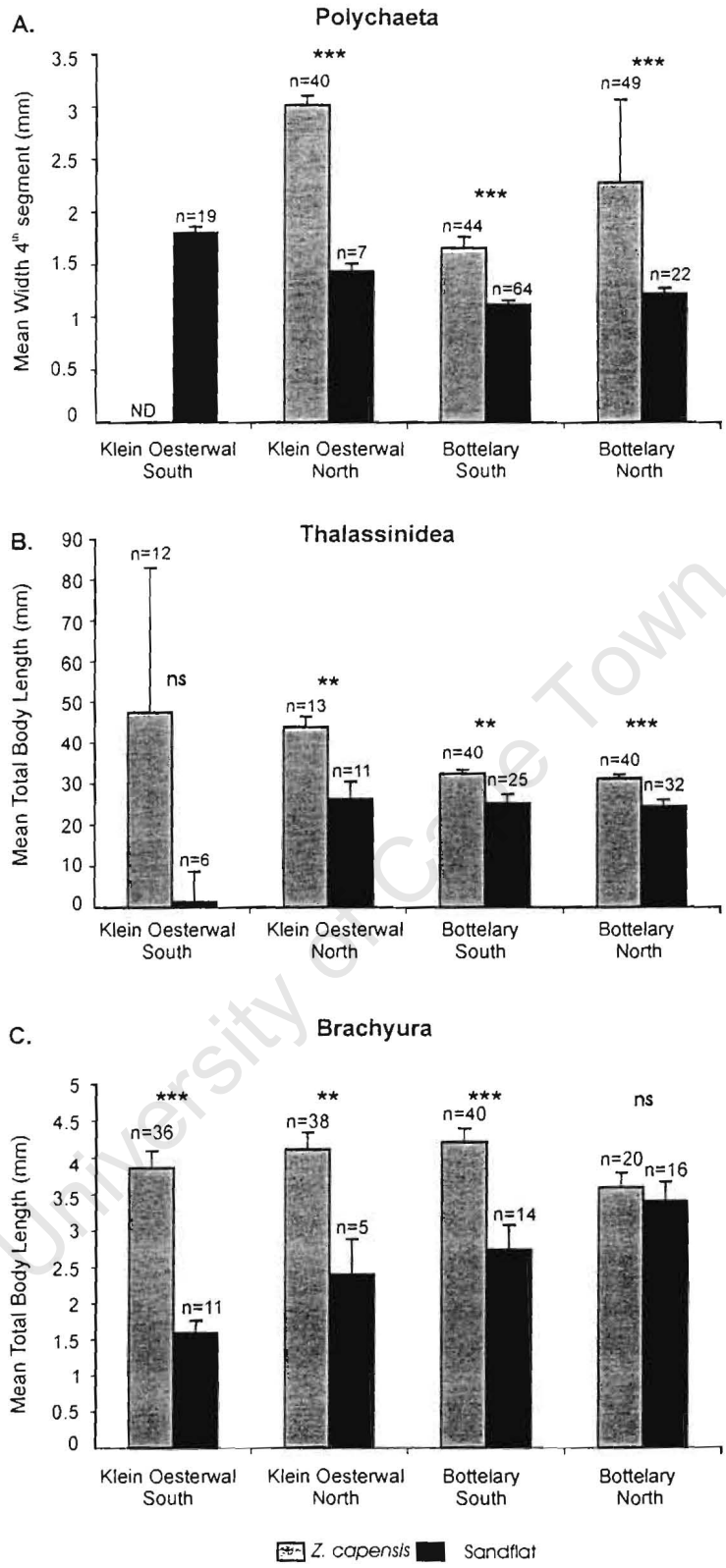


Figure 3.9: Mean sizes (+SE) of (A) Polychaeta, (B) thalassinidean prawns and (C) Brachyura sampled within *Z. capensis* beds and in sandflats; ** and *** denotes significant differences between habitats at $p< 0.01$ and $p< 0.001$ respectively (Mann-Whitney U tests). ND indicates the absence of individual; n= sample sizes for each observation.

3.3.6 *Invertebrate Size*

Body sizes of three taxa (Polychaeta, Thalassinidea and Brachyura), encompassing the major forms of locomotion among macrofauna, were measured at four sites to test the hypothesis that larger individuals, and larger representatives of morphologically similar species should be relatively less abundant within eelgrass beds than in sandflats (Brenchley, 1982). In the three taxa considered, the mean sizes of individuals present within *Z. capensis* were significantly larger than those of their sandflat counterparts in all but one case (Thalassinidea at Klein Oesterwal South), for which there was no significant difference between the habitats (Figure 3.9). Thus, the data contradict Brenchley's hypothesis.

3.4 Discussion

It is well known that natural assemblages in marine habitats are patchy and often unpredictably variable through space and time (Underwood, 2000). Such variability is likely to manifest itself in changes in community composition. In particular, the availability and quality of habitat can affect abundances and diversity of faunal communities; either directly by providing appropriate habitat in some places only, or indirectly by modifying biological interactions among different species (Menge *et al.*, 1985; Fairweather, 1988 in Underwood, 2000). The presence or absence of *Z. capensis* beds within Langebaan Lagoon emulate this, as results from field surveys presented in the previous chapter showed distinct eelgrass/sandflat habitats, with *Z. capensis* markedly restricted in its distribution. A consequence of this may be a ripple of indirect effects due to mediation of biological interactions by eelgrass. For example, the potentially negative effects of bioturbation by *C. kraussi* on *U. africana* may be prevented by sediment stabilisation by *Z. capensis*.

3.4.1 *Differences in faunal composition between habitats*

Vegetated sediments generally support different assemblages of species from nearby unvegetated sediments, manifested in distinct differences in species composition, numerical abundance, and diversity (Orth, 1977; Heck & Wetstone, 1977; Stoner, 1980; Homziak *et al.*, 1982; Fitzhardinge, 1983; Heck *et al.*, 1989; Edgar, 1990; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1997). Consideration of this dates back to as early as 1937 when, for example, Stauffer found that after the disappearance of *Zostera marina* in a Massachusetts estuarine lagoon, all species previously found on or amongst the seagrass disappeared and the only invertebrates remaining were those previously restricted to the surrounding substratum (Whitfield, 1989).

In my study, the faunal communities associated with both eelgrass beds and adjacent *Callianassa*-dominated, un-vegetated sandflats were surveyed at several sites around the lagoon to explore the degree to which unique faunal assemblages are associated with each of these habitats. As predicted, marked differences in community composition existed, with the fauna among *Z. capensis* stands clearly distinct from that of adjacent sandflats. *Z. capensis* beds were fundamentally represented by *Upogebia africana*, *Perinereis nuntia vallata*, *Assiminea globulus* and *Cleistostoma edwardsii,* with the notable addition of *Lumbrineris tetraura* in 2000. Sandflat areas on the other hand, were principally dominated by *Orbinia angrapequensis*, *Urothoe grimaldii* and *Callianassa kraussi*. Accordingly, many of the species sampled could be classified as either '*Zostera*-associated' or 'Sandflat-associated', with species representative of each habitat either absent or present in very low densities in the other habitat. Analogous results have been found in nearly all comparative studies of seagrass and unvegetated habitats, revealing differences in the dominant species present in each habitat (e.g. Homziak *et al.*, 1982; Hily & Bouteille, 1999).

Dissimilarities were further reflected in descriptive techniques (hierarchical cluster analysis and MDS ordination plots) comparing the two habitat regions. Quantitative analysis of both years showed substantial differences in community structure between *Zostera* and sandflat sites (Figures 3.1 and 3.2), with the faunal communities associated with each habitat forming two distinct assemblages, more than 75% dissimilar in composition. This was predominantly attributable to the handful of species listed above as distinguishing between the two habitats. Only two species (*Lumbrineris tetraura* and *Scoloplos johnstonei*) earmarked as fundamental to the divergence between the two communities were not consistently characteristic in both 1999 and 2000.

Although the number of species considered here as primarily responsible for the compositional differences between the two infaunal communities was small, confidence in these results is amplified by the agreement between the species identified as consistently characteristic of each habitat, first by simple univariate analyses (Table 3.1 and 3.2) and second via multivariate techniques. Furthermore, species identified as symptomatic of each habitat were either absent or present in very low densities in the other habitat (Figure 3.3), signifying two divergent macrofaunal communities, one associated with *Z. capensis* beds and the other with *Callianassa*-dominated sandflats. Despite some variability in this spatial pattern at certain sample sites, site differences were negligible relative to habitat differences, especially in the light of the consistency of the results between 1999 and 2000.

The complex spatial patterns produced by patchily distributed *Z. capensis* beds among vast intertidal sandflats may generate a specialized habitat, offering refugia for species that prefer more stable and structurally complex environments in contrast to the dynamic, unstable, homogenous environments that sandflats offer (Bostrom & Bonsdorff, 1997). Aspects of the structural complexity of seagrasses have been evoked in previous studies to explain faunal composition (e.g. shoot density, Homziak *et al.*, 1982; plant surface areas, Stoner & Lewis, 1985) and several means by which seagrass complexity exerts an influence on the infauna have been postulated (Webster *et al.*, 1998). For instance, increases in detrital food availability as a function of detritus-trapping by seagrass blades may attract particular species. Another factor likely to influence community structure between eelgrass and sandflat areas is predation. Although many predators such as fish and crustaceans reside in and around seagrass beds, predation efficiency may be reduced due to seagrass structural complexity (Heck & Wetstone, 1977; Bell & Westoby, 1986).

In addition to food availability and predation, indirect interactions between functional groups may play important roles in determining community composition. The concept of 'trophic group amensalism' has been widely used to explain negative interactions between soft-sediment organisms, for example between filter-feeders and deposit-feeders or between tube-dwellers and burrowers (e.g. Rhoads & Young, 1970; Aller & Dodge, 1974; Woodin, 1976; Myers, 1977; Weinberg, 1984; Levinton, 1985 and others). Such interactions can result in the exclusion of certain species by others and may orchestrate differences in community structure.

3.4.2 *Species Diversity, Richness and Abundance*

Several previous studies have shown significantly higher animal abundance and species diversity in vegetated areas than in adjacent bare substrates (Orth, 1977; Stoner, 1980; Fitzhardinge, 1983; Heck *et al.*, 1989; Edgar, 1990; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1997; Hily & Bouteille, 1999; Lee *et al.*, 2001). Blanket explanations for the higher abundance of macrofauna in vegetated habitats include (1) increased habitat heterogeneity (Heck & Wetstone, 1977), (2) stabilisation of sediments and subsequent accruement of organic material (Orth, 1977), (3) increased food supply from both accumulated detritus (Thayer *et al.*, 1975) and associated epifauna and epiflora (Kikuchi, 1980 in Fitzhardinge, 1983), and (4) decreased predation efficiency due to high habitat complexity (Bell & Westoby, 1986; Nelson & Bonsdorff, 1990 in Bostrom & Bonsdorff, 1997). My results contradict these studies. In 1999, the fauna associated with *Callianassa*-dominated sandflats in Langebaan Lagoon was richer and

more diverse than that of *Z. capensis* beds, and in 2000, the two habitats were statistically indistinguishable in terms of richness and diversity (Tables 3.7 and 3.10).

However, one of the central criticisms of diversity indices is that they can be particularly susceptible to sampling bias. Consequently, direct comparisons of univariate measures of the faunal community can only be made with caution (Lewis & Stoner, 1981 in Webster *et al.*, 1998). Indeed, community data are inherently highly multivariate and best analysed with multivariate techniques (Clarke & Warrick, 1994). In effect, univariate measures collapse a full set of species abundance data into a single co-efficient, which results in the loss of a host of information (Sink, 2001). Nevertheless, the univariate measures did indicate, that infaunal species diversity and richness were never greater (and often significantly less) in *Zostera* than in sandflat communities. Abundance was, however, always greater in *Zostera* than in adjacent sandflat communities.

The findings regarding diversity and richness are also in direct opposition to trends identified in several Southern African estuaries. Even estuaries with physical conditions similar to Langebaan Lagoon (e.g. the Kariega Estuary, which has a mouth that is permanently open to the sea and a freshwater input that is sporadic: see Hodgson, 1987) show greater diversity of fauna within *Z. capensis* beds than in adjacent bare substratum. Whitfield (1989) described the existence of two distinct faunal communities in the Swartvlei estuary and recorded higher species diversity in areas vegetated by *Z. capensis*. Similarly, Kaletja & Hockey (1991) found differences in the distribution of invertebrates in the Berg River, which they also attributed to vegetation cover.

The reversed trends in richness and diversity shown here are probably a function of site-specific biotic and abiotic interactions. Whereas certain components of the fauna may be directly limited by *C. kraussi* bioturbation (Suchanek, 1983), thus reducing species diversity and richness, others may benefit from the disturbance. For example, Flint & Kalke (1986) have reported that bioturbation may promote faunal assemblages by enhancing the colonisation of certain infaunal species. Increased penetrability and oxygenation associated with bioturbation (Kristensen *et al.*, 1985) may also favour particular organisms. Thus the balance between the adverse and positive biological effects of bioturbation may offer some explanation for higher diversity within *Callianassa*-dominated sandflats compared to eelgrass beds. Furthermore, some of the 'blanket' explanations for the higher diversity and richness in eelgrass beds may not always be applicable. For instance, if food is not limiting, then the elevated levels of detritus available in eelgrass beds may have no influence on richness and diversity (Webster *et al*, 1998). Similarly, various authors have suggested that predation can be more intense in eelgrass beds than in bare sandflats

(Whitfield, 1988; Young & Young, 1978 cited in Whitfield, 1989), perhaps accounting for the lower diversity recorded in the seagrass beds.

However, such causative explanations need to take into account the unique physical conditions inherent to Langebaan Lagoon. Edgar & Barrett (2002) determined that variation associated with faunal composition was higher between localities within estuaries than between different estuaries, suggesting that the interactions between physical conditions intrinsic to different parts of each estuary are important in driving community response and structure. Ultimately, the physical characteristics of the environment may be so extreme that they override the buffering effect that the structural complexity of seagrass imparts. Low species richness in seagrasses is generally associated with habitats that undergo extreme environmental changes (Jackson, 1973 in Lee *et al.*, 2001). In the present context, however, it is unlikely that physical conditions are ever extreme in Langebaan Lagoon. The system is almost entirely marine, so salinities scarcely depart from those of normal seawater levels, and temperatures are moderate and vary comparatively little seasonally (Day, 1959; Mazure & Branch, 1979; Christie, 1981). Differences in the nature of the sediments, dictated by tidal currents and wind-driven distribution of particles (Flemming, 1977) do impose limits on where *Zostera* is likely to exist within the system, but in those areas where it is established, there are no obvious extremes of salinity or water temperature that might limit the fauna associated with the eelgrass beds. One important fact is, however, the limitation of *Zostera* beds to the upper shore by *C. kraussi* bioturbation lower down the shore. Although our samples were deliberately taken within a narrow tidal range, greater physical stress in the high–shore may have contributed to the lower diversity and richness in the *Zostera* beds.

3.4.3 *Sediment Penetrability*

Amongst the host of different explanations proposed in the introduction to account for differences in faunal community composition between *Z. capensis* beds and adjacent sandflats is sediment penetrability. More specifically, seagrass canopies reduce water flow and trap fine sediment and organic detritus (Lee *et al.*, 2001). Ultimately, consolidation occurs around the matrix of root-rhizome systems, and in the absence of mechanical disturbance, the sediment becomes more stable. In contrast, the sandflats in the lagoon are dominated by the dynamic burrower *C. kraussi*.

As predicted, the penetrability of the sediment within the *Callianassa*-dominated sandflat was significantly higher than that within the *Z. capensis* bed (Figure 3.4), associated with respectively binding of the sediment in the eelgrass beds and bioturbation by *C. kraussi* in the

sandflat. Apart from Geelbek, which is situated at the head of the lagoon and is characterised by finer and predominantly anaerobic muddy sand (Puttick, 1977), this trend was consistent at all sites in both 1999 and 2000.

The direct consequences of such sedimentary modifications are potentially acute for the faunal communities associated with each habitat. In particular, sediment compaction restricts the movement of burrowing organisms (Brenchley, 1982 and reference therein) as it causes the sedimentary fabric to become 'tighter' (Rhoads, 1974). The potential complexity of these patterns is further underscored by the fact that the density of other burrowers in the sediment will influence burrowing ability and may either enhance conditions or be detrimental (Wynberg, 1991), over and above other physical obstacles such as eelgrass root-rhizomes.

3.4.4 *Morphological Characteristics*

Brenchley (1981, 1982) has specifically hypothesised that mobility (and to a certain extent size), rather than feeding type, will determine the nature of biological interactions in soft sediments. This is especially pertinent given the incompatibility between sediment stabilisers such as *Z. capensis*, and destabilisers such as *C. kraussi* (Brenchley, 1982; Gallagher *et al.*, 1983; Suchanek, 1983; Jumars & Nowell, 1984; Murphy, 1985; Posey, 1986; Thrush, 1991). In particular, Brenchley (1982) demonstrated that the mobility of burrowing taxa is significantly reduced in substrata containing *Zostera marina* roots.

A variety of burrowers were included in Brenchley's (1982) study, which demonstrated that species with dissimilar forms of morphology may be differently affected by sediment stability. More specifically, hard-bodied taxa were most inhibited, as soft-bodied taxa were more capable of changing shape. Larger individuals were also affected to a greater degree, with the restrictions imposed on mobility increasing disproportionately with size. This implies that invertebrates residing among seagrass roots, should, on average, be smaller in size than those in unvegetated areas (Brenchley, 1982). Consequently, the faunal assemblage associated with *Z. capensis* should be characterised by smaller, more flexible-bodied, non-burrowing species that are less restricted by having to negotiate compact, cohesive sediments and the physical obstructions presented by rhizome-root networks. Conversely, loosely configured sediment associated with extreme bioturbation in *Callianassa*-dominated sandflats should facilitate the existence of larger, harder-bodied, burrowing infauna.

Species categorised in accordance with Brenchley's (1982) functional groups i.e. burrowing *vs.* non-burrowing and hard-bodied *vs.* soft-bodied showed ambivalent responses to *Zostera* and

Callianassa habitats. There was no evidence that *Zostera* beds contained proportionately fewer hard-bodied and more soft-bodied fauna than would be expected by chance - whether this was assessed in terms of the proportions of species or the proportions of individuals. There was, however, support for her hypothesis that non-burrowers should be disproportionately more abundant in *Zostera* beds and burrowers in sandflats, particularly when considered in terms of the numbers of individuals. The most credible positive evidence thus supported the idea that *Zostera* inhibits burrowing individuals. Although some sites failed to differ significantly in terms of the number of burrowers and non-burrowers occurring within the two habitats, the general trend at all sites was consistent over both years sampled. Whether this was attributable to direct physical effects of sediment stability, or rather a result of indirect biogenic effects of eelgrass root-mats, is uncertain, especially as the potential set of interactions that could be generated between sediment characteristics and the relative mobility of burrowers is complex (Brenchley, 1982).

Further disparity with Brenchley's (1982) hypotheses arose from comparisons of the sizes of individuals within eelgrass and adjacent sandflat areas. Contrary to Brenchley's predictions, individuals from *Z. capensis* beds were markedly larger than their sandflat counterparts (Table 3.13 and Figure 3.9). Bird & Jenkins (1999) showed interesting differences in the size structure of macrofaunal assemblages of seagrass beds associated with different levels of wave energy. Individuals in a low-energy sheltered environment were significantly larger than those from more exposed environments (Bird & Jenkins, 1999). Similar logic can be applied to the size structure of invertebrates sampled within *Z. capensis* beds and *Callianassa*-dominated sandflats. It is possible that the unstable sandprawn-dominated environment can be likened to that of the dynamic, high-energy environment described by Bird and Jenkins (1999), whereas *Z. capensis* beds mimic the sheltered environment characterised by increased accumulations of debris, drift algae and finer sediment.

3.4.5 Conclusion

As Woodin (1981) has noted, patterns of distribution and abundance of organisms involve a dynamic interplay between relationships among organisms and the structure of the habitat. My results have provided circumstantial evidence that discordant interactions between *Z. capensis* and *C. kraussi* (see Chapter 2) are responsible for structuring associated faunal communities within Langebaan Lagoon, due to sediment stabilisation caused by *Z. capensis* and the intense effects of *C. kraussi* bioturbation in the surrounding sandflats.

As predicted by the hypotheses proposed in the introduction, distinct faunal assemblages exist within the lagoon, one associated with *Z. capensis* beds and the other with *Callianassa*-dominated sandflats. These assemblages were dominated by a divergent suite of species, each of which was either absent or present in very low densities within the alternative habitat. However, species diversity and richness were lower in *Zostera* beds than in un-vegetated sandflats, contradicting trends established by previous investigators (See Orth, 1977; Stoner, 1980; Fitzhardinge, 1983; Hodgson, 1987; Heck *et al.*, 1989; Whitfield, 1989; Edgar, 1990; Kaletja & Hockey, 1991; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1997; Hily & Bouteille, 1999; Lee *et al.*, 2001).

There was evidence supporting the idea that burrowing organisms are inhibited by *Zostera,* as proposed by Brenchley (1982). This was further corroborated by sediment penetrability data, which revealed greater penetrability of substrata in *Callianassa*-dominated areas and less penetrability where *Zostera* binds the sediment. There was, however, no evidence that *Zostera* excludes hard-bodied or large species: indeed the *Zostera* beds housed larger polychaetes, thalassinideans and brachyurans than did the sandflats. The *Zostera* beds did support greater densities of individuals compared to the adjacent sandflats, probably because of their higher organic content and accumulation of detritus (Mazure & Branch, 1979).

All of these results are the outcome of an observational study that can only serve as an exploratory tool to identify agents that have the potential to determine community structure. The strict conclusion that any of these factors are causal agents shaping intertidal assemblages is not valid. Although the factors maintaining macrofaunal assemblages can be suggested, their mechanisms and inter–relationships are still somewhat unclear (Orth, 1977). The biotic and abiotic factors potentially structuring the *Zostera* and sandflat habitats are numerous (Figure 3.10), and the network of their couplings is complex (Bostrom & Bonsdorff, 1997). In theory, this could lead to site–specific conditions that lack generality. In reality however, many of the differences identified between *Zostera* beds and sandflats were consistent between sites, and site effects were seldom significant.

Assemblages were sampled from sites encompassing a wide spectrum of physical conditions (sheltered eastern bank versus more exposed western bank) yet, despite these physical differences, all *Zostera*-associated and *Callianassa*-associated faunal communities were consistent in both structure and composition. The consistency with which the communities were related to habitat differences rather than site differences implies that biological regulation of conditions plays a major role.

The overall picture emerging is that physical factors such as currents and winds dictate sedimentary characteristics, with coarse, unstable sediments prevalent on the western bank of the lagoon, and finer, more stable sediments deposited on the eastern bank. As a consequence, *Z. capensis* is limited to the eastern bank, where it is confined to the high-shore by the bioturbation activities of *C. kraussi*. In turn, *Z. capensis* stabilises the sediments and thus antagonises *C. kraussi* burrowing. Accordingly, two contrasting habitats are established, each with a distinct assemblage of species. The sandflat assemblage was characterised by greater species richness and diversity, but considerably lower abundance of individuals than the *Zostera* beds. Furthermore, sandflats contained a disproportionately larger number of burrowing fauna than the *Zostera* beds.

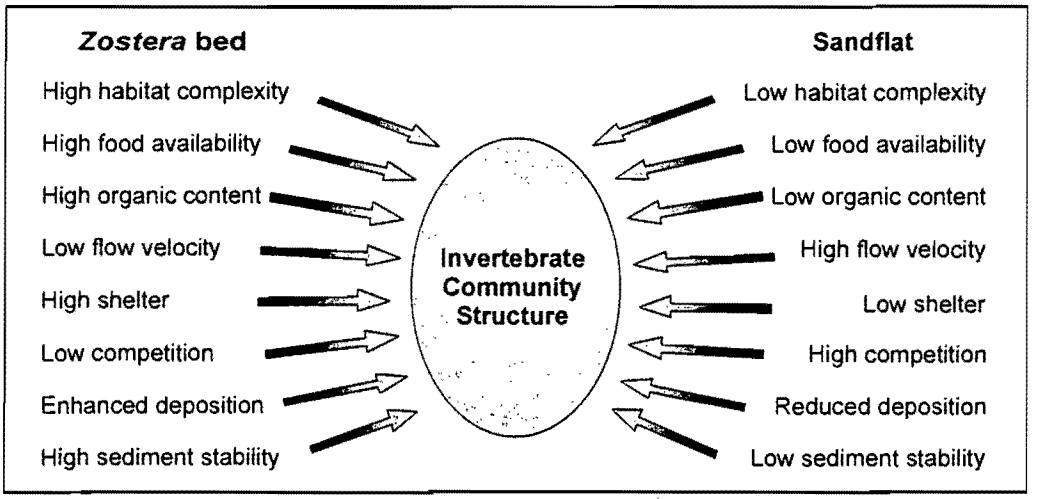


Figure 3.10: A generalised model of abiotic and biotic factors regulating benthic community structure in the *Zostera*-associated and sandflat-associated habitat (after Bostrom & Bonsdorff, 1997).

species richness and diversity, but considerably lower abundance of individuals than the *Zostera* beds. Furthermore, sandflats contained a disproportionately larger number of burrowing fauna than the *Zostera* beds.

