Macrobenthic community structure across an inter- and subtidal gradient in a mangrove estuary

By

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Abstract

Macrozoobenthic community structure and composition was investigated along a subtidal-intertidal gradient in the Mngazana Estuary. Six transects were sampled between the spring high water mark (HWST) and the bottom of the river channel in the lower estuary. Fifteen replicate samples were collected along each transect using a Van Veen type grab (211 cm^2 bite) during each of three sampling sessions. Samples were sieved through a 500 μm mesh bag and the invertebrates stored in bottles for further analysis in the laboratory. Additional grab samples were collected for sediment particle size analysis and organic matter. Physical variables measured at each transect included: salinity, temperature, dissolved oxygen, depth, pH, percentage mud, organic content and turbidity. Sediment compactness was measured at all intertidal transects and additional sediment samples were collected at mid shore and high shore transects for percentage water content analysis.

A total of 104 species were recorded along the intertidal-subtidal gradient in the sampling area. Species richness was higher in the subtidal zone compared to the intertidal zone and polychaetes numerically dominated the macrozoobenthic community at most transects, during all three sessions. At high shore transects the community was characterised by having fewer species, consisting mostly of brachyurans, polychaetes and gastropods.

Shannon diversity index (H') was generally higher for subtidal transects ($\overline{x}$ = 2.3; range: 2.8 to 1) than for intertidal transects ($\overline{x}$ = 1.4; range: 2.2 to 0.6) indicating that the distribution of individuals among species in the intertidal zone experienced greater variability. Results for Hill's numbers followed the same trend as Shannon diversity with subtidal communities mostly consisting of abundant species followed by very abundant species. Intertidal communities generally exhibited lower numbers of abundant and very abundant species.

Sedimentary characteristics played a major role in structuring benthic communities in comparison to other physico-chemical variables. Organic content and mud content of the substrate were identified as important factors influencing community patterns observed along the subtidal-intertidal gradient. In addition, sediment compactness and water content of the substrate was found to influence intertidal community structure. Subtidal community structure possibly had a greater dependence on seasonal variations in abiotic and/or biotic factors.

Cluster dendrograms used in conjunction with MDS ordination mapping revealed that macrozoobenthic communities were generally distinct between high shore intertidal transects

and subtidal transects. Most species exhibited a broad spatial distribution along the subtidal-intertidal gradient with mid and high shore transects being the exception. Most species also exhibited marked shifts in abundance and this was especially noticeable at the transition between the subtidal and intertidal zone. Two polychaete species, *Prionospio sexoculata* and *Capitella capitata,* were very abundant species and featured amongst the most numerically dominant species collected during each sampling session.

Key words: *subtidal, intertidal, macrozoobenthos, community structure, environmental variables, sedimentary characteristics.*

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Chapter 1. Introduction

Estuarine zoobenthic zonation is relatively well studied throughout the world with available evidence linking macrozoobenthic community structure to both biological and environmental variables. The multitude of factors found in estuaries demonstrates a continuous and irregular pattern of change causing an unpredictable and unstable environment (Wolff 1983). However, extreme and not average conditions are important in limiting distribution and abundance patterns of benthic species (Day 1981a). Therefore, the limiting factor for any species is that distinct variable that exceeds the tolerance range of the species in question.

Some invertebrate literature (e.g. the meiofauna), suggests that zonation patterns in tidal estuaries are not consistent. Such variations in faunal patterns are attributed to spatial and temporal variations of the physico-chemical/biotic environment, changes in sediment granulometry and abundances of microbial food (Alongi 1987a). Zonation of salt marsh animals is also largely determined by variation in the character of the substrate, the degree of inundation and the presence of salinity gradients (Daiber 1977). These factors may have a great influence on macrozoobenthic fauna whether the effects are expressed directly or indirectly. Similarly there exist many factors, which in combination may affect benthic community structure in estuaries. These are classified by Kneib (1984) as:

- various density-dependent processes (e.g., adult-larval interactions, agonistic behaviour, interspecific competition),
- selective larval settlement or mortality,
- predator-prey interactions,
- the influence of physical factors expressed through habitat preferences,
- unpredictable or cyclic physical disturbances.

Elaborating further on this, Edgar and Barrett (2002) cite numerous hypotheses that have been proposed to explain patterns of macrofaunal distribution in localised areas that include:

- faunal biomass and productivity in estuaries are affected by nutrient loadings and primary production,
- faunal density, biomass and species richness are affected by periodic anoxia,
- faunal biomass and species richness are affected by freshwater flushing and salinity,
- faunal biomass, productivity and species richness are affected by seagrass biomass,
- faunal biomass and species richness are affected by differences in sediment particle size.

In the following sections, specific factors that influence macrozoobenthic communities are examined.

1.1. Sediment characteristics

Distribution and deposition of sediments in estuaries exhibits a broad temporal and spatial variability that can be related to factors such as tidal currents, wind or waves (Quijon and Jaramillo 1993). Individual sedimentation events also smother estuarine flats with terrigenous sediments, creating a significant disturbance to local benthic communities (Hewitt *et al.* 2003).

Sediments are also variable in terms of particle size that has a significant effect on benthic estuarine assemblages (e.g. Puttick 1977, Teske and Wooldridge 2001, Nanami *et al.* 2005). Estuarine sediments are characteristically poorly sorted and have a relatively high silt/clay content (Dye 1983a). Teske and Wooldridge (2001) determined in a survey of 13 Eastern Cape estuaries that mud content (< 63 μm paticle size) was the most important environmental variable responsible for the biotic patterns found in these estuaries.

The particle size of sediments affects different benthic species in different ways. Deposit-feeding and suspension-feeding species in Buzzards Bay (Massachusetts, USA) show marked spatial separation; suspension feeders are largely confined to sandy or firm mud bottoms while deposit feeders attain high densities on soft muddy substrata (Rhoads and Young 1970). Rhoads and Young (1970) stated that organisms feeding exclusively on deposited food would, *a priori*, be expected to reach maximum diversity and biomass on fine-grained organic muds containing an abundant food supply. Populations feeding on suspended material however, may be less influenced in their distribution by the type of substratum and instead may be dependent on the quantity and quality of the suspended material in the water column (Rhoads and Young 1970).

Apart from influencing the feeding strategies of benthic species, particle size also affects the ability of fauna to colonize the substratum. A study by Pinedo *et al.* (2000) concluded that the large grain size of sediment particles had a significant negative impact on the construction of tubes by the tubicolous polychaete *Owenia fusiformis*. Coull and Fleeger (1977) found that comparisons between meiobenthic copepod communities from different substrata types were different in species composition, seasonal responses, environmental regimes, dominance relationships, and controlling factors. Despite these differences, the community investigated

maintained equal diversity. Diversity in this instance appeared to have been upheld by diverse and independent mechanisms.

There are other sediment characteristics that have been shown to influence the biota living in the substrata. Research by Dye (1983b) in the intertidal zone of the Mngazana Estuary showed a lower abundance and diversity of meiofauna occupying the top three to four centimetres of sediment compared to slightly deeper horizons. This was related to the oxygen consumption of the sediments, but possibly also due to partial desiccation. In strongly stratified estuaries, concentration of organic matter in the sediment can result in oxygen depletion, which is not favourable for the survival of infauna (Le Bris and Glémarec 1996). There is further reason to suggest that in certain cases, the fauna at a given study site may be composed of species representing various habitat types, i.e. sand, silt-clay, marine and estuarine (Maurer *et al.* 1976, Desroy *et al.* 2002). Maurer *et al.* (1976) cites various causes that may be held accountable for this phenomenon including the bottom topography of the benthos, the degree of organic load, pollution and different estuarine processes. Research by Linton and Taghon (2000) on marine soft-bottom benthic habitats, established that the disappearance of opportunistic species as succession proceeded following an enrichment or disturbance event could be related to the exhaustion of a food resource such as availability of organic matter.

1.2. Salinity

In the Gamtoos estuary Schlacher and Wooldridge (1996a) noted that salinity emerged as the main factor controlling subtidal macrofaunal assemblages at both extremes of the salinity gradient, whereas sediment type delineated between communities in the mesohaline to polyhaline reaches. Although salinity is an important factor influencing the distribution of organisms in estuaries, the distribution of true euryhaline species appears to be more independent of the salinity found in the adjacent water (Teske and Wooldridge 2001, 2003). This is probably related to the naturally wide tolerance range characteristic of this group and the less pronounced salinity fluctuations in the substratum than in the free water above (Kinne 1967).

Owing to the relative independence of true estuarine species to variations in salinity, and because of their numerical dominance, Teske and Wooldridge (2004) argued that it was more

appropriate to divide Eastern Cape estuaries into regions characterised by certain types of sediment in order to explain some of the observed macroinvertebrate distribution patterns.

1.3. Tidal inundation

Intertidal habitats are subject to strong physical and biological gradients related to the frequency and duration of tidal inundation (Kneib 1984). Desiccation, temperature and exposure are important variables regulating differences in community structure between high-shore and subtidal sites, and between sites of varying elevation (Bursey and Wooldridge 2002, 2003).

Studies on South African estuaries have established that macrozoobenthic species richness and diversity increased from the high shore to the low shore where the environment is less harsh and where habitat diversity may be greater (Puttick 1977, Bursey and Wooldridge 2002). Similarly, total meiobenthic faunal densities decreased with increasing elevation in estuaries (Alongi 1987a). However, some evidence suggests that species composition of intertidal and shallow-water habitats may be more stable than that of deeper subtidal habitats, due to the presence of short-lived opportunistic species in deeper areas after periods of deoxygenation (Rainer 1981). A stable community structure and species composition found at intertidal and shallow-water habitats indicates that greater environmental harshness does not necessarily imply less faunal stability (Rainer 1981). In addition, Branch and Grindley (1979) found that in the intertidal middle reaches of the Mngazana Estuary, benthic faunal biomass was far higher than subtidally. These middle reaches of the Mngazana Estuary were characterised by fine muddy sediments. Generally, in the intertidal zone there was an increase in density towards the high tide mark, because of the many burrowing crabs that inhabited the area. Branch and Grindley (1979) related these findings to low levels of oxygen just below the surface of the mud, which excluded all, but tolerant species. Thus, abundance and density of macrofauna are closely related to the composition of the sediment. De Decker and Bally (1985) supported this conclusion, as richest sediments in terms of species in the Bot River estuary's littoral and subtidal zone were those with the lowest mud fractions.

Tidal ebb and flow is capable of physically altering intertidal as well as subtidal habitats. Hanekom *et al.* (1988) showed that numbers of *Upogebia africana* were much lower in the subtidal channel, where strong currents resulted in a relatively coarse substratum with a subsieve content too low for colonisation by *U. africana*. Tidal currents also influence the

stability of the sediment, the nature of the food supply for benthic organisms and, in extreme cases, impose direct physical stresses on epifaunal communities (Warwick and Uncles 1980). Bayliss-Smith *et al.* (1979) hypothesized that extreme tides resulting from storm surges resulted in significant erosion and deposition in high marsh areas and could account for the rapidity of geomorphic change on lower marsh areas. Other studies have shown that the low shore portion of a tidal flat is subject to constant re-suspension and deposition, whilst the upper shore is primarily subject to deposition of particulate matter (Anderson 1976). Barnett (1984) found reduced abundance and small differences in species composition between the low shore fauna and the 'community' in the upper half of the shore in the Humber estuary. Barnett (1984) ascribed these differences to constant re-working of low shore sediments by wave and current action. In all mangrove estuaries studied by Alongi (1987b), sediments in the high intertidal zones were coarser, drier and had significantly less organic nitrogen compared to sediments in the low and mid intertidal zones. In all of the estuaries studied, sediments in mid intertidal zones were significantly more organic-rich (as total organic matter, organic N and C) compared to the high and low intertidal zones (Alongi 1987a). Such tidal effects on intertidal substrata may also depend on the local tidal range and gradient of the intertidal zone. Areas with a large tidal range may possess relatively strong tidal currents, whereas areas with a low tidal range have negligible water flow (Edgar and Barrett 2002).

Tides may also have a positive influence on fauna. Alongi (1987a) stated that the potential for rapid repopulation of mangrove sediments by meiofauna due to tidal action is good, considering the warm temperatures and considerable tidal range usually encountered in these types of estuaries. Evidence indicates that meiofauna are continually dispersed and transported by wind waves and tidal currents and quickly repopulate intertidal and shallow-water habitats (Alongi *et al.* 1983).

Research also suggests that biomass differences and mean size of *Upogebia africana* among levels within mud banks reflect differences in the duration of exposure to tidal currents and the ability to filter-feed (Dubula and Lasiak 2003). According to Dubula and Lasiak (2003) mudprawns occupying burrows on the lower part of the mud bank are able to feed longer and, as a result, grow faster than those living higher up on the bank. However, the variability at a smaller scale (e.g. between replicates) could be attributable to the influence of small-scale water movements on larval supply, availability of food and oxygen, sediment type, disturbance by predators, activities of other benthic animals and the presence of various biogenic structures (Morrisey *et al.* 1993 as quoted by Dubula and Lasiak 2003). Similar

trends for the bivalve *Dosinia hepatica* indicated that clam size decreased upshore from low water as a result of decreased feeding time higher in the intertidal zone (McLachlan 1974). Although constant water coverage is certainly an advantage in coping physiologically with the environment, habitat heterogeneity, providing refuges from predators, and other biotic components of the area influence infauna densities as well (Coull *et al*. 1979).

1.4. Biological interactions as factors influencing benthic communities

The effects of environmental factors are further complicated by biological interactions that are influenced by the presence of particular species (Edgar and Barrett 2002). However, specific biological interactions have been shown to play an important role in influencing community structure, both in the intertidal and subtidal zones.

1.4.1. Aquatic vegetation

Salt-marsh type environments are particularly harsh habitats for intertidal organisms. Animals found in these habitats must possess structural, physiological or behavioural capabilities that enable them to adjust to or avoid wide-ranging levels of salinity, temperature, humidity, desiccation and inundation (Daiber 1977). The presence of macrophytes for example, provides many species with microhabitats (Alfaro 2006) and may result in an increase in macrofauna biomass toward the high shore (De Decker and Bally 1985, Hodgson 1987). This is possibly due to the capillary effect of the algae filaments that prevents the desiccation of the sediment surface (Furota and Emmett 1993). Hodgson (1987) noted that in the Kariega estuary, one possible reason for high macrozoobenthic species diversity, when compared to other Eastern Cape estuaries, is the growth of *Zostera capensis* along the entire length of the estuary. Edgar and Barrett (2002) also found that macrophyte beds supported substantially more diverse faunas than un-vegetated habitats. Thus, the presence or absence of macrophytes influences the characteristics of the benthos (Puttick 1977).

Previous research has positively correlated crab community structure and species number with mangrove tree and seedling community structure and diversity, suggesting that mangroves were important to the crab fauna as a habitat and as a food source (Ashton *et al.* 2003). In mangals, other factors may also influence the associated benthic fauna. Morrisey *et al.* (2003) found that there were substantial differences in the abundance and composition of the fauna between younger and older mangrove areas. Sediments in older stands were more compacted and contained more organic matter and leaf litter compared to younger

stands. It was also shown that for sediments under *Enteromorpha* algal mats, percentage water, organic and silt / clay contents, medium phi and sorting coefficient significantly increased, and became significantly more reduced between 1 and 8 cm depth (Bolam *et al.* 2000).

Marine algal forms can also negatively influence benthic faunal species. Cardoso *et al.* (2004) found that the physical barrier created by mats of macroalgal species interfered negatively with the feeding mechanism of the isopod *Cyathura carinata* at the sediment–water interface. This species is both a deposit feeder and a predator. Aquatic vegetation can play an important role in stabilizing sediments creating suitable environments in which to make burrows for certain benthic invertebrates (Pinedo *et al.* 2000). However, the movement of burrowing animals may also be interrupted by vegetation as cited by Furota and Emmett (1993).

1.4.2. Bioturbation

The effects of bioturbation on the sediment and the benthic fauna have indicated that in some cases burrowing may significantly affect the composition and chemistry of sediments. Katz (1980) found that the burrowing activities of the fiddler crab, *Uca pugnax,* turned over approximately 18% of the upper 15 cm of sediment annually and burrows increased the surface area by 59% in experimental quadrats. In doing this, buried organic material can be brought back to the surface making it available to other benthic fauna. Bioturbation by crabs also results in changes in surface topography, particle size distribution and degree of aeration and, thus, the concentration of phytotoxins in the substratum (Lee 1998). The burrows of the mudprawn, *Upogebia africana*, tend to render the substratum softer where they are abundant (McLachlan and Grindley 1974). This bioturbation of muddy substrata could then make it easier for other less efficient burrowing infauna to occupy muddy sediments. Bacterial numbers have also been shown to increase in the presence of burrowing sandprawns, *Callianassa kraussi* (Branch and Pringle 1987).

The intensive reworking of the upper few centimeters of a muddy bottom by some deposit feeders produces a fluid fecal-rich surface that is easily resuspended by low-velocity tidal currents (Rhoads and Young 1970). Rhoads and Young (1970) suggested that the physical instability of this fecal surface tends to:

- clog the filtering structures of suspension-feeding organisms,
- bury newly settled larvae or discourage the settling of suspension-feeding larvae,

- prevent sessile epifauna from attaching to an unstable mud bottom.

Observations made by Morrisey *et al.* (1992a) raised the possibility that the presence of the tubes built by chaetopterid polychaetes was in some way facilitating the presence of other taxa. For example, initial differences in recolonization of experimental plots by *Pygospio elegans* influenced near-bed hydrodynamic effects (Bolam and Fernandes 2002). Burrows enhanced local sediment stabilization and the presence of *P. elegans* enhanced successful conspecific colonisation. Additionally, mineralization of organic matter is enhanced and bacterial production stimulated in the presence of meiofauna and many of the important meiofaunal functions take place in very muddy substrata (Coull 1999).

1.4.3. Predation

Activities of aquatic predators are often accountable for invertebrate distribution patterns and have been investigated in intertidal salt marshes (Kneib 1984), estuarine culture pens (Soares *et al.* 2004) and in mangrove stands (Schrijvers *et al.* 1998). The comparative significance of epibenthic predation on endobenthic fauna also increases down the intertidal to subtidal gradient, possibly at the cost of exploitative competition (Reise 1985). According to Rochette and Dill (2000) predators can affect the vertical distribution of mobile intertidal invertebrates in two ways:

- cause greater mortality of prey at certain intertidal levels,
- induce prey to seek safer intertidal areas.

Such effects were witnessed in the anti-predator behaviour of littorinid gastropods as their intertidal zonation was controlled by predatory crabs (Rochette and Dill 2000). Fish predation on benthic amphipods has also been shown to influence sex and size class distribution. Schlacher and Wooldridge (1996b) found that the amphipod, *Grandidierella lignorum*, showed prominent behavioural differences between sexes; males were markedly more active than females on the sediment surface in their search for receptive females and consequently were more vulnerable to predatory fish. This was reflected in the predominance of females in samples (Schlacher and Wooldridge 1996b). Past studies have also recorded that recruitment of infauna can be controlled by intense predation (Valderhaug and Gray 1984). However, in the case of meiofauna, predators cannot significantly reduce their population size due to a high abundance resulting from high reproductive rates (Coull 1999) and can thus be assumed to be, in most cases, a non-limiting factor for organisms feeding on these fauna.

1.4.4. Recruitment

In open tidal estuaries, many larval invertebrates are recruited from the sea (De Decker and Bally 1985). The recruitment of the mudprawn *Upogebia africana* into estuarine mudbanks, for example, is linked to the supply of larvae; larval behaviour; flood tidal currents that transport post-larvae into estuaries; and successful settlement and subsequent survival of juveniles (Wooldridge and Loubser 1996, Dubula and Lasiak 2003). Hanekom and Erasmus (1988) recorded the largest standing biomass of *U. africana* in the Swartkops estuary at stations bordering the tidal channels in the lower reaches; while prawn densities decreased markedly in the upper reaches. According to Hanekom and Erasmus (1988) this indicated a strong likelihood that water movement and its associated transport of oxygen and food material may influence the growth of this anomuran.

Apart from battling tidal currents, benthic larvae face many other challenges during the recruitment phase. Other physical processes that have been found to influence larval recruitment include the effects of wind on tides and currents. The analysis of settlement data gathered by Paula *et al.* (2003) suggested a significant effect of wind-driven transport on onshore migration of brachyuran megalopae into a mangrove swamp on Inhaca Island, Mozambique. However, the modes of transport for new recruits and newly settled benthic larvae vary with developmental stages. Armonies and Hellwig-Armonies (1992) concluded that for the bivalve *Macoma balthica* initial spatfall was mainly ruled by hydrographic features without active sediment selection. It was also found that *Macoma,* by having successive post-larval migrations, could several times change the intertidal site occupied during their first year of life (Armonies and Hellwig-Armonies 1992).

Apart from physical processes, various biological factors need to be considered when studying recruitment patterns. Bolam *et al*. (2000) determined that the negative effect of *Enteromorpha prolifera* on the polychaete *Pygospio elegans* was mainly due to larval filtering, suggesting that the weed was likely to have detrimental effects on population maintenance of most species, which rely on planktonic larval recruitment. Hill (1979) stated that post-larvae of the mud crab, *Scylla serrata* appeared to prefer conditions of shallow water, muddy substratum and shelter provided by mangrove roots, macrophytes or reeds.

The patch effect (dense aggregations of a species) related to adult conspecifics has been recorded in several studies. For example, the successful recruitment of the polychaete *Owenia fusiformis* could be influenced by certain substratum characteristics resulting from the

tube construction phase of burrowing adults (Pinedo *et al.* 2000). As previously mentioned, such patch effects have also been recorded for *P. elegans* by Bolam and Fernandes (2002) where existing tubes helped increase sediment stability and further recruitment. Armonies and Hellwig-Armonies (1992) correlated the faster growth of *Macoma balthica* juveniles in the upper intertidal with a higher density of larger recruits at these sites and found that indirectly, the faster growth of juveniles at these sites could result from the higher density of larger recruits.

1.5. Motivation for benthic studies

Numerous studies have focused on the intertidal and subtidal macrozoobenthic community structure of estuaries (e.g. McLachlan and Grindley 1974, Barnett 1984, Kneib 1984, Netto and Lana 1997, De Villiers *et al.* 1999, Teske and Wooldridge 2001) although comparatively few studies have concentrated on subtidal benthic communities in local estuaries. Studies in South African estuaries on the subtidal community include work done by Hodgson (1987) and more recently Schlacher and Wooldridge (1996a), Teske and Wooldridge (2001) and Thwala (2005). In addition, experimental results from soft sediment habitats are frequently opposing and appear to challenge generalization, whereas most studies on hard-substratum habitats have produced regular and corresponding results. One reason for this disparity according to Kneib (1984) is that much of the well known hard-substrata research has been conducted in a single habitat, the rocky intertidal, while soft-substrata findings are derived from many different habitats, including both vegetated and non-vegetated subtidal as well as intertidal environments.

Results from subtidal benthic studies in South Africa have identified a rich fauna (e.g. Hodgson 1987, Schlacher and Wooldridge 1996a,Teske and Wooldridge 2001, Thwala 2005) but no extensive comparison has occurred between intertidal and subtidal communities locally. However, some data suggest that subtidal communities are distinct from intertidal communities with a relatively well-developed community structure (Bazaïri *et al.* 2003, Bursey and Wooldridge 2003). Subtidal benthos are not affected by the same strong gradients found in intertidal areas, and comparisons between the organization of subtidal and intertidal communities are not expected to produce many similarities (Kneib 1984). Soft sediment intertidal habitats are typically wide-ranging with hidden distribution patterns due to the small size of the benthic infauna. Consequently, instead of concentrating on large-scale distribution patterns, individual soft-substratum community studies have usually put emphasis on the

importance of a single factor, such as predation (Schrijvers and Vincx 1997); and the influence on the abundance of benthic organisms at one point along the tidal gradient (Kneib 1984).

In order to construct an articulate model for soft-sediment benthic community structure, such as existing models for rocky shores, additional broad ranging research is needed on the comparative significance of different environmental and biological variables influencing the dispersal of benthic fauna along the inter- and subtidal continuum. Descriptions of the cryptic intertidal distribution patterns of soft-substratum organisms are prerequisite to an understanding of community dynamics in these forms of habitat but are conspicuously deficient in the literature (Kneib 1984). There are currently only a handful of studies on the productivity of the macrozoobenthos or macrozoobenthic communities of South African subtropical estuaries; this represents a serious gap in our knowledge of such systems as at the turn of the millennium quantitative data for macrozoobenthos existed for only 13% of the 259 estuaries found on the Southern African coastline (De Villiers *et al.* 1999). Research on macrozoobenthos is important in order to obtain a good grasp on estuarine ecosystem functioning and the necessary implementation of effective conservation measures (MCM, DEA&T and CSIR Environtek 2000).

1.6. Previous benthic research on the Mngazana Estuary

Like warm temperate estuaries, the macrozoobenthos of subtropical estuaries is dominated by crustaceans, which in turn are largely dominated by brachyuran taxa (De Villiers *et al.* 1999). During a survey of the Mngazana Estuary by Branch and Grindley (1979) it was established that 209 invertebrate species, including species living on hard substrata, inhabited the estuary. The invertebrate fauna (retained by a 1 mm mesh) was dominated by a temperate fauna in the lower reaches and a tropical-subtropical fauna in the upper reaches (Branch and Grindley 1979). Furthermore, their findings showed that brachyuran detritivores constituted 80-100% of the biomass, compared to warm temperate estuaries where deposit and filter feeders dominated the benthic fauna. A more recent study at Mngazana focussing on the subtidal macrobenthos, found that the dominant taxa comprised polychaetes while the presence of other taxonomic groups varied greatly along the estuary, although deposit feeding species were found to dominate (Thwala 2005). Organic matter and percentage mud often emerged as the most important variables influencing the subtidal benthic community (Thwala 2005). Dye (1983c) encountered highest meiofaunal densities in the top 10cm of

intertidal sediments within the Mngazana Estuary and distribution was found to correlate most consistently with mean redox potential (Eh). Dye (1983c) recorded few macrofaunal organisms in meiofauna cores having a volume usually less than 1% of the total and stated that apart from crabs the macro-infaunal density was low.

Branch and Grindley (1979) related the high invertebrate species diversity in the Mngazana Estuary to the favourable physical conditions (i.e. minimum silt load and a permanently open mouth). De Villiers *et al.* (1999) stated that species diversity in such subtropical estuaries is correlated with factors such as freshwater input and whether the estuary mouth is open or closed. Furthermore, the sediments found in subtropical estuaries favour deposit feeding guilds as a result of the physical nature and high organic content of the sediment (De Villiers *et al.* 1999). Emmerson and McGwynne (1992) estimated that 43.6% of *Avicennia marina* leaf-fall at Mngazana was consumed by the deposit feeding crab, *Sesarma meinerti*.

1.7. Purpose of the study

This study forms part of a broader initiative on the Mngazana Estuary. The overall project incorporates multidisciplinary approaches to the various aspects relating to the estuary and its inhabitants including: zoology, botany, socio-economics, hydrology and geography.

The aims of this study were to:

1. Investigate and compare macrozoobenthic invertebrate community structure[1] and composition between adjacent intertidal and subtidal transects in muddy substrata.
2. Identify physical variables that influence macrozoobenthic community structure along the intertidal and subtidal gradient in the study area.

[1] Note: In this study the term *community structure* will refer to the species composition.

Chapter 2. Description of the estuary and study area

2.1. Location and physiography

The Mngazana Estuary is a mangrove system approximately 10km south of Port St Johns (31^{o} 42' S 29^{o} 25' E - Fig 2.1.) in the subtropical - warm temperate biogeographical transition zone. This estuary supports the third largest area of mangroves in South Africa (Rajkaran *et al.* 2004). The mangrove plant community comprises *Avicennia marina*, *Bruguieria gymnorhiza* and *Rhizophora mucronata*. The Mngazana River is 35 km long and has a catchment area of 275 km^2. The estuary is only 5.6 km in length (Wooldridge 1977). Two creeks are located near the estuary mouth and meander through extensive mangrove stands. First creek (Mbazwa) situated close to the estuary mouth is 1.5 km long and drains a large section of the Mngazana mangal forest and the eastern coastal hills. Second Creek is 2 km long and is located a short distance upstream of the mouth (Thwala 2005). The mangroves found growing in the estuary play an important role in stabilizing the riverbanks, especially along the outer bends (Rajkaran *et al.* 2004). The estuary is also ranked 15^{th} among the 259 South African estuaries in terms of biodiversity importance (Turpie 2004).

The Mngazana Estuary maintains a permanently open mouth due to a strong tidal prism and a rocky promontory on the southern side (Branch and Grindley 1979). A strong marine influence leads to a weak horizontal salinity gradient, with little vertical stratification. According to Branch and Grindley (1979) tidal effects are felt for the full length of the estuary, declining from a spring tide range of approximately 1.7 m just inside the mouth to 0.7 m at the bridge in the upper reaches. The silt load is also relatively low compared to other estuaries in the subtropical region and results in a relatively clear water column (Branch and Grindley 1979). The estuary contains an array of habitats, including salt marshes, mangrove forests, sand banks, rocky shores and a sheltered water body (Branch and Grindley 1979).

River inflow is low most of the time (average monthly flow was 0.34 m^3 per second for the three sampling sessions, van Niekerk and Huizinga 2007). December to March (summer) represent the high rainfall runoff period for the estuary, with average monthly volumes greater than 2 million cubic metres recorded. May to August (winter) represent the low flow period with monthly volumes around 1 million cubic metres or less (van Niekerk and Huizinga 2007). The years 2002 to 2005 were considered a drought period for the Mngazana Estuary. During this time the recorded monthly river flow volumes were often significantly lower than average

inflows. A previous estimate of annual rainfall for the estuary was 805 mm, which was much lower than that of neighbouring Port St. Johns where 1035 mm on average was documented (Wooldridge 1977).

The estuary has significant conservation potential and high ecological value (Whitfield 2000 as quoted by Thwala 2005; Branch and Grindley 1979). Although there are no major developments or commercial activities in the catchment of the estuary there is some utilisation of the estuarine resources at a subsistence level (Thwala 2005). One of the more important anthropogenic impacts on the estuary is the harvesting of mangroves. Mangrove harvesting at Mngazana takes place throughout the forest although *Rhizophora mucronata* is favoured (Rajkaran *et al.* 2004).

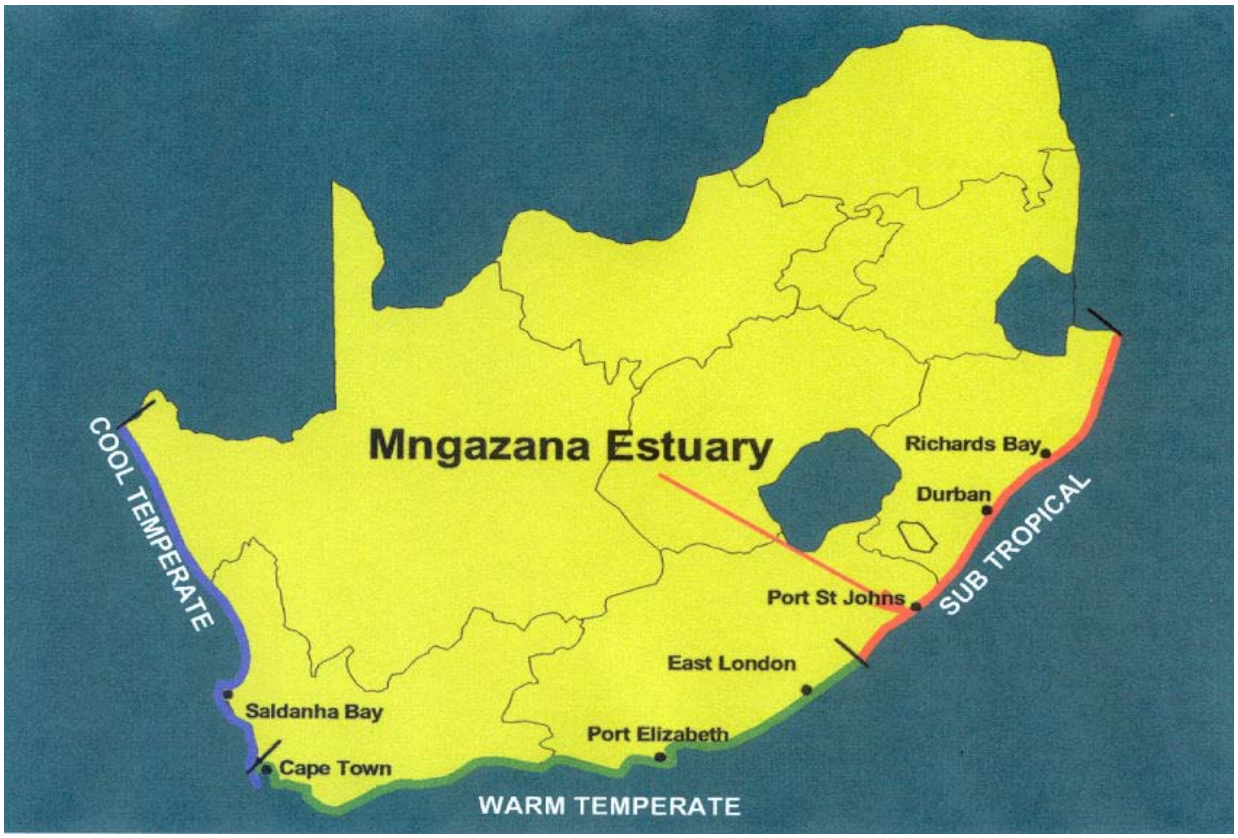


Fig 2.1. Location of the Mngazana Estuary on the east coast of South Africa (CSIR 2005).

2.2. Study site

Three sampling trips were made to the Mngazana Estuary (June 2004, November 2004 and January 2005). The locale designated for sampling covered an area of approximately 30 m x 40 m and was located approximately 1 km upstream of the mouth and a short distance

upstream from the confluence of 2nd Creek and the main estuary (Fig 2.2). Muddy substrata dominated the study area. This locale was chosen as it provided a relatively gradual transition between the intertidal to subtidal zone that was devoid of vegetation.

The survey by Branch and Grindley (1979) described the middle reaches of the Mngazana Estuary as having a relatively constant salinity and relatively low current velocities. Well-developed mangrove stands with some *Zostera capensis* beds characterise these middle reaches where euryhaline marine faunal species dominate. The sampling area chosen for this study was non-vegetated, but was bordered by the white mangrove, *Avicennia marina*. This species is exposed to a low level of harvesting by the local human communities (Rajkaran *et al.* 2004). Organic-rich mud is usually associated with the stilt roots and pneumatophores of *Avicennia* spp. trees (Boto and Wellington 1984). The majority of the substrata found in the middle reaches and the creeks of the estuary contain black mud with a high organic content and are characteristic of mangrove soils (Branch and Grindley 1979).

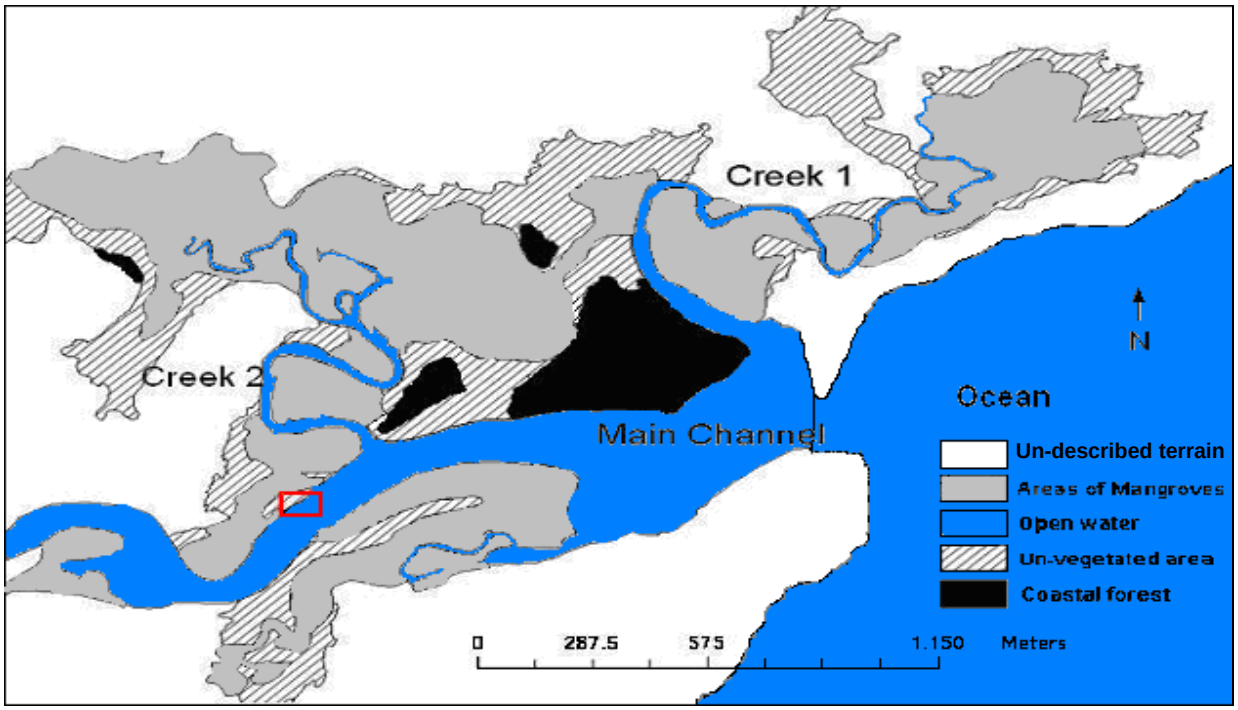


Fig 2.2. Location of the study area within Mngazana (the red rectangle denotes the sampling area, Modified from Rajkaran *et al.* 2004).

Chapter 3. Materials and Methods

3.1. Field sampling procedure

3.1.1. Experimental design

Six transect lines were located between the spring high water tide (HWST) mark and the channel bottom of the estuary (Fig 3.1) at about three metres water depth (measured at HWST). Three of these transect lines were located in the intertidal and three in the subtidal area. The intertidal group consisted of a transect line positioned along the low water tide mark of spring low tide (LWST, Transect 4); a transect line with a vertical height of 0.5 m above LWST at the mid shore (Transect 5); and a transect with a vertical height of 1 m above LWST on the high shore (Transect 6).

Transect 3 was located along the subtidal gradient and had a vertical depth of 0.5 m below the LWST; the subtidal intermediate transect was located on the channel margin (about 1.5 m water depth at HWST, Transect 2); and the deepest transect was in the main channel (Transect 1 at 3 m water depth at HWST). All transects were GPS-marked, but the positions changed marginally each sampling session as a result of change in tidal amplitude at the time and the position of the river channel. Each transect line ran parallel to the shore for a distance of 10 m. Intertidal transects were always sampled when submerged by the incoming or outgoing tide and were therefore sampled in the same way as subtidal sites.