Chapter 4

An experimental examination of interactions between *Zostera capensis* and *Callianassa kraussi*, and their indirect effects on *Upogebia africana*.

4.1 Introduction

Marine communities are structured by interactions between a large number of biotic and abiotic processes, which occur at and across a range of different scales, resulting in highly complex systems. Much of our understanding of these systems has been generated by attempting to reduce this complexity (Levin, 1988), and field experiments have proved to be powerful tools that allow tests of hypotheses regarding the importance of particular processes (Cummings *et al.*, 2001).

Biological interactions seem of great importance in governing the communities of Langebaan Lagoon. In particular, the bioturbator *Callianassa kraussi* continually reworks vast amounts of sediment during the course of feeding and burrowing (Branch & Pringle, 1997). In addition to transporting sediment (Jumars & Nowell, 1985), callianassids increase oxygen and mineralization (Kristensen *et al.*, 1985), alter sediment geochemistry (Aller *et al.*, 1983), enhance bacterial numbers, bury and alter the depth-distribution of micro-algae and reduce the meiofauna (Koike & Mukai, 1983; Bell & Woodin, 1984; Probert, 1984; Alongi, 1985; Branch & Pringle, 1997). Bioturbation also has indirect effects on community structure. Thus, although the effects of *C. kraussi* are biological in origin, its influence on other organisms is mediated through physical processes that are the consequence of its burrowing and feeding activities (Suchanek, 1983).

Other *Callianassa* spp. are renowned for their amensal interactions with certain groups of organisms, notably seagrasses (e.g. Rhoads & Young, 1970; Suchanek, 1983). In my study, field observations (Chapters 2 and 3) have shown that the seagrass *Zostera capensis* and the sandprawn *Callianassa kraussi* are mutually exclusive of each other, with *Z. capensis* patchily distributed and limited to the high-shore by *C. kraussi*, which dominates the rest of the shore. In addition, *C. kraussi* also appears to exclude the mudprawn *Upogebia africana* from its domain. Being predominantly a filter-feeder, *U. africana* requires stable sediments to construct its semi-permanent U-tubes and it achieves these conditions through co-habitation with *Z. capensis*. Large established beds of eelgrass may inhibit or exclude *C. kraussi*, because their complex root-rhizome networks obstruct active burrowing (Brenchley, 1983). In contrast, active bioturbation by *C. kraussi* is likely to result in resuspension of sediments, smothering *Z.*

capensis as a result and causing fragmentation of seagrass meadows. It is also believed to clog the filtering apparatus of filter–feeders such as *U. africana* and collapse its burrows (Rhoads & Young, 1970; Brenchley, 1982, 1983; Suchanek, 1983).

These relationships have, however, been proposed on the basis of data that are purely observational in nature, involving simultaneous comparisons of vegetated and unvegetated areas. Further understanding of the causality sustaining these interactions requires rigorous exploration of responses of one species when the other is manipulated, particularly as interactions may be site-specific and/or species-specific. This is clearly demonstrated by conflicting results reported in previous studies. For example, Thompson & Pritchard (1969) found that the colonisation of intertidal sandflats by *Zostera marina* and *Z. japonica* was accompanied by drastic reductions in the population range of *Callianassa californiensis* – a response they attributed to the inhibition of burrowing activities by dense root-rhizome mats (Harrison, 1987). On the contrary, however, Suchanek (1983) revealed that *Callianassa rathbunae* excludes *Thalassia testudinum* by smothering or reducing the penetration of light as a result of the suspension of particles.

This background prompted the establishment of a field experiment to elucidate the mechanisms involved in the putative limitation of *Z. capensis* or *U. africana* by *C. kraussi* within Langebaan Lagoon. Essentially, the experiment involved transplanting healthy sods of eelgrass into nearby areas within *Callianassa*-dominated intertidal sandflats. In half of these areas, *C. kraussi* was experimentally removed prior to transplantation, while in the other half *C. kraussi* populations remained undisturbed. Previous studies indicate that *Z. capensis* responds well to being transplanted and to environmental change (salinity, temperature, photoperiod, and light intensity) (Edgcumbe, 1980). Furthermore, it is probable that *Zostera* will grow in most substrates, provided the organic content is sufficiently high at the time of initial colonisation (Edgcumbe, 1980).

Using transplants of eelgrass into areas with and without *C. kraussi*, coupled with controls and disturbance controls, my experiments tested the following hypotheses:

1. *Z. capensis* transplants will increase in area and cover in the absence of *C. kraussi* bioturbation, but will decrease and be eliminated if *C. kraussi* is present.
2. *U. africana* will be more numerous in association with *Z. capensis* than in its absence, and more abundant in areas devoid of *C. kraussi* than in the presence of *C. kraussi*.
3. *C. kraussi* will be absent or occur at low densities in the presence of established beds of *Z. capensis*.

4.2 Methods

The experiment was conducted at Bottelary (see Figure 1.1) on the eastern shore of the lagoon, on the same intertidal sandflat investigated in preceding chapters. This site was selected as it is characterised by extensive open sandflats dominated by the sandprawn *Callianassa kraussi*, and large beds of the eelgrass *Zostera capensis* on the high-shore.

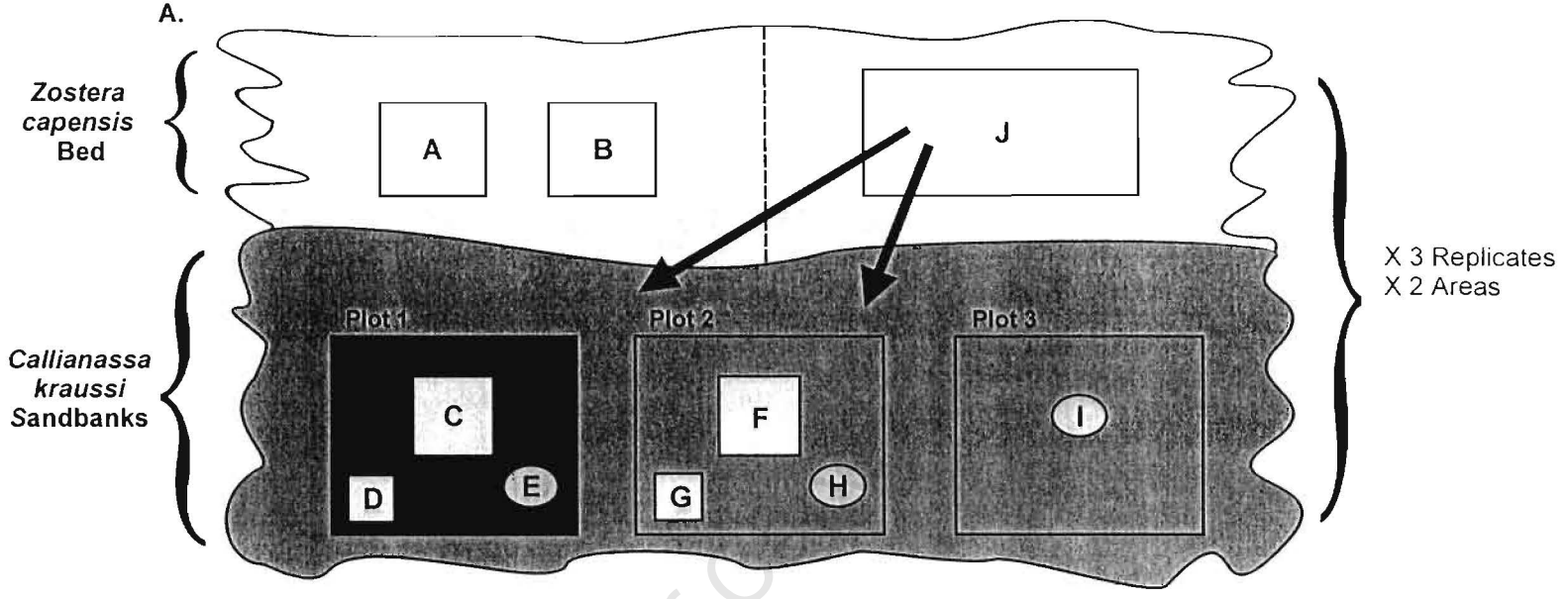
4.2.1 *Experimental Design*

Two areas, about 100 m apart, were selected and within each area ten different treatments were established as summarised in Figure 4.1. For most of the treatments (C-J) three replicates were created in each of the two areas but for two treatments (A and B) the three replicates were limited to one area.

Treatments A, B and J were established within the eelgrass bed. Treatment A was an undisturbed '*Zostera* Control' that was monitored over time to record if there were any natural changes in the *Z. capensis* bed. Treatment B was a procedural control (the '*Zostera* Disturbance Control'). Within it, a $1m^2$ plot of *Z. capensis* was dug down to 20 cm, lifted and removed in the same manner as in the transplant treatments described below, but then returned to its original position to monitor for any affects of the disturbance on the eelgrass. Treatment J (*Zostera* Removal) was an area of 5 X 2 m in which *Z. capensis* was dug down to a depth of 20 cm and removed, and in which recovery of above-ground and below-ground biomass of *Z. capensis* was monitored after 12 months.

Treatments C-I were all established within the *Callianassa*-dominated sandflats immediately below the *Zostera* beds. Four of these treatments, C, D, F, and G all involved transplanting plots of *Z. capensis* from the *Z. capensis* bed down into the sandflats dominated by *C. kraussi*, and comprised different combinations of two factors: the size of the transplanted unit and whether it was introduced into a plot that possessed *C. kraussi* or one from which all *C. kraussi* had been experimentally eliminated. Treatment C (termed *-Callianassa +Zostera* 1 m^2) was a transplant of 1 m^2 of *Z. capensis* into a plot where *C. kraussi* had been eliminated. Treatment D (termed *–Callianassa +Zostera* 0.5 m^2) was identical but the transplanted *Z. capensis* was only 0.5 m^2 in area. Treatment E (*–Callianassa –Zostera*) also fell in a plot from which *C. kraussi* had been eliminated but constituted unvegetated sandflat. Treatments F and G (respectively termed *+Callianassa +Zostera* 1 m^2 and *+Callianassa +Zostera* 0.5 m^2) were identical to C and D but

A.



B.

Key	Treatment	Abbreviation	Sampling 1d	1w	2w	3w	4w	2m	3m	4m	5m	6m	12m	18m
A	*Zostera* Control	*Zost* Control	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓[2,3]	✓[4]
B	*Zostera* Disturbance Control	*Zost* Dist Control	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓[2,3]	✓
C	- *Callianassa* + *Zostera* 1m²	-*Call*+*Zost* (1m²)	✓	✓	✓	✓	✓	✓[3]	✓	✓[3]	✓	✓[1,3]	✓[2,3]	✓[1,4]
D	- *Callianassa* + *Zostera* 0.5m²	-*Call*+*Zost* (0.5m²)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓[1]	✓[2,3]	✓[1]
E	- *Callianassa* - *Zostera*	-*Call*-*Zost*	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓[3]	✓[4]
F	+ *Callianassa* + *Zostera* 1m²	+*Call*+*Zost* (1m²)	✓	✓	✓	✓	✓	✓[3]	✓	✓	✓	✓[1,3]	✓[2,3]	✓[1,4]
G	+ *Callianassa* + *Zostera* 0.5m²	+*Call*+*Zost* (0.5m²)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓[1]	✓[2,3]	✓[1]
H	+ *Callianassa* - *Zostera*	+*Call*-*Zost*	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
I	*Callianassa* Control	*Call* Control	✓	✓	✓	✓	✓	✓[3]	✓	✓	✓	✓[3]	✓[3]	✓[4]
J	*Zostera* Removal	*Zost* Removal											✓[2,3]	

Figure 4.1: Schematic diagram (A) illustrating experimental treatments. (B) Key showing experimental treatments, abbreviations and sampling strategy. In Plot 1, *C. kraussi* was eliminated by defaunation of the sediment; in Plots 2 and 3 it was left undisturbed. Prawn-hole counts and *Z. capensis* cover were recorded at all time intervals, indicated by tick symbols. Total area and biomass of *Z. capensis* were only sampled at selected times and are shown by superscripts[1] and [2] respectively. Sediment penetrability and sediment flux and suspension were sampled at times indicated by superscripts [3] and [4] respectively (d = days, w = weeks, m = months).

involved the transplantation of 1 m^2 or 0.5 m^2 of *Z. capensis* into a plot where *C. kraussi* was left undisturbed. Treatment H (*+Callianassa –Zostera)* also fell within the *+Callianassa* plot but again constituted unvegetated sandflat. Treatment I (*Callianassa* Control) was an undisturbed area in the *Callianassa*-dominated sandflats. The procedures involved in the transplantation of *Z. capensis* and the elimination of *C. kraussi* are given in detail below.

From the outset it should be appreciated that the experimental removal of *C. kraussi* cannot be undertaken without side effects. Previous attempts to remove sandprawns by digging or using a prawn pump have never succeeded in completely eliminating them. Worse, these procedures result in substantial disturbance of the sedimentary fabric (Wynberg & Branch, 1994). This precluded the use of these methods as a means of removing sandprawns in the present experiment, as sedimentary stability was an integral part of the hypotheses being tested. Defaunation by smothering had the benefit of eliminating all sandprawns without disturbing the sediment but inevitably eliminated other infauna as well. To establish treatments C-I, three randomly chosen plots of 5 X 5 m, approximately 10–m apart were marked out in the *Callianassa*-dominated sandflat immediately below the *Z. capensis* bed. One of these (plot 1 in Figure 4.1) was defaunated by covering the sediment surface with thick plastic sheeting weighted at the edges with 25 kg fertiliser bags filled with sand. This procedure enabled me to consistently defaunate a large plot of sediment, thus eliminating bioturbation without having to modify the sediment structure and stratigraphy.

The defaunated plot was monitored monthly for 6 months until it was completely devoid of all macrofauna (particularly *C. kraussi*). A second plot (plot 2 in Figure 4.1) was left undisturbed for the duration. Following this, 1 m^2 and 0.5 m^2 areas of *Z. capensis* were respectively transplanted into plots 1 and 2. Sods were taken from the eelgrass bed by cutting it into 0.25 m^2 squares with a spade to a depth of 20 cm, the depth to which *Zostera* spp. generally extend, according to Homziak *et al.* (1982). At each plot where *Zostera* transplants were being installed, holes were first dug in the sediment to accommodate the transplanted sods. The sods were lifted out of the *Z. capensis* bed, carried on a steel sheet and lowered into the pre-dug holes. The 1 m^2 areas of *Z. capensis* were implanted in the centre of each plot, followed by the 0.5 m^2 areas towards the edge of the plot. The two implanted areas of *Z. capensis* were always at least 1 m apart and at least 1 m from the edge of the plot so that they constituted independent treatments and were unaffected by each other or by conditions in the surrounding area. An adjacent area (Plot 3 see Figure 4.1) was left undisturbed and served as a *Callianassa* control (Treatment I) in which the densities of *C. kraussi* were monitored.

4.2.2 *Sampling*

After the treatments were established, the responses of *Z. capensis, C. kraussi* and *U. africana* were monitored by evaluating *Z. capensis* cover, biomass and area, and by counting prawn holes as described in Chapter 2. Sampling was undertaken once weekly for the first month, thereafter once monthly until termination of the experiment after 12-18 months. Figure 4.1 B illustrates the dates on which samples were taken. Although data were gathered on all of these dates, I condensed the graphical presentation by depicting the data at monthly or three-monthly intervals only, as they were representative of the intervening dates.

The condition of *Zostera capensis* was determined by scoring its percentage cover, total area of transplanted sods and the wet-weight of above-ground and below-ground plant biomass. Percentage cover was estimated within a 0.25 m^2 quadrat placed in the centre of each treatment and was measured at all sampling intervals. Biomass was determined from two 10 X 20 cm samples in the centre of each treatment in which *Z. capensis* was present. *Z. capensis* surface biomass was sampled by cutting surface shoots at ground level, rinsing, blotting, and wet-weighing them to 0.01g accuracy. Once this had been completed, the sediment was removed down to a depth of 20 cm using a sediment corer, sieved through a 2-mm mesh sieve, and all sub-surface *Z. capensis* root–rhizomes and debris retained and wet-weighed. *Z. capensis* biomass was only sampled once (after 12 months) as the methods involved were destructive and would have biased subsequent measurements.

Total area of *Z. capensis* was determined by scoring the above-ground expansion of eelgrass outwards from the original transplanted plots, and was measured twice, at 6 months and 12 months.

Prawn densities were assessed by counting burrow holes within 0.25 m^2 quadrats in each treatment, and were counted at all sampling intervals. Prawn holes were considered to represent 1:1 holes per adult *C. kraussi* and 2:1 holes per adult *U. africana*, as determined by Forbes (1973) and Wynberg & Branch (1991).

Penetrability of the sediment within control and experimental treatments was measured at 2, 4, 6, and 12 months. Ten random penetrability measurements were taken at each site by dropping a standardized steel rod 1 m long and 8 mm in diameter from a height of 1 m above the substratum. The distance of penetration into the substratum was used as an index of penetrability.

Net sediment flux at the sediment–water interface and the distribution of suspended sediment above treatments A, C, E, F and I were measured after 18 months to determine whether *Z. capensis* transplants modified hydrodynamics thus influencing sediment movement on the intertidal sandflat. Sediment flux was measured using depth of disturbance rods – a simple, inexpensive procedure for the measurement of both the total volume of sediment in transport and the net volume flux of the sediment (Greenwood & Hale, 1980). A round steel rod (0.5 cm diameter, 1.5 m long) was driven vertically into the sand until 0.45 m was left exposed above the sediment surface. A loose–fitting washer (0.6 cm internal diameter) placed over the rod provided the control for determining bed surface scour or aggradation. Rods were deployed at spring ebb and left for the duration of one tidal cycle. Sediment aggradation was measured as the depth to which the washer became buried.

Suspended sediment above treatments A, C, E, F, I was measured by means of sediment traps consisting of vials (polyethylene film canisters, height: 50 mm, diameter 25 mm) arranged in tiers at intervals of: 0, 1.3, 7.7, 15.3, 22.9 and 30.6 cm above the sediment bottom, following Cook and Gorsline (1972). The devise was buried so that the lip of the lowest vial was flush with the sediment-water interface. After installation, the containers were uncapped and left for the duration of one spring tidal cycle. The contents of each vial were filtered through Whatman filters via a filtration syringe, oven–dried at 40°C and weighed to 0.0001g accuracy. Although the vial design does not sample all sediment passing the trap, it is designed to collect a representative sample over a continuous range (Cook & Gorsline, 1972).

4.2.3 *Statistical Analysis*

Data were tested for normality and homogeneity of variance by means of Kolmogorov-Smirnov test and Levene's test respectively (alpha set at 0.05). If necessary, data were transformed to meet the assumptions of parametric tests. In some cases, equality of variance was achieved but not normality; but graphical inspection revealed that the data were sufficiently normal not to compromise the ANOVAs (Quinn & Keough, 2002). In cases where the data were uniformly zero (and therefore had zero variance), they were excluded from statistical analysis. Before proceeding to test the primary hypotheses, a separate one-way ANOVA was used to compare the results from the *Zostera* Control and *Zostera* Disturbance Control. There were no significant differences between these ($p > 0.25$ in all cases) so the data for these two treatments were pooled in subsequent tests, increasing the replicates to six and therefore balancing the design when comparing these data with those of other treatments for which there were six replicates. Initially, I used repeated-measure (RM)-ANOVA models to analyse *Z. capensis* cover, total areas and prawn densities, because I had sampled the same plots more than once and thus

compromised the independence of variables. As significant time X treatment interactions were detected, separate ANOVAs were computed for each of the sampling periods following the protocol advocated by Williams (1990) and Worm & Reusch (2000). Differences in these variables between treatments were thus evaluated at each time interval by two-way ANOVA, with area as a random factor and treatment as a fixed factor. As differences between the two areas proved significant on isolated occasions only, I simplified the graphical presentations by pooling the data for the two areas, although they were distinguished when running the statistical analyses. In a few cases, there was a significant interaction between area and treatment. In these instances, the means of one factor were compared separately at each level of the other factor and *vice versa* by multiple-comparison Tukey tests (Underwood, 1997). Where significant main effects were detected in the ANOVA and there was no interaction between the main effects, Tukey HSD posteriori tests (Tukey, 1953 in Zar, 1984) were employed to analyse differences among levels of the treatments.

Differences in sediment penetrability, net sediment flux and suspended sediment between control and experimental treatments were assessed by ANOVA and followed by multiple comparison Tukey tests when appropriate. Initial analyses of penetrability (after 2, 4 and 6 months) were confined to the *Callianassa* Control, the -Callianassa +*Zostera* and +*Callianassa* +*Zostera* treatments and compared the effects of area as a random factor and treatment as a fixed factor in a 2–way ANOVA. After 12 months penetrability was analysed for all treatments but as two of the treatments were not replicated in both areas, the data were analysed by one–way ANOVA with treatment as the sole factor. Statistical analyses were conducted using StatSoft, Inc. (2000) STATISTICA version 6 for Windows.

4.3 Results

4.3.1 *Zostera capensis* Cover

The percentage cover of *Z. capensis* was compared among all treatments that possessed seagrass after 1 day, 3 months, 6 months, 12 months and 18 months (Figure 4.2). Its cover was equal in all treatments at the start and did not display any obvious changes until 3 months after the experiment began. Thereafter, cover in both –*Callianassa* +*Zostera* plots and +*Callianassa* +*Zostera* plots declined. After 6 months, *Z. capensis* cover in all –*Callianassa* +*Zostera* plots began to recover, while in +*Callianassa* +*Zostera* treatments it continued to decline. Two-way ANOVAs (Table 4.1) performed separately for each sampling date indicated significant differences in *Z. capensis* cover between treatments from 6 months onwards but, apart from 6 months never between areas. There was never any significant area X treatment interaction.

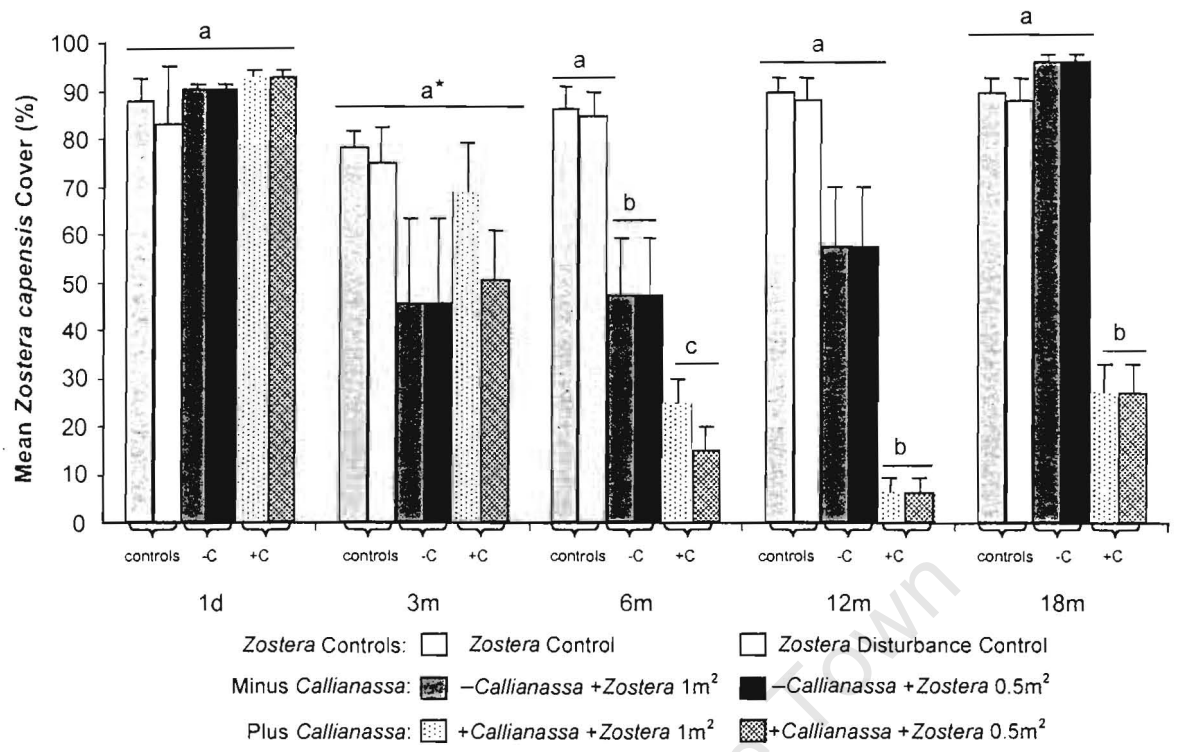


Figure 4.2: A comparison of the mean (+ SE) *Z. capensis* cover (%) in control and treatment areas, in relation to time after installation of *Z. capensis* transplants (d = days, m = months). Different letters indicate significant differences between treatments ($p < 0.01$). Solid lines above the bar columns connect treatments that were not significantly different from each other ($p > 0.05$). * No ANOVA was possible for the 3-month data due to inequality of variances even after transformation, but inspection of the error bars suggests an absence of any significant difference between treatments.