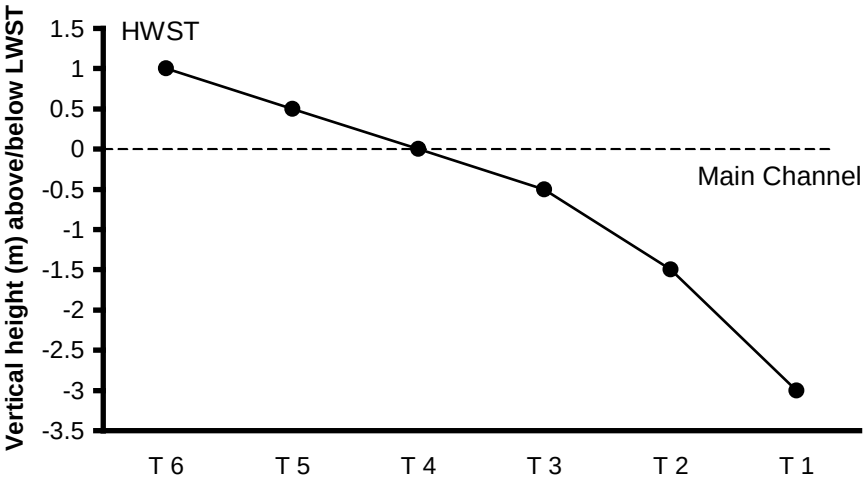


Fig 3.1. Relative position of transect lines (T1 to T6) along the subtidal to intertidal gradient (LWST=0m). Transects were located approximately 5 to 7 metres apart, along the gradient.

3.1.2. Biological sampling

The macrozoobenthic fauna and substrata were sampled using a van Veen-type grab. The area covered by the van Veen grab measured 211 cm^2 with a bite of approximately 10 cm deep. This was considered an adequate sampling depth as Branch and Grindley (1979) found that almost all benthic fauna in the estuary's middle reaches were confined to the top 10 cm of the substrata, with the lower layers consisting of black anoxic mud. In the case of subtidal transects, sampling was always performed from a small boat. Grab samples were transferred to plastic bags for later sieving on the shore. Sampling always commenced down-current of the direction in which replicates were to be collected as to ensure that the next sample would not be disturbed by previous activity. The volume sampled by each grab and the number of replicates per transect were previously determined for muddy and sandy substrata in the Nxaxo- Ngqusi estuary (Wavecrest) immediately south of Mngazana (Tsotsobe 2001). Tsotsobe (2001) found that when comparing the sampling efficiency of two Van Veen type grabs with bite sizes of 211 and 564 cm^2 on the macrozoobenthos, the larger grab size was more efficient although at a cost of effort. This meant that a greater number of replicates had to be collected by the small grab to ensure the inclusion of most species present. Fifteen replicates per transect were collected in this study, approximately 40% more than the number of replicates suggested by Tsotsobe (2001) to sample 80-90% of the infauna present.

Each sampling session commenced close to or during a spring tide. The position of LWST was marked using two 1 m poles, 10 m apart and sampling of intertidal transects commenced about four hours before and continued up to the time of high water. Subtidal transects were sampled directly before or after the intertidal session as subtidal sites were permanently submerged. Total duration of each sampling session was about six hours. All samples collected with the grab were sieved through 500 μm mesh bags and the animals retained and preserved in a 10% formaldehyde solution. Various mesh sizes have been used in research focusing on benthic assemblages in Eastern Cape estuaries (e.g. 4 mm and 5 mm by McLachlan and Grindley 1974, 1 mm by Branch and Grindley 1979, 0.5 mm by Teske and Wooldridge 2003, 0.25 mm by Schlacher and Wooldridge 1996a), depending on factors such as biogeographic zone and the main objectives of a particular study. Given the variability of retention efficiencies, the final choice should, however, fall on the smallest mesh possible (Schlacher and Wooldridge 1996c). Accordingly, a 500 μm mesh was used in this study, complimenting the work done by Thwala (2005).

3.1.3. Physico-chemical sampling

The physical variables measured at each transect included: salinity, temperature, oxygen content (mg/l and % saturation), depth, pH and turbidity. These measurements were taken with a YSI 6 600 Multiparameter probe at both the water surface and bottom of the water column at each transect. Physical variables at intertidal transects could only be measured at high tide. Due to problems with the multiparameter probe, some physical data for Transects 5 and 6 were not measured during the June 2004 sampling session.

An additional sub sample was collected from each transect with a grab for later sediment particle size (%mud: <63 μm and %sand: 2 mm – 63 μm) and organic content analyses. Sediment compactness was also measured at all three intertidal transects using a blunt stainless steel rod. The diameter of the rod measured 5 mm; the weight 448 g; and length 1.8 m. The rod was dropped from a constant height of 1 m and penetration into the substratum was measured. Ten independent penetration measurements were taken along each intertidal transect from which a mean could be calculated. Additional sediment samples were collected by means of a grab along intertidal Transects 5 and 6 when the tide was at lowest ebb and at full high tide. These samples were stored in plastic honey jars and were sealed with plastic tape and were used for sediment water content analysis. Samples were immediately stored in a portable freezer to prevent evaporation during transport to the laboratory.

3.2. Laboratory procedures

Following the method outlined by Schlacher and Wooldridge (1996a), macrozoobenthic fauna were extracted from grab samples after treatment with Rose Bengal and repeated decantation (min. five times). The remaining debris was then carefully examined for the presence of macrozoobenthic species too heavy to be successfully extracted by decantation or for organisms that adhered to plant and algal debris. All individual organisms gathered from these samples were identified to the lowest taxon possible.

Sediment particle size was determined in the laboratory by the dry sieve method using a graded series of standard sieves listed in Table 3.1. Sediment samples were first ashed in a furnace for 8 hours at 550 ^{0}C to remove all organic debris and water vapour. Thirty-five gram sediment samples were then weighed and softly ground in a pestle and mortar. The mud fraction (i.e. silt and clay) was separated by washing it through a 63 μm sieve before drying at

60 ^{0}C for 48 hours to constant weight. Each sample was then reweighed to calculate the loss of weight of the mud fraction. The remaining sediment (i.e. larger than 63 μm) was placed in a mechanical sieve shaker with a graded series of sieves (Table 3.1) and shaken for 15 minutes per sample. Each fraction in the series could then be weighed and expressed as a percentage of the total initial dry mass of that particular sample.

Table 3.1. Sediment particle size categories (modified from Thwala 2005).

Particle size (mm)	Category
2.000 – 1.000	Very coarse sand
1.000 – 0.500	Coarse sand
0.500 – 0.250	Medium sand
0.250 – 0.125	Fine sand
0.125 – 0.063	Very fine sand
<0.063	Silt/Mud

Water content of substrate samples collected from intertidal transects was determined by recording the weight of each sample, before oven drying for 48 hours at 60 ^{0}C. Samples were then reweighed and the percentage water content calculated. Organic content was determined after drying sediment samples in an oven at 60 ^{0}C for 48 hours in order to evaporate moisture. Samples were then weighed to obtain the dry weight. Each sample was then ashed (total combustion of a sample of known weight) in a furnace at 550 ^{0}C for 8 hours and reweighed to calculate the percentage organic matter content.

3.3. Data analysis

Bursey (1998) and Thwala (2005) provided a detailed description of some of the methods and programs used in the analysis of benthic data. Two separate data sets were analysed:

- One set included biological data comprising the macrozoobenthic fauna collected at the study site.
- The second set comprised the physical parameters measured in the field as well as sediment particle size and water content analyses completed in the laboratory.

3.3.1. Environmental data analysis

A multivariate analysis of the environmental data was performed using PRIMER v.6 (Plymouth Routines in Multivariate Ecological Research, 2006). Environmental data were first normalised by employing Euclidean distances. Euclidean distances collapse environmental data into an analogous, dimensionless scale as environmental variables were measured on dissimilar scales. This procedure allowed for the clustering of transects in accordance with their similarities in relation to the set of environmental variables. Comparisons between transects based on the measured environmental variables were performed using group average cluster analysis and Principal Component Analysis (PCA) available in the PRIMER package. These procedures are ordination methods and provide a visual presentation or map of sites (transects) over a single dimension. The relative distance between sites is a reflection of the degree/similarity between them (Clarke and Warwick 1994). The environmental data collected from each field trip (i.e. June and November 2004 and January 2005) were treated discretely due to variation in community structure and variability between sampling trips. As mentioned previously, some environmental data in June 2004 for Transects 5 and 6 were not available for comparison.

Sediment particle size was analysed separately. A Bray-Curtis similarity matrix and group average cluster was employed as the various fractions of the sediment size groups outlined in Table 3.1 were based on the same scale. Non-metric multidimensional ordination plots of the similarity matrix were used to point out associations between transects.

3.3.2. Community structure

Species composition was first comprehensively described and the relevant data expressed by way of graphs, charts and tables. Macrozoobenthic community structure was described for each transect on the basis of the following parameters: diversity, evenness, richness and abundance. Species diversity comprises two separate categories namely; species richness referring to the total number of species; and evenness referring to the abundance of individuals as distributed among the species. Species richness was expressed as the total number of species found at each transect consisting of 15 replicates.

Diversity indices that take both components of species diversity (richness and evenness) into account provide a single number that allows a statistical comparison of biota between sites Bursey (1998). The PRIMER 6 program, DIVERSE was used to calculate the Shannon diversity index (H'). The Shannon index is a popular diversity measure, despite some

criticism (Shannon and Weaver 1949 quoted by Magurran 1988). The 15 replicate samples collected from each of the six transects allowed for the testing of significance of dissimilarity between transects and replicates.

DIVERSE (PRIMER) was also used to compute Hill's numbers, N0 (number of species), N1 (number of abundant species) and N2 (number of very abundant species). Hill's numbers presents an important method for concentrating on various parts of species evenness and provides a method for underlining the degree of dominance of frequently encountered species or the input of rare species (Hill 1973).

3.3.3. Multivariate species analysis

Using multivariate analysis, community structure was evaluated according to the extent to which replicates shared certain species at analogous levels of abundance. The PRIMER 6 software package was employed to manipulate and analyze the data obtained. The PRIMER package follows Clarke's (1993) strategy of community analysis and incorporates different programmes to perform the steps outlined by Clarke:

- Data are root-root transformed to reduce the weighting of abundant species or the domination by large-bodied species (biomass),
- Definition of similarity between replicates,
- Cluster analysis and non-metric multidimensional scaling (MDS),
- Numerous techniques are applied to recognize the species determining the observed trends across replicates including:

  a) Species analysis, where cluster analysis and MDS were used to express groups of species whose abundance fluctuates in parallel across sites,

  b) Similarity breakdown, recognising the species that displays the greatest similarity and dissimilarity between sites or groups of sites.

All species abundance data was square root transformed and standardised. The square root transformation is applicable when the group variances are proportional to the means and by transforming such data, by utilising their square roots results in a sample whose underlying distribution is normal (Zar 1998). As suggested for biological data, Bray-Curtis similarity matrices and non-metric Multidimensional Scaling (MDS) were used in order to perform the group average cluster analyses needed for ordination. Both methods were used to show similarities in order to improve accuracy in the interpretation of results (Field 1982 as quoted by Thwala 2005). One of the strengths of cluster analysis lies in the methods ability to show

the levels of similarity. However, after a specific site has been grouped its association with sites in other groups is difficult to determine. By using MDS this problem is overcome.

3.3.4. SIMPROF

The program SIMPROF (similarity profile) in the PRIMER v.6 package was used to indicate groups of transects (identified by Bray-Curtis similarity matrices and Euclidean distance) that were significantly different from each other. SIMPROF tests for structure in the data. The first step is to create a resemblance profile by ranking the resemblance matrix for the data. A mean profile is then calculated by randomising the order of each variables values and re-calculating the profile (Clarke and Gorley 2006). The pi statistic is calculated as the deviation of the actual data profile with the mean one and is then compared with the deviations of further randomly generated profiles to test for significance (Clarke and Gorley 2006). The null hypothesis states that there is no structure and therefore randomisation is allowed.

3.3.5. Connecting community structure and environmental data

Biotic and abiotic MDS and PCA ordination plots could be contrasted to examine the extent to which the measured physical data “clarified” any patterns in community structure. This provided a visual method for linking biological and physical data.

As described by Bursey (1998), an analytical method was used to connect community patterns to physical variables to determine which of the latter were important in manipulating community structure. The BIO-ENV program (Clarke and Warwick 1994) in the PRIMER package was used to evaluate and compare the relative importance of physico-chemical variables and sedimentary characteristic data measured and their influence on the invertebrate communities identified. This allowed for the easy identification of the physical variables that had the greatest effect on community structure. BIO-ENV concurrently uses both the Bray-Curtis similarity matrix constructed from the biological abundance data and the Euclidean distance dissimilarity matrix from the physical data and contrasts them. At the same time it computes a variable or assemblage of variables that maximise the rank correlation between the two variables.

3.3.6. Similarity breakdown and species analysis

The SIMPER program (Similarity Percentages) in the PRIMER package was used to identify species that were most responsible for similarity between separate transects or separate groups of transects. Transects and groups of transects were chosen on the basis of the initial

cluster dendrograms and MDS plots constructed, as explained in Section 3.4.3. According to Clarke and Warwick (1994) the average similarity within each group of sites and the average dissimilarity between all pairs of inter-group sites being compared is based exclusively on the average contribution made by each of the species present or absent at the sites found in a particular group (average similarity) or in each or both groups of sites (average dissimilarity). This procedure also aided the identification of “indicator species” that were accountable for discriminating between transects that were separate from all other transects as well as identifying species discriminating between different groups of transects. The Statistica package was used to perform multiple regression analyses and Spearman rank correlations in order to determine whether the species abundance of certain dominant species correlated significantly to the specified physical variables.

Chapter 4. Results

4.1. Physico-chemical variables

Environmental data from each of the six transects and for each of the three sampling sessions is listed in Table 4.1. For some of the measured variables readings were taken at both the top of the water column and just above the surface of the substrate. In certain instances the shallow nature of transects precluded more than one reading. No data are available for some of the variables in June 2004 due to calibration problems of the multi-parameter probe. Bottom values for salinity, temperature, oxygen content, percentage mud (<63 µm) and organic matter are also represented graphically (Fig 4.1).

4.1.1. Salinity

Salinity values (measured in Practical Salinity Units or PSU) for both subtidal and intertidal transects, during the three sampling sessions generally indicated that the water column was well mixed. Salinity values were also similar at both intertidal and subtidal transects during November 2004 and January 2005, indicating that there was little change along the sub- and intertidal gradient. Salinity readings, at all transects, were also higher during November 2004 ($\bar{x}$ = 40.5; range: 40.3 to 40.9). The lowest salinity readings were recorded during June 2004 ($\bar{x}$ = 33.9; range: 33.4 to 36), while slightly higher values were recorded during January 2005 ($\bar{x}$ = 34.9; range: 34.9 to 34.9), (Fig 4.1). In general, salinity showed only minor change from subtidal to intertidal transects during the three sampling sessions.

4.1.2. Temperature

A small temperature difference between the surface and bottom waters was recorded at all transects (Table 4.1). During June 2004 and January 2005 temperature readings showed little variation between subtidal and intertidal transects. In November 2004 temperature readings were slightly higher at intertidal transects compared to subtidal transects. Transect 6 in particular showed an approximate increase of 4 ^{0}C compared to subtidal transects. Maximum temperatures were recorded during January 2005 ($\bar{x}$ = 25^{0}C; range: 24.9 ^{0}C to 25.1 ^{0}C) and the lowest temperatures during June 2004 ($\bar{x}$ = 18.9 ^{0}C; range: 18.7 ^{0}C to 19^{0}C) as expected, with November 2004 readings ($\bar{x}$ = 23.1 ^{0}C; range: 22.1 ^{0}C to 26^{0}C) reflecting intermediate values (Fig 4.1). Temperature readings during November 2004 showed greater fluctuation across transects than during the other two sampling periods.

4.1.3. Dissolved oxygen

The water column appeared to be well oxygenated during all three sampling sessions (Table 4.1). During June 2004, dissolved oxygen readings stayed relatively stable across Transects 1 to 4 ($\bar{x}$ = 6.8 mg/l; range: 6.7 mg/l to 6.9 mg/l), (Fig 4.1). For both the November 2004 ($\bar{x}$ = 7.9 mg/l; range: 4.2 mg/l to 10mg/l) and January 2005 ($\bar{x}$ = 6.4 mg/l; range: 4.4 mg/l to 8.9 mg/l) sampling sessions dissolved oxygen readings fluctuated across the intertidal and subtidal gradient. Dissolved oxygen values were higher in intertidal transects compared to subtidal transects in November 2004. During January 2005 dissolved oxygen values were relatively high at deep subtidal transects and the high intertidal transect. Intermediate transects reflected lower values.

4.1.4. Mud and silt fraction

The mud/silt fraction present in the sediment fluctuated between transects, although similar trends were observed between different sampling sessions (Fig 4.1). The percentage mud was generally higher at the deep subtidal transects (T1 & T2) and the high intertidal transect (T6). Intermediate transects reflected a lower percentage mud content. The mud fraction varied most at Transect 5, between different sampling sessions. The mean mud fraction during June 2004, November 2004 and January 2005 was 53.3% (range 32.4% to 73.9%), 57% (range 40.9% to 90.5%) and 58.4% (range 39.5% to 71.2%) respectively.

4.1.5. Organic matter

The organic content of the sediment at all transects was on average higher during January 2005 ($\bar{x}$ = 4.7%; range: 3.1% to 6.3%) compared to June 2004 ($\bar{x}$ = 2.3%; range: 1.5% to 3.3%) and November 2004 ($\bar{x}$ = 3.1%; range: 1.9% to 6.6%), which followed a very similar trend in relation to each other (Fig 4.1). Percentage organic content also showed some variation between transects along the subtidal to intertidal gradient during all sampling sessions.

Percentage organic matter and percentage mud followed a similar trend during all sampling sessions (Fig 4.2). A Spearman ranked correlation test indicated a positive correlation (at the 95% confidence level) between organic content and percentage mud at all intertidal transects during all sampling sessions combined ($r = 0.783$). However, there was no correlation between these two sedimentary variables when tested for all transects during each session. Depth was positively correlated with percentage organic matter content during January 2005 ($r = 0.829$).

4.1.6. Sediment water content

Substrate water content indicated a decrease in percentage water content up the intertidal gradient from Transects 5 to 6 during all sampling sessions except for the sample taken at high tide during January 2005 when a small increase was recorded (Table 4.1). As can be expected, sediment percentage water content was higher at high tide ($\overline{x}$ = 35.6% for June 2004 and $\overline{x}$ = 26.7% for January 2005) compared to low tide ($\overline{x}$ = 23.6% for June 2004 and $\overline{x}$ = 20.4% for January 2005) for both Transects 5 and 6 during June 2004 and January 2005. In November 2004, only a slight change in percentage water content was measured between high tide ($\overline{x}$ = 24.8%) and low tide ($\overline{x}$ = 24.3%) sediment samples.

A Spearman ranked correlation test indicated a negative correlation, at the 95% confidence level, between the water content of the sediment at low tide and percentage mud during all three sampling sessions combined (r = -0.712). The water content of the sediment at low tide also showed a positive correlation with the water content of the sediment at high tide for all three sampling sessions combined (r = 0.724).

4.1.7. Compactness of the sediment

Table 4.1 show that for all sampling sessions there was a general increase in sediment compactness moving up the intertidal gradient from the low intertidal (Transect 4) to the high intertidal (Transect 6). Mean sediment compactness during June 2004, November 2004 and January 2005 was 102.5 mm (range 53.5 mm to 137 mm), 143.5 mm (range 139.5 mm to 149 mm) and 112 mm (range 48.5 mm to 168 mm) respectively.

Table 4.1: Environmental variables measured at each of the transects during each sampling session (X denotes no measurement taken).

	Subtidal			Intertidal		
Transect	**1**	**2**	**3**	**4**	**5**	**6**
June 2004						
Salinity (surface PSU)	33.4	33.4	33.5	X	X	X
Salinity (bottom PSU)	33.3	33.4	33.5	33.5	36.0	X
Temperature (surface ^{o}C)	18.7	18.8	18.8	X	X	X
Temperature (bottom ^{o}C)	18.7	18.8	18.9	19.0	X	X
Oxygen (bottom mg/l)	6.7	6.7	6.7	6.9	X	X
Oxygen (% saturation bottom)	87.9	87.7	88.3	90.7	X	X
Depth (m)	2.0	1.5	1.0	0.0	X	X
Sediment - % mud (<0.065 mm)	67.7	66.6	39.5	39.5	32.4	73.9
Sediment organic matter (%)	3.3	2.4	2.4	1.5	1.8	2.6
Sediment water% content @ LT	X	X	X	X	28.3	18.8
Sediment water% content @ HT	X	X	X	X	40.3	30.8
Compactness (penetration in mm)	X	X	X	117.0	137.0	53.5
November 2004						
Salinity (surface PSU)	40.5	40.4	40.5	40.5	40.5	X
Salinity (bottom PSU)	40.4	40.1	40.4	40.4	40.4	40.9
Temperature (surface ^{o}C)	22.9	22.8	22.9	22.8	24.3	X
Temperature (bottom ^{o}C)	21.8	21.9	21.2	22.2	22.4	26.0
Oxygen (bottom mg/l)	7.6	4.2	6.9	10.0	9.4	9.1
Oxygen (% saturation bottom)	111.0	73.0	118.3	145.3	144.2	142.2
Depth (m)	3.5	3.7	3.3	1.5	0.3	0.1
Sediment - % mud (<0.065 mm)	65.0	90.5	42.5	40.9	41.2	62.2
Sediment organic matter (%)	3.4	6.6	2.3	1.9	1.9	2.5
Sediment water% content @ LT	X	X	X	X	26.5	22.0
Sediment water% content @ HT	X	X	X	X	26.6	22.9
Compactness (penetration in mm)	X	X	X	149.0	142.0	139.5
January 2005						
Salinity (surface PSU)	35.0	35.0	35.0	34.9	34.9	34.9
Salinity (bottom PSU)	34.9	34.9	34.9	34.9	34.9	34.9
Temperature (surface ^{o}C)	25.1	25.1	24.8	25.0	25.0	25.1
Temperature (bottom ^{o}C)	25.1	25.1	24.9	25.0	25.0	25.0
Oxygen (bottom mg/l)	7.4	8.9	3.5	4.4	5.8	8.0
Oxygen (% saturation bottom)	110.1	132.7	52.1	65.4	85.5	118.6
Depth (m)	4.0	3.0	1.3	0.8	0.5	0.4
Sediment - % mud (<0.065 mm)	68.7	71.2	39.5	47.3	62.7	60.9
Sediment organic matter (%)	6.3	6.0	3.9	3.8	5.1	3.1
Sediment water% content @ LT	X	X	X	X	23.7	17.0
Sediment water% content @ HT	X	X	X	X	26.6	26.7
Compactness (penetration in mm)	X	X	X	168.0	119.5	48.5

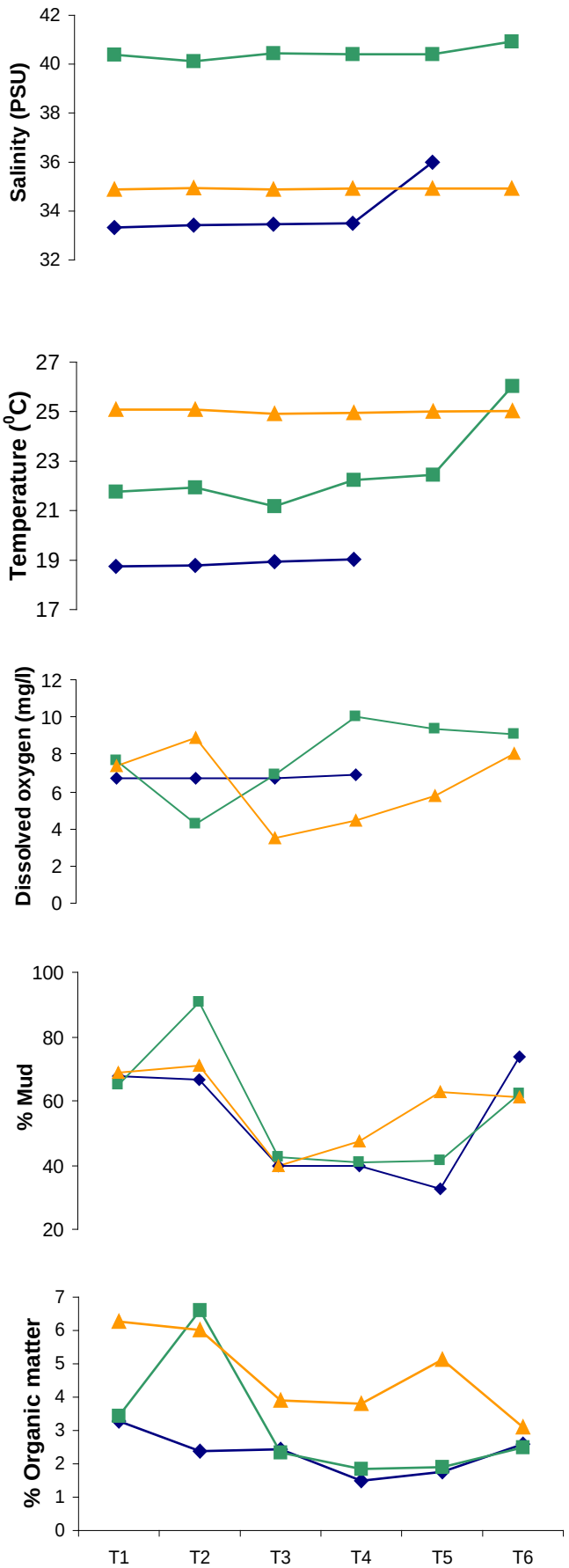


Fig 4.1: Physico-chemical variables measured at each transect (T1 – T6) during each sampling session (June 2004 -◆; November 2004 –■; January 2005 –▲).

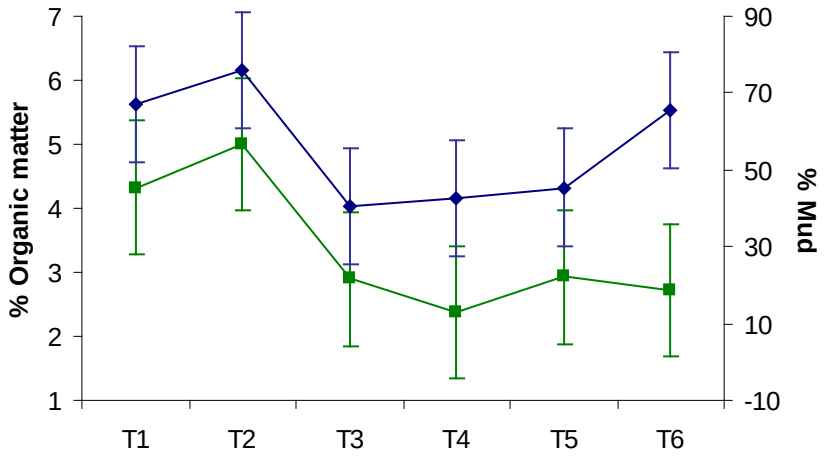


Fig 4.2: Mean (± standard deviation) percentage mud content (◆) and percentage organic matter content (■) at each transect (T1 – T6) for all three sampling sessions combined.

4.2. Multivariate analysis of environmental data

The letters A-C will be used in this and subsequent sections as a prefix to Transects 1 to 6 in order to denote the different sampling sessions, where: A denotes June 2004; B denotes November 2004; and C denotes January 2005.

4.2.1. Physico-chemical analyses

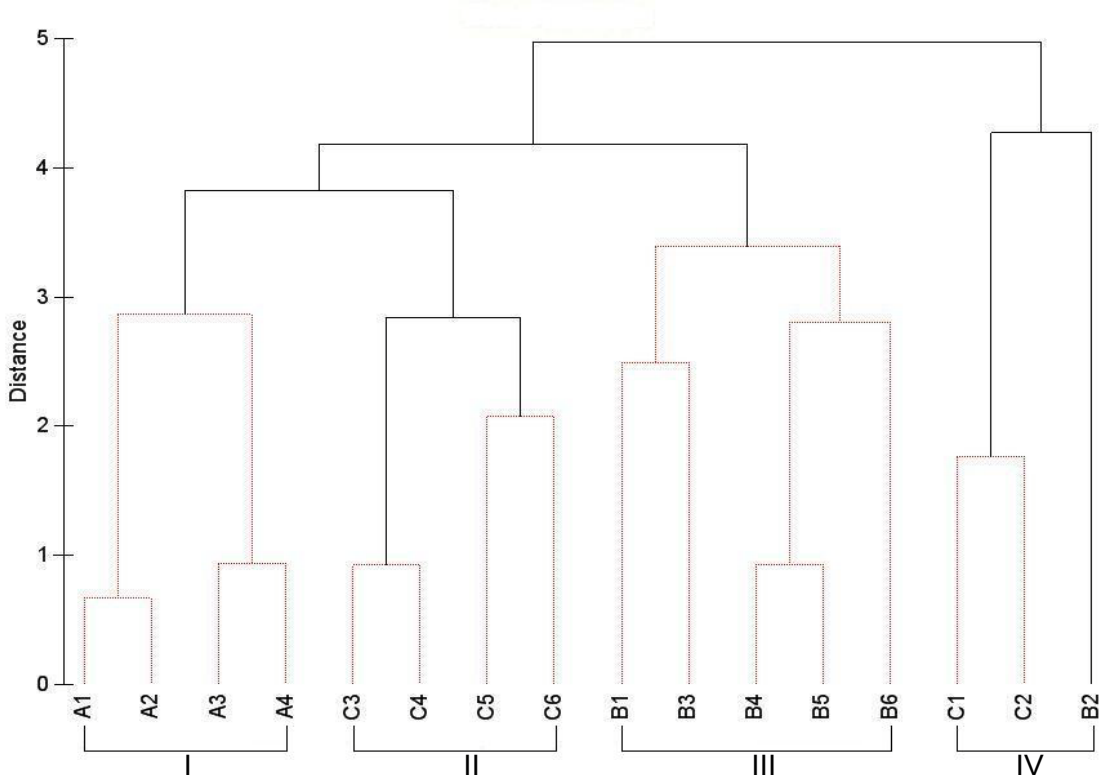
Physico-chemical data were analysed using cluster analysis (Fig 4.3.A) and include salinity (bottom), temperature (bottom), dissolved oxygen (mg/l at the bottom), water depth, pH, and percentage mud and percentage sand. Note that Transects 5 and 6 - June 2004 were excluded from the analysis (see Section 3.1.3). Red dashed lines indicated no significant difference between substructures (SIMPROF, p = >0.05) and solid black lines indicated a significant difference (SIMPROF, p = <0.05). Cluster analyses in conjunction with PCA were used to identify four groups:

- Group I contained Transects A1 to A4. There was no significant difference between the substructures making up this group (SIMPROF, p = >0.05),
- Group II contained Transects C3 to C6. Substructures C3 and C4 and substructures C5 and C6 clustered separately within this group and differed significantly from each other (SIMPROF, p = <0.05),

- Group III contained all transects from the November 2004 sampling series except for Transect B2. There was no significant difference between the substructures making up this group (SIMPROF, p = >0.05),
- Group IV consisted of Transects C1 and C2. Transect B2 was also grouped with these transects although it was significantly different from Transects C1 and C2 (SIMPROF, p = <0.05).

The grouping of transects indicated that transects sampled during the same sampling session generally clustered together. Subtidal transects sampled during the same sampling session also shared greater levels of similarity with one another. Similarly, most intertidal transects sampled in the same session shared greater similarity. A PCA ordination map (Fig 4.3.B) of the physico-chemical data points toward a similar grouping of transects as was presented by cluster analysis. Transects that had a resemblance value of 2 or lower (Fig 4.3.A) were closely situated to one another on the PCA ordination map (Fig 4.3.B). However, the separation between the different groups of transects (Groups I to IV) was more ambiguous.

A



B

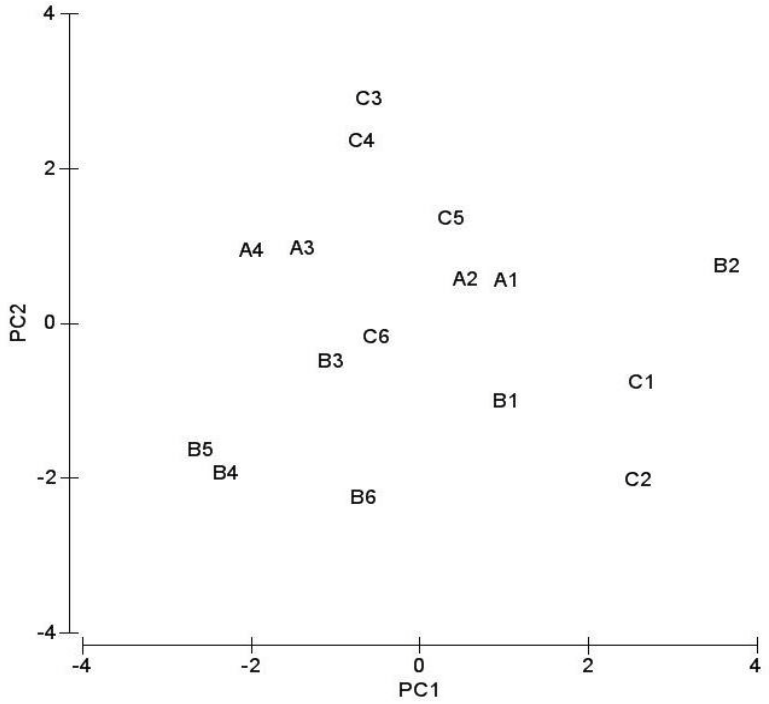


Fig 4.3.A: Dendrogram showing resemblance between transects in terms of physico-chemical variables by means of Normalised Euclidean distance during June (A1 - A4), November 2004 (B1 – B6) and January 2005 (C1 – C6; Red dashed lines indicate p = >0.05); **B:** PCA plot for the same data as in **A**. Transects A5 and A6 were excluded as some data were lost due to instrument failure.

4.2.2. Particle size analysis

Bray-Curtis similarity analysis (Fig 4.4) of all transects during the three sampling sessions identified three major groups based on the mean particle size distribution at the 80% resemblance level. Only one transect (B2) fell outside these three groups. All transects were characterised by a high fraction of fine sediments that indicated a similarity level of greater than 60%. Red dashed lines (Fig 4.4) between separate transects (substructures) represent groups of transects that were not significantly different from one another whereas solid black lines signify groups that are significantly different (i.e. SIMPROF, p = <0.05). Cluster analyses together with MDS plots were used to characterise three groups:

- Transects in Group I were mainly associated with the deeper subtidal area with the exception of one high intertidal transect (A6), which shared greatest similarity with transects from this group although it was significantly different from these transects (SIMPROF, p = <0.05). Sediments from these transects consisted mostly of very fine sand and muddy sediments with smaller fractions of fine and medium sand,
- Transects in Group II were also characterised by sediments having a relatively even particle size distribution across the medium sand to mud fractions. However, the very fine sand and mud fractions constituted a larger proportion compared to the other groups. There was also a small coarse sand fraction (Transect C6). This group consisted of two high intertidal transects and one mid intertidal transect that were not significantly different from each other,
- Transects in Group III were characterised by sediments having a relatively even particle size distribution across the medium to mud/silt fractions. A small component also consisted of coarse sand (Transect C3). The majority of transects in this group were located in the shallow subtidal and low to mid intertidal levels and were not significantly different from each other,
- Transect B2 was located in the deep subtidal and contained mostly muddy sediments and was significantly different from all other substructures (SIMPROF, p = <0.05).

The importance of fine sediments in characterising Groups I, II and III (Fig 4.4) is further illustrated by bubble plots (Fig 4.5) that indicate a distinct gradient across transects for both the medium and fine sand fractions. These sediment fractions increased from Transect B2 to Group I. No clear gradient was visible for the other sediment particle fractions.

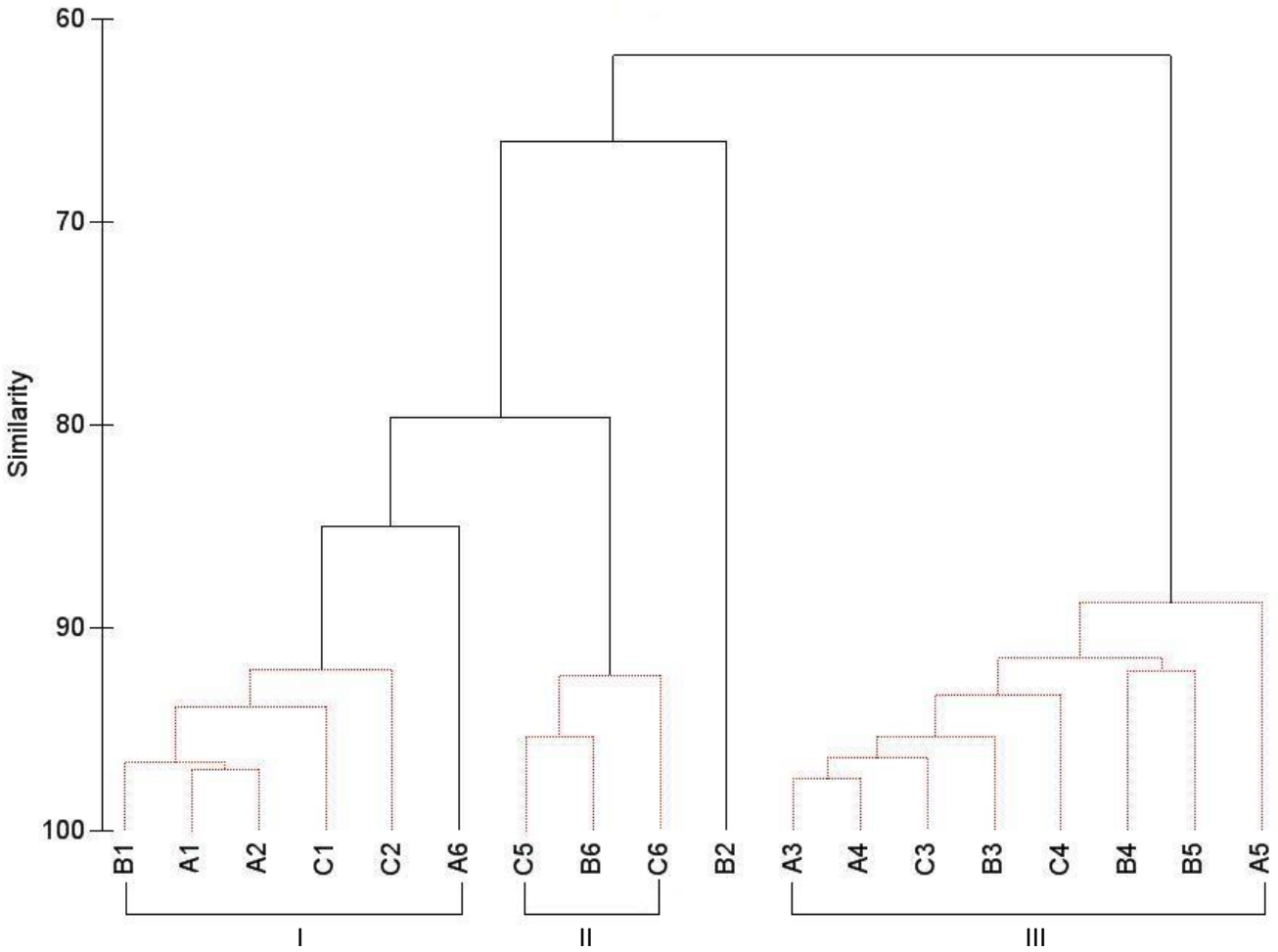


Fig 4.4: Cluster analysis of transects during the three sampling sessions showing the degree of similarity between transects in terms of mean particle size distribution. Red dashed lines indicate no significant difference between transects (SIMPER, p = >0.05). Data represent all sampling sessions (A, B and C) and transects (1 - 6) sampled.