Table 4.1: Results of two-way ANOVAs performed separately on the effects of treatment and area on *Z. capensis* cover 1 day, 6 months and 12 months after initiation of the experiment. Data for 3 months were excluded due to inequalities of variance.

Two-Way ANOVA					
1 day	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	7.5	0.143	0.709	Not Significant
Treatment	4	56.3	1.071	0.396	Not Significant
Area X Treatment	4	17.9	0.341	0.847	Not Significant
6 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	1687.5	4.8913	0.039	Significant
Treatment	4	5159.58	14.955	<0.001	Significant
Area X Treatment	4	364.58	1.056	0.403	Not Significant
12 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	907.5	2.556	0.125	Not Significant
Treatment	4	7786.25	21.933	<0.001	Significant
Area X Treatment	4	376.25	1.059	0.402	Not Significant
18 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.00	0.00	1.000	Not Significant
Treatment	4	9522.00	93.13	<0.001	Significant
Area X Treatment	4	12.50	0.12	0.744	Not Significant

Post-hoc Tukey tests indicated an absence of any differences between *Z. capensis* cover among any of the treatments at the start of the experiment. After 6-12 months, however, *Z. capensis* cover in the *Zostera* Controls and the *–Callianassa +Zostera* treatments were consistently significantly higher than the *+Callianassa +Zostera* treatments, irrespective of the size of the *Zostera* transplants ($1m^2$ or $0.5m^2$). There were never any significant differences between transplants of different sizes. After 18 months *Z. capensis* cover in *–Callianassa +Zostera* treatments had recovered to almost 100%. In contrast, eelgrass cover in *+Callianassa +Zostera* treatments remained <30 % (Figure 4.2). *Z. capensis* was consistently absent from all other treatments, which were thus excluded from the statistical analyses

4.3.2 *Zostera capensis Biomass*

Comparisons of *Z. capensis* biomass among control and experimental treatments were made after 12 months for both above-ground and below-ground biomass (Figure 4.3). Surface biomass of *Z. capensis* (Figure 4.3 A) differed significantly between both treatments and areas, although differences between areas were marginal ($p \approx 0.04$). Interaction between these main effects was insignificant (Table 4.2). Post-hoc Tukey tests showed that the two *Zostera* controls had consistently higher values than any of the transplanted treatments (most of which did not differ from each other irrespective of whether *C. kraussi* was present or absent, despite a trend of higher values in the *–Callianassa* treatments compared with *+Callianassa* treatments). The *Zostera* Removal treatment always had the lowest values and significantly differed from all other treatments.

Below-ground samples (Figure 4.3 B) also showed significant differences in biomass between treatments, but not for area effects or interactions (Table 4.2). The biomass in the control plots was significantly higher and that in the *Zostera* Removal area significantly lower than any of the other treatments. No significant differences in biomass were found among the four transplant treatments.

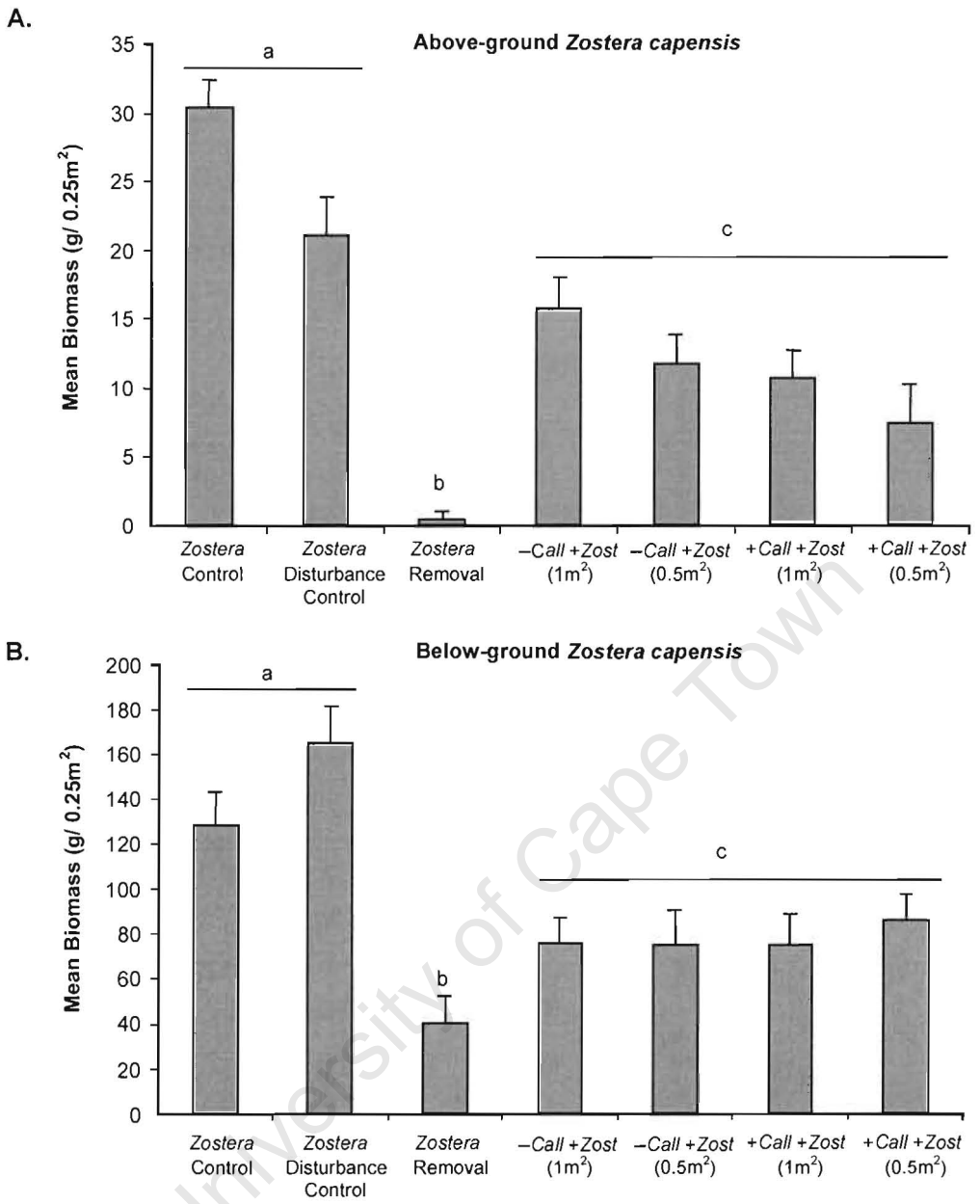


Figure 4.3: A comparison of the mean (+SE) biomass (g/0.25m^2) of (A) above-ground *Z. capensis* and (B) below-ground *Z. capensis* biomass within control and experimental treatments. Treatments that share the same letters were not significantly different (Tukey post-hoc tests, p> 0.05).

Table 4.2: Results of two-way ANOVAs on the effects of area and experimental treatment on above-ground and below-ground *Z. capensis* biomass.

Two-Way ANOVA					
Surface Biomass	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	216.45	4.39	0.039	Significant
Treatment	6	1130.67	22.98	<0.001	Significant
Area X Treatment	6	97.83	1.99	0.078	Not Significant
Below-ground Biomass	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	47.0	0.05	0.828	Not Significant
Treatment	6	10316.3	10.33	<0.001	Significant
Area X Treatment	6	1037.5	1.04	0.402	Not Significant

4.3.3 *Zostera capensis Area*

Expansions of *Z. capensis* transplant plots from the original $1m^2$ and $0.5m^2$ areas were measured after 6 and 18 months in all *+Callianassa +Zostera* and *–Callianassa +Zostera* treatments to determine the effects of the presence or absence of *C. kraussi* on *Z. capensis* growth. In the absence of *C. kraussi*, the area of *Z. capensis* doubled relative to the original (combined) areas of $1.5m^2$, while in the presence of *C. kraussi*, it halved so that the area of *Z. capensis* within *–Callianassa* treatments was ultimately approximately 3.5 times greater than that in the *+Callianassa* treatments (Figure 4.4 and 4.5).

Two-way ANOVAs performed on root transformed data for 6 and 18 months both yielded significant differences between the *–Callianassa* and *+Callianassa* treatments but no difference between areas nor any significant area X treatment interaction (Table 4.3).

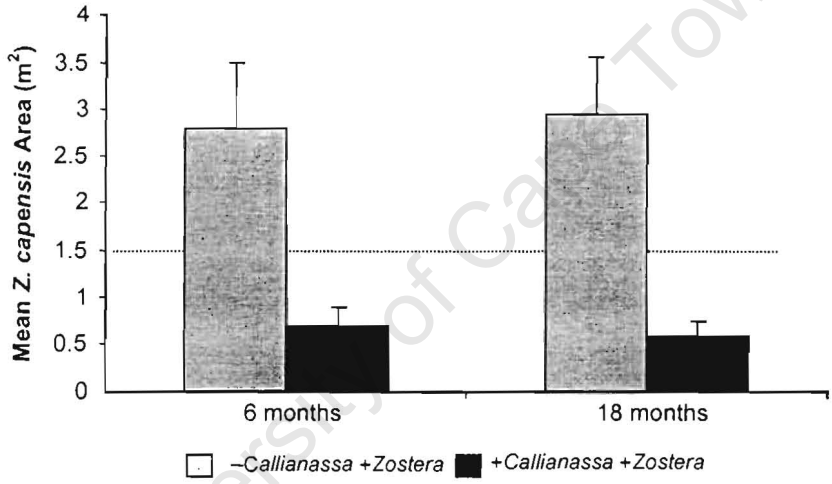
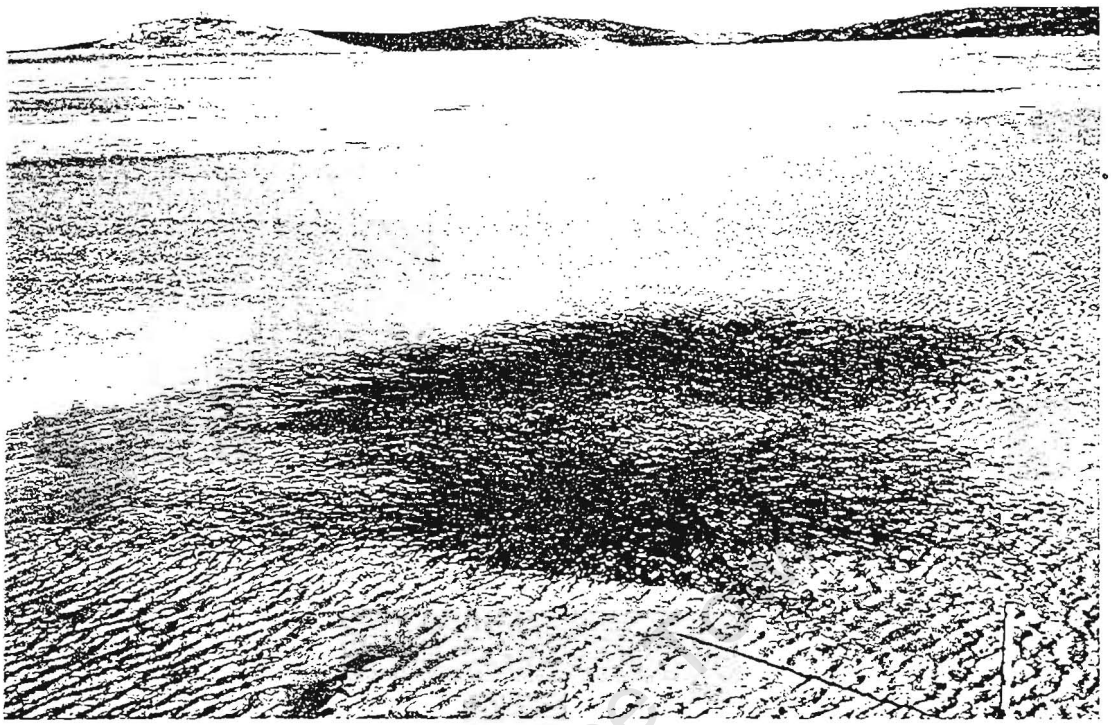


Figure 4.4: Mean (+SE) *Z. capensis* area (m^2) in *–Callianassa +Zostera* and *+Callianassa +Zostera* areas at 6 months and 18 months after installation of *Z. capensis* transplants. The data combine both $1m^2$ and $0.5m^2$ transplants, as expansion of *Z. capensis* in *–Callianassa +Zostera* areas had merged the two. The dotted line indicates the original (combined) area of the two transplants.

Table 4.3: Results of a Two-way ANOVA comparing *Z. capensis* expansion within *–Callianassa +Zostera* and *+Callianassa +Zostera* sites, with area as a random factor and treatment as fixed factor.

Two-way ANOVA					
6 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.51	3.35	0.105	Not Significant
Treatment	1	1.35	8.83	0.018	Significant
Areas X Treatment	1	0.15	0.97	0.354	Not Significant
18 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.01	0.37	0.576	Not Significant
Treatment	1	1.83	100.63	<0.001	Significant
Areas X Treatment	1	0.02	0.96	0.383	Not Significant

A



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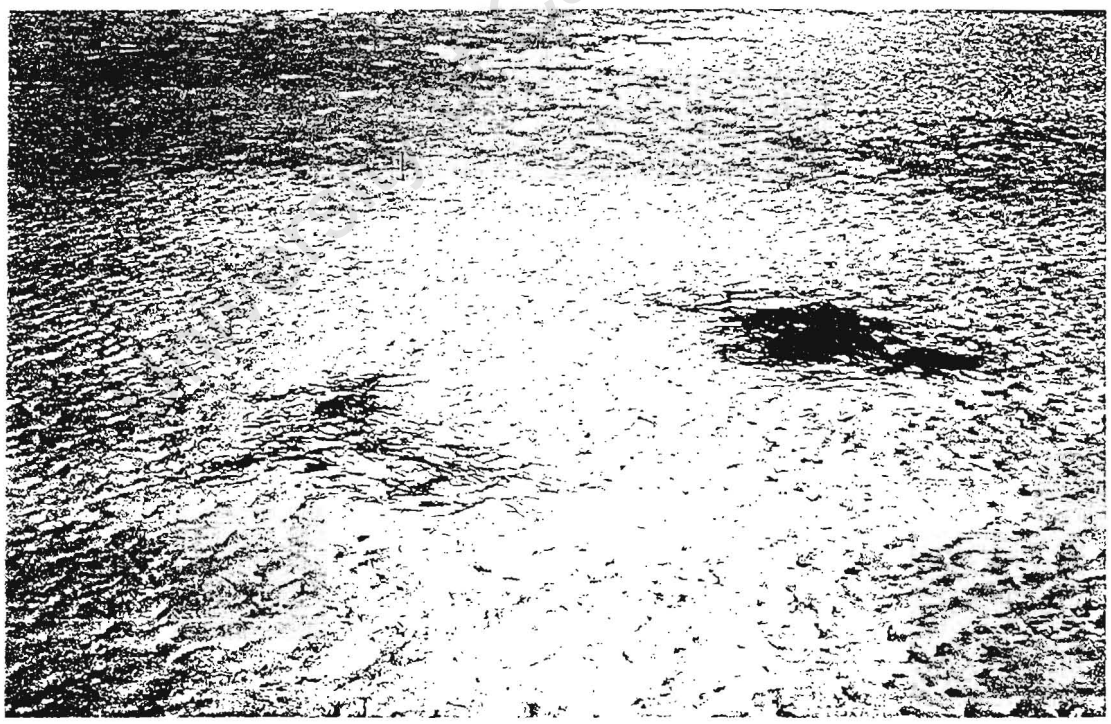


Figure 4.5: Examples of (A) *Z. capensis* transplanted into areas where *C. kraussi* was eliminated by defaunation (*–Callianassa +Zostera*) and (B) *Z. capensis* transplanted into areas with natural densities of *C. kraussi* (*+Callianassa +Zostera*).

4.3.4 *Prawn Densities*

Figure 4.6 A compares the mean densities of *Upogebia africana* among all treatments. Two-way ANOVAs conducted at 2 weeks, 3, 4, 5 and 6 months (Table 4.4) showed significant differences between *U. africana* densities between treatments, but area affects were only evident at 2 weeks and 4 months. Interactions between the main effects were never significant. After three months, three trends were consistently evident from post–hoc Tukey tests. First, highest densities of *U. africana* were always recorded in the *Zostera* Controls. In the *Zostera* Removal treatment (which was monitored once only, after 12 months) the densities of *U. africana* were identical to those in the *Zostera* Controls. Second, densities in *–Callianassa +Zostera* treatments always exceeded those in *+Callianassa +Zostera*. Third, densities were lowest in treatments that lacked *Z. capensis*, regardless of the presence or absence of *C. kraussi*.

Two-way ANOVAs showed that densities of *Callianassa kraussi* were significantly different between treatments on all occasions (Table 4.5). With one exception, differences between areas and interactions between area X treatment were never significant. The solitary exception was after 3 months when an outlier in the *+Callianassa +Zostera* $1m^2$ treatment induced an interaction. Post-hoc Tukey tests were applied to determine which treatments differed and the results are summarised in Figure 4.6 B.

Four trends emerged from post–hoc Tukey tests, all of which were diametrically opposite from those recorded for *U. africana*. First, *C. kraussi* was consistently absent from the *Zostera* Controls and *Zostera* Disturbance Controls in the *Zostera* bed. Although the *Zostera* Removal treatment was monitored only once (after 12 months), densities of *C. kraussi* in it remained at zero. Second, in the three '*–Callianassa*' treatments in which *C. kraussi* was eliminated (*–Callianassa +Zostera* $1m^2$, *–Callianassa +Zostera* $0.5m^2$, *–Callianassa –Zostera*), densities of *C. kraussi* remained very low and differed significantly from those in the '*+Callianassa'* treatments for the first five months, although they began to recover in the sixth month. Third, after *Z. capensis* was transplanted into '*+Callianassa*' treatments it initially reduced densities of *C. kraussi* to almost half those in the *Callianassa* Control and the *+Callianassa –Zostera* treatments, although they did partly recover (relative to the controls) and from the fourth month onwards were not statistically distinguishable from these treatments. Finally, up to the sixth month the *Callianassa* Control and the *+Callianassa –Zostera* treatments always contained the highest densities of *C. kraussi*.

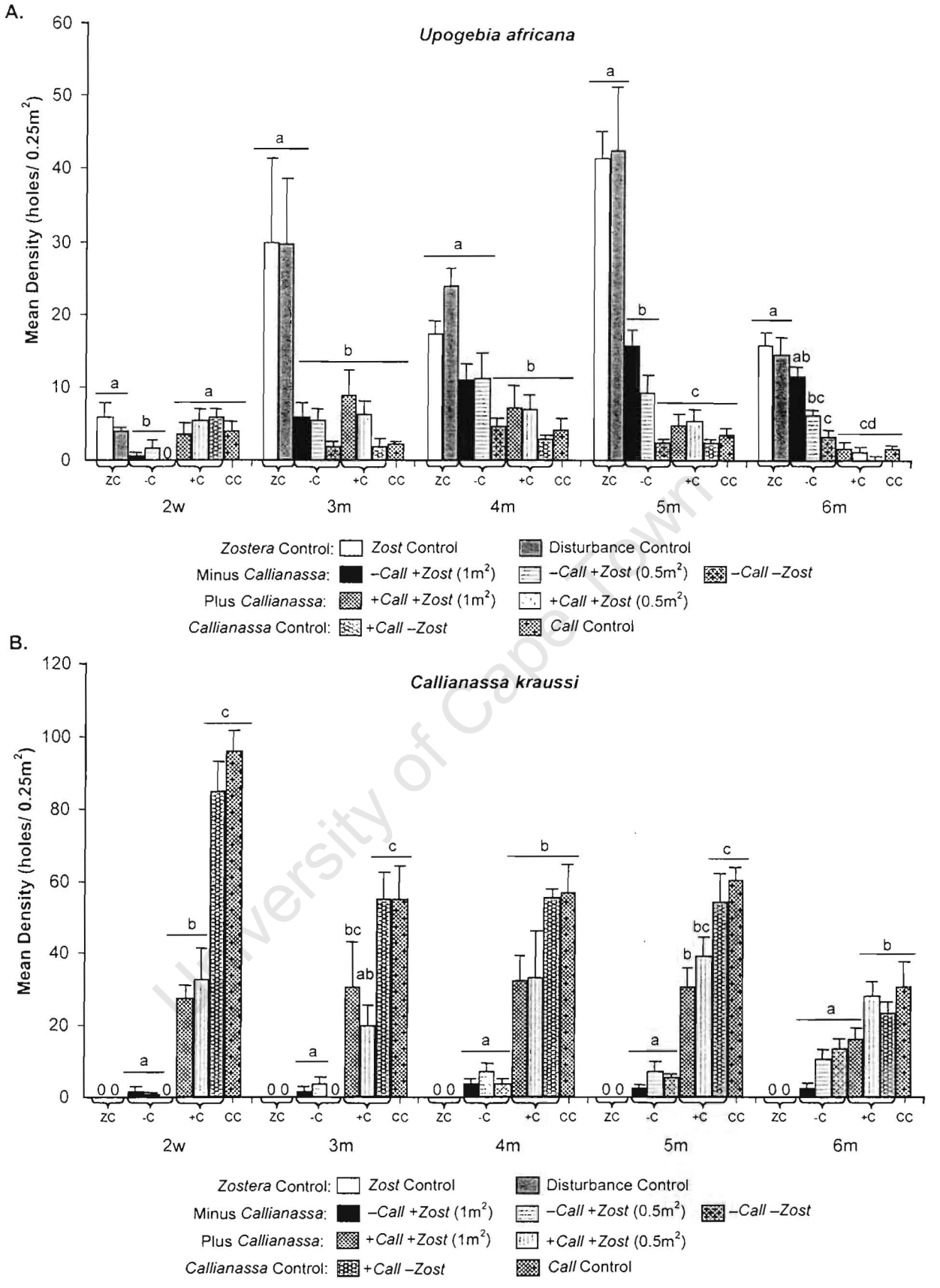


Figure 4.6: A comparison of the mean (+SE) densities of (A) *U. africana* and (B) *C. kraussi* densities (holes/0.25m^2) within control and experimental treatments (d = days, m = months). Treatments that share letters were not significantly different (Tukey post-hoc tests, p> 0.05). Zeros indicate absence of either species.

Table 4.4: Results of Two-way ANOVAs comparing *U. africana* densities (holes/0.25m^2) recorded in *–Callianassa +Zostera* and *+Callianassa +Zostera* areas at 2 weeks, 3 months, 4 months, 5 months and 6 months after initiation of the experiment.

U. africana	Two-way ANOVA				
2 weeks	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	96.33	21.51	<0.001	Significant
Treatment	7	31.62	7.06	<0.001	Significant
Areas X Treatment	7	4.52	1.01	0.443	Not Significant
3 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.083	0.01	0.981	Not Significant
Treatment	7	2894.62	19.39	<0.001	Significant
Areas X Treatment	7	64.70	0.43	0.874	Not Significant
4 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	6.49	10.53	0.002	Significant
Treatment	7	4.76	7.72	<0.001	Significant
Areas X Treatment	7	0.92	1.49	0.203	Not Significant
5 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.23	3.77	0.061	Not Significant
Treatment	7	1.09	18.23	<0.001	Significant
Areas X Treatment	7	0.05	0.78	0.612	Not Significant
6 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.09	0.37	0.549	Not Significant
Treatment	7	7.66	31.59	<0.001	Significant
Areas X Treatment	7	0.36	1.49	0.205	Not Significant

Table 4.5: Results of Two-way ANOVAs comparing *C. kraussi* densities in the different treatments at 2 weeks, 3 months, 4 months, 5 months and 6 months. Two treatments were excluded from this analysis (*Zostera* Control and Disturbance Control) as *C. kraussi* was consistently absent from them.

C. kraussi	Two-way ANOVA				
2 weeks	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	535.71	4.03	0.054	Not Significant
Treatment	6	9834.38	73.99	<0.001	Significant
Areas X Treatment	6	209.71	1.58	0.190	Not Significant
3 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	2704.02	18.06	<0.001	Significant
Treatment	6	3491.78	23.33	<0.001	Significant
Areas X Treatment	6	457.30	3.05	<0.001	Significant
4 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	5.68	3.31	0.079	Not Significant
Treatment	6	37.18	21.65	<0.001	Significant
Areas X Treatment	6	1.20	0.70	0.652	Not Significant
5 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.01	0.02	0.905	Not Significant
Treatment	6	39.06	45.66	<0.001	Significant
Areas X Treatment	6	1.36	1.59	0.186	Not Significant
6 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	17.36	0.19	0.659	Not Significant
Treatment	6	608.60	6.94	<0.001	Significant
Areas X Treatment	6	72.52	0.83	0.559	Not Significant

4.3.5 *Sediment Penetrability*

The physical penetrability of the sediment at 2, 4 and 6 months was consistently higher within *+Callianassa +Zostera* and *Callianassa* Control treatments compared to that in *–Callianassa +Zostera* treatments (Figure 4.7 A), suggesting that both binding of the sediment by *Z. capensis* and mechanical disturbance via bioturbation have marked effects on the sediment within the corresponding habitats. More detailed investigations at 12 months revealed similar trends

(Figure 4.7 B). Penetrability was lowest in the *–Callianassa* treatments (*-Callianassa +Zostera*, *Zostera* bed, *-Callianassa +Zostera* 1m^2 and *–Callianassa +Zostera* 0.5m^2 treatments) and greatest within treatments in which *C. kraussi* was present.

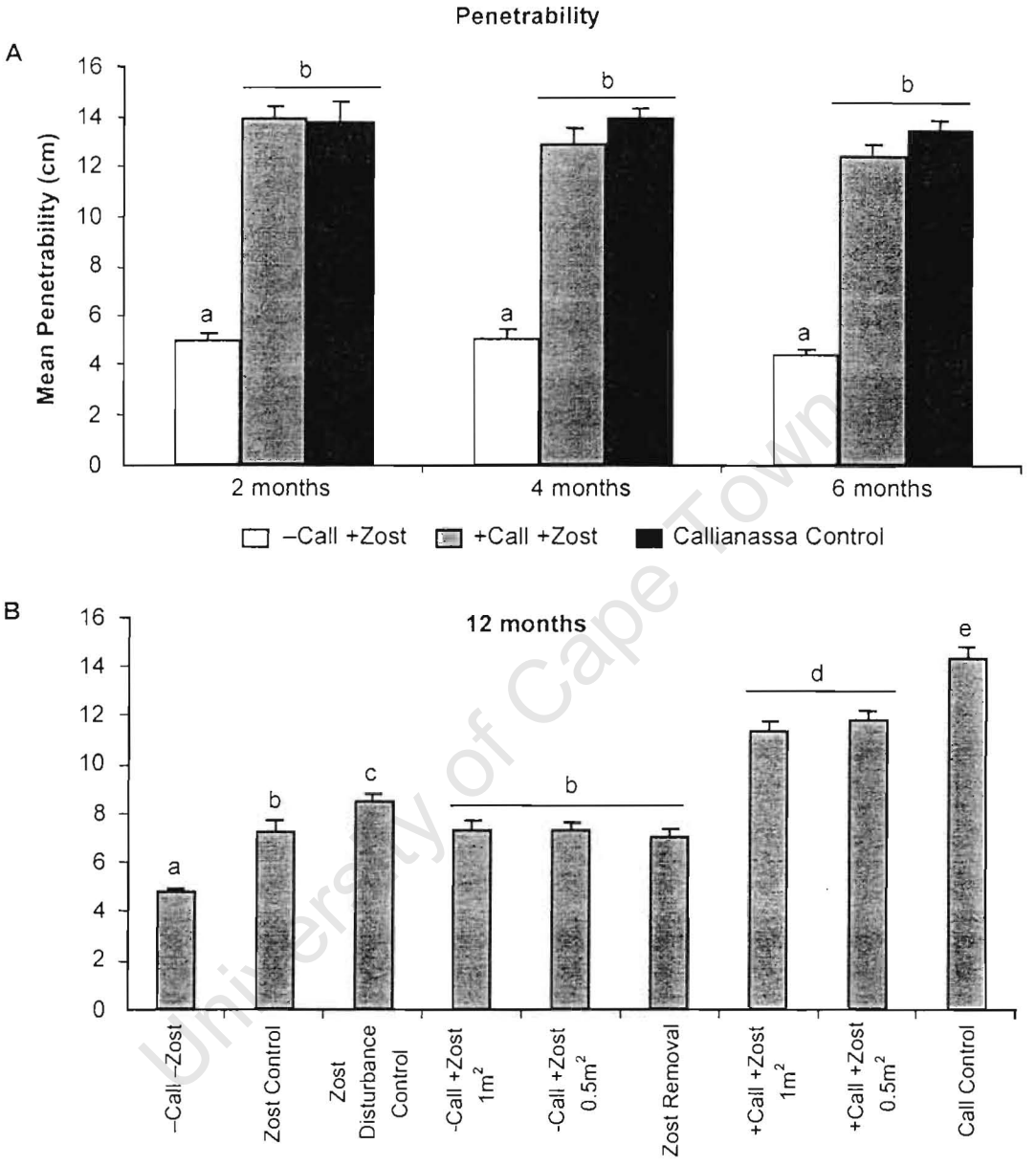


Figure 4.6: A comparison of the mean (+SE) penetrability of sediment (mm) in *–Callianassa +Zostera*, *+Callianassa +Zostera* and *Callianassa* Control sites at 2 months, 4 months and 6 months. B illustrates sediment penetrability in all control and experimental treatments at 12 months. Letters indicate significant differences between treatments ($p < 0.05$). Solid lines above the bar columns connect treatments that were not significantly different from each other ($p > 0.05$).

These results were confirmed by two-way ANOVAs comparing the effects of area and treatment on penetrability (Table 4.6). Data from 2 months and 4 months produced significant results for both main effects, but no interaction between them. Penetrability at 6 months was affected only by treatment. Post-hoc Tukey tests showed that the sediment in *–Callianassa +Zostera*

treatments was consistently less penetrable than that in *+Callianassa +Zostera* and *Callianassa* Control treatments (Figure 4.7 A). A one-way ANOVA performed on sediment penetrability at 12 months showed highly significant differences in penetrability between treatments (Table 4.6). Post-hoc Tukey test results indicate that penetrability within *–Callianassa –Zostera* treatments were significantly lower than all other treatments. Treatments occurring either in the natural eelgrass bed or those containing *Z. capensis* transplanted in the absence of *C. kraussi* showed equally low penetrability values compared to those that where transplanted in the presence of *C. kraussi*. Penetrability was consistently significantly higher within the *Callianassa* Control versus all other treatments (Figure 4.7 B).

Table 4.6: Results of Two–way ANOVAs (A) performed separately on the effects of treatment and area on the penetrability of the sediment within treatment plots at 2 months, 4 months and 6 months. A separate One–way ANOVA (B) was performed for data collected at 12 months.

A		Two-Way ANOVA			
2 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.53	5.08	0.029	Significant
Treatment	2	12.38	118.61	<0.001	Significant
Area X Treatment	2	0.19	1.85	0.167	Not Significant
4 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.58	8.53	0.005	Significant
Treatment	2	11.21	165.14	<0.001	Significant
Area X Treatment	2	0.20	2.96	0.06	Not Significant
6 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.03	0.67	0.417	Not Significant
Treatment	2	12.65	261.69	<0.001	Significant
Area X Treatment	2	0.01	0.22	0.799	Not Significant
B		One-Way ANOVA			
12 months	**df Effect**	**MS Effect**	**F**	**p-level**	
Treatment	8	69.51	82.09	<0.001	Significant

4.3.6 *Net Sediment Flux*

Net sediment flux at the sediment–water interface was greatest within *Callianassa* Control treatments, whereas sediment movement within all other treatments were comparably low (Figure 4.8), suggesting that both resuspension of sediment by bioturbation and trapping of sediment by *Z. capensis* have noticeable effects on sediment flux at the sediment-water interface.

A Two-way ANOVA testing the effects of area and treatment showed highly significant differences between treatments, but no area effect or any interaction between them (Table 4.7). Post-hoc Tukey tests revealed significant differences in sediment flux within *Callianassa* Control treatments only when compared to all other treatments, which were statistically indistinguishable.

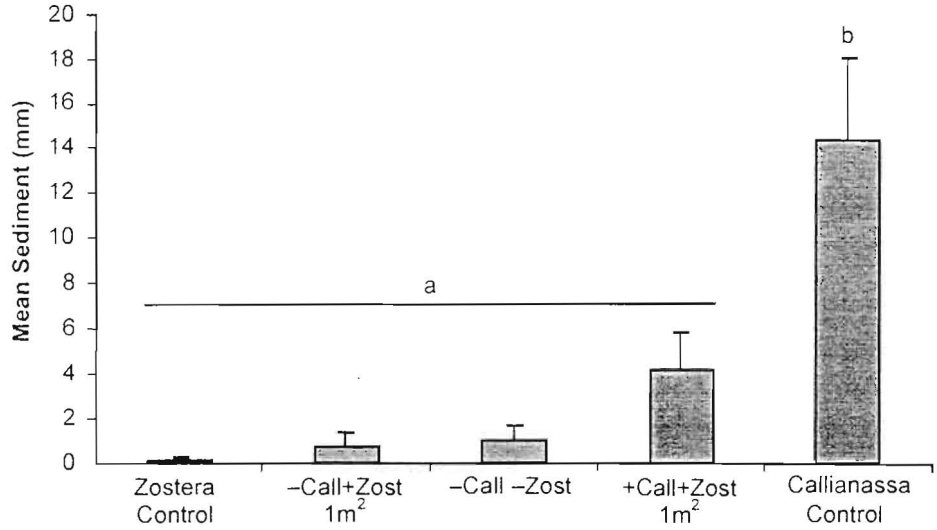


Figure 4.8: A comparison of the mean (+SE) nearshore sediment flux (mm) within control and experimental treatments, as determined by depth of burial of washers on disturbance rods. Letters indicate significant differences between treatments ($p < 0.01$). Solid lines above the bar columns connect treatments that were not significantly different from each other ($p > 0.05$).

Table 4.7: Results of a Two–Way ANOVA on the effects of area and treatment on nearshore sediment flux, as determined by depth of disturbance rods in control and treatment sites.

Two-Way ANOVA					
	df Effect	MS Effect	F	p-level	
Area	1	0.05	0.07	0.795	Not Significant
Treatment	4	8.36	12.04	<0.001	Significant
Area X Treatment	4	0.30	0.43	0.783	Not Significant

4.3.7 *Suspended Sediment*

The volume of sediment settling in sediment traps within control and experimental treatments was measured to determine whether the presence of *Z. capensis* and/or *C. kraussi* influences the amount of suspended sediment. The most notable differences in sediment volume occurred at the sediment-water interface (corroborating results from the depth–of–disturbance rods), but became more ambiguous as depth above the sediment bottom increased. Generally, lower volumes of sediment were associated with treatments that either contained *Z. capensis* or lacked *C. kraussi* whereas highest volumes were recorded within *Callianassa*–associated treatments (Figure 4.9). Two-way ANOVAs testing the effect of area and treatment at each height level separately are shown in Table 4.8. Significant differences between treatments were evident at

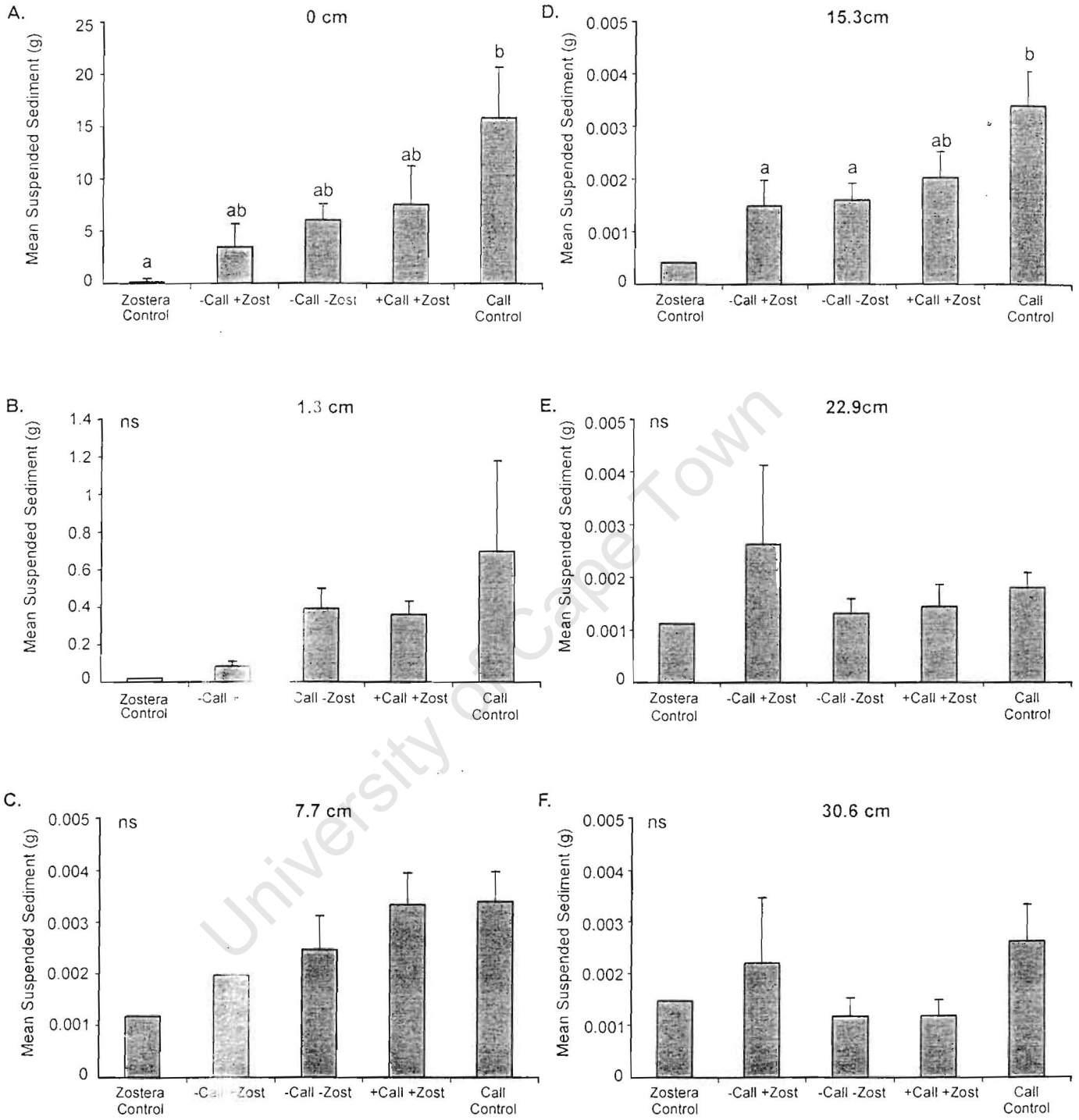


Figure 4.9: A comparison of the mean (+SE) vertical distribution of suspended sediment at set height intervals (A-F) above the sediment-water interface within experimental treatments. Letters indicate significant differences ($p < 0.05$) between treatments. ns indicates sample intervals at which treatments were not significantly different.

two height intervals only. At the 0 cm level, post-hoc Tukey tests revealed significant differences in the volume of suspended sediment within *Zostera* Control and *Callianassa* Control treatments (Figure 4.9 A). At the 15.3 cm level, significant differences occurred between –*Callianassa* –*Zostera* and *Callianassa* Control treatments (Figure 4.9 D).

Table 4.8: Results of Two–Way ANOVAs on the effects of area and treatment on suspended sediment in control and treatment sites. No ANOVA was possible for the 22.9 cm data due to inequality of variances even after transformation.

Two-Way ANOVA					
0 cm	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.01	0.00	0.984	Not Significant
Treatment	4	6.74	4.52	0.009	Significant
Area X Treatment	4	2.17	1.46	0.253	Not Significant
1.3 cm	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.07	1.38	0.257	Not Significant
Treatment	3	0.07	1.36	0.291	Not Significant
Area X Treatment	3	0.09	1.79	0.189	Not Significant
7.7 cm	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.00	4.2	0.058	Not Significant
Treatment	3	0.00	1.4	0.278	Not Significant
Area X Treatment	3	0.00	0.2	0.898	Not Significant
15.3 cm	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.00	4.8	0.044	Not Significant
Treatment	3	0.00	3.5	0.039	Significant
Area X Treatment	3	0.00	0.8	0.526	Not Significant
30.6 cm	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.00	6.10	0.025	Significant
Treatment	3	0.00	1.19	0.345	Not Significant
Area X Treatment	3	0.00	1.17	0.353	Not Significant

4.4 Discussion

The dynamic nature of shallow-water soft-bottom communities has led to the development of conceptual models interpreting communities in terms of their state of ecological 'neighbourhood stability' (Gray, 1977 in Probert, 1984), i.e. where the biological effects of one species may render an environment more or less suitable for another species or set of species (Gray, 1974).

Descriptive techniques employed in the preceding two chapters provided circumstantial evidence that bioturbation by *C. kraussi* has dramatic negative impacts on the distribution and abundance of *Z. capensis* and *U. africana*, resulting in mutually exclusive distribution patterns. On the other hand, there was also evidence that *Z. capensis* stabilises the sediment, excluding *C. kraussi* but allowing co-habitation by *U. africana*. Although these observations form the basis for understanding the ecological processes controlling the distribution patterns of these species, confirmation of the causality of these interactions was sought through the experimental manipulations described in this chapter.

The potential negative influence of *C. kraussi* bioturbation on *Z. capensis* stands was assessed experimentally by transplanting replicated sods of the eelgrass from a healthy bed to adjacent areas within the *Callianassa*-dominated sandflats. In half of these areas, *C. kraussi* was experimentally removed prior to transplantation while in the other half, *C. kraussi* remained undisturbed. I hypothesised that *Z. capensis* would flourish in the absence of *C. kraussi* bioturbation but deteriorate in areas where *C. kraussi* was present in its natural densities. Similarly, *U. africana* was expected to be more prevalent in association with *Z. capensis*, and in areas devoid of *C. kraussi*, but less abundant in the presence of *C. kraussi*.

During the early phases of the experiment, the response of *Z. capensis* transplants in both the presence and absence of *C. kraussi* were ambiguous, and initial establishment of the transplants may have been retarded by procedural disturbances due to transplanting and relocating the eelgrass sods. However, the transplanted sods of *Z. capensis* did become established, and after about six months the health of *Z. capensis* plants in the presence or absence of *C. kraussi* began to parallel trends consistent with those predicted in earlier chapters and hypothesised in the introduction. In areas where *C. kraussi* had been experimentally removed, the eelgrass became established and expanded to form healthy, lush beds (> 75% cover). Initial declines in *Z. capensis* cover were short-lived, and were followed by a steady recovery until cover reached levels equivalent to that in the Controls (Figure 4.2). Furthermore, in the *–Callianassa* treatments, *Z. capensis* generated growth via extensions of its rhizomes through the sediment, resulting in a fourfold increase in the area covered by the seagrass (Figure 4.4 and 4.5). In contrast, the health of *Z. capensis* plants in sites dominated by *C. kraussi* began to decline. Blades in these areas physically deteriorated, with many showing signs of invasion by diatoms. *Z. capensis* cover decreased to <30% (Figure 4.2) and the total area of the seagrass diminished to less than that of its original transplant size (Figure 4.4 and 4.5).

These responses were closely mirrored by differences in the sediment characteristics of *–Callianassa* and *+Callianassa* treatments. Levels of both sediment flux and sediment suspended within the water column were greater in areas dominated by *C. kraussi*, and less in treatments in which either *Z. capensis* was present or *C. kraussi* was absent were largely unaffected (Figures 4.8 and 4.9). Furthermore, the penetrability of the sediment in areas where *C. kraussi* was present was significantly higher than that within *Zostera*–associated treatments (Figure 4.7). Several authors (Rhoads & Young, 1970; Brenchley, 1982; Suchanek, 1983) have proposed that sediment resuspension by active bioturbators can negatively affect seagrass populations by physically smothering the plants. These results indicate strongly that where *C. kraussi* occur in high densities, not only is biologically–enhanced sediment transport high, but *Z. capensis* is diminished as well. Unexpectedly, though, biomasses of *Z. capensis* from

–Callianassa and *+Callianassa* treatments were statistically indistinguishable, although there was some suggestion of less surface biomass in areas dominated by *C. kraussi* compared to areas where the sandprawn was experimentally removed (Figure 4.3). Biomass in the *Zostera* Removal treatment remained lower than that in any of the other treatments even after 12 months, indicating that recovery after removal is slow.

As anticipated, the decline of *Z. capensis* health in *+Callianassa* treatments was mirrored by the encroachment of *C. kraussi* from the adjacent sandflat. Although the abundance of the sandprawn was initially diminished by the implanted sods of *Z. capensis*, invasion soon took place in the *+Callianassa* treatments, and after four months there was no statistical difference between its densities inside the *Zostera* transplants and those in the *Callianassa* Controls. This effect was more obvious within the smaller patch sizes (0.5 m^2), indicating the importance of seagrass patch size in mediating recovery after disturbance (e.g. Worm & Reusch, 2000). Encroachment of *C. kraussi* in the *–Callianassa* treatments was, however, far slower, and even after 6 months low densities of *C. kraussi* occurred within the transplanted sods and even in the adjacent defaunated areas that lacked *Z. capensis* (Figure 4.6). Although it is tempting to conclude that *Z. capensis* alone inhibited invasion by *Callianassa*, the exclusion of *C. kraussi* may in part be largely due to the physical changes in the sediment associated with the defaunation procedure. As discussed earlier, sediment compaction is known to restrict the movement of burrowing organisms (Brenchley, 1982) and accordingly may explain the slow recovery of the prawn. Indeed, the penetrability of the sediment within defaunated areas was significantly lower than any other treatment, and the penetrability within *–Callianassa* treatments was lower than that in the *+Callianassa* treatments (Figure 4.7). *C. kraussi* was never recorded in the eelgrass bed, in either the *Zostera* Control plots or in the *Zostera* Disturbance Control. It also failed to colonise the *Zostera* Removal treatment in spite of a substantial reduction of *Zostera* biomass.

Conversely, *U. africana* was consistently more numerous in association with *Z. capensis*, most obviously in the absence of *C. kraussi*. Where *C. kraussi* was present in high densities (*+Callianassa* treatments and *Callianassa* Control sites), *U. africana* was virtually absent (Figure 4.6). In *Zostera* transplants, *U. africana* reached higher densities in *–Callianassa* than in the *+Callianassa* treatments.

The results clearly indicate that *C. kraussi* has a negative effect on *Z. capensis*, and has the ability to control its distribution and abundance. Previous research has shown *Zostera* spp. to be adaptable to a variety of environmental conditions (see Edgcumbe, 1980). Indeed, in other South African estuaries (e.g. Kromme Estuary) intertidal beds grow in a wide range of substrata,

from coarse sand to very fine sand and cover a variety of tidal heights (Hanekom & Baird, 1988). However, in Langebaan Lagoon, *Z. capensis* is persistently limited to the high-shore as a consequence of bioturbation by *C. kraussi*. This was particularly evident from the ability of *Z. capensis* to establish healthy beds in sandflats once bioturbation had been experimentally eliminated. Because of the procedure I used to create '*–Callianassa*' treatments (see methods), all infaunal species were eliminated by defaunation, leaving open the question of the agents of bioturbation. However, past experiments implicate *C. kraussi* as the main culprit. Experiments by Branch & Pringle (1987), in which only the densities of *C. kraussi* was experimentally manipulated (i.e. all other infaunal species were left undisturbed), revealed an almost a total absence of any turnover of sediment in cages lacking *C. kraussi*. Consequently, Branch & Pringle (1987) argued that *C. kraussi* was the only important bioturbator operating within Langebaan Lagoon causing ~94% of the sediment turnover. Similarly, in the lagoon of Enewetak Atoll, callianassids accounted for ~83% of the sediment processed by invertebrates (Suchanek, 1986).

Z. capensis clearly has the ability to persist and expand in the sandflats where it is normally absent, provided that bioturbation is eliminated. This was apparent in the substantial increase in size of the transplanted sods in the *–Callianassa* treatments (Figure 4.5). As a result of vegetative extensions of their rhizomes through the sediment, seagrasses can expand their cover, adding new biomass and contributing to increased population growth rate (Phillips *et al.*, 1983; cited in Ewanchuk & Williams, 1995). Although seagrasses reproduce sexually by producing fruits and seeds, asexual or vegetative reproduction is commonly considered to be the most important mode of reproduction, particularly for recolonisation following disturbance. Rasheed (1999) found that recolonisation of disturbed plots of *Zostera capricorni* in the Ellie Point (Australia) seagrass meadows was purely by asexual reproduction, confirming that vegetative propagation is fundamental for both the spread and recovery of seagrass beds (Patriquin, 1975; Clarke & Kirkman, 1989; Duarte & Sand-Jensen, 1990). Williams (1990) discovered that vegetative propagation was the sole mechanism of recovery for experimentally cleared plots in a Caribbean seagrass meadow and vegetative growth is also responsible for the recolonisation of gaps created by dugongs feeding in seagrass beds in Australia (Preen, 1995).