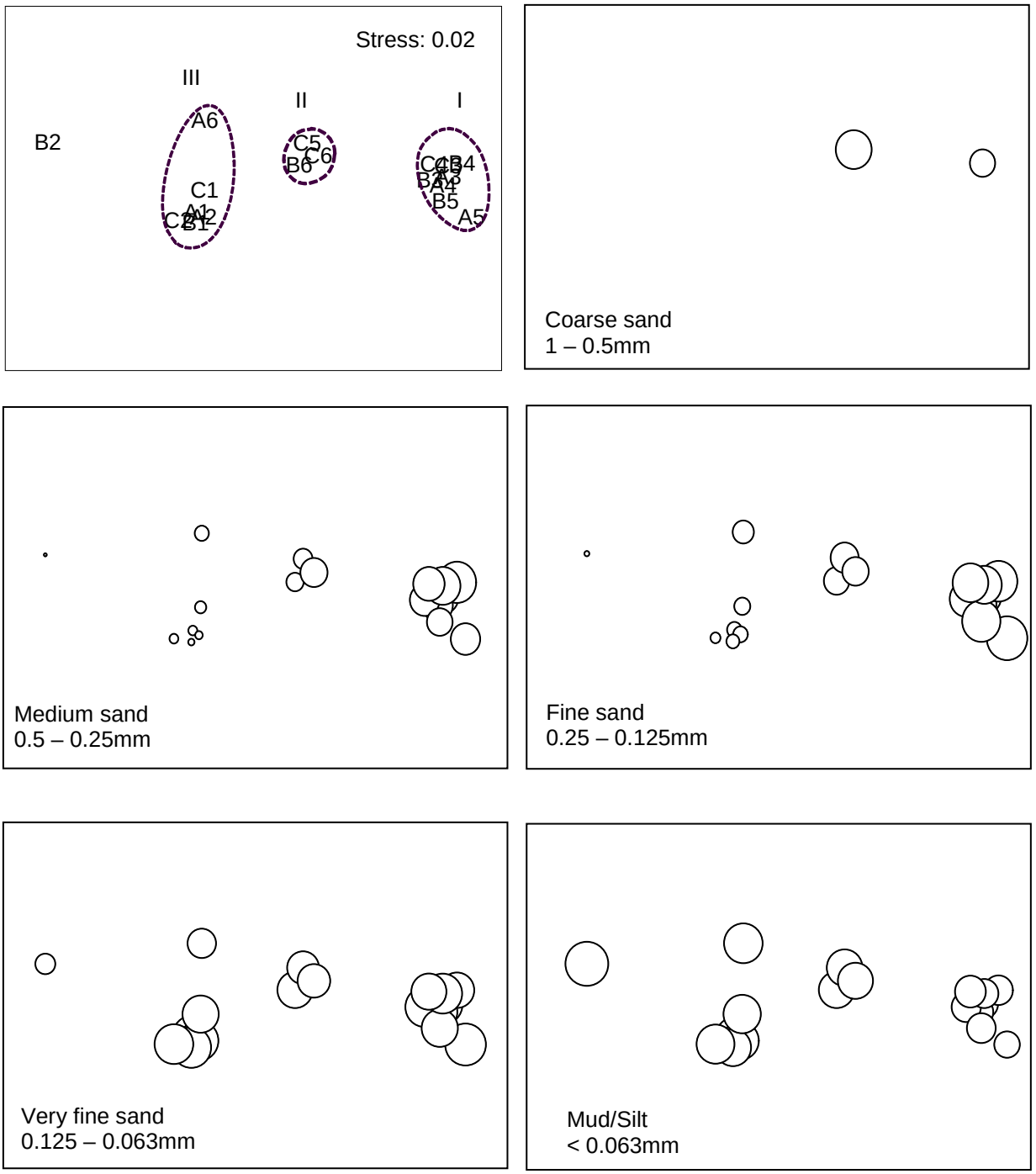


Fig 4.5: MDS plots of transects during the three sampling sessions indicating resemblance in terms of mean sediment particle size (I, II, and III represents groups of transects indicated in Fig 4.4). Data represent all sampling sessions (A, B and C) and transects (1 - 6) sampled.

4.2.3. Sedimentary characteristics of intertidal transects

Sedimentary data describing intertidal Transects 4, 5 and 6 during each of the three sampling sessions were analysed using cluster analysis in order to determine the level of similarity (Fig 4.6.A). The variables analysed included percentage mud content of the sediment, organic matter content, sediment water content during both high and low tide and the compactness of the sediments. Subtidal transects were excluded as the purpose of this analysis was to examine the effects of aerial exposure on macrozoobenthic communities in the intertidal zone. With the aid of cluster analysis and PCA (Fig 4.6.B) three groups were identified:

- Group I contained all the low intertidal transects located at the low tide mark, Transects A4, B4 and C4,
- Group II consisted of mid intertidal transects (A5 and B5),
- Group III contained all the high intertidal transects (Transects 6) with Transect C5 included.

The groups of transects identified suggested that transects generally clustered together on the basis of their location along the intertidal gradient. There was no significant difference between the substructures of Groups I and II (SIMPROF, p = >0.05) although they did show some separation between them. Group III was significantly different from substructures in Groups I and II (SIMPROF, p = <0.05). A PCA ordination map of the same sedimentary data suggested a similar grouping of transects as was found with the cluster analysis.

PCA ordination maps reflecting sedimentary characteristics during each sampling session for each intertidal transect are given in Fig 4.7. Sedimentary data were also superimposed on the ordination maps by means of bubbles in order to indicate the comparative values of these variables at each transect. It can be seen that the percentage mud content of the sediments was on average higher at high intertidal transects, while lower values were recorded at the lower intertidal transects. However, sediment penetrability together with sediment water content (during both high and low tide) was higher at the lower intertidal transects.

Fig 4.7 indicates that for Group III the percentage mud content of the sediment was a relatively important variable in separating this group from the other two groups. Mud content was also responsible for the separation of Group I although values at Transect B5 (Group II) were more similar to that of Group I. The main variable responsible for the separation of Group I was the water content of the sediment at both high and low tide. Organic content showed no clear pattern across intertidal transects. Sediment penetrability was relatively

constant at all transects except for Transects A6 and C6 where sediments were more compact.

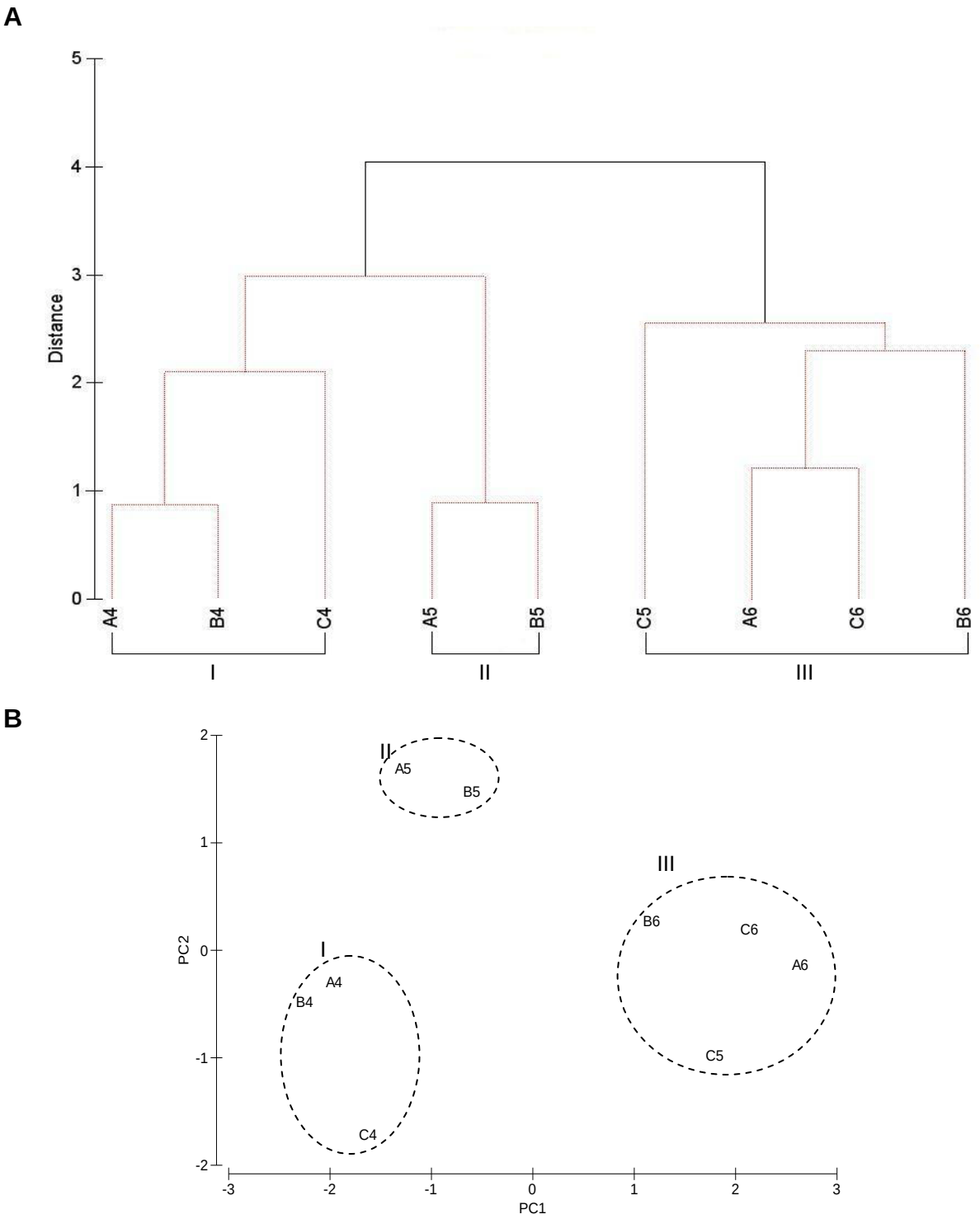


Fig 4.6.A: Dendrogram showing resemblance between transects in terms of sedimentary characteristics of intertidal transect by means of Normalised Euclidean distance during June/November 2004 and January 2005 (Red dashed lines indicate no significant difference, p = >0.05); **B:** PCA plot for the same data as in **A**. Data represent all sampling sessions (A, B and C) and all intertidal transects (4 - 6) sampled.

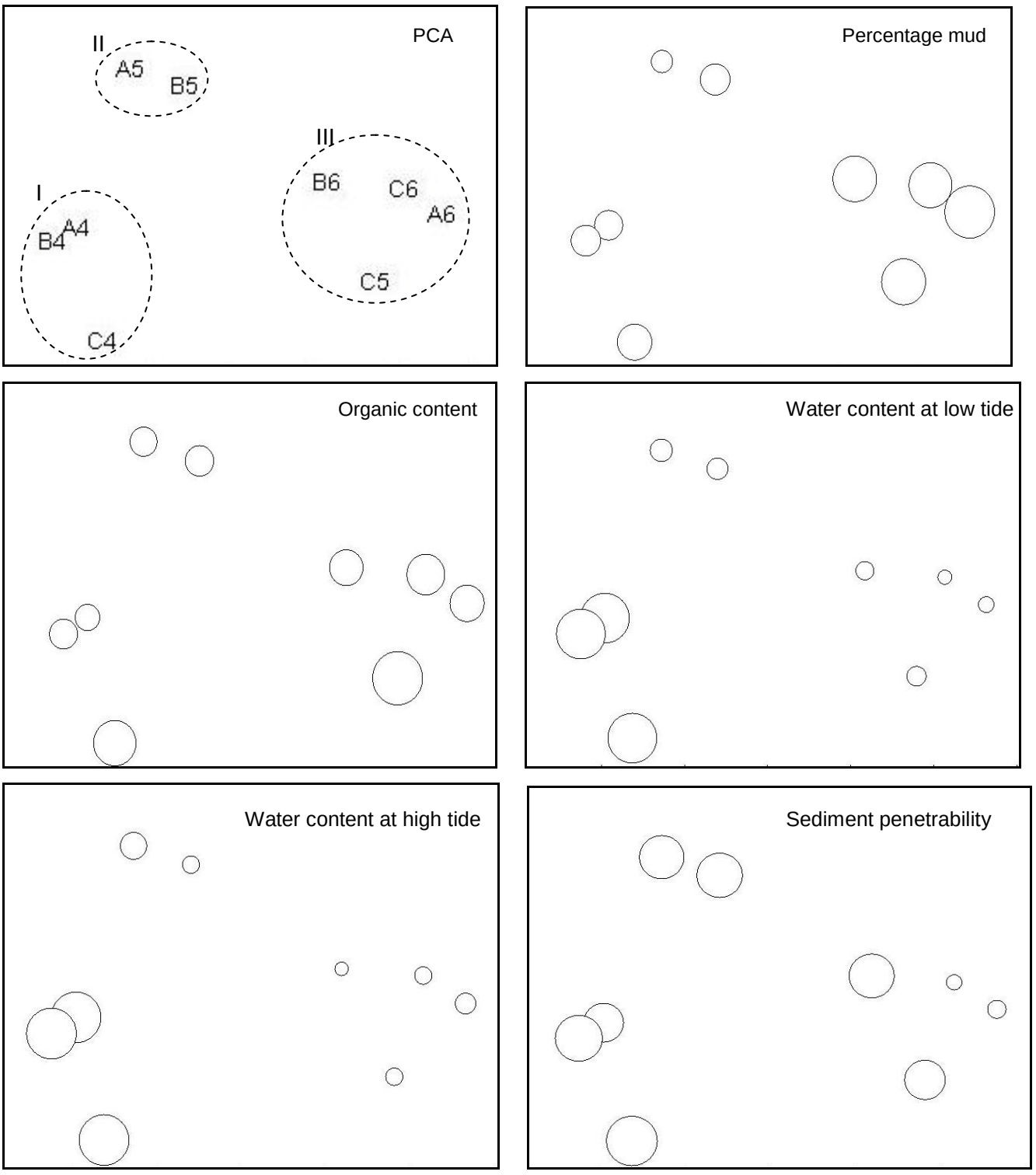


Fig 4.7: PCA plot of intertidal transects during each sampling session indicating resemblance in terms sedimentary characteristics. Data represent all sampling sessions (A, B and C) and all intertidal transects (4 - 6) sampled.

4.3. Biological analysis

4.3.1. Taxonomic composition

Fig 4.8.A-C indicates that generally, subtidal transects (T1 - T3) had a higher number of ind.m^{-2} (individuals per square metre) than intertidal transects (T4 - T6) during all sampling sessions. The number of ind.m^{-2} also decreased up the intertidal gradient from Transects 4 to 6 during each session. T6 consistently reflected very low macrofaunal densities.

Highest numbers of ind.m^{-2} were recorded in winter (June 2004) at Transect 1 (13220.m^{-2}) and 3 (14487.m^{-2}). The number of ind.m^{-2} was lower during the remaining two sampling sessions; for example, in November 2004 the highest numbers that were recorded were 4803.m^{-2} (Transect 2) and 4573.m^{-2} (Transect 3). In January 2005 highest numbers of ind.m^{-2} were recorded at Transect 2 (4037.m^{-2}), while abundance levels for Transect 1 and 3 were similar.

A total of 104 species was collected over the three sampling sessions (Appendices A to C). Twenty-four species were excluded from all subsequent analyses as these were only represented by one individual (Appendix D). Included were three foraminifera species, represented by foram tests, but no live specimens were found. The total number of species collected (at all transects) decreased during each sampling session: 87 species in June 2004; 51 species in November 2004; and 30 species during January 2005. More species were collected from the subtidal than from the intertidal zone during each sampling session and species numbers decreased along the intertidal gradient (Fig 4.9.A-C).

The taxonomic composition (Fig 4.10, column A; expressed as the percentage of listed number of individuals) reflects the dominance of polychaete species, while column B (Fig 4.10) indicates the composition of other taxa after the removal of polychaetes from the data. Polychaetes made up the dominant component of the macrozoobenthic community (over 70%) in relation to number of species (Fig 4.9.A-C) and number of ind.m^{-2} (Fig 4.10, column A) during each sampling session and were found to dominate at all transects, except at Transect 6 at the extreme high tide mark. At Transect 6 fewer species were encountered with mostly brachyurans, polychaetes and gastropods. Although polychaetes dominated all three sampling sessions, composition of other taxa showed much variability and no clear trends of distribution were apparent along the subtidal-intertidal gradient. Other species that were found to be relatively abundant at most transects included molluscs, brachyurans and

nematodes. Polychaete species that were present in high numbers during all sampling sessions included *Capitella capitata, Timarete tentaculata, Prionospio sexoculata* and *Paraonides lyra capensis.*

During all sampling sessions species richness (total number of species) was relatively higher for Transects 1 to 4, decreasing at Transects 5 and 6. Bivalves, gastropods and brachyurans were present at all transects during June 2004 and November 2004. Brachyurans were also present at all transects during January 2005. During November 2004 Anomura and Nematoda were present at all transects.

Amphipods, Anomurans, Copepods, Cumaceans, Isopods, Nematodes, Nemerteans and Tanaieds were present from deep subtidal transects to low-intertidal transects. The distribution of other taxa was scattered over transects and these taxa were represented by a low number of species.

4.3.2. Shannon diversity (H') and Hill's numbers

During all sampling sessions, Shannon diversity trends (Fig 4.11.A) corresponded to the trends shown for species richness (Fig.4.11.B). Each index reflected similar and relatively high values at Transects 1 and 2 during all sampling sessions. In general, intertidal transects reflected lower values for both the diversity index and measures of species richness when compared to the subtidal transects. There were no clear and consistent patterns along the gradient (T1 to T6) between sampling sessions.