Obviously, the rates of seagrass recolonisation and recovery depend on the magnitude of the disturbance combined with the growth characteristics of the seagrass species. Previous studies have determined that disturbances that created small gaps in the seagrass meadow were likely to recover within 12 months by vegetative propagation (Rasheed, 1999). However, these studies were set where seagrass meadows surrounded the disturbance area. Within Langebaan Lagoon, disturbance occurs predominately at the bed margins, which may then expand to occupy new

space via vegetative expansion on one front only (i.e. down-shore), as the upper limit is probably determined by desiccation (Talbot & Bate, 1987). Consequently, expansion occurs far more slowly (if at all) than in these previous studies, particularly if there is continual disturbance of the adjacent sand (Townsend & Fonseca, 1998). Essentially, the extreme concentration of disturbance near bed margins of *Z. capensis* by high densities of *C. kraussi* in the adjacent sandflats may overwhelm the colonisation capabilities of the eelgrass. Additionally, rhizome damage may take place as bioturbators burrow into and fragment existing margins (Townsend & Fonseca, 1998), and may significantly impair the expansion of *Z. capensis* meadows.

Comparative studies investigating *Zostera-Callianassa* interactions have also pointed to the mutually exclusive relationship of the two species. On one hand, *Z. capensis* seems able to limit *C. kraussi*, excluding it from healthy beds. Thompson & Pritchard (1969) noted that the colonisation of intertidal sandflats by *Zostera marina* and *Z. japonica* was accompanied by drastic reductions in the population range of the burrowing shrimp *Callianassa californiensis* (see also Harrison, 1987). Distributional data showed that the lower limit of the zone of abundant shrimp burrows coincided with the upper limit of eelgrass (opposite to the zonation pattern in Langebaan Lagoon, but based on the same mechanisms). Furthermore, in artificially established plots of *Z. japonica*, the prawn populations were temporarily reduced. Later in the season, when the eelgrass beds became denuded, the prawn burrows re-appeared in the sediment from which they had been excluded (Thompson & Pritchard, 1969; Harrison, 1987).

Following Brenchley (1982), it is plausible that these results were due to restrictions imposed on the burrowing activities of the callianassids by the root-rhizome mat of the encroaching seagrasses. But while it is conceivable that a healthy stand of eelgrass with its complex rhizome mat will inhibit *Callianassa*, seagrass beds can be invaded successfully (Suchanek, 1983). Thus, on the other hand, the physical disturbance associated with the normal burrowing and feeding activities of sandprawns may sometimes be too intense for the survival of seagrass. Experimental transplants of *Thalassia testudinum* by Suchanek (1983) revealed that once *Callianassa rathbunae* has invaded seagrass stands, it excludes or inhibits the seagrass by smothering it, or by reducing the penetration of light as a result of suspension of particles.

The results of this chapter provide experimental evidence of the causality of the processes governing the interactions between *Zostera capensis* and *Callianassa kraussi*. These include the following. (1) In the absence of bioturbation, *Z. capensis* is able to survive and expand in areas within sandflats. (2) In the presence of *C. kraussi*, the eelgrass steadily deteriorates, both in cover and aerial extent. (3) *U. africana* was consistently associated with *Z. capensis* and was common in areas lacking *C. kraussi* but virtually absent in the presence of *C. kraussi*. (4)

Densities of *C. kraussi* within *Z. capensis* transplants were considerably reduced compared to background levels although this effect was relatively short-lived. (5) Penetrability, sediment flux and suspension of sediment were all greater in the presence of *C. kraussi* than in its absence, and least in *Zostera* beds or transplants. Collectively, this implies that bioturbation by *C. kraussi* had a more significant impact on structuring *Z. capensis* than *vice versa*, although seagrass did inhibit *C. kraussi* to a certain extent. Furthermore, these results support the concept of amensal interactions between deposit-feeding species (e.g. *C. kraussi*) and suspension-feeding species (e.g. *U. africana*), as first reported by Rhoads & Young (1970, 1971).

In regions where *C. kraussi* does limit or eliminate seagrass beds it will also affect the extremely complex assemblage of other species that are either directly or indirectly dependent on the seagrass beds (Ogden, 1980; Suchanek, 1983). In Langebaan Lagoon, eelgrass beds house a distinct suite of species very different from that of the adjacent *Callianassa*-dominated sandflats (Chapter 3). Consequently, experimental transplants of *Z. capensis* into areas originally dominated by *C. kraussi* may cause a shift in community structure, from one characterised by sandflat-associated species to one with *Zostera*-associated species. This is the topic of Chapter 5.

Chapter 5

An experimental examination of the influence of biological interactions on community structure within *Zostera capensis* beds and sandprawn–dominated sandflats.

5.1 Introduction

It has been widely acknowledged that seagrass habitats support an invertebrate fauna that is more prolific in species richness, diversity, abundance and biomass than unvegetated areas (O'Gower & Wacasey, 1967; Orth, 1977; Stoner, 1980; Homziak *et al.*, 1982; Fitzhardinge, 1983; Suchanek, 1983; Lewis, 1984; Heck *et al.*, 1989; Edgar, 1990; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1977; Lee *et al.*, 2001). Recently, experimental studies have investigated mechanisms that may explain this, such as increased food abundance, sediment stability, protection from predation or habitat complexity (Orth, 1977; Heck & Wetstone, 1977; Stoner, 1980; Orth *et al.*, 1984; Summerson & Peterson, 1984), all of which interact to underpin the seagrass faunal community.

In particular, habitat structure strongly influences processes that govern the abundance and distribution of organisms in space and time (Hovel & Lipcius, 2002). For instance, the leaves and root–rhizome system of seagrass create habitats of relatively high structural complexity which, in contrast to bare sediments, provide many spatial niches for a variety of fauna (Heck & Wetstone, 1977) and afford shelter from predation (Lewis, 1984). By reducing the effects of currents and wave–action at the sediment–water interface, seagrass beds also encourage the deposition of fine organic sediments and thus alter the particle size–structure of the substrata on which they grow (Fonseca *et al.*, 1983; Bowden *et al.*, 2001) and the availability of food for benthic fauna (Lewis, 1984; Edgar & Barrett, 2002). The increased productivity, habitat modification and generation of spatial refugia in otherwise unvegetated areas make it likely that seagrass beds are important in maintaining biodiversity (Bowden *et al.*, 2001).

Furthermore, fragmentation of continuous areas of habitat to small, spatially isolated remnant patches, may additionally impact on biotic interactions that structure communities (Hovel & Lipcius, 2002 and references therein). Indeed, seagrass meadows may be extensive and continuous, but they are more often fragmented by forces such as waves and currents, animal foraging and boating into mosaics of discrete patches surrounded by a matrix of unvegetated sediments (Fonseca *et al.*, 1983; Hovel & Lipcius, 2002).

Biological disturbances, in particular, have important consequences for the structure and distribution of benthic communities in soft–sediment environments (Myers, 1977; Suchanek, 1983; Alongi, 1985; Rowden & Jones, 1993; Berkenbusch *et al.*, 2000), and the role that physical disturbance plays in modifying the strength and importance of these interactions, are widely acknowledged (Orth, 1977; Sousa, 1979; Paine & Levine, 1981; Woodin, 1981; Suchanek, 1981; Bell & Woodin, 1984). Feeding and burrowing activities by a variety of bioturbators can cause substantial sediment disturbance in intertidal habitats (Rhoads & Young, 1977; Grant, 1983), resulting in both negative and positive effects for the abundance of associated organisms (Peterson, 1977; Suchanek, 1983; DeWitt & Levinton, 1985; Townsend & Fonseca, 1998; Berkenbusch *et al.*, 2000). Given the proposed importance of bioturbators (especially burrowing deposit–feeders such as *Callianassa kraussi*) in modifying the physical environment in soft–sediments (Rhoads & Young, 1970; Woodin, 1976; Brenchley, 1981; Posey, 1986, 1987; Branch & Pringle, 1987), it is probable that they exert a powerful influence on the composition of the faunal communities in which they are dominant (Wynberg & Branch, 1991).

The descriptive field studies presented in Chapters 2 and 3 explored the importance of biological interactions in influencing the distribution and abundance of soft–bottom communities at Langebaan Lagoon. Although these results were largely correlative, they suggested that two distinct habitats exist within the lagoon: one comprising beds of the eelgrass *Zostera capensis*, and the other sandflats dominated by the sandprawn *C. kraussi*, each with a distinctive faunal composition. However, the complexity of these patterns, the interdependence between the components of the sandflat and the observational nature of these results makes it difficult to confidently assign causality to the relationships between *Z. capensis* and *C. kraussi* and their associated faunas. This issue was addressed in Chapter 4, which employed manipulative experimental techniques to elucidate the interactions between seagrass and sandprawns. The results showed that bioturbation by *C. kraussi* has a negative influence on the health and biomass of *Z. capensis* and, in turn, *Z. capensis* inhibits the distribution and density of the sandprawn.

This chapter considers further whether mutually exclusive *Z. capensis* and *C. kraussi* habitats may influence the faunal composition associated with each habitat, and relied on the manipulative experiments described in Chapter 4 to examine macrofaunal community composition and species abundance in relation to experimental transplants of *Z. capensis* into areas with and without *C. kraussi*. As in Chapter 3, I also used this analysis to test hypotheses advanced by Brenchley (1981, 1982) who argued that because eelgrass stabilises sediment, the fauna of eelgrass beds should mainly comprise species characterised by flexible bodies and

non–burrowing habit. Conversely, sandprawn–dominated areas, which will experience substantial bioturbation, will house species that are relatively larger, inflexible and burrowing. Specifically, I tested the following hypotheses:

1. Differentiation in biological community composition will exist between sediments disturbed by *C. kraussi* and those stabilised by *Z. capensis* (following Suchanek, 1982 and others) and between experimental transplants of *Z. capensis* into areas with and without *C. kraussi*.
2. Differences in the composition of each experimental and control treatment's associated faunal assemblage will be explained by Brenchley's (1982) hypothesis, which distinguishes taxa according to mobility and morphology, and argues that *Zostera*–associated fauna will be disproportionately represented by non–burrowing and soft–bodied species and those in unvegetated, bioturbated sediments by burrowing and hard–bodied species.

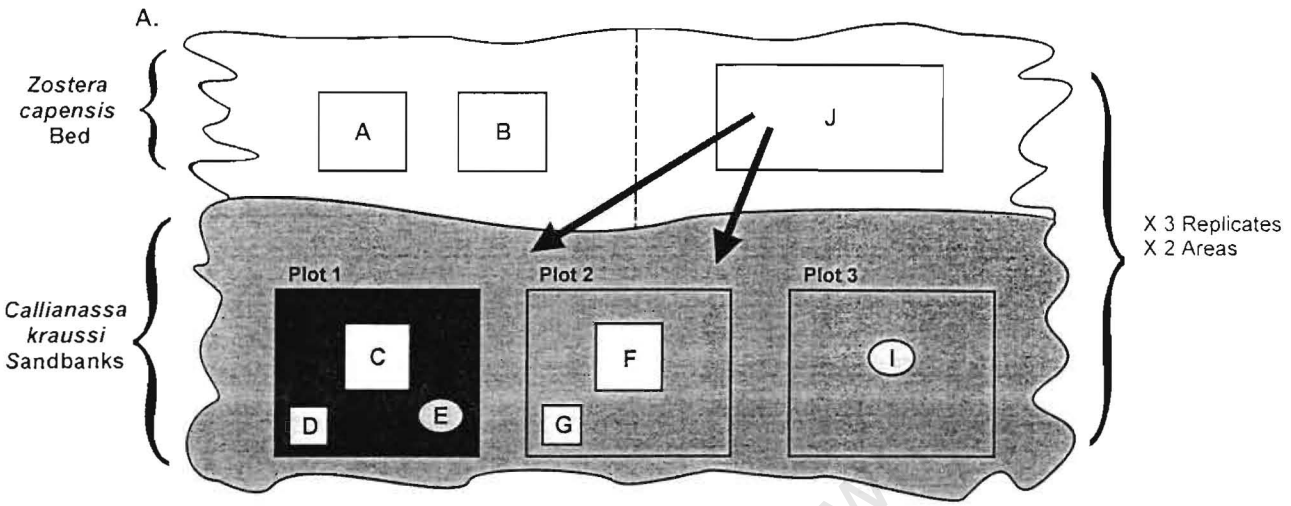
5.2 Methods

The sampling site at Bottelary and the experimental procedures are described in detail in Section 4.2.1 of the previous chapter. In brief, the experiment involved transplanting areas or either 1 m^2 or 0.5 m^2 of *Z. capensis* into unvegetated sandflats that either contained normal densities of the sandprawn *C. kraussi*, or from which the sandprawn had been eliminated by faunal suffocation. In addition to these experimental treatments, undisturbed *Callianassa* Controls and *Zostera* Controls and *Zostera* Disturbance Controls were conducted. Figure 5.1 summarises the experimental design. The experiment was established in two areas, with three replicates of each control or treatment per area.

5.2.1 *Biological Communities*

Surveys of community composition were conducted within the controls and experimental treatments at 12 and 18 months. At 12 months, all treatments were sampled. Surveys at 18 months were confined to treatments A, C, F and I for two reasons. First, the *Zostera* disturbance Control and the *Zostera* Removal treatments proved identical with the *Zostera* Control. Second, the 0.5 m^2 and 1 m^2 transplants of *Zostera* had merged (at least in the –*Callianassa* treatments), so they were treated as a single unit. Only two replicates were sampled in each area after 18 months due to the loss of some replicates. For each replicate, two randomly selected 0.1 m^2

A.



B.

Key	Treatment	Abbreviation	Sampling 12m	Sampling 18m
A	*Zostera* Control	*Zost* Control	✓	✓
B	*Zostera* Disturbance Control	*Zost* Dist Control	✓	
C	- *Callianassa* + *Zostera* $1m^2$	*-Call+Zost* ($1m^2$)	✓	✓
D	- *Callianassa* + *Zostera* $0.5m^2$	*-Call+Zost* ($0.5m^2$)	✓	
E	- *Callianassa* - *Zostera*	*-Call-Zost*	✓	
F	+ *Callianassa* + *Zostera* $1m^2$	*+Call+Zost* ($1m^2$)	✓	✓
G	+ *Callianassa* + *Zostera* $0.5m^2$	*+Call+Zost* ($0.5m^2$)	✓	
I	*Callianassa* Control	*Call* Control	✓	✓
J	*Zostera* Removal	*Zost* Removal	✓	

Figure 5.1: Schematic diagram (A) illustrating experimental treatments. (B) Key showing experimental treatments, abbreviations and sampling strategy. In Plot 1, *C. kraussi* was eliminated by defaunation of the sediment; in Plots 2 and 3 it was left undisturbed. Tick symbols indicate the control and experiment treatments sampled after 12 and 18 months.(d = days, w = weeks, m = months).

samples were taken. Sediment was dug down to a depth of 20 cm and sieved through a 1–mm mesh sieve. All living macrofauna retained by the sieve was preserved in 10% formalin and identified to species level using Branch *et al.* (1994), Day (1981), Griffiths (1976), Kensley (1972) and Kilburn & Rippey (1981). Species were categorised according to whether they were 'hard–bodied' or 'soft–bodied', and 'burrowing' or 'non–burrowing', following categories of relative mobility and functional morphology identified by Brenchley (1981).

5.2.2 *Statistical Analysis*

Data were tested for normality and homogeneity of variance by Kolmogorov–Smirnov tests and Levene's tests respectively (alpha set at 0.05). If necessary, data were transformed to meet the assumptions of parametric tests. When this failed, equivalent nonparametric statistical tests were applied. Differences in the densities of macrofaunal species within control and experimental treatments were assessed by Mann–Whitney U tests. Comparisons of species diversity and species richness between treatments were assessed by ANOVA. The Shannon diversity index (H'=-sum (Pi*Log (Pi)), where Pi is the proportion of the total count arising from the *i*th species), was used to establish species diversity, and Margalef's richness index (d'= (S-1)/Log (N), where S is the total number of species and N the total number of individuals) determined species richness. When appropriate, ANOVAs were followed by multiple comparison Tukey tests. Statistical analyses were conducted using StatSoft, Inc. (2000) STATISTICA version 6 for Windows. Differences in relative mobility and functional morphology (hard–bodied vs. soft–bodied and burrowing vs. non–burrowing) of macrofaunal assemblages sampled within control and experimental treatments were assessed by Chi–square analyses.

PRIMER (Plymouth Routines in Multivariate Ecological Research, version 5, 2001) was used for analysis of species composition and abundance (Clarke & Warrick, 1994). Biological data were fourth-root transformed to weight the contribution of less abundant species. Hierarchical cluster analysis using Bray-Curtis similarity and multidimensional scaling (MDS) were used to compare community composition between control and experimental treatments. Similarity percentage breakdown analysis (SIMPER) allowed the identification of the relative contribution of single species to differences in community structure. Species were only considered if they cumulatively accounted for at least 80% of the overall similarity or dissimilarity within or between treatments.

5.3 Results

5.3.1 *Community Structure*

The experimental transplant of *Z. capensis* into intertidal sandflats produced clear changes in community structure.

The dendrogram and MDS plot for 12 months (Figures 5.2 and 5.3) indicated a distinct separation of communities between the natural *Zostera* bed, transplanted treatments and unvegetated treatments. On the whole, samples clustered into five discrete groups more than 70% dissimilar, based primarily on habitat differences and size of the original transplant plot. Cluster I comprised samples from the *Zostera* Control, *Zostera* Disturbance Control and *Zostera* Removal plots, resulting in a unique '*Zostera* bed' faunal community. Samples from the transplanted areas (*-Callianassa +Zostera* and *+Callianassa +Zostera*) in 1 m^2 plots (Cluster II, '*+Zostera* 1 m^2') were distinct from 0.5 m^2 transplanted plots (Clusters IV and V, '*+Zostera* 0.5m^2'), regardless of the presence or absence of *C. kraussi*. All samples that constituted unvegetated sandflat (*-Callianassa –Zostera* and *Callianassa* Control) grouped together in Cluster III, with sub-clusters forming as a result of divergence between sample areas (sub-groups III a-d). Apart from Cluster III, area differences accounted for none of the divergence between faunal groups.

The dendrogram for 18 months showed more clear–cut differences in the community structure of macrofaunal assemblages sampled from control and experimental treatments (Figure 5.4 A). Four distinct groups of samples were evident, consistent with differences in habitat. These results were supported by the MDS plot (Figure 5.4 B), which clearly separated treatments, and associated those treatments that were characterised by the absence of *C. kraussi* (*Zostera* Control and *–Callianassa +Zostera*) and those that were characterised by the presence of *C. kraussi* (*+Callianassa +Zostera* and *Callianassa* Control).

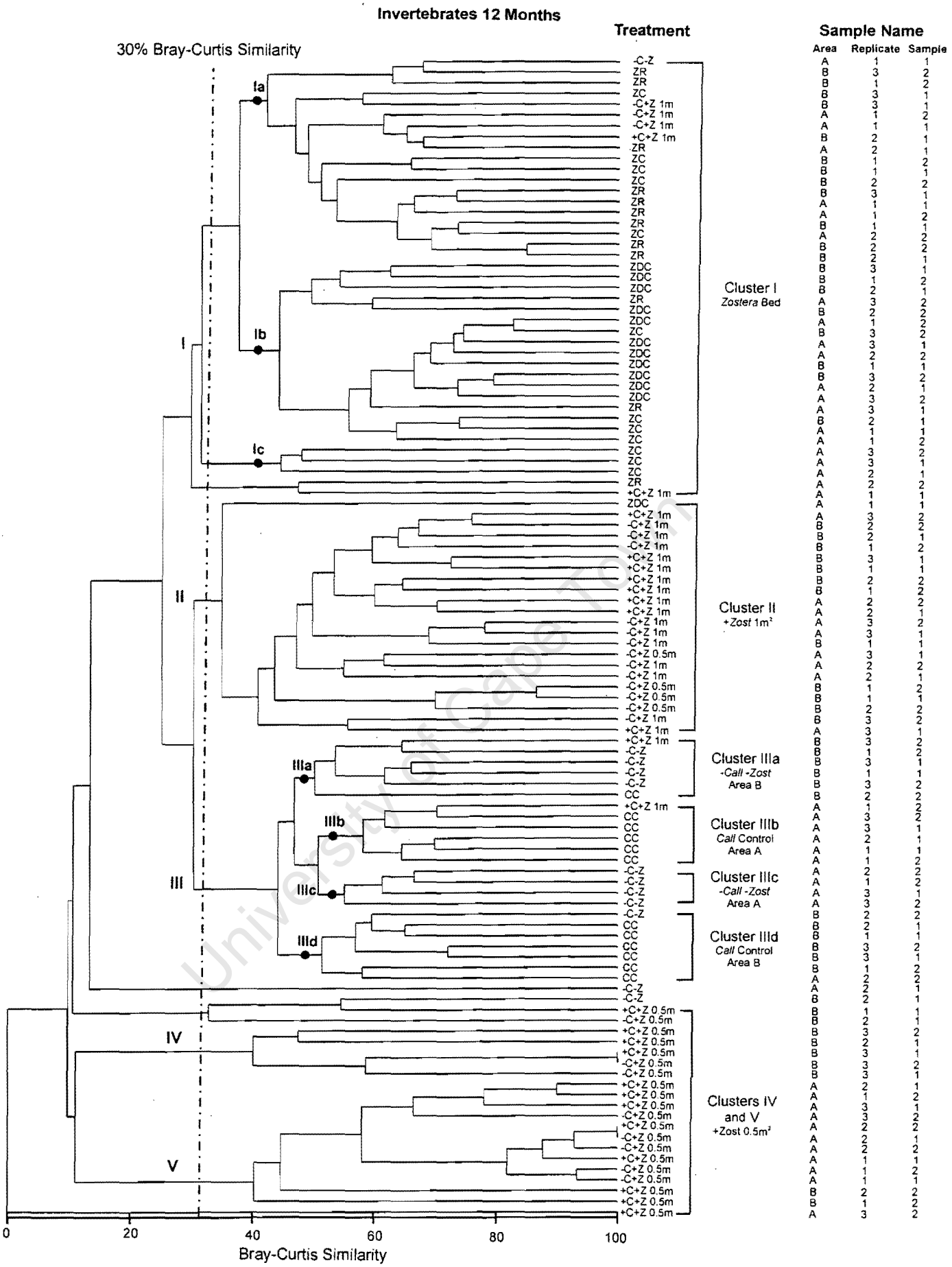


Figure 5.2: Dendrogram showing results of hierarchical cluster analysis based on fourth-root transformed invertebrate data from control and experimental sites sampled 12 months after experiment initiation. Treatments: -C-Z= *-Callianassa -Zostera*, ZC= *Zostera* Control, ZDC= *Zostera* Disturbance Control, ZR= *Zostera* Removal, -C+Z 1m²= *-Callianassa +Zostera* 1m², -C+Z 0.5m²= *-Callianassa +Zostera* 0.5m², +C+Z 1m²= *+Callianassa +Zostera* 1m², +C+Z 0.5m²= *+Callianassa +Zostera* 0.5m², CC= *Callianassa* Control.

B.