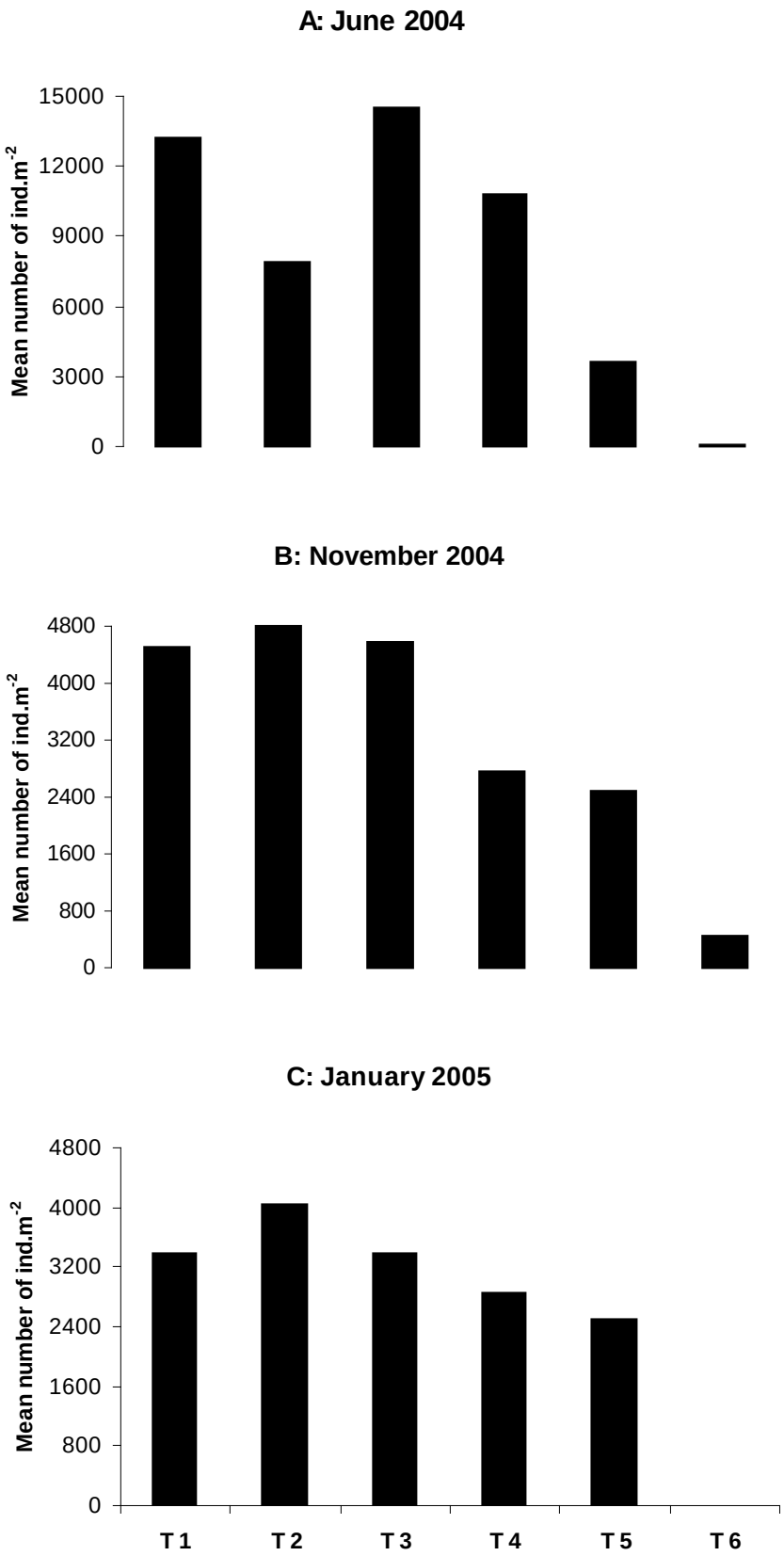


Fig 4.8.A-C: The mean number of ind.m^{-2} recorded at each transect (T 1 to T 6) during each of the three sampling sessions.

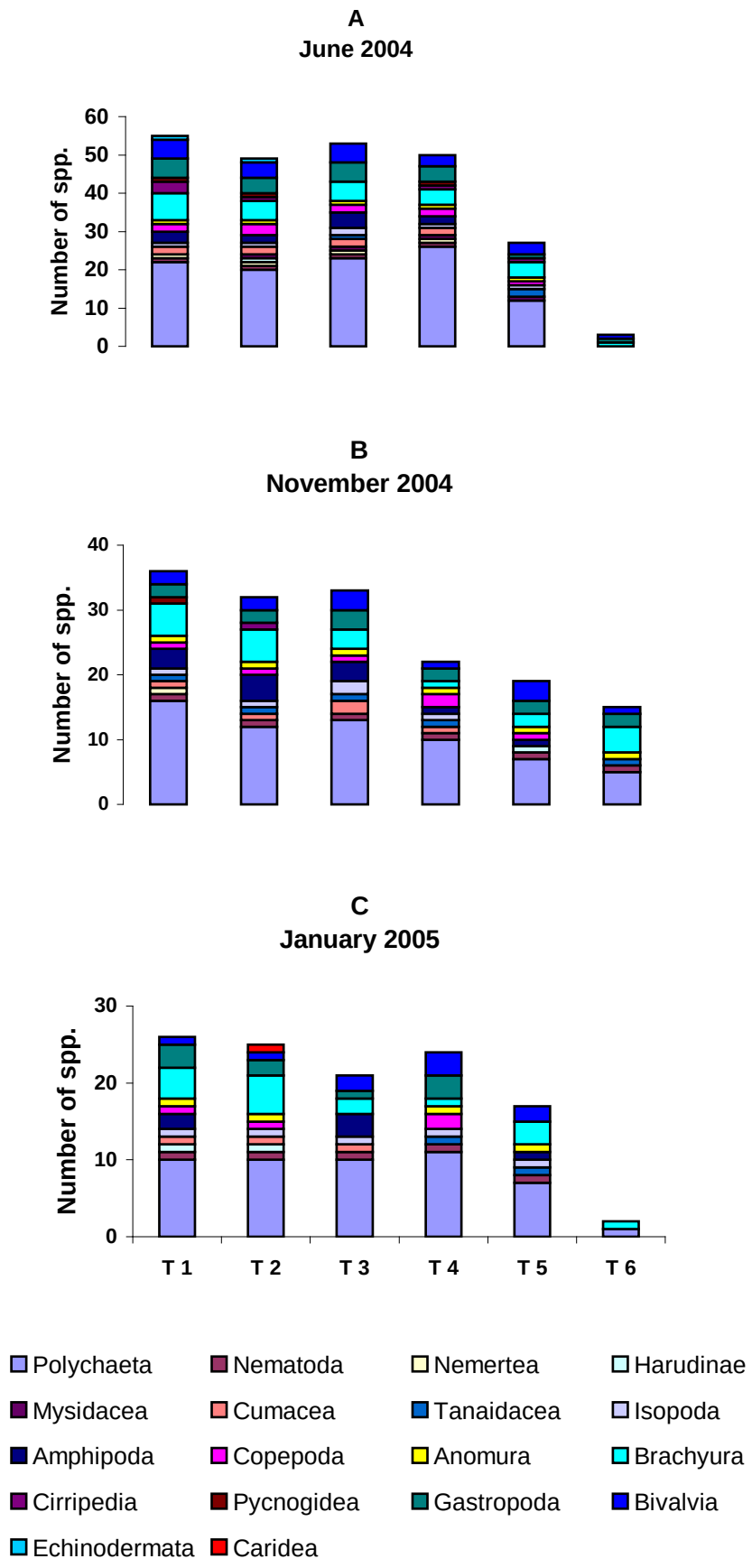


Fig 4.9.A – C: Number of species recorded for each Taxon at Transects 1 to 6 during each sampling session.

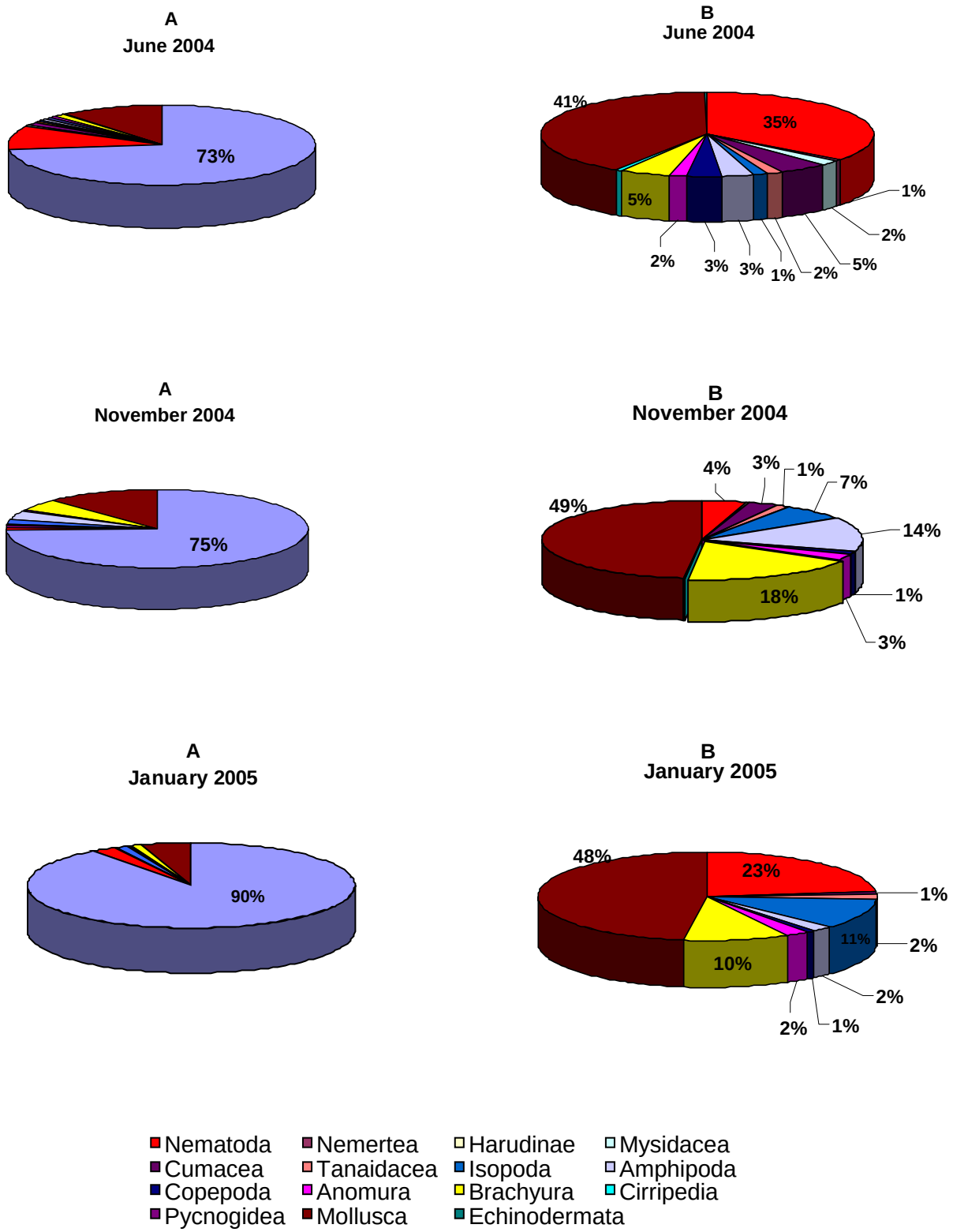


Fig 4.10: Taxonomic composition (as percentage of total number of individuals) during each sampling session. Column A reflects the true taxonomic composition during each sampling session indicating dominance by polychaete species. Column B reflects the proportions of other taxa after exclusion of polychaete species.

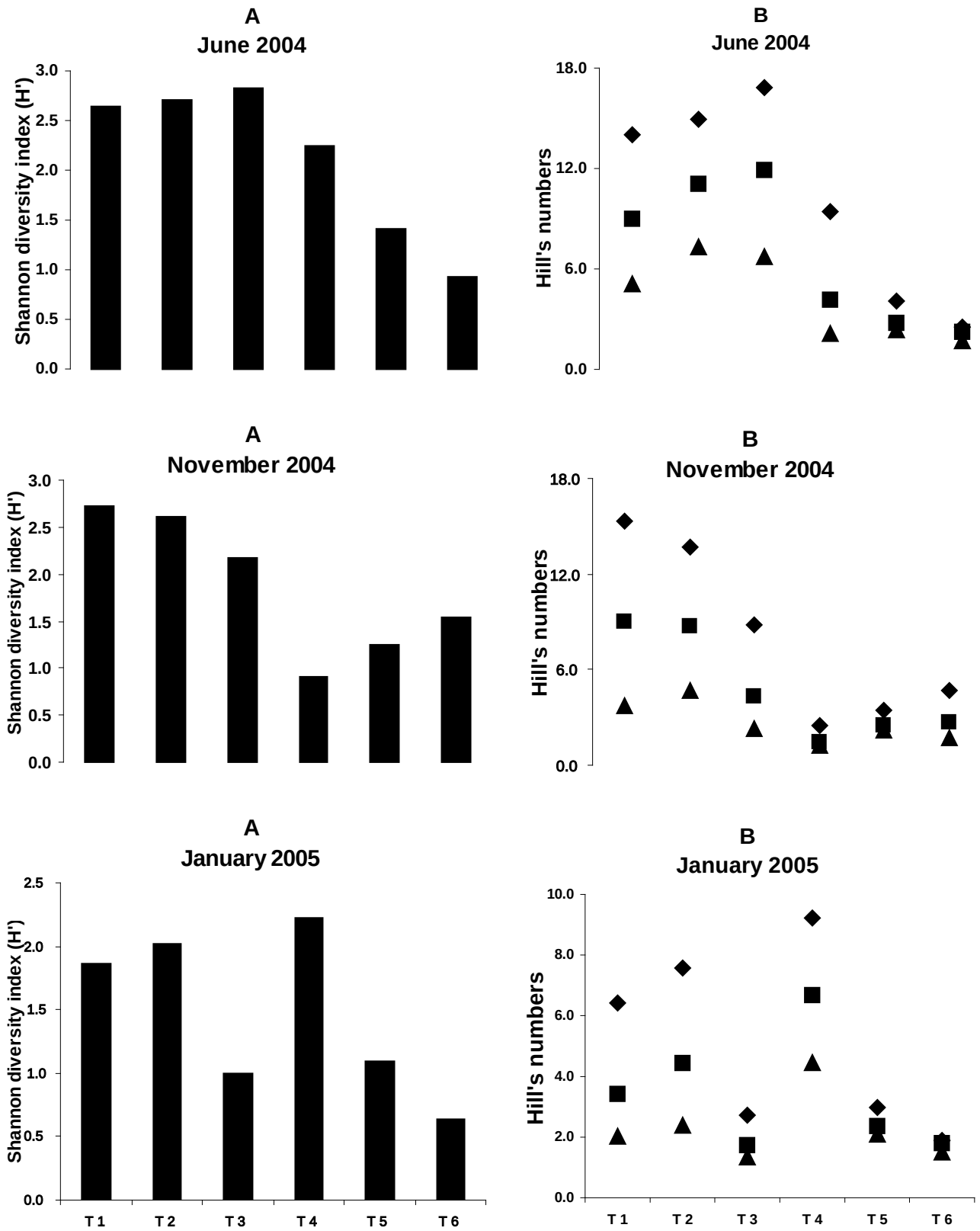


Fig 4.11: Column A reflects Shannon diversity (H') indices for Transects T 1 to T 6 during each sampling session. Column B reflects measures of species richness (Hill's numbers) for each transect (T 1 to T6) during each session. N1 (◆) reflects abundant species; N2 (■) reflects very abundant species; and N0 (▲) reflects total number of species.

4.4. Multivariate analyses of biological data

Cluster diagrams and their associated MDS plots were used to illustrate the degree of similarity in terms of species composition and abundance between transects for November 2004 and January 2005 (Fig 4.12). The analysis for June 2004 is not included, as the criteria needed by the different analyses were not met due to the lack of specific physico-chemical variables.

Cluster analysis distinguished three groups at approximately 45% similarity and 40% similarity during November 2004 and January 2005 respectively (Fig 4.12). The same general pattern was revealed by the MDS plots for the two sampling sessions. During each sampling session Transects 1 and 2 shared the greatest level of similarity and were not significantly different. Similarly, during both sessions Transect 6 was the transect that was the least similar to the other transects sampled and was significantly different from all other groups and substructures.

During November 2004 subtidal transects (B1 to B3) grouped together (Group B I). Substructures B1 and B2 were not significantly different from each other. Although B3 was significantly different from B1 and B2 (SIMPROF, $p = <0.05$), these substructures were grouped together as they shared more than 60% similarity and were closely clustered according to the MDS plot. During January 2005 Group C(I) comprised Transects C1, C2 and C4 and these substructures were not significantly different from each other as indicated by SIMPROF ($p = >0.05$). Group B(II) consisted of two Transects B4 and B5 and shared over 50% similarity and were not significantly different from one another. Group C(II) consisted of Transects C5 and C3 and were approximately 60% similar with no significant difference between them.

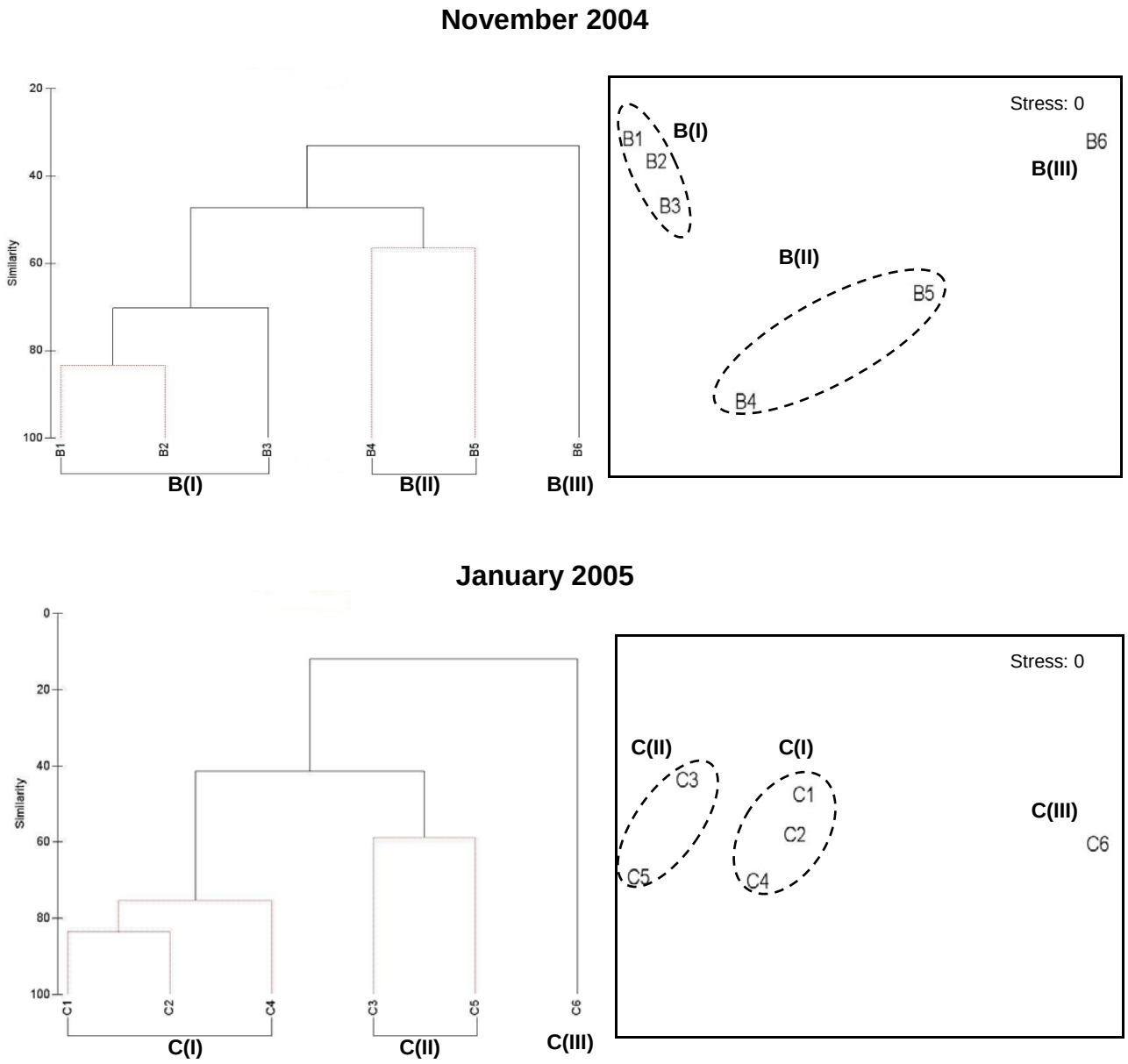


Fig 4.12: Dendrograms (Red dashed lines indicate p = >0.05) and associated MDS plots illustrating percentage similarity between transects within sampling sessions, based on benthic community composition and structure. Data represent November 2004 and January 2005 sampling sessions (B and C respectively) and the six transects (1 - 6) sampled on each occasion.