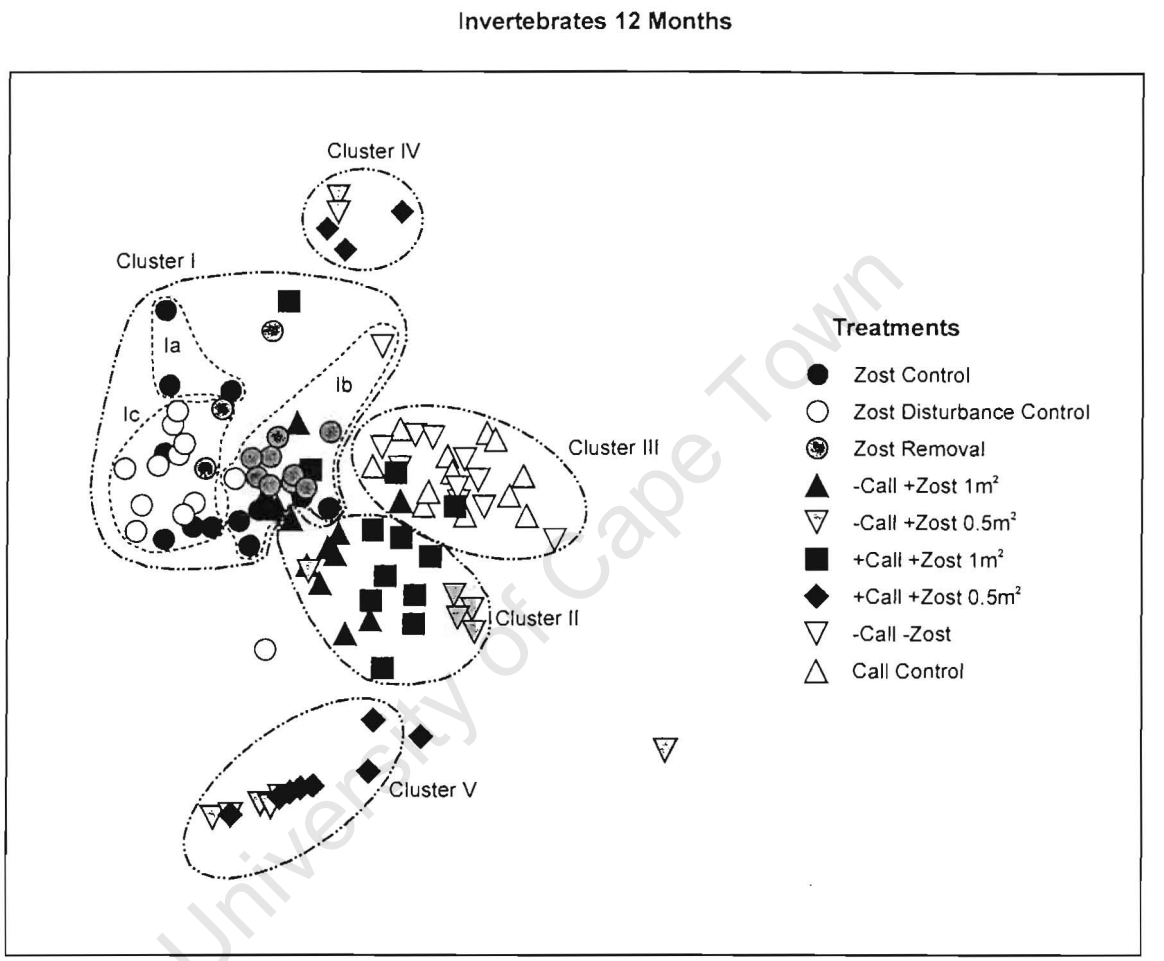


Figure 5.3 : MDS plot (stress=0.17) based on fourth-root transformed invertebrate data from control and experiment sites sampled 12 months after experiment initiation.

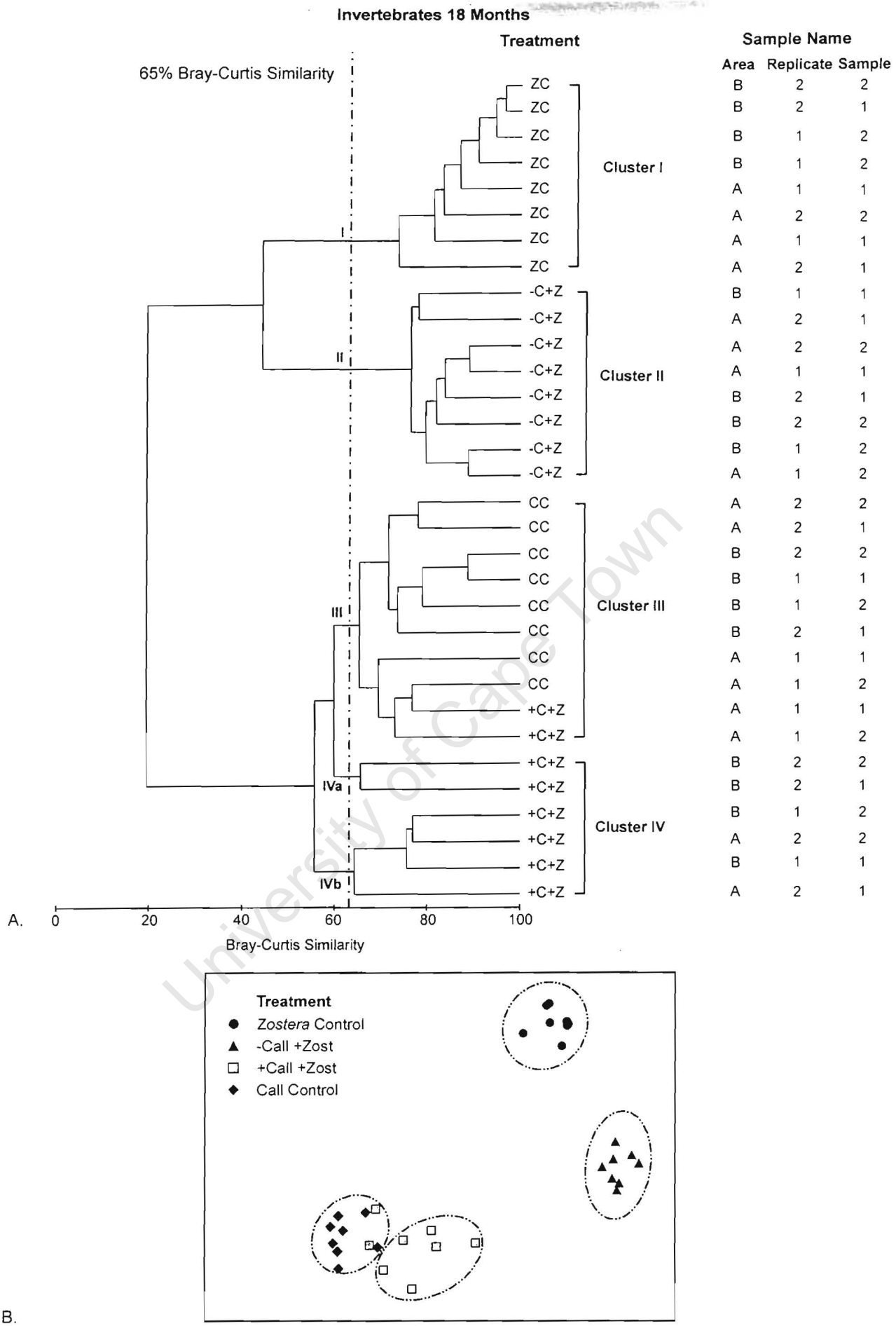


Figure 5.4: Dendrogram (A) showing results of the hierarchical cluster analysis and (B) MDS plot (stress=0.01) based on fourth-root transformed invertebrate data from control and experiment sites sampled 18 months after experiment inititation. Treatments: ZC= *Zostera* Control, -C+Z= *-Callianassa +Zostera*, +C+Z= *+Callianassa +Zostera*, CC= *Callianassa* Control.

5.3.2 *Community Composition*

Differences in the macrofauna sampled within control and experimental treatments indicated that distinct assemblages existed. Figure 5.5 A shows the suite of indicator species identified by SIMPER as being principally responsible for distinguishing between treatments at 12 months. Communities showed marked divergence in abundances and composition, with different taxa responding differently to the presence or absence of *Zostera* and/or *Callianassa*. This was most evident from examination of the two most extreme treatments, the *Zostera* Control and the *Callianassa* Control. Species typical of *Zostera*–associated habitats were consistently more abundant in the *Zostera* Control, while sandflat–associated species consistently dominated the *Callianassa* Control. Typical *Zostera*–associated species included *Assiminea globulus* and *Hydrobia* sp. (the most important characteristic species), *Siphonaria compressa*, *Ceratonereis erythraeensis*, *Paramoera capensis*, *Cleistostoma edwardsii*, *Perinereis nuntia vallata* and *Upogebia africana*. In contrast, the *Callianassa* Control was consistently dominated by *Orbinia angrapequensis* (the most important characteristic species), *Urothoe grimaldii*, *Notomastus latericeus*, *Callianassa kraussi*, *Scoloplos johnstonei* and *Carditella rugosa*. In both cases, species that were indicative of one of these treatments were either absent or present in very low densities in the other treatment, thus exhibiting patterns similar to those described in Chapter 3.

Furthermore, this list of species corresponded closely with those identified in Chapter 3 as characteristic of either *Zostera* or sandflat habitats. The one exception was the addition of *Paramoera capensis* to the *Zostera*–associated species–list. To simplify the graphical representation, the *Zostera* Disturbance Control and *Zostera* Removal Control treatments were excluded (as they showed patterns almost identical to the *Zostera* Control) and only samples from the *Zostera* Control treatments presented, although all three were distinguished when running PRIMER analyses. SIMPER showed no consistent differences between the composition of faunal communities within *Zostera* Control, *Zostera* Disturbance Control and *Zostera* Removal treatments, nor did cluster analysis or the MDS plots, which grouped these three treatments together as a cluster (Figures 5.2 and 5.3).

The faunal composition within *–Callianassa +Zostera* 1m^2 and *+Callianassa +Zostera* 1m^2 treatments was more diverse than either control treatments, comprising moderate abundances of both *Zostera*–associated and sandflat–associated species. There was almost no difference between the species present in these two treatments, except for the presence or absence of *C. kraussi*. Divergence between *–Callianassa* and *+Callianassa* treatments was largely due to a greater abundance of *Zostera*–associated species in the absence of *C. kraussi* (*Siphonaria compressa*, *Paramoera capensis*, *Perinereis nuntia vallata* and *Cleistostoma edwardsii*), and a

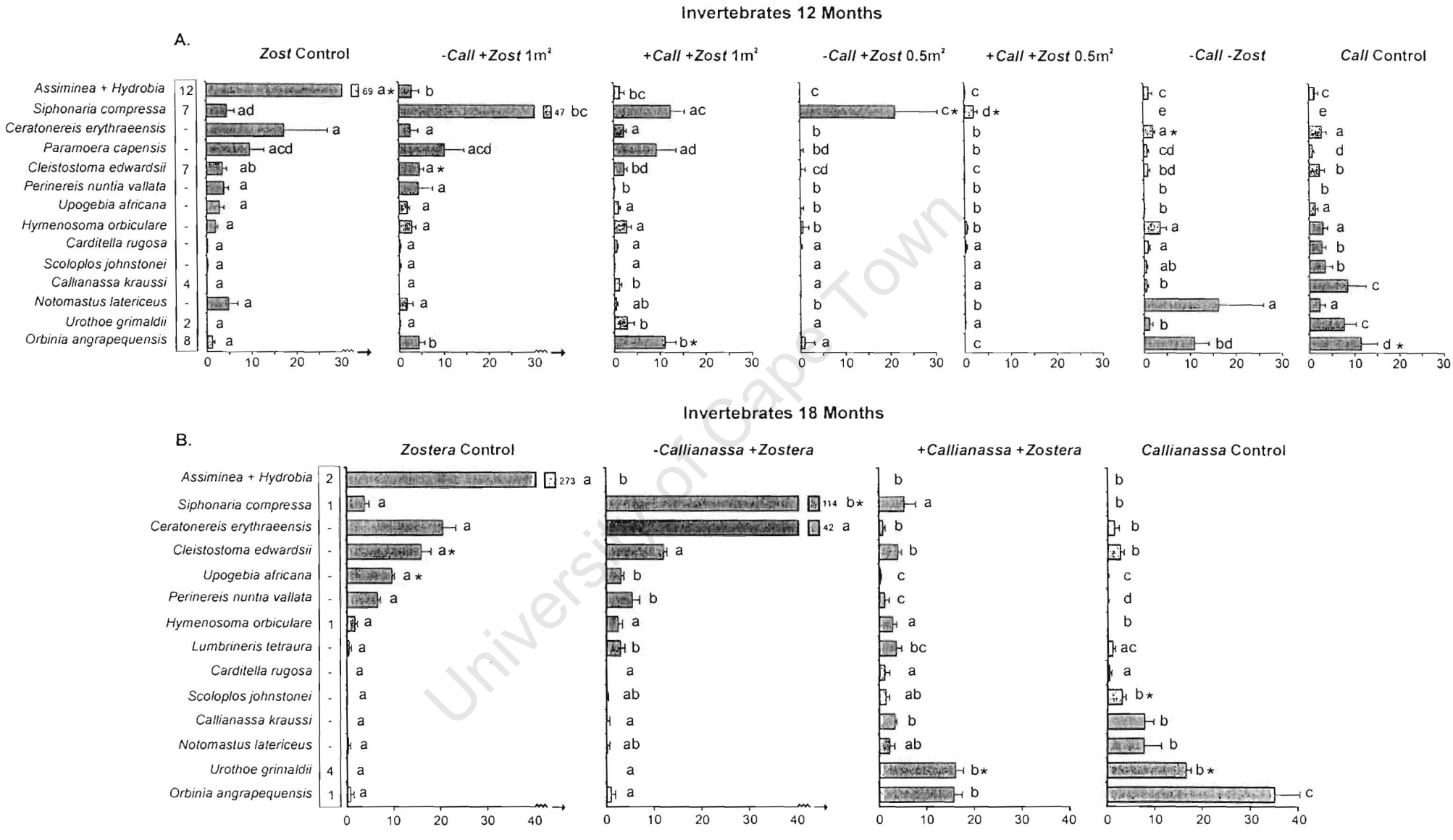


Figure 5.5: Mean density (+SE) of indicator species sampled in control and experimental treatments that consistently distingished between treatments after (A) 12 months and (B) 18 months, as determined by SIMPER analyses. Taxa accounting for 80 % of the cumulative similarity are shown: taxa that share letters indicate an absence of significant differences between treatments ($p > 0.05$), as determined by Mann-Whitney U tests. Numbers following the names of species indicate the number of times a species consistently distinguished between treatments; * indicates species most consistently characteristic of each treatment.

greater abundance of sandflat–associated species in the presence of *C. kraussi* (most notably *Orbinia angrapequensis* and *Urothoe grimaldii*). The two most important distinguishing species were *Siphonaria compressa* (characteristically *Zostera*–associated) and *Orbinia angrapequensis* (characteristically sandflat–associated).

Of particular interest, are the species distinguishing between *+Zostera* 1m^2 and *Zostera* Control treatments. The most abundant species within the *Zostera* Control, the gastropods *Assiminea globulus* and *Hydrobia* (predominantly high–shore species) were present in very low densities within the transplanted treatments, regardless of the absence or presence of *C. kraussi*. In contrast, *Siphonaria compressa* was much more abundant within the transplanted treatments compared to the higher–shore *Zostera* bed, particularly in the absence of *C. kraussi*.

Communities within 0.5 m^2 treatments were very different in abundances and composition from other treatments, mainly because few species were present and most occurred in low abundances. The only notable exception was *Siphonaria compressa*, which occurred in relatively high densities within the *–Callianassa* treatment and was the most consistently characteristic species.

Communities associated with *–Callianassa –Zostera* treatments responded differently from what was expected, comprising mainly species characteristic of sandflat–associated habitats. The most abundant species within the treatment, *Notomastus latericeus* and *Orbinia angrapequensis*, were present in greater or equal densities to those recorded in the *Callianassa* Control, despite the absence of *C. kraussi*. The most consistently characteristic species was *Cleistostoma edwardsii*.

The simplified data set at 18 months, which concentrated on the basic treatments, showed clear trends in faunal composition (Figure 5.5 B). The *Zostera* Control was dominated by high abundances of *Zostera*–associated species, whereas sandflat–associated species were more abundant within the *Callianassa* Control. Furthermore, there was little overlap between the species characteristic of these two divergent controls. *Cleistostoma edwardsii* and *Upogebia africana* were the most consistently characteristic species within the *Zostera* Control, while *Scoloplos johnstonei* and *Urothoe grimaldii* consistently characterised the *Callianassa* Control. Differences in the faunal composition between the two *+Zostera* treatments were more pronounced than at 12 months, with very few sandflat–associated species occurring within the *–Callianassa* treatment. The distinction between *Zostera*–associated and sandflat–associated species was more ambiguous within *+Callianassa* treatments, but the most important characteristic species dominating the samples were the sandflat–associated species *Urothoe*

grimaldii and *Orbinia angrapequensis*. The two high–shore species *Assiminea* and *Hydrobia*, which were abundant in the *Zostera* Controls, where absent from the *Zostera* transplants, which were situated slightly lower on the shore than the *Zostera* Controls. Conversely, *Siphonaria compressa* was approximately twenty times more abundant in the *–Callianassa* treatment than in the *Zostera* Control, and even in the *+Callianassa* treatment it achieved about 1.5 times its density in the *Zostera* Controls.

Patterns were thus remarkably consistent between 12 months and 18 months in terms of the indicator species distinguishing between macrofaunal assemblages in control and experimental treatments (Figure 5.5). Most striking were the differences between treatment extremes (e.g. *Zostera* Control and *Callianassa* Control). Also of particular interest, was the divergence between 1 m^2 plots and 0.5 m^2 plots after 12 months, indicating the importance of seagrass patch size for macrofaunal assemblages.

5.3.3 *Species Richness and Diversity*

A comparison was made of the richness and diversity indices of species sampled within control and experimental treatments. At 12 months, few discernible patterns emerged. Briefly, richness and diversity of species was comparable between most treatments except for 0.5 m^2 plots, which in all cases were the least rich and diverse. The total number of species (S) was highest within *+Callianassa* + *Zostera* 1 m^2 plots, but also comparatively high in the *Zostera* bed treatments (*Zostera* Control, *Zostera* Removal and *Zostera* Disturbance Control), *Callianassa* Control, –Callianassa *+Zostera* 1 m^2 and *–Callianassa –Zostera* treatments. All 0.5 m^2 treatments were characterised by low numbers of species (five times less than the *Zostera* bed treatments), regardless of the presence or absence of *C. kraussi* (Table 5.1). The same pattern was exhibited by Margalef's richness indices (d', Table 5.1). The total number of individuals (N) was highest in the eelgrass bed (notably in the *Zostera* Disturbance Control and *Zostera* Control), and clearly lowest in the two 0.5 m^2 treatments. The highest Shannon diversity indices were recorded in the *Callianassa* Control, the *Zostera* Control and the *Zostera* Disturbance Control treatments (Table 5.1). Diversity within 0.5m^2 plots was four times less than that of the most diverse treatments.

Analyses of the four indices comparing area and treatment by means of two-way factorial ANOVA are shown in Table 5.2. All indices showed significant differences among treatments ($p < 0.001$), but not between areas. Species richness indices (both total species and Margalef's richness) showed highly significant results ($p < 0.001$) among treatments. Interpretation of the total species was, however, clouded by a significant interaction between both main effects (area and treatment). When this occurs, tests of the main effects are unreliable. As a result, the

means of one factor were compared separately at each level of the other factor and vice versa by multiple comparison Tukey-tests. These indicated that significant differences between areas were marginal and occurred in only 38% of cases. For all four indices, values within 0.5 m^2 plots were significantly lower than some or all of the other treatments (Post-hoc Tukey tests, $p < 0.05$; see Table 5.1).

Table 5.1: Indices of species richness, diversity and abundance for invertebrates sampled 12 months after experiment initiation. Species richness is given as the Total Number of Species (S) and Margalef's richness index (d'). Shannon Diversity was determined by PRIMER analyses based on fourth-root transformed data. Letters appearing after the mean values differ between treatments if the results were significantly different (Tukey post–hoc tests, $p < 0.05$)

	Indices							
12 Months	**Total Species (S)**		**Margalef's Richness (d')**		**Total Individuals (N)**		**Shannon Diversity (H')**	
Treatment	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Zostera Control	14.6 a	1.6	2.6 ab	0.1	255.0 a	90.9	1.9 a	0.1
Zostera Disturbance Control	12.3 a	0.4	2.1 ab	0.1	297.2 a	82.6	1.5 a	0.1
Zostera Removal	13.1 a	0.6	2.4 ab	0.1	181.5 a	40.3	2.0 a	0.1
–Call +Zost 1m^2	12.5 a	0.9	2.3 ab	0.1	176.8 ab	48.2	1.6 a	0.2
+Call +Zost 1m^2	15.3 a	0.8	3.1 a	0.1	107.7 ab	14.2	1.8 a	0.2
–Call +Zost 0.5m^2	3.3 b	0.9	0.6 c	0.2	48.3 b	16.5	0.5 b	0.2
+Call +Zost 0.5m^2	3.0 b	1.0	1.1 b	0.5	8.0 b	1.9	0.7 b	0.3
–Call –Zost	11.5 a	0.9	2.4 ab	0.1	98.5 ab	26.5	1.8 a	0.1
Callianassa Control	13.8 a	1.2	2.7 ab	0.2	116.6 ab	32.2	2.1 a	0.1

Table 5.2: Results of Two-way ANOVA's on the effects of treatment and area on diversity indices sampled 12 months after experiment installation. Species Richness is represented by Total number of species (S) and Margalef's Richness (d'). Abundance is represented by Total number of individuals (N) and Species Diversity by the Shannon Diversity Index, as determined by PRIMER analyses based on fourth-root transformed data.

12 Months	**Two-Way ANOVA**				
Total Species (S)	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	3.63	0.72	0.401	Not Significant
Treatment	8	128.96	25.60	<0.001	Significant
Area X Treatment	8	11.88	2.36	0.037	Significant
Margalef's Richness (d')	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.00	0.01	0.947	Not Significant
Treatment	8	1.31	8.83	<0.001	Significant
Area X Treatment	8	0.16	1.09	0.397	Not Significant
Total Individuals (N)	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	1.94	0.11	0.742	Not Significant
Treatment	8	103.57	5.85	<0.001	Significant
Area X Treatment	8	20.27	1.14	0.358	Not Significant
Shannon Diversity (H')	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.06	0.42	0.520	Not Significant
Treatment	8	0.56	4.11	0.001	Significant
Area X Treatment	8	0.12	0.89	0.535	Not Significant

At 18 months the patterns were more clear-cut (Table 5.3). Species richness (both total number of species and Margalef's richness) was greatest within *+Callianassa +Zostera* treatments. Abundance was highest in the *Zostera* Control treatment and lowest in the *Callianassa* Control and the *+Callianassa +Zostera* treatment. Individuals were five times more abundant within the *Zostera* Control than in the *+Callianassa +Zostera* treatment or the *Callianassa* Control. Conversely, this pattern was reversed when comparing Shannon Diversity between treatments: *+Callianassa +Zostera* treatments were 1.5 to 2.1 times more diverse than other treatments.

Table 5.3: Indices of species richness, diversity and abundance for invertebrates sampled 18 months after experiment initiation. Species richness is given as the Total Number of Species (S) and Margalef's richness index (d'). Shannon Diversity was determined by PRIMER analyses based on fourth-root transformed data. Letters appearing after the mean values differ if the treatments were significantly different (Tukey post–hoc tests, $p < 0.05$).

	Indices							
18 Months	**Total Species (S)**		**Margalef's Richness (d')**		**Total Individuals (N)**		**Shannon Diversity (H')**	
Treatment	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Zostera Control	9.1 b	0.7	1.4 b	0.1	338.2 a	42.4	0.9 b	0.1
–Call +Zost	9.3 ab	0.6	1.6 b	0.1	187.0 b	19.1	1.2 b	0.1
+Call +Zost	11.5 a	0.5	2.5 a	0.1	64.7 c	6.4	2.0 a	0.1
Callianassa Control	8.0 b	0.6	1.6 b	0.1	77.6 c	6.9	1.4 b	0.1

Table 5.4: Results of Two-way ANOVA's on the effects of treatment and area on diversity indices sampled 18 months. Species Richness is represented by Total number of species (S) and Margalef's Richness (d'). Abundance is represented by Total number of individuals (N) and Species Diversity by the Shannon Diversity Index, as determined by PRIMER analyses based on fourth-root transformed data.

18 Months	**Two-Way ANOVA**				
Total Species (S)	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	16.53	5.90	0.231	Not Significant
Treatment	3	17.19	6.14	0.002	Significant
Area X Treatment	3	1.53	0.55	0.655	Not Significant
Margalef's Richness (d')	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	1.22	12.48	0.001	Significant
Treatment	3	2.08	21.32	<0.001	Significant
Area X Treatment	3	0.05	0.52	0.67	Not Significant
Total Individuals (N)	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.07	4.04	0.056	Not Significant
Treatment	3	0.85	48.89	<0.001	Significant
Area X Treatment	3	0.01	0.39	0.761	Not Significant
Shannon Diversity (H')	**df Effect**	**MS Effect**	**F**	**p-level**	
Area	1	0.04	0.61	0.440	Not Significant
Treatment	3	1.91	30.69	<0.001	Significant
Area X Treatment	3	0.04	0.64	0.59	Not Significant

Two-way ANOVAs performed on each of the four indices are shown in Table 5.4. All indices showed highly significant differences ($p < 0.002$) between treatments and only Margalef's richness was affected by area. None of the indices were affected by interactions between the main effects. Post-hoc Tukey tests confirmed the trends described above. The total number of species, Margalef's richness and Shannon diversity were all highest in the *+Callianassa +Zostera* treatment. Conversely, the total number of individuals within *Zostera* Control and the *–Callianassa +Zostera* treatments were significantly greater than within *+Callianassa +Zostera* and the *Callianassa* Control.

Considering the two periods of sampling together, the total number of species (S) and Margalef's richness (d') were consistently highest in *+Callianassa +Zostera* treatments. Shannon Diversity however, was initially highest in the *Callianassa* control treatments (in agreement with previous findings, see Chapter 3) but later proved more diverse within *+Callianassa +Zostera* treatments. The abundance of individuals was consistently highest within the *Zostera* bed (*Zostera* Control, *Zostera* Disturbance Control and *Zostera* Removal), also corresponding to previous findings (Chapter 3). The 0.5 m^2 treatments (sampled at 12 months only) were consistently the least diverse and species rich regardless of the presence or absence of *C. kraussi*. None of the other treatments revealed any discernable trends and in most cases exhibited comparable richness and diversity values.

5.3.4 *Morphological Characteristics*

To test hypotheses advanced by Brenchley (1981, 1982), differences between macrofaunal assemblages sampled within control and experimental treatments were assessed according to their relative mobility and functional morphology (burrowing vs. non-burrowing; hard-bodies vs. soft-bodied). Two sets of data were considered: 12 months and 18 months.

Brenchley's first hypothesis proposed that a disproportionately greater number of hard-bodied fauna should reside in bare, unvegetated sandflats, whereas *Zostera* beds should sustain more soft-bodied, flexible fauna. As in Chapter 3, two methods were employed to address this question. The first was to explore the proportions of species representative of the different morphological categories in control and experimental treatments. However, Chi-square analysis proved insignificant with reference to the proportion of species representing either hard-bodied or soft-bodied taxa within each treatment (Table 5.5). This approach was, however, of questionable value, as the numbers of species sampled within each habitat were in some cases less than those recommended for valid Chi-square analyses (Zar, 1984; Garvin, 1986).

Table 5.5: Total number of observed and expected numbers of hard–bodied and soft–bodied; and burrowing and non–burrowing species sampled within control and experimental treatments after 12 and 18 months. Chi–square analysis proved insignificant with reference to the proportions of species representing hard–bodied versus soft–bodied or burrowing versus non–burrowing taxa within each treatment.

Species 12 Months	**Brenchley Hypothesis**							
Treatments	**Hard–bodied**		**Soft–bodied**		**Burrowing**		**Non–burrowing**	
	Exp	***Obs***	***Exp***	***Obs***	***Exp***	***Obs***	***Exp***	***Obs***
Zost Control	18.2	16	5.9	8	13.0	14	10.9	10
–Call +Zost 1m^2	17.4	16	5.9	7	12.5	11	10.5	12
+Call +Zost 1m^2	21.9	22	7.0	7	15.7	14	13.2	15
–Call +Zost 0.5m^2	9.1	11	2.9	1	6.5	6	5.5	6
+Call +Zost 0.5m^2	7.6	10	2.4	0	5.4	4	4.6	6
–Call –Zost	14.4	14	4.6	5	10.3	13	8.7	6
Call Control	17.4	17	5.6	6	2.5	14	10.5	9
Chi–Square	$X^2_{0.05,\ 6} = 6.493$				$X^2_{0.05,\ 6} = 3.809$			
18 Months	**Brenchley Hypothesis**							
Treatments	**Hard–bodied**		**Soft–bodied**		**Burrowing**		**Non–burrowing**	
	Exp	***Obs***	***Exp***	***Obs***	***Exp***	***Obs***	***Exp***	***Obs***
Zost Control	9.4	9	7.6	8	11.6	10	5.4	7
–Call +Zost	9.9	10	8.0	8	12.3	11	5.7	7
+Call +Zost	13.3	15	10.7	9	17.8	17	8.2	9
Call Control	8.3	7	6.7	8	10.3	14	4.7	1
Chi–Square	$X^2_{0.05,\ 3} = 0.994$				$X^2_{0.05,\ 3} = 5.589$			

The same hypothesis can, however, be assessed in a different manner by examining the proportions of individuals representing the same morphological categories (Figure 5.6 A). Of the seven cases explored at 12 months, nearly all yielded results in opposition to the hypothesis. In treatments that possessed *Zostera*, there were fewer soft-bodied species and more hard-bodied species than expected by chance. Of the two treatments that lacked *Zostera* (*–Callianassa –Zostera* and *Callianassa* Control) both opposed the hypothesis (Figure 5.6 A). Analysis of the simpler data set sampled at 18 months showed equally little support for the hypothesis (Figure 5.6 B). Two of the three *Zostera* treatments showed support for the hypothesis while the *Callianassa* Control opposed it. Overall, with 64% of the cases in opposition to the hypothesis Brenchley's first hypothesis can be rejected, whether the results are considered in terms of the number of species or the number of individuals within each habitat.

Brenchley's second hypothesis proposed that burrowing fauna would be disproportionately more abundant within sandflats as opposed to *Z. capensis* beds, with the reverse trend among non-burrowing fauna. Again, the data can be explored in terms of the number of species or the number of individuals. With reference to the proportions of species, the data showed no significant differences in the frequency of burrowing versus non-burrowing species from those expected by chance (Table 5.5).

HYPOTHESIS 1:
Hard Bodied Individuals *vs.* Soft Bodied Individuals

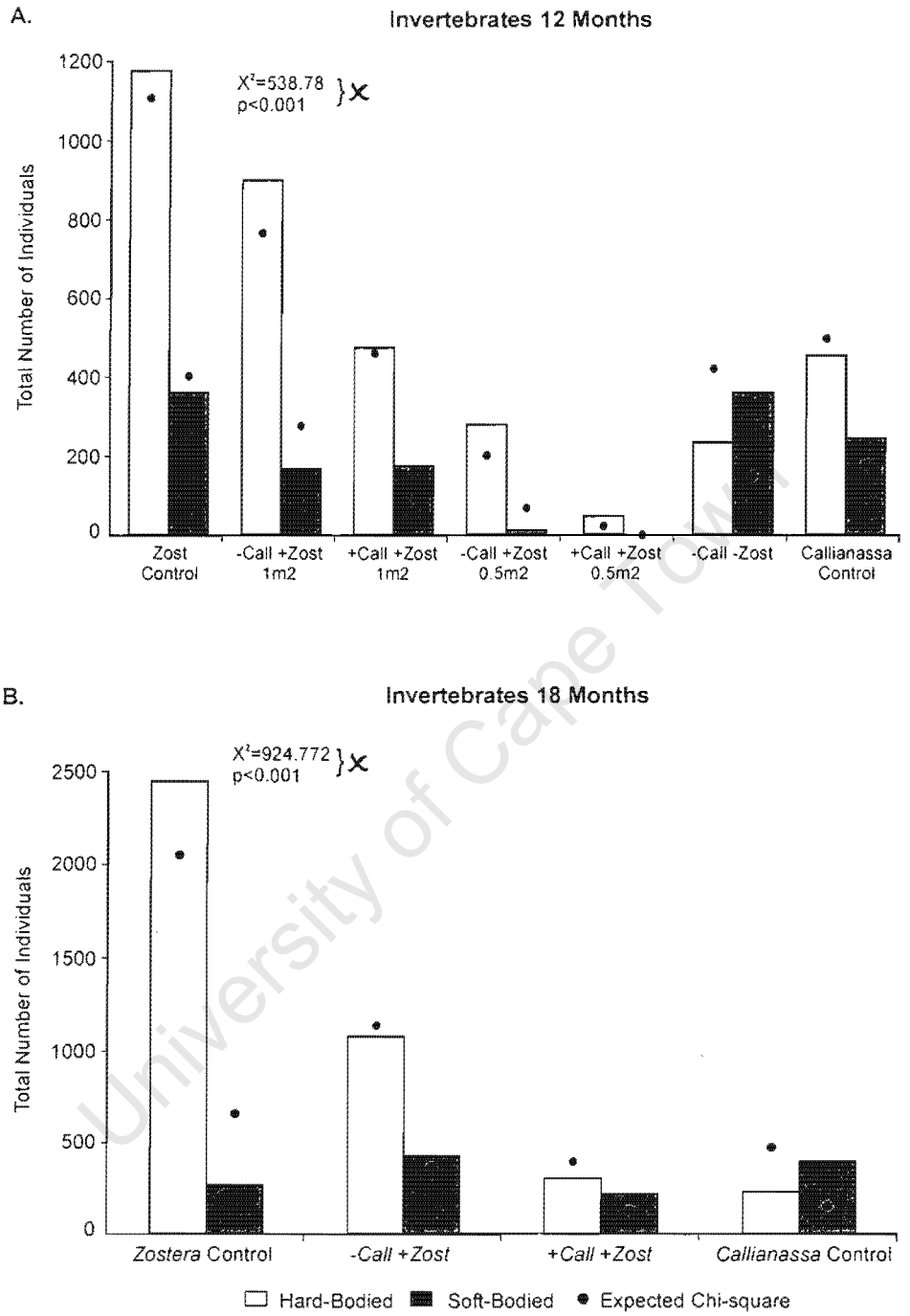


Figure 5.6: Histograms showing the total numbers of hard-bodied and soft-bodied individuals sampled within control and experimental treatments after (A) 12 months and (B) 18 months. Dots indicate expected values. Chi-square analyses and corresponding p-values shows significant differences between expected and observed values. In cases where there were significant departures from the expected values, tick or cross symbols show either support for or opposition to Brenchley (1982).

HYPOTHESIS 2:
Burrowing Individuals *vs.* Non-burrowing Individuals

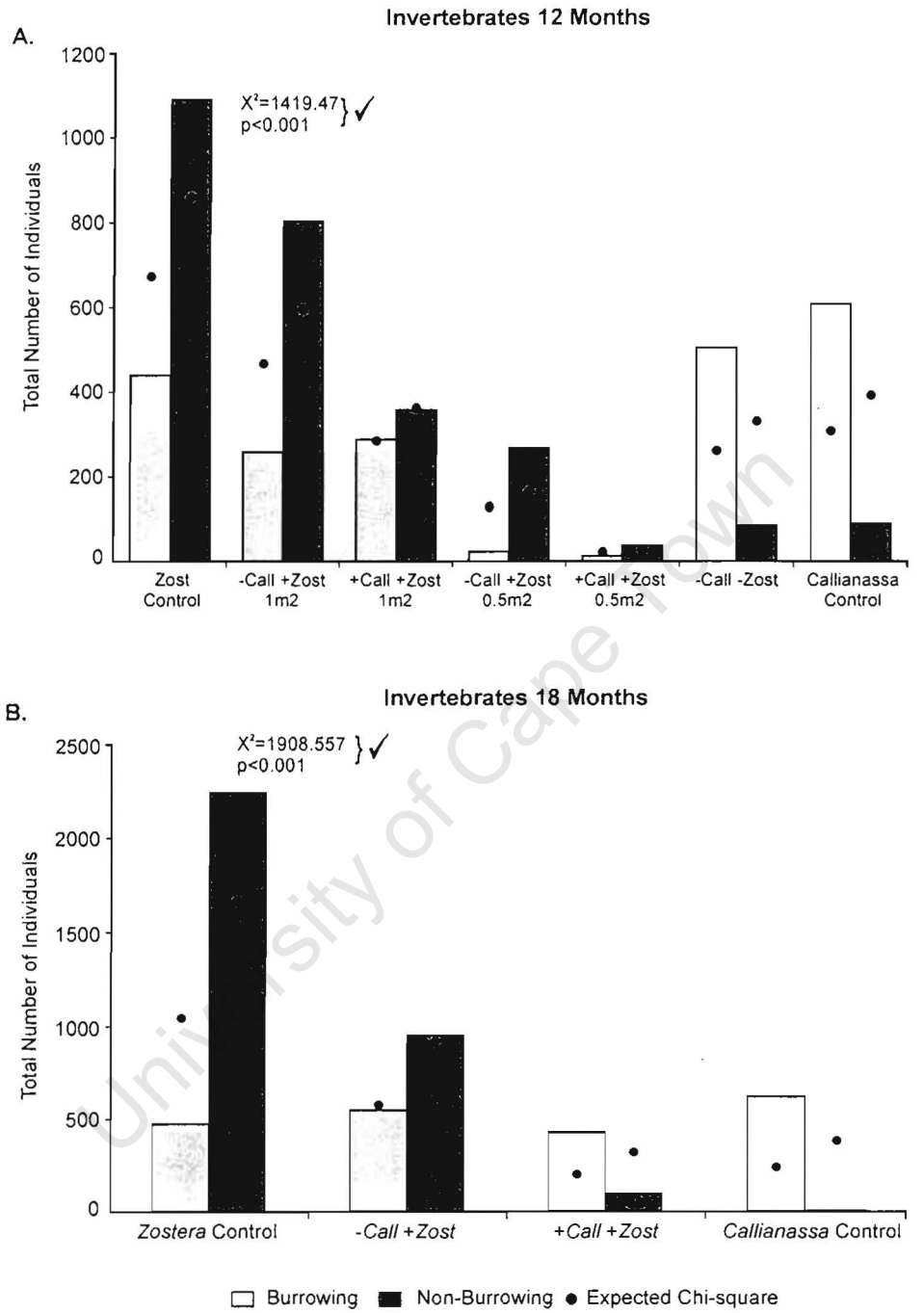


Figure 5.7: Histograms showing the total numbers of burrowing and non-burrowing individuals sampled within control and experimental treatments after (A) 12 months and (B) 18 months. Dots indicate expected values. Chi-square analyses and corresponding p-values shows significant differences between expected and observed values. In cases where there were significant departures from the expected values, tick or cross symbols show either support for or opposition to Brenchley (1982).

In contrast, analysis of the proportion of individuals from each category provided more convincing support for Brenchley's second hypothesis. Combining months, ten of the eleven cases explored conformed to her predictions (Figure 5.7), with fewer burrowing species and more non-burrowing species represented in treatments that possessed *Zostera*, and *vice versa* for treatments that lacked *Zostera*. In general, there was little support for the hypothesis when considering the number of species, but stronger support when analysing the number of individuals.

5.4 Discussion

Intense biological interactions coupled with physical disturbances have often been thought to be primarily responsible for regulating intertidal assemblages (Paine & Levine, 1981). Results from field surveys presented in previous chapters (2 and 3) provided circumstantial evidence suggesting that bioturbation by *Callianassa kraussi* limits the distribution of the seagrass *Zostera capensis* and influences community composition of the macrofaunal assemblages associated with either species. Experimental manipulations employed to test the amensal relationship between *Z. capensis* and *C. kraussi* then showed causality of the processes governing these interactions (Chapter 4). Briefly, experimental transplants of *Z. capensis* into areas dominated by *C. kraussi* were severely limited in both cover and aerial extent, whereas *Z. capensis* transplanted into areas in which *C. kraussi* had been experimentally eliminated flourished and even expanded in areas within the intertidal sandflat.

Similar studies elsewhere have reported that where *Callianassa* does limit or eliminate seagrass beds it also affects the extremely complex assemblage of other populations, which are either directly or indirectly dependent upon the seagrass beds (Ogden, 1980; Suchanek, 1983). Species that are sensitive to bioturbators may seek refuge in seagrass, as it functions primarily as a 'buffer', compensating for any possible negative effects of high sediment turnover activity by *Callianassa* (Berkenbusch *et al.*, 2000). Generally, vegetated sediments support different assemblages of species from nearby un–vegetated sediments, which are manifested in distinct differences in species composition, numerical abundance and diversity (O'Gower & Wacasey, 1967; Orth, 1977; Stoner, 1980; Homziak *et al.*, 1982; Fitzhardinge, 1983; Suchanek, 1983; Lewis, 1984; Heck *et al.*, 1989; Edgar, 1990; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1977; Lee *et al.*, 2001). This has been explained by decreased predation efficiency due to high habitat complexity (Lewis, 1984), correlated with macrophyte biomass (Stoner, 1980), or as a result of habitat preference for dense seagrass by prey as an escape mechanism from predation (Bell & Westoby, 1986). Seagrass beds can also stabilise sediment and accumulate organic material,

allowing increased settlement and growth of infauna. Juveniles are also prevented from being resuspended and transported away (Orth, 1977; Bostrom & Bonsdorff, 1997).

The faunal communities of Langebaan Lagoon similarly show marked differences in community composition between vegetated and unvegetated sediments, with the fauna among *Zostera capensis* stands clearly distinct from that of adjacent sandflats (Chapter 3). This study, while confirming previous investigations of the role of *Zostera* and *Callianassa* on macrofaunal assemblages in Chapter 3, extends these observations to different degrees of *Zostera–Callianassa* interactions, established through manipulative field experiments.

5.4.1 *Differences in faunal composition*

Dissimilarities in community structure between control and experimental treatments showed significant differences in benthic community composition, the cause of which appears to be related to the bioturbatory activity of *C. kraussi*, the presence of *Z. capensis* or a combination of both. Fauna clustered into five distinct groups, corresponding to the degree of association with either *Z. capensis* or *C. kraussi*. On one side of the spectrum was the *Zostera* Control and on the other, the *Callianassa* Control, which showed the largest divergence between communities and presented the most extreme case of 'habitat–association'. In these two treatments, the abundance of the dominating species were clearly respectively *Zostera*–associated or sandflat–associated, with species representative of each habitat either absent or present in very low densities in the other treatment (Figure 5.5).

The trends among the faunal assemblages associated with the remaining treatments were more ambiguous. Originally, it was hypothesized that the various treatments would represent unique faunal communities, depending on the degree of association with *Z. capensis* and/or *C. kraussi*. That is, situations in which *Z. capensis* was the dominating factor (i.e. *Zostera* Control, *Zostera* Disturbance Control, *–Callianassa +Zostera*) would be largely characterised by *Zostera*–associated species and share similarities in faunal composition. The opposite was predicted for situations where *C. kraussi* was dominant (i.e. *Callianassa* Control, *+Callianassa –Zostera*). Furthermore, the largest dissimilarity was expected in situations where neither species was present i.e. *Zostera* Removal and *–Callianassa –Zostera*. But, in reality, the overriding factors contributing to the dissimilarity between faunal communities among treatments were the presence or absence of *Zostera* and the size of the original transplant plot.

Multivariate dissimilarities in community structure (Figure 5.2 and 5.3) occurred between five clusters of samples, namely Cluster I: *Zostera* bed samples (*Zostera* Control, *Zostera*

Disturbance Control and *Zostera* Removal), Cluster II: +*Zostera* 1 m^2 transplant treatments (irrespective of the presence or absence of *Callianassa*), Clusters IV and V: +*Zostera* 0.5 m^2 transplant plots (again irrespective of the presence or absence of *Callianassa*), and Cluster III: unvegetated sandflat (*Callianassa* Control and –*Callianassa* –*Zostera*). These results suggest that whilst bioturbation appears to have a significant and explainable influence on the spatial variation of macrofauna community composition (see Berkenbusch *et al.*, 2000), the presence of *Z. capensis* appears to be more important in structuring the associated faunal community. Several studies have made a connection between the above–ground biomass or cover of seagrass and infaunal community composition (Orth, 1977; Stoner, 1980; Webster *et al.*, 1998). Additionally, below–ground root–rhizomes of seagrasses may impose restrictions on burrowing infauna (Brenchley, 1982; Suchanek, 1983) as well as influencing physical changes in the sediment (e.g. decreased penetrability within Z. *capensis* transplants, Figure 4.7). Even though plant biomass was highly varied between +*Zostera* treatments (Chapter 4, Figure 4.3), it is plausible that *Z. capensis* mediates the negative effects of high sediment turnover or disturbance by *C. kraussi*.

This may also explain the unexpected similarities in the faunal communities of *Zostera* Removal treatments and *Zostera* Control and *Zostera* Disturbance Controls. Within the *Zostera* Removal, all *Z. capensis* and below–ground biomass was removed to a depth of 20 cm, thus creating a bare unvegetated area. However, re–colonisation of the sediment by 'sandflat' species may have been prevented, as the removal area was surrounded by the original *Zostera* bed and contained remnants of root–rhizome networks, and its penetrability remained low, forming a 'frontier zone' habitat similar to that at the lower edge of the *Zostera* bed (Chapter 2). Consequently, the sediment would probably have been sufficiently stable to provide a favourable environment for sedentary organisms commonly associated with *Zostera* environments, while impeding active burrowers.

Faunal communities were also distinguished according to the size of the original transplants. Relatively few species were present within 0.5 m^2 transplants, and then in very low abundances when compared to 1 m^2 plots. Dissimilarity in the effects of transplanted plots of different sizes was also observed in the previous chapter, which pointed to the importance of seagrass patch size in mediating recovery after disturbance (e.g. Worm & Reusch, 2000), as 0.5 m^2 transplant plots showed lower resistance to the invasion of *C. kraussi* than 1 m^2 transplant plots. Furthermore, smaller patches with high edge–to–area ratios are subject to greater overall disturbance than large patches (Irlandi *et al.* 1995 in Bowden *et al.*, 2001). In this light, it is likely that the encroachment of *C. kraussi* and its associated disturbance may have overridden the moderating effects of *Z. capensis* in smaller patches while, the presence of *Z. capensis*

prohibited colonisation by sandflat–associated species. Few of the dissimilarities between samples were attributable to differences between the two experimental areas, between replicates or between sub–samples within the replicates, suggesting consistency in the observed patterns. The only exception was the interaction of area X treatment in the case of *–Callianassa –Zostera* and *Callianassa* Controls, which formed sub–clusters as a result of divergence between sample areas (Clusters IIIa–IIId, Figure 5.2).

Clear–cut trends were evident from the results of the simplified analysis after 18 months, which concentrated on the basic treatments only. In this case, multivariate analyses identified four distinct faunal communities, which closely corresponded to the individual treatments (Figure 5.4). These results were consistent with both the original hypotheses presented here and those in Chapter 3 and showed no trace of any area, replicate or sample effects. *Zostera*–associated faunal communities were distinct in the absence of *C. kraussi* while sandflat–associated species dominated faunal communities in the presence of *C. kraussi*. Again, these differences were most pronounced in comparisons of the two extreme treatments, the *Zostera* Control and the *Callianassa* Control. Furthermore, there were greatest affinities between the composition of the faunal communities associated with the presence of *C. kraussi* (*+Callianassa +Zostera* and *Callianassa* Control) and between those lacking *C. kraussi* (*–Callianassa +Zostera* and *Zostera* Control), suggesting that *C. kraussi* plays a powerful role in structuring community composition.

The dissimilarities between treatments were largely dictated by a relatively small set of species, showing definite affinities for either *Zostera* or sandflat habitats. Previous investigations comparing the faunal communities associated with seagrass and unvegetated habitats have similarly reported differences in the dominant species representative of each habitat (Homziak *et al.*, 1982; Hily & Bouteille, 1999). Results from Chapter 3 established that *Z. capensis* beds were fundamentally represented by *Upogebia africana*, *Perinereis nuntia vallata*, *Assiminea globulus* and *Cleistostoma edwardsii*, with the notable addition of *Lumbrineris tetraura* in 2000. Sandflat areas on the other hand, were principally dominated by *Orbinia angrapequensis*, *Urothoe grimaldii*, and *Callianassa kraussi*. With the exception of a few additional species, the same suite of species was identified as being primarily responsible for the divergence between the *Zostera*–associated treatments and *Callianassa*–associated treatments (Figure 5.5). Typical *Zostera*–associated species included *Assiminea globulus*, *Hydrobia*, *Siphonaria compressa*, *Ceratonereis erythraeensis*, *Paramoera capensis*, *Cleistostoma edwardsii*, *Perinereis nuntia vallata* and *Upogebia africana*. In contrast, sandflat or *Callianassa*–associated treatments were consistently dominated by *Orbinia angrapequensis*, *Urothoe grimaldii*, *Notomastus latericeus*, *Callianassa kraussi*, *Scoloplos johnstonei* and *Carditella rugosa*.

Comparable with Chapter 3, the macrofaunal assemblages within the two habitat extremes (*Zostera* Control vs. *Callianassa* Control) showed marked differences in composition and abundance, with different taxa responding differently to the presence or absence of *Zostera* and/or *Callianassa* (Figure 5.5). These patterns were fairly consistent, though more varied within the less extreme treatments. The transplantation of *Z. capensis* into areas both with and without *C. kraussi* presented an opportunity to isolate the direct effects of *C. kraussi* on macrofauna community composition, as both transplant treatments were identical, except for the absence or presence of *C. kraussi*. From this comparison, there were definite indications that bioturbation influences macrofaunal composition in small localised areas. Treatments containing *Z. capensis* in the absence of *C. kraussi* comprised higher abundances of *Zostera*–associated species (notably *Siphonaria compressa*, *Paramoera capensis*, *Perinereis nuntia vallata* and *Cleistostoma edwardsii*) and fewer sandflat species, whereas transplants into areas containing *C. kraussi* were dominated by fauna more characteristic of sandflat areas (*Orbinia angrapequensis* and *Urothoe grimaldii*) than *Zostera* areas.