Bray Curtis similarity analysis between all transects for all sampling sessions is given in Fig 4.13. There was a relatively high degree of similarity between most subtidal transects, especially between Transects 1 and 2. Transect 3 and intertidal transects were more variable in terms of similarity. Transect 5 however, reflected a relatively high degree of similarity between sampling sessions. Three broad cluster groups were identified based on the dendrogram together with MDS plots (Fig 4.14):

- Group I was mainly comprised of subtidal transects: Transects A1 to A4, Transects B1 to B3, and Transects C1, C2 and C4,
- Group II included mainly intertidal transects: Transects A5, B4, B5, B6, C3 and C5,
- Group III consisted of only two transects, A6 and C6. These transects shared a low level of similarity (~30%).

Within Group I five substructures that differed significantly from each other were identified. These were grouped together into a single set as they were closely clustered together (Fig 4.14.B) and were more than 60% similar in terms of their biotic assemblage. There was a significant difference between Groups II, III and the substructures forming Group I (SIMPROF, $p = <0.05$). There was no significant difference between the substructures within Group II or the substructures within Group III. Fig 4.14.A illustrates the MDS ordination of transects during all three sampling sessions. Fig 4.14.B presents the same pattern as Fig 4.14.A, but focuses on the ordination of Group I and II transects. Comparing Figures 4.13, 4.14.A and B revealed the same general relationship between transects. Group III transects were well separated and shared less than 10% similarity with the other groups, indicating that a distinct community characterised Group III. The MDS plot revealed a separation between transects in Groups I and II (similar to that in Fig 4.13), which again indicated two distinct biological communities. These transects also shared a greater level of similarity when compared to Group III.

A separate multivariate analysis of subtidal transects for the combined sessions was not presented as cluster dendrograms and ordination plots revealed the same trend as found in Fig 4.13 and Fig 4.14.A and B.

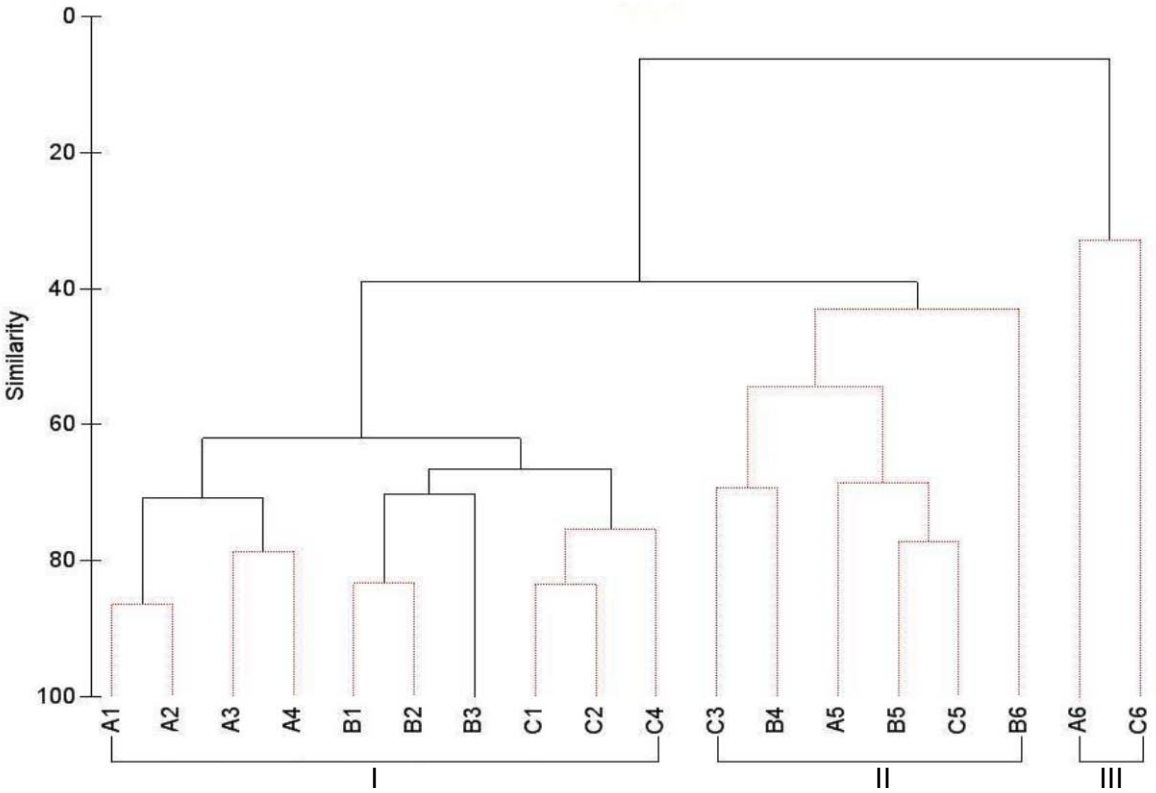


Fig 4.13: Cluster dendrogram indicating similarity of transects in terms of species abundance at all transects during each sampling session (Red dashed lines indicate p = >0.05). Data represent all sampling sessions (A, B and C) and transects (1 - 6).

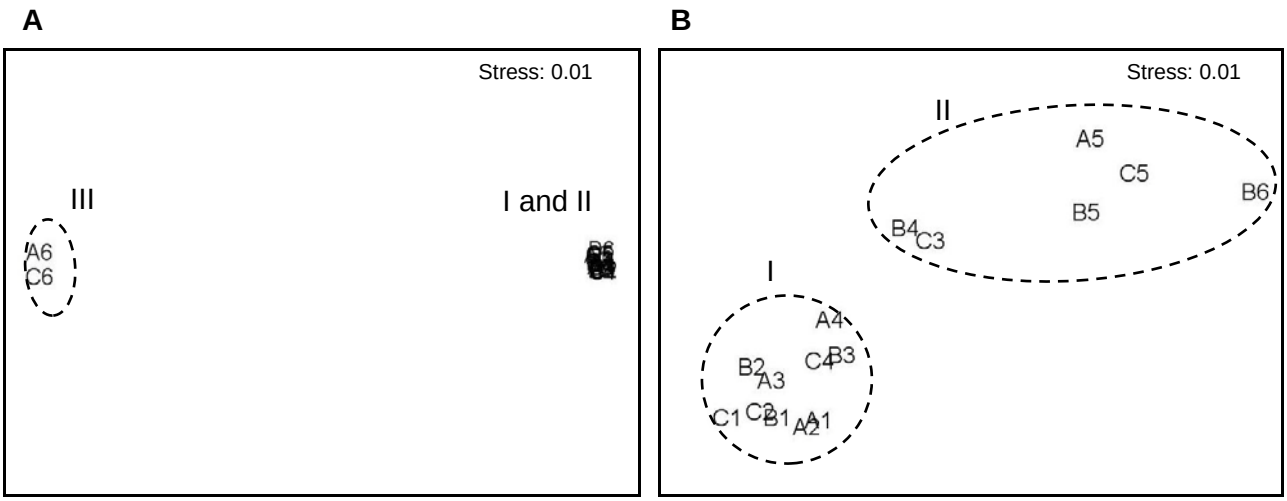


Fig 4.14.A: MDS plot demonstrating similarity (at the 60% level) of transects in terms of species abundance at all transects during each sampling session; **B:** MDS plot for same data as in **A,** but excluding Transects C6 and A6. Data represent all sampling sessions (A, B and C) and transects (1 - 6).

4.5. Multivariate analyses of intertidal data

Intertidal transects (T4, T5 and T6) were further analysed using Bray-Curtis similarity analysis for all sampling sessions (Fig 4.15). Three groups based on community composition and structure were significantly different from each other (SIMPROF, $p = <0.05$).

- Group I included all low intertidal transects (A4, B4 and C4). Transects A4 and C4 were approximately 60% similar. There was no significant difference between substructures within the group,
- Group II mostly comprised mid intertidal transects (A5, B5 and C5), but included one high intertidal transect (B6). Transects B5 and C5 shared approximately 70% similarity and were more than 65% similar to Transect A5. Transect B6 was approximately 50% similar to the mid intertidal transects. There was no significant difference between the substructures within this group,
- Group III included two high intertidal transects, A6 and C6. These two transects shared little similarity with any of the other transects, although there was no significant difference in the substructures between these two transects (SIMPROF, $p = > 0.05$).

Fig 4.16.A presents the MDS ordination plot of intertidal transects during each sampling session. Fig 4.16.B shows the same pattern as Fig 4.16.A, but focuses on the ordination of Groups I and II only. Fig 4.15 and 4.16 both reveal the same general trend in terms of grouping of transects. Fig 4.15 also indicated that Group III did not cluster with the other two groups and shared little similarity, indicating a distinct biotic community at A6 and C6. Groups I and II were closer and shared a greater percentage of similarity (~40%) than with Group III.

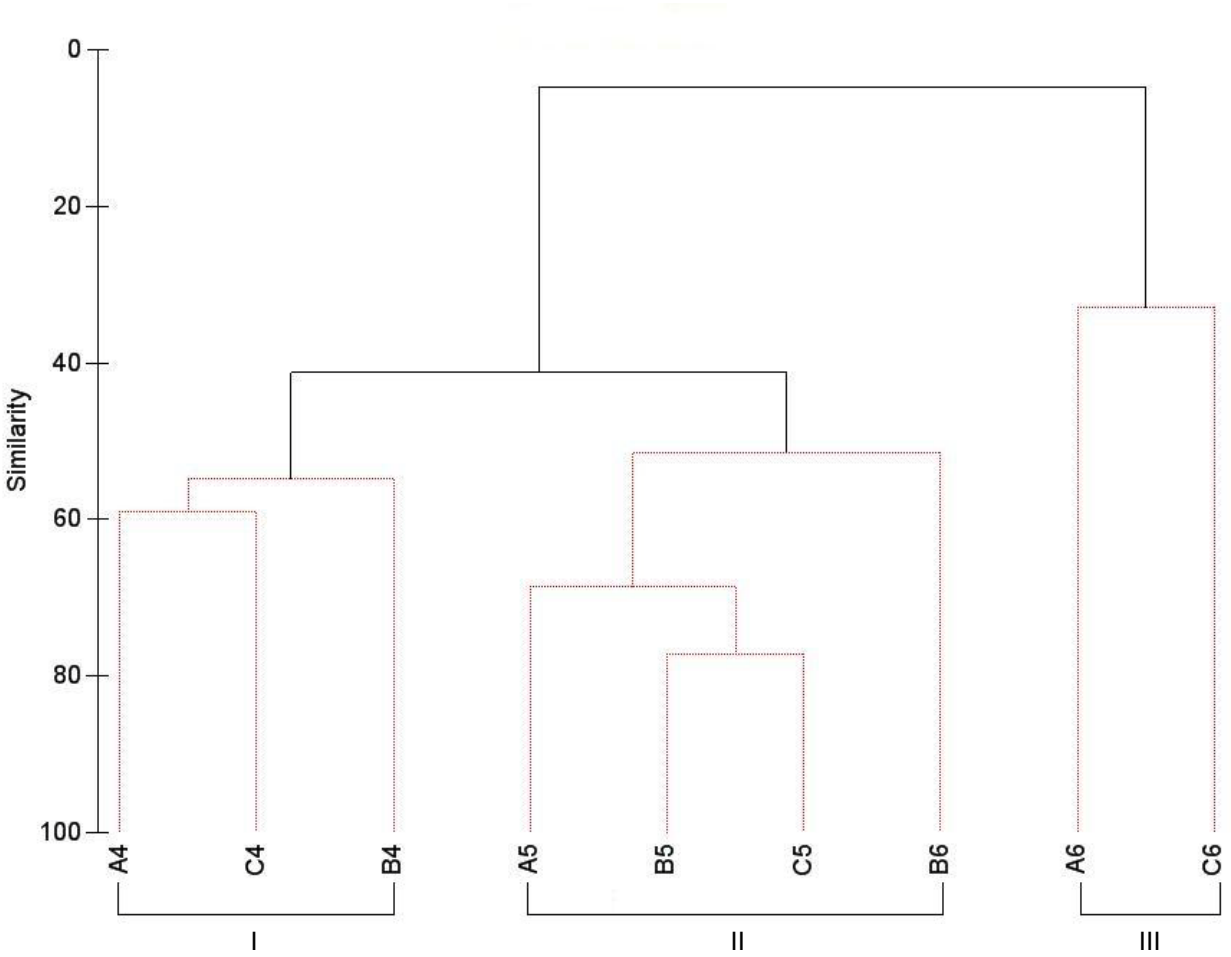


Fig 4.15: Cluster dendrogram demonstrating similarity of transects in terms of species abundance at all intertidal transects (T4, T5 and T6) during all sampling sessions (A, B and C). Red dashed lines indicate p = >0.05.

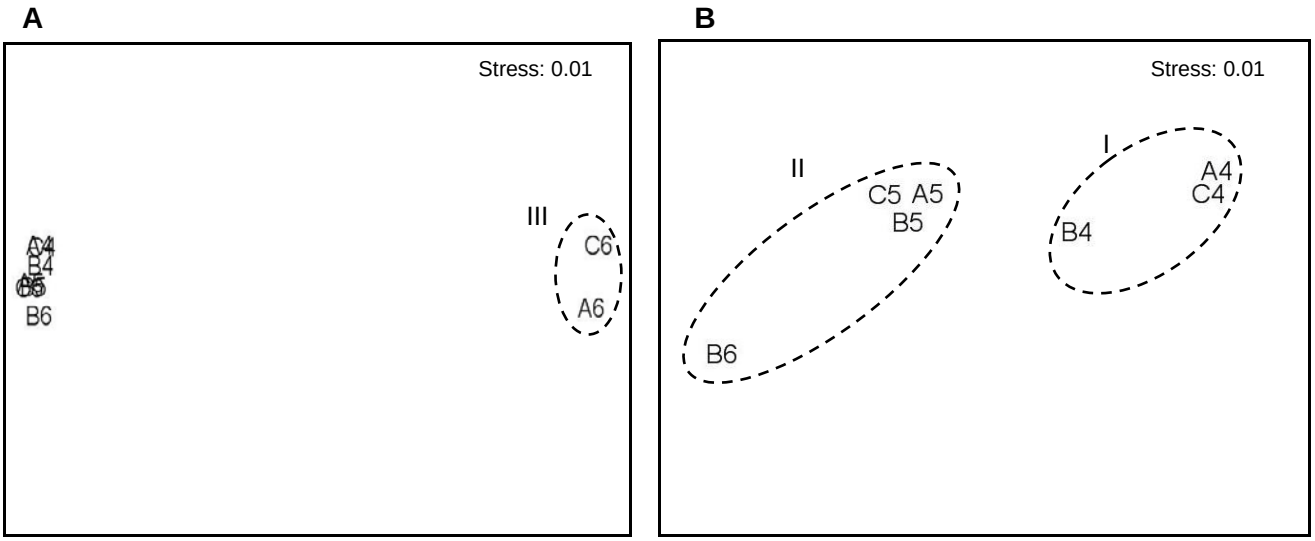


Fig 4.16.A: MDS plot demonstrating similarity of transects in terms of species composition and abundance at all intertidal transects (T4, T5 and T6) during each sampling session (A, B and C); **B:** MDS plot for same data as in **A,** but excluding Transects C6 and A6.

4.6. Linking biotic community patterns to physico-chemical variables

Table 4.2 presents the strongest correlation between ordination maps for the combinations of physico-chemical variables and the biological community plots for November 2004 and January 2005 (PRIMER 6 BIO-ENV). A similar analysis for June 2004 was excluded, as the physico-chemical data set was not complete. The BIO-ENV analysis provided single and combinations of abiotic variables that were found to describe the observed spatial distribution patterns of biotic communities (Thwala 2005) and from this the most important correlations were identified.

For November 2004 the correlations between the biological variables and the six environmental variables (i.e. salinity, temperature, oxygen saturation, depth, mud content of the sediment and organic content of the sediment) were high, while correlations for January 2005 were very low. A combination of depth and temperature provided the highest correlation (0.904) during November 2004. Depth was also the single most important variable (p=0.861) in November 2004 and was included in all variable combinations. A combination of oxygen content, depth and organic content provided the highest correlation (p=0.57) for January 2005. Organic content provided the single best variable (p=0.43) for January 2005 and was included in the majority of variable combinations.

Table 4.2: Best correlations between physico-chemical variables and biotic communities produced by BIO-ENV analysis during November 2004 and January 2005. Variables that provide highest correlations are shown and explained.

Date	Variable	Correlation	Comment
November 2004	Temperature, Depth	0.904	Depth was the single best variable, explaining 86.1% of the correlation
January 2005	Oxygen content, Depth, Organic content of the sediment	0.57	Organic content was included in most variable combinations and was the single best variable during this session.

4.6.1. Linking intertidal biotic community patterns to intertidal variables

Table 4.3 presents the correlation between the ordination maps for the combinations of sedimentary variables and the intertidal biological community plots for all sampling sessions (BIO-ENV). The same procedure was followed as described in Section 4.6.1.

Correlations between intertidal communities and the five sedimentary variables were relatively high. Sediment compactness was the single most important variable (p=0.685) and was included in most of the variable combinations. The two-variable combination of mud content and sediment compactness produced the highest correlation (p=0.709). Sediment water content at LT and compactness yielded another important combination with a correlation of p=0.655.

Table 4.3: Best correlations between sedimentary variables and intertidal biotic communities produced by BIO-ENV analysis for the combined sampling sessions. Combinations of variables with the highest correlations are presented and explained.

Variable	Correlation	Comment
Mud content, Compactness	0.709	Compactness was included in most variable combinations and was the single best variable during this session.

4.7. Species similarity breakdown

A SIMPER (PRIMER 6) analysis was used to determine the level of similarity within groups and average dissimilarity between groups, based on the percentage contribution of individual species to average similarity and dissimilarity respectively (the June 2004 sampling session was excluded). Groups were based on data represented in MDS plots (Fig 4.12 and Fig 4.16) and were analysed to reflect the contribution of numerically important species that cumulatively contributed 90% of total abundance. The SIMPER program is not able to calculate similarity within groups that contain only one transect.

4.7.1. Average dissimilarity

Appendix E provides a detailed analysis of average dissimilarity between groups of transects and individual transects for November 2004. Average dissimilarity for November 2004 (Table 4.4) was highest between Group B I and Transect B6 (74.1%), with *Capitella capitata* contributing 15.2% to average total dissimilarity. Lowest average dissimilarity for this sampling session was between Group B I and Group B II (52.7%), with *Prionospio sexoculata* contributing 19.1% to average total dissimilarity. *C. capitata* was among the three main species contributing to total average dissimilarity for each of the *inter*-group comparisons, while *Timarete tentaculata* and *P. sexoculata* were among the main contributing species for two of the *inter*-group comparisons. *Paraonides lyra capensis* was a discriminator species for

two of the *inter*-group comparisons. The discriminator species include four polychaete and one copepod species.

Appendix F provides a detailed analysis of average dissimilarity between groups of transects and individual transects for January 2005. Average dissimilarity for January 2005 (Table 4.4) was highest between Group C II and Transect C6 (96.7%), with *Timarete tentaculata* contributing 29.1% to average total dissimilarity. Lowest average dissimilarity for this sampling session was between Group C I and Group C II (59%), with *Prionospio sexoculata* contributing 21.3% to average total dissimilarity. *T. tentaculata* was among the three main species contributing to total average dissimilarity for each of the *inter*-group comparisons, while *P. sexoculata* and *Uca annulipes* were among the main contributing species for two of the *inter*-group comparisons. Discriminator species for the three *inter*-group comparisons include three polychaete species, one copepod species, one mollusc species and one brachyuran species.

Table 4.4: Summary of species dissimilarity between groups during each sampling session. Group B I includes Transects B1, B2 and B3. Group B II includes Transects B4 and B5. Group C I includes Transects C1, C2 and C4. Group C II includes Transects C3 and C5.

Comparing:	Av. Diss. %	Main contributing species	% Contribution	Discriminator
November 2004				
Group B I	52.7	*Prionospio sexoculata*	19.1	*Paraonides lyra capensis*
Group B II		*Capitella capitata*	11.3	*Cossura* sp.
		Timarete tentaculata	9.1	
Group B I	74.1	*Capitella capitata*	15.2	Polychaete sp.A
Transect B6		*Nassarius kraussianus*	7.9	
				Phyllodoce malmgreni
		Timarete tentaculata	7.4	
Group B II	56.4	*Prionospio sexoculata*	23.8	*Paraonides lyra capensis*
Transect B6		*Nassarius kraussianus*	10.4	*Pseudodiaptomus charteri*
		Capitella capitata	9.4	
January 2005				
Group C I	59	*Prionospio sexoculata*	21.3	*Prionospio sexoculata*
				Pseudodiaptomus
Group C II		*Capitella capitata*	11.8	*charteri*
		Timarete tentaculata	11.7	
Group C I	83.3	*Timarete tentaculata*	25.3	*Timarete tentaculata*
Transect C6		*Uca annulipes*	24.7	*Nassarius kraussianus*
		Paraonides lyra capensis	7.4	
Group C II	96.7	*Timarete tentaculata*	29.1	*Uca annulipes*
Transect C6		*Uca annulipes*	20.9	*Ceratonereis keiskamma*
		Prionospio sexoculata	16.7	

4.7.2. Average similarity

Appendix H provides a detailed analysis of average similarity within groups of transects for November 2004. Average similarity between transects in Group B I was 74.6% (Table 4.5), with *Timarete tentaculata* contributing 14.4% to average total abundance. Group B II contained two transects (B4 and B5) with an average similarity of 56.6%. *Prionospio sexoculata* contributed 43.9% to the average total abundance within Group B II.

Appendix I provides a detailed analysis of average similarity within groups of transects for January 2005. Average similarity between transects in Group C I was 78.2% (Table 4.5), with *Timarete tentaculata* contributing 18.6% to average total abundance. Group C II contained two transects with an average similarity of 58.8%. *Prionospio sexoculata* contributed 49.3% to the average total abundance within Group C II.

Table 4.5: Summary of species similarity within groups during each sampling session Group B I includes Transects B1, B2 and B3. Group B II includes Transects B4 and B5. Group C I includes Transects C1, C2 and C4. Group C II includes Transects C3 and C5.

Comparing:	Av. Sim. %	Main contributing species	% Contribution
November 2004			
Group B I	74.6	*Timarete tentaculata*	14.4
		Prionospio sexoculata	8.5
		Cossura sp.	6.6
Group B II	56.6	*Prionospio sexoculata*	43.9
		Capitella capitata	15.2
		Nematode sp.	6
January 2005			
Group C I	78.2	*Timarete tentaculata*	18.6
		Paraonides lyra capensis	14.7
		Capitella capitata	9.5
Group C II	58.8	*Prionospio sexoculata*	49.3
		Capitella capitata	26.4
		Nematode sp.	6.9

4.7.3. Dominant species

The dominant species present at each of the six transects during each sampling session were identified (Table 4.6) by examining the average similarity (Table 4.5, Appendices H and I) and the mean abundance data (Appendix A, B and C). The dominant species during June 2004 were identified from Appendix A, as no SIMPER analysis was available for this session.

Table 4.6: Dominant species at each of six transects during each sampling session based on average similarity and mean abundance data.

Transect	Dominant species
June 2004	
A1	*Timarete tentaculata,* Nematode sp., *Capitella capitata, Heteromastus* sp., *Paraonides lyra capensis*
A2	*Capitella capitata, Timarete tentaculata, Heteromastus* sp., Nematode sp., *Paraonides lyra capensis*
A3	*Timarete tentaculata, Prionospio sexoculata, Dosinia hepatica, Paraonides lyra capensis, Nicomache* sp.
A4	*Prionospio sexoculata, Timarete tentaculata, Capitella capitata*
A5	*Capitella capitata, Prionospio sexoculata*
A6	*Nassarius kraussianus, Uca annulipes*
November 2004	
B1	*Timarete tentaculata*, *Dosinia hepatica*, *Capitella capitata, Heteromastus* sp., *Paratylodiplax blephariskios*
B2	*Timarete tentaculata,* Gastropod spat. A*, Prionospio sexoculata, Dosinia hepatica, Capitella capitata, Cossura* sp*.*
B3	*Prionospio sexoculata, Timarete tentaculata, Capitella capitata, Grandidierella bonnieroides*
B4	*Prionospio sexoculata, Capitella capitata*
B5	*Capitella capitata, Prionospio sexoculata*
B6	*Capitella capitata, Nassarius kraussianus*
January 2005	
C1	*Timarete tentaculata*, *Paraonides lyra capensis, Capitella capitata*
C2	*Timarete tentaculata*, *Paraonides lyra capensis, Capitella capitata*
C3	*Prionospio sexoculata, Capitella capitata, Timarete tentaculata*
C4	*Paraonides lyra capensis, Timarete tentacualata, Prionospio sexoculata, Capitella capitata*
C5	*Capitella capitata, Prionospio sexoculata*
C6	*Timarete tentaculata, Uca* sp*.*

4.7.4. SIMPER analysis for all intertidal transects during the combined sampling sessions

Appendix G provides a detailed analysis of average dissimilarity between groups of intertidal transects during the combined sampling sessions. Average dissimilarity for the combined sessions (Table 4.7) was highest between Group II and Group III (95.7%), with *Uca annulipes* contributing 18.4% to average total dissimilarity. Lowest average dissimilarity for the combined sampling sessions was between Group I and Group II (58.8%), with C*apitella capitata* contributing 15.6% to average total dissimilarity. *Timarete tentaculata* was among the three main species contributing to total average dissimilarity for each of the *inter*-group comparisons, while *C. capitata* and *U. annulipes* were among the main contributing species for two of the *inter*-group comparisons. Discriminator species for the three *inter*-group

comparisons include three polychaete species, one nematode species and one brachyuran species.

Table 4.7: Summary of species dissimilarity for intertidal groups during all sampling sessions combined. Group I includes Transects A4, B4 and C4. Group II includes Transects A5, B5, C5 and B6. Group III includes Transects A6 and C6.

Groups	Av. Diss. %	Main contributing species	% Contribution	Discriminator
Group I	58.8	*Capitella capitata*	15.6	*Phyllodoce malmgreni*
Group II		*Prionospio sexoculata*	11	*Capitella capitata*
		Timarete tentaculata	6.4	
Group I	94.5	*Uca annulipes*	19.5	*Uca annulipes*
Group III		*Timarete tentaculata*	15.6	Nematode sp.
		Nassarius kraussianus	12.3	
Group II	95.7	*Uca annulipes*	18.4	*Capitella capitata*
Group III		*Timarete tentaculata*	15.4	*Uca annulipes*
		Capitella capitata	13.9	

Appendix J provides a detailed analysis of average similarity within groups of intertidal transects for all sampling sessions combined. Average similarity between transects in Group I was 56.2% (Table 4.8), with *Prionospio sexoculata* contributing 22.5% to average total abundance. Group II contained four transects with an average similarity of 61.4%. *Capitella capitata* contributed 39.8% to the average total abundance within Group II. Group III contained two transects with an average similarity of 32.8%. An average total abundance of 100% was attributed to *Uca annulipes.*

Table 4.8: Summary of species similarity within intertidal groups during all sampling sessions combined. Group I includes Transects A4, B4 and C4. Group II includes Transects A5, B5, C5 and B6. Group III includes Transects A6 and C6.

Comparing:	Av. Sim. %	Main contributing species	% Contribution
Group I	56.2	*Prionospio sexoculata*	22.5
		Capitella capitata	11.8
		Timarete tentaculata	7.6
Group II	61.4	*Capitella capitata*	39.8
		Prionospio sexoculata	21.6
		Nematode sp.	5.2
Group III	32.8	*Uca annulipes*	100

4.7.5. Dominant species at intertidal transects

The dominant species present at each of the three intertidal groups were identified (Table 4.9) by examining the average similarity data (Table 4.8) and the mean abundance data (Appendix A to C).

Table 4.9: Dominant species at each of the groups of intertidal transects for all sampling sessions combined based on average similarity and mean abundance data.

Group	Dominant species
Group I	*Prionospio sexoculata, Timarete tentaculata, Capitella capitata*
Group II	*Capitella capitata, Prionospio sexoculata*
Group III	*Nassarius kraussianus, Uca annulipes*

4.8. Species abundance for each sampling session

SIMPER analyses were used to identify all numerically important species that cumulatively contributed more than 90% to total abundance of all species, between the six transects sampled during all sampling sessions (Appendix K), as well as for the intertidal transects from the three sessions combined (Appendix L).

Table 4.10 indicated that the average similarity between Transects 1 to 6 was 40.1% during June 2004, 48.6% in November 2004 and 40.1% in January 2005. During all three sessions *Capitella capitata* and *Prionospio sexoculata* were among the four highest ranked species in relation to average total abundance. Similarly, *Timarete tentaculata* was one of the four highest ranked species for June 2004 and January 2005. During June 2004 and January 2005, Nematode sp. and *Paraonides lyra capensis* were among the four highest ranked species respectively. *Dosinia hepatica* and *Nassarius kraussianus* were among the four highest ranked species during November 2004.

Fig 4.17.A-C presents the abundance for each of the four highest contributing species at all six transects during June 2004, November 2004 and January 2005. During all sampling sessions the abundance of *Capitella capitata* decreased from deep subtidal transects to the intertidal transect (T4) with a sharp increase in abundance at Transect 5. The abundance of *Prionospio sexoculata* generally increased from deep subtidal transects with highest numbers recorded between shallow subtidal and mid intertidal transects. Other species were generally more abundant in subtidal transects than in intertidal transects.

Table 4.10: Summary of species similarity and species contributions to all six transects for each sampling session.

Comparing:	Av. Sim. %	Main contributing species	% Contribution
June 2004	40.1	*Capitella capitata*	9.7
		Prionospio sexoculata	8.5
		Timarete tentaculata	7.5
		Nematode sp.	5.8
November 2004	48.6	*Prionospio sexoculata*	16.8
		Capitella capitata	14.3
		Dosinia hepatica	7.3
		Nassarius kraussianus	6.4
January 2005	40.1	*Timarete tentaculata*	20.3
		Capitella capitata	15.3
		Prionospio sexoculata	14.2
		Paraonides lyra capensis	8.3

4.8.1. Species abundance for intertidal transects during all sampling sessions

Average similarity was 31.4% (Table 4.11). *Prionospio sexoculata, Capitella capitata,* Nematode sp. and *Nassarius kraussianus* were the four highest ranked species in relation to average total abundance.

The abundance for each of the dominant species is presented (Fig 4.18). Intertidal abundance of *Capitella capitata* was highest at Transect 5 during all sampling sessions. The intertidal abundance of *Prionospio sexoculata* and Nematode sp. was highest at Transect 4 during June and November 2004 and at Transect 5 during January 2005. *Nassarius kraussianus* was most abundant at Transect 4 during June 2004 and January 2005 and at Transect 6 during November 2004.

Table 4.11: Summary of similarity and species contributions to all intertidal transects for all sampling sessions combined.

Comparing:	Av. Sim. %	Main contributing species	% Contribution
All intertidal transects	31.4	*Prionospio sexoculata*	25.1
		Capitella capitata	23.4
		Nematode sp.	6
		Nassarius kraussianus	5.8

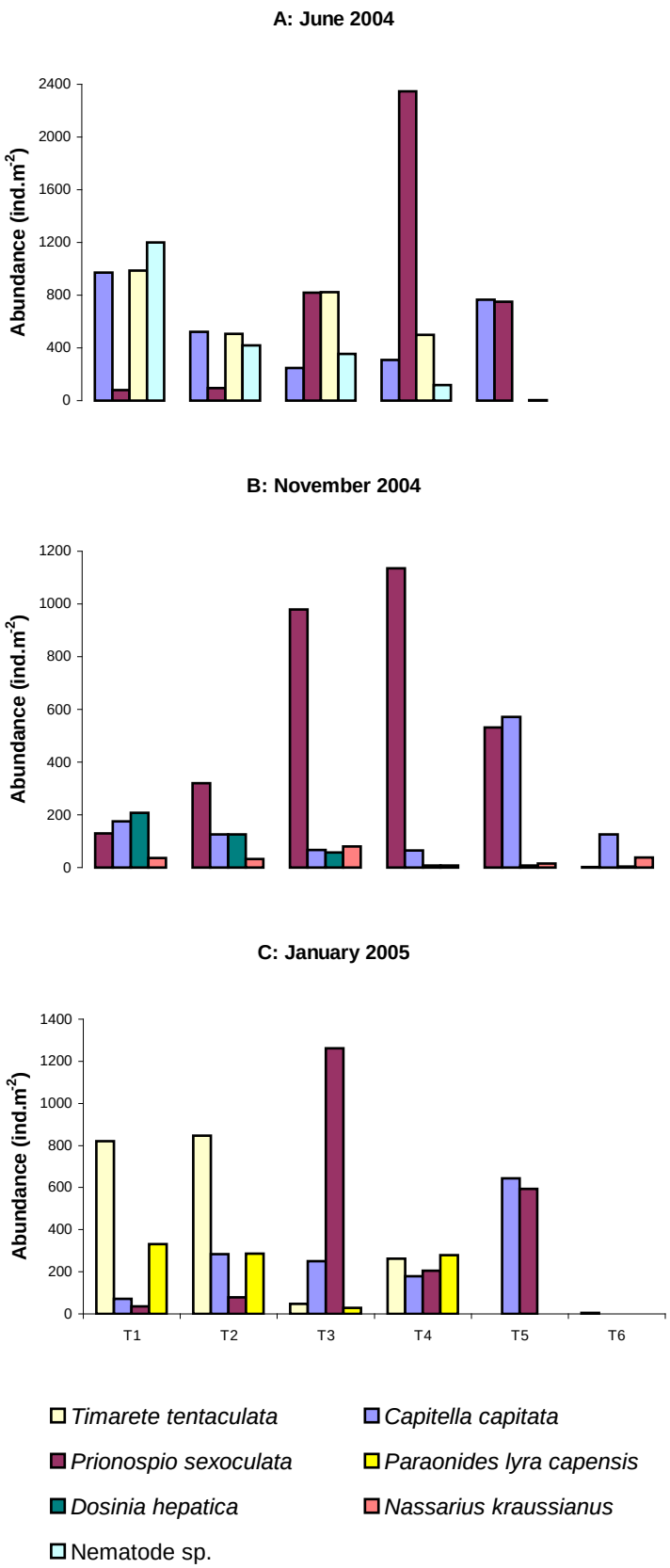


Fig 4.17. A-C: Dominant species abundances at Transects 1 to 6 during each sampling session.

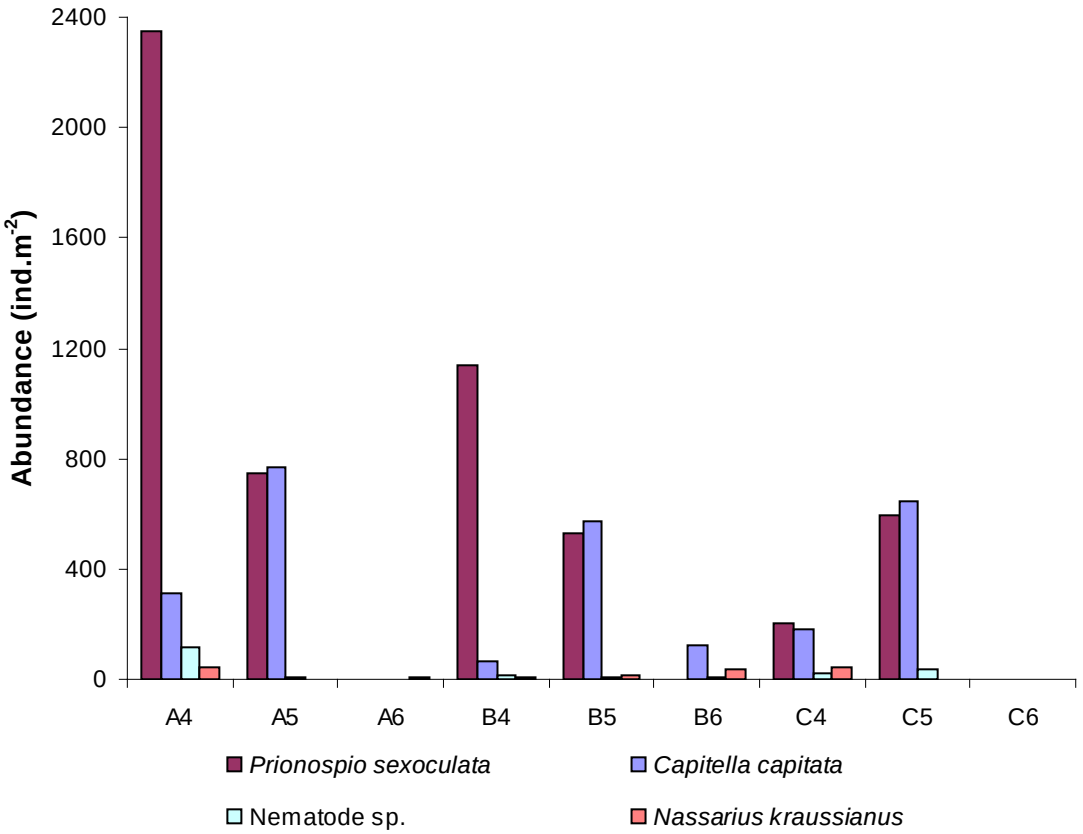


Fig 4.18: Dominant species abundances at each intertidal transect sampled during all three sampling sessions.

4.9. Correlating species abundance to environmental variables

Spearman rank correlations indicating significant correlations between species abundance for the dominant species identified in the previous section and the physical variables are presented in Table 4.12.

There was no significant correlation between the dominant species and the environmental variables measured during June 2004. Note that only Transects A1 to A4 were included for the analysis (physical data was absent for Transects A5 and A6). *Dosinia hepatica* was negatively correlated with temperature (-0.812) and positively correlated with depth (0.928) during November 2004. During January 2005 *Timarete tentaculata* (0.829) and *Paraonides lyra capensis* (0.928) were positively correlated with depth.

Table 4.12 also presents significant Spearman rank correlations between species abundance for the dominant species identified in the intertidal transects and the intertidal variables

measured. Both *Prionospio sexoculata* (0.809) and Nematode sp. (0.723) positively correlated with sediment water content at low tide.

Table 4.12: Spearman rank correlations indicating significant correlations between species abundance and physico-chemical/sedimentary data (Significant correlations at 95% confidence levels; n represents number of transects).

Sampling session	Variable	Species	n	Correlation
November 2004	Temperature	*Dosinia hepatica*	6	-0.812
	Depth	*Dosinia hepatica*	6	0.928
January 2005	Depth	*Timarete tentaculata*	6	0.829
	Depth	*Paraonides lyra capensis*	6	0.928
Intertidal transects during all three sampling trips	Water content at LT	*Prionospio sexoculata*	9	0.809
	Water content at LT	Nematode sp.	9	0.723

Chapter 5. Discussion

5.1. Community structure and species richness

The Mngazana Estuary is a remarkably species rich subtropical estuary due to the favourable physical conditions within it (Branch and Grindley 1979). Branch and Grindley (1979) recorded 209 invertebrate species (retained by a 1mm mesh) that were mostly found in the intertidal zone of the estuary. Only five of these species were collected in the subtidal zone. A possible reason for the low number of subtidal species collected was that the sampling methods used were not suitable for subtidal benthic sampling (Bursey 1998). However, reasons for low macrozoobenthic species diversity in subtidal regions could also be related to strong tidal currents and sediment instability (Ysebaert *et al.* 2003). Bazaïri *et al.* (2003) found that in a North West African lagoon that functioned like an estuary, the macrozoobenthic community structure was controlled by edaphic factors