In the absence of *C. kraussi*, the majority of species associated with *Z. capensis*, but normally confined to the *Zostera* bed in the high–shore, achieved abundances equal to those recorded in the *Zostera* bed when the *Zostera* was transplanted into the sandflats at a slightly lower level on the shore. There were two exceptions. First, in the *+Zostera –Callianassa* treatment, the limpet *Siphonaria compressa* rose to densities almost five times greater than in the *Z. capensis* bed. In *+Zostera +Callianassa* treatments however, the limpet was much less abundant. Second, and in contrast, the gastropods *Assiminea globulus* and *Hydrobia* sp., remained confined to the *Zostera* bed, never becoming established on *Z. capensis* transplanted into the intertidal sandflats, even in treatments that were *Callianassa*–free. As both these taxa commonly occur near the high water mark on lagoonal mudflats (Flemming, 1977; Branch *et al.*, 1994), Mazure & Branch (1979) considered that they were excluded from intertidal sandflats because *C. kraussi* bioturbation disturbs their food source. However, my results dispute this and suggest that perhaps its distribution and abundance is due to a preference for habitat higher on the shore (see Bell & Westoby, 1986) rather than an avoidance of disturbance by *C. kraussi*.

In areas where *C. kraussi* was left undisturbed, the effect of *Z. capensis* on the infaunal community was short–lived, and the presence of *C. kraussi* ultimately led to the assemblages resembling those of sandflats. Numerous hypotheses have been proposed to explain the impact of bioturbators on the distribution of organisms in soft sediments (see Posey, 1987). Generally, burrowing deposit–feeders modify habitats indirectly through physical processes, which are a consequence of normal burrowing or feeding activities, thereby excluding certain organisms with different lifestyles (Rhoads & Young, 1970; Woodin, 1976; Brenchley, 1981). For

instance, Brenchley (1978) noted a negative correlation between the abundance of several sedentary organisms and dense *Callianassa californiensis* beds, while Aller & Dodge (1974) and Suchanek (1983), observed that certain Caribbean species of *Callianassa* negatively affect suspension–feeding organisms and the seagrass *Thalassia testudinum* respectively.

But perhaps the most interesting patterns of faunal composition were observed within the *–Callianassa –Zostera* treatments. A marked feature of these was that the sediment compacted as a consequence of the defaunation process and penetrability noticeably decreased to less than a third of that recorded within undisturbed, unvegetated sandflat (Figure 4.7 B). Furthermore, without the addition of *Z. capensis* and its associated advantages (e.g. increased habitat complexity, food availability, shelter from predation and hydrodynamic forces), it was expected that few species, if any at all, would re–colonise these defaunated unvegetated areas. Despite this, however, results indicated a faunal composition similar to that of the *Callianassa* Control (Figure 5.2, 5.3, 5.5), and similar total numbers of taxa and individuals. The two most numerically abundant species were *Notomastus latericeus* and *Orbinia angrapequensis*, both characteristically sandflat–associated species. This suggests that with sufficient time, mobility and larval dispersion, species can re–colonise these areas regardless of the extreme impenetrability of the sediment.

5.4.2 *Species Diversity, Richness and Abundance*

In contrast to the findings of other workers (e.g. O'Gower & Wacasey, 1967; Orth, 1977; Stoner, 1980; Homziak *et al.*, 1982; Fitzhardinge, 1983; Suchanek, 1983; Lewis, 1984; Heck *et al.*, 1989; Edgar, 1990; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1977; Lee *et al.*, 2001), diversity values showed few differences in species richness and diversity between vegetated treatments compared to unvegetated treatments. This is surprising, as numerous studies involving the manipulation of natural and artificial seagrass plots have shown that the presence of seagrass directly increases the number of colonising species (Homziak *et al.*, 1982; Fitzhardinge, 1983; Harrison, 1987; Fonseca *et al.*, 1990; Edgar & Barrett, 2002).

In general, there were few differences in infaunal species diversity and richness between treatments, except for 0.5 m^2 transplant plots, which in all cases exhibited the lowest diversity values. Combining the two sampling periods, the diversity and richness of species was never greater within *Zostera* treatments compared to *Callianassa* treatments, although the combination of both species (*+Callianassa +Zostera*) showed the highest species richness (S and d') and diversity (H') at 18 months (Table 5.3). Abundance was, however, always greater within the *Zostera* bed compared to any other treatment. These results agree with those in Chapter 3,

which showed that where differences in richness and diversity were identified between treatments, the trends were in direct opposition to those recognized by other studies (see references above).

In Chapter 3, I proposed that the reversed trends in richness and diversity are probably a function of site–specific biotic and abiotic interactions. For instance, whereas certain components of the fauna maybe directly limited by *C. kraussi* bioturbation (Suchanek, 1983), thus reducing species diversity and richness, others may benefit from its disturbance. Widdicombe & Austen (1999), for example, proposed that increased diversity at intermediate levels of bioturbation may be due to the effect of bioturbation on the sediments rather than the physical disruption of dominant species. Consequently, the balance between the adverse and positive biological effects of bioturbation may offer some explanation for the higher diversity within *Callianassa*–dominated treatments compared to *Zostera*–dominated treatments. The combination of *Z. capensis* and *C. kraussi* may offer a unique situation for the colonisation of *Zostera*–associated species that are able to withstand moderate sediment disturbance by *C. kraussi* and *vice versa* for *Callianassa*–associated species, thereby increasing species diversity. Differences between diversity of large versus small seagrass transplants may be attributed to differences in macrophyte biomass (Stoner & Lewis, 1985). Webster *et al.* (1998) found that infaunal species diversity within a seagrass bed differed significantly between areas exhibiting relatively small differences in shoot density. Once again, the importance of seagrass patch size in maintaining different faunal communities is evidenced.

5.4.3 *Morphological Characteristics*

Brenchley (1981, 1982) has specifically hypothesised that mobility rather that feeding type will determine the nature of biological interactions in soft–sediments. Several laboratory and field manipulations have investigated Brenchley's hypothesis and have indicated that mobile animals can exclude sedentary organisms through burial and disruption while sedentary species may bind the sediment or physically obstruct mobile burrowers (Peterson, 1977; Brenchley, 1981; Wilson, 1981; Suchanek, 1983, Dewitt & Levinton, 1985; Murphy, 1985, Posey, 1985). In particular, Brenchley (1982) demonstrated that mobility of burrowing taxa is significantly reduced in substrata containing *Zostera marina* roots.

A variety of burrowers were included in Brenchley's (1982) study, which demonstrated that species with dissimilar forms of morphology may be differently affected by sediment stability. More specifically, hard–bodied taxa were most inhibited, as soft–bodied taxa were capable of changing shape. This implies that invertebrates residing among seagrass roots should be

characterised by more flexible–bodied, non–burrowing species whereas invertebrates commonly associated with *Callianassa*–dominated sandflats should be harder–bodied and burrowing.

Species categorised in accordance with Brenchley's (1982) functional groups i.e. hard–bodied vs. soft–bodied and burrowing vs. non–burrowing showed ambivalent responses to experimental treatments. There was no evidence that *Zostera* treatments contained proportionately fewer hard–bodied species and more soft–bodied fauna than would be expected by chance – whether this was assessed in terms of the proportions of species or the proportions of individuals. Indeed, where the ratios of hard: soft–bodied animals departed from those expected by chance, they did so in a manner contradicting Brenchley's hypothesis.

There was, however, support for Brenchley's hypothesis that non–burrowers should be disproportionately more abundant in association with *Zostera* and burrowers in association with *Callianassa*, especially when considered in terms of the numbers of individuals (Figure 5.7). Furthermore, treatments that comprised both *Z. capensis* and *C. kraussi* (*+Callianassa +Zostera*) contained proportionately more burrowing individuals, again implying that *C. kraussi* may supersede the stabilising effect of *Z. capensis* and suggesting the importance of mobility in producing patterns in faunal community composition.

A further aspect known to influence the mobility of burrowing organisms involves the physical properties of the sediment (Brenchley, 1982). In particular, mobility is reduced in poorly sorted sediments because the sedimentary fabric becomes 'tighter' as a result of compaction (e.g. Rhoads, 1974). Consequently, areas of low sediment penetrability should impose similar restrictions on infauna as the root–rhizomes of *Z. capensis*, inhibiting organisms that are characteristically hard–bodied and burrowing. This was tested by the *–Callianassa –Zostera* treatment, as the combination of the defaunation process used to eliminate *C. kraussi* and the absence of *Z. capensis* resulted in markedly compacted sediment with low penetrability (Figure 4.7 B). But, in contrast to Brenchley's hypothesis, the fauna residing within this treatment comprised disproportionately more burrowing individuals than non–burrowing individuals and their proportions were similar to those in the *Callianassa* Control (Figure 5.7). Overall, the most credible positive evidence in support of Brenchley's hypotheses (1981, 1982) corroborated the idea that *Z. capensis* and *C. kraussi* mutually influence the mobility of infauna. Where *C. kraussi* is completely excluded, *Zostera* inhibits burrowing individuals, but in the presence of *C. kraussi*, disturbance by the bioturbator may dominate in determining community composition by inhibiting non–burrowing individuals. This trend was consistent over both periods sampled and confirms the results from the previous investigations reported in Chapter 3.

5.4.4 Conclusion

My results experimentally demonstrate that discordant interactions between *Z. capensis* and *C. kraussi* are responsible for structuring associated faunal communities within Langebaan Lagoon, due to sediment stabilisation caused by *Z. capensis* and the intense effects of *C. kraussi* bioturbation in intertidal sandflats.

These effects were observed in varying degrees by the experimental transplantation of *Z. capensis* into areas with and without *C. kraussi*. Treatments containing *Z. capensis* in the absence of *C. kraussi* developed faunal communities very similar to those identified as being *Zostera*–associated in Chapter 3. Conversely, treatments containing *Z. capensis* in the presence of *C. kraussi* were more similar in composition to those identified as being sandflat/ *Callianassa*–associated (although these treatments were represented by a combination of both *Zostera*–associated and *Callianassa*–associated species). As in Chapter 3, the divergence between faunal assemblages could be ascribed to a limited suite of species. This was most apparent in the two habitat 'extremes', the *Zostera* Control and the *Callianassa* Control, which provided the most direct comparison with the habitats sampled in Chapter 3 (i.e. the *Zostera* bed and the *Callianassa*–dominated sandflat). Habitats lacking both *Z. capensis* and *C. kraussi* were colonised predominantly by sandflat–associated species. However, species diversity and richness in *Zostera*–associated treatments where lower than or equal to those in *Callianassa*–associated treatments, contradicting trends established by previous investigators (See Orth, 1977; Stoner, 1980; Fitzhardinge, 1983; Hodgson & Whitfield, 1989; Heck *et al.*, 1989; Edgar, 1990; Kaletja & Hockey, 1991; Edgar *et al.*, 1994; Bostrom & Bonsdorff, 1997; Hily & Bouteille, 1999; Lee *et al.*, 2001), but corroborating similar trends established in Chapter 3.

There was evidence supporting the idea that burrowing organisms are inhibited by *Zostera* as proposed by Brenchley (1982), but no evidence to suggest that *Zostera* diminishes hard–bodied species. There was also no evidence that sediment compaction *per se*, as measured by sediment penetrability, excludes burrowing organisms. The *Zostera* beds did support greater densities of individuals compared to any other treatment, probably because of their high organic content and accumulation of detritus (Mazure & Branch, 1979).

These results imply that both *Zostera capensis* and *Callianassa kraussi* can be considered as 'structural' species i.e. they are both singularly important for structuring the macrofaunal communities within Langebaan Lagoon. While it was impossible to assign direct causality for the observed patterns based on the field observations in Chapter 3, the experimental

manipulations of *Z. capensis* in the presence and absence of *C. kraussi* provide more compelling evidence that the sandprawn and the seagrass are primary agents driving macrofaunal community structure and composition acting, respectively, by bioturbation and by stabilisation of the sediment.

"But, wherever... they meet, and come into competition, if one has the slightest advantage over the other, that other will decrease in numbers or be quite swept away"

Charles Darwin: 1856–1858
(Stauffer, 1975).

Biological interactions have been frequently implicated as a major force structuring marine soft–bottom communities. In particular, the structure of benthic communities is often defined by the sedimentary requirements of some species and the changes to the sediment affected by others. The focus of this thesis was two–fold. First, it focused on the interaction between the eelgrass *Zostera capensis* and the sandprawn *Callianassa kraussi*, and their indirect effects on the mudprawn *U. africana*, in the intertidal sandflats at Langebaan Lagoon, South Africa. Second, it assessed the macrofaunal assemblages associated with *Z. capensis* or *Callianassa*–dominated sandflats. Comparative, correlative and experimental approaches were combined to establish the existence, and the process and consequences, of this biologically–mediated interaction.

The results of the different approaches revealed an overall pattern, which is summarised in Figure 6.1. First, field surveys conducted at several sites around the Lagoon provided an indication of the distribution and abundance of the three main species examined (Chapter 2). The distribution and density of *Z. capensis* and *U. africana* were closely associated (Figure 6.1 C), and both were mainly limited to a narrow band along the high–shore by *C. kraussi* bioturbation. The rest of the shore was dominated by *C. kraussi*, which occurred at high densities from immediately below the eelgrass beds downwards to a depth of at least 2 meters into the subtidal zone. *Z. capensis* and *C. kraussi* were always largely mutually exclusive (Figure 6.1 A) and, under most sedimentary circumstances, the same was true of *U. africana* and *C. kraussi* (Figure 6.1 B). Correlative data confirmed these relationships and the existence of two distinct habitats within the Lagoon were established: one associated with *Z. capensis*, and the other with *C. kraussi*.

In Chapter 3, the macrofaunal communities associated with *Z. capensis* and *C. kraussi* were surveyed to determine the degree to which they are distinct. Comparative field surveys showed the infaunal community associated with *Z. capensis* and the *Callianassa*–dominated sandflat are markedly different, in terms of both community structure and composition (Figure 6.1 J). The

sandflat–assemblage was characterised by greater species richness and diversity, but lower abundance of individuals than the *Zostera* beds. When the fauna was assessed in terms of

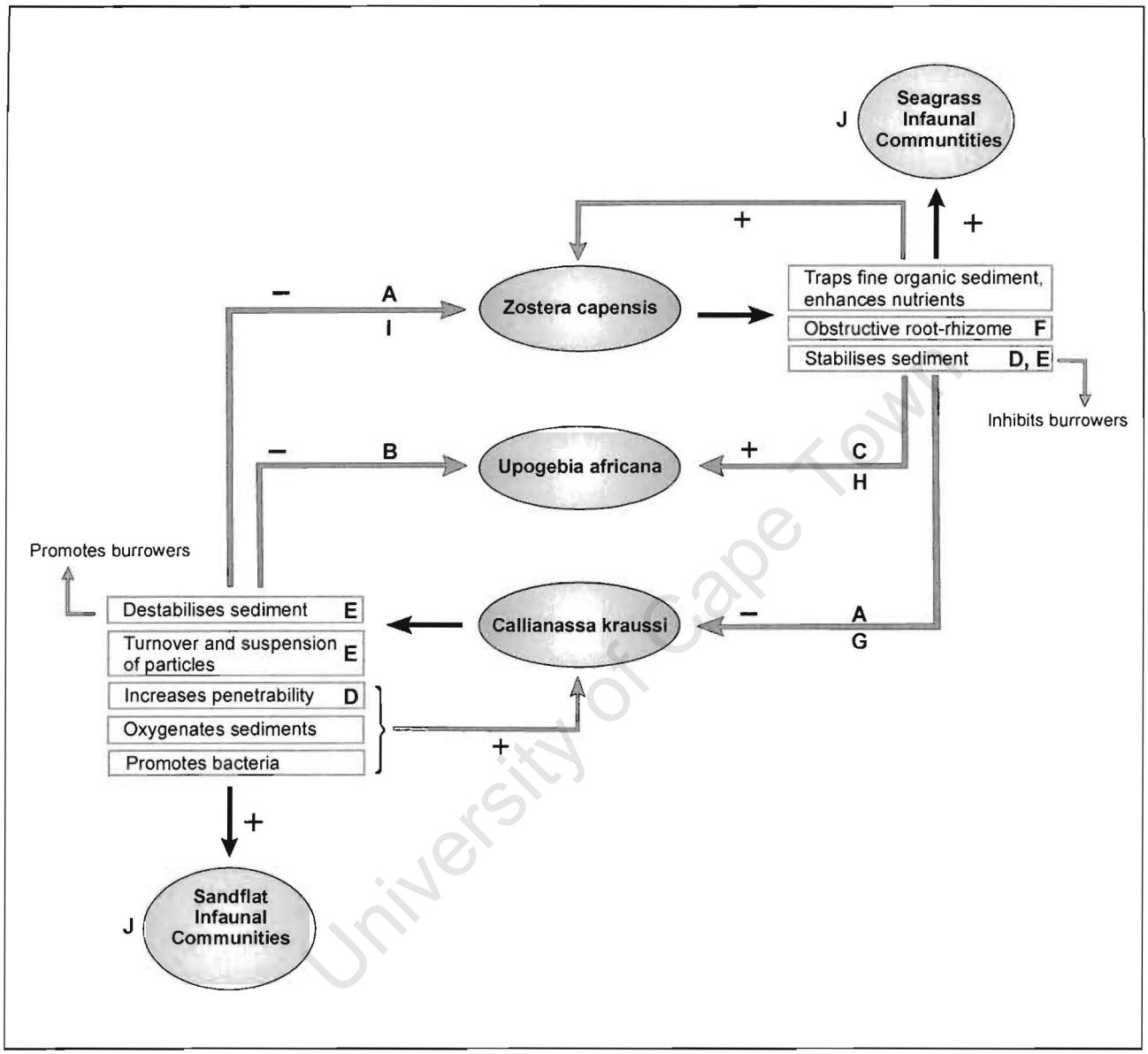


Figure 6.1: Schematic summary of the observed interaction between *C. kraussi* and *Z. capensis*, and the indirect cascade effects on *U. africana* and associated macrofauna community structure. + = positive effects, - = negative effects. The letters A-J correspond to those showed opposite, depicting idealised representations of the results.

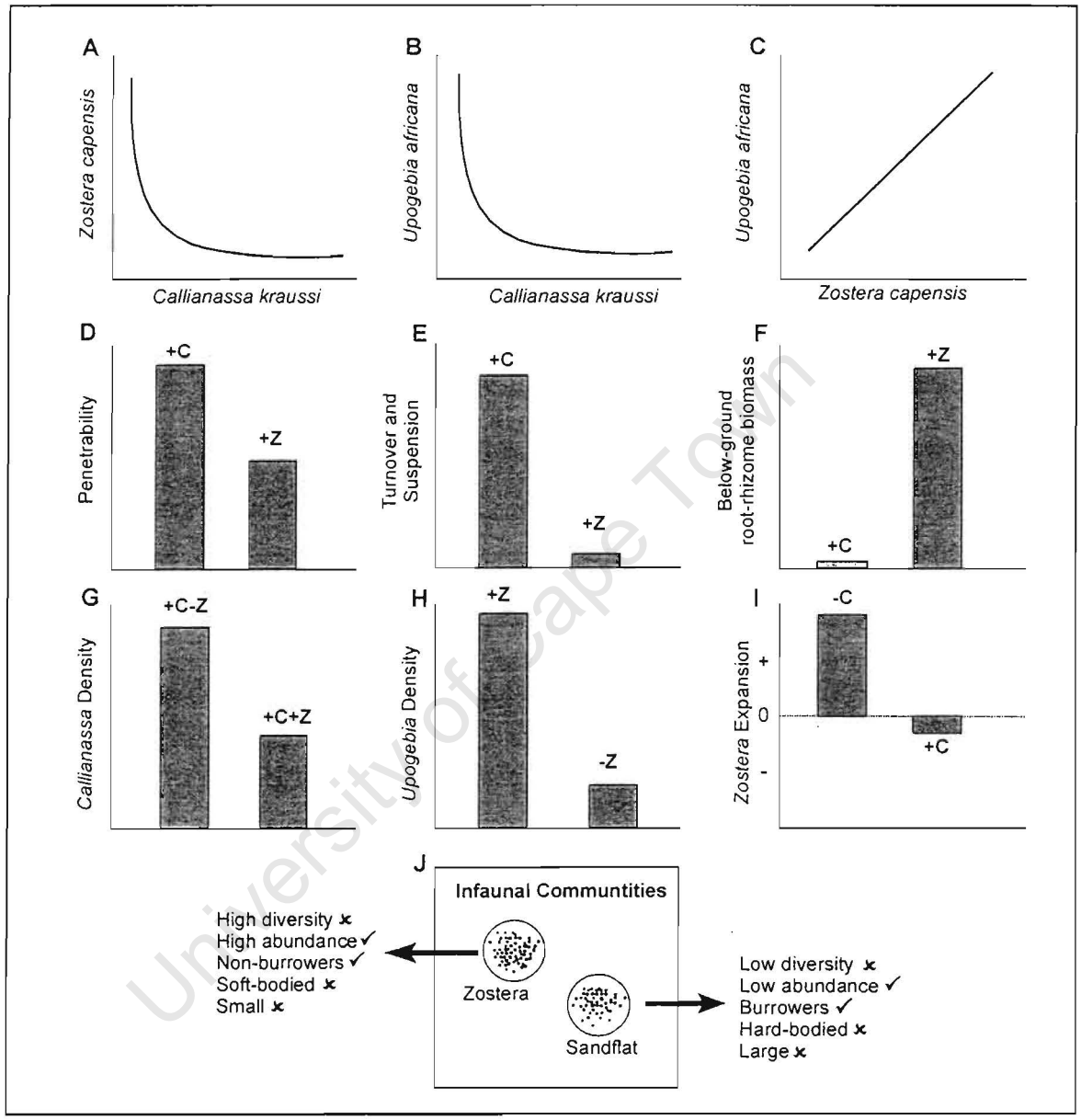


Figure 6.1 (Continued): Summary diagram of idealised results obtained from field surveys (A-C), and experimental transplants (D-I) and analyses of community structure (J). The letters A-J cross-refer to processes identified in the facing figure.

Brenchley's (1982) functional–mobility hypothesis, it had a disproportionately high number of burrowing individuals in sandflats when compared to *Zostera* beds, but contrary to the hypothesis, hard–bodied large individuals were not more prevalent in sandbanks relative to seagrass beds.

Second, a manipulative experiment was undertaken to further understand the causality sustaining the relationship between *Z. capensis, C. kraussi* and their associated faunal communities (Chapter 4). The experiment involved transplanting healthy sods of eelgrass into nearby areas within the *Callianassa*–dominated intertidal sandflats. In half of these areas, *C. kraussi* was experimentally removed prior to transplantation, while in the other half *C. kraussi* populations remained undisturbed. In the absence of *C. kraussi*, *Z. capensis* was able to persist and expand, whereas in the presence of *C. kraussi* the eelgrass steadily deteriorated (Figure 6.1 I). Although *C. kraussi* was initially limited to a certain extent by the implantation of *Z. capensis* (Figure 6.1 G), this effect was short–lived. *C. kraussi* was also shown to indirectly affect *U. africana*, which occurred in greatest densities in association with *Z. capensis* but was virtually absent in the presence of *C. kraussi* (Figure 6.1 H).

The above responses prompted further analyses of the structure, abundances and composition of faunal communities to assess the effects of experimental transplants of *Z. capensis* into areas originally dominated by *C. kraussi* (Chapter 5). The introduction of *Z. capensis* resulted in a shift in community structure, from one characterised by sandflat–associated species to one with *Zostera*–associated species. Species diversity and richness were not statistically different between *Callianassa*–dominated treatments and *Zostera* bed treatments, but the total number of individuals was considerably lower. Significantly more burrowing organisms were found in the presence of *C. kraussi* (Figure 6.1 J).

The combined results lead to the conclusion that *C. kraussi*, because of its bioturbating burrowing and feeding activities, is singularly important in structuring the soft–bottom communities within Langebaan Lagoon. In the high–shore, *Z. capensis* offers refuge from the disturbance effects of *C. kraussi* bioturbation. Lower on the shore, the marked increase in penetrability, sediment turnover and suspension associated with *C. kraussi* bioturbation may override the stabilising effect of *Zostera capensis* (Figure 6.1 D, E, F). The direct effects of *C. kraussi* on *Z. capensis* and *vice versa* extend further to the complex assemblage of fauna associated with each habitat, profoundly influencing the structure, composition and mobility of these faunal communities (Figure 6.1 J).

These relationships are likely to have important consequences for the sustainability of the soft–bottom communities within Langebaan Lagoon, particularly as "our continued multiplicity of demands on estuarine environments as producers of food, avenues of transportation, receptacles of wastes, living space, and sources of recreational and aesthetic pleasures intensifies" (Thayer *et al.*, 1975, p 288). Thus it is imperative that we understand the functioning of these nearshore ecosystems to predict the consequences of human interventions.

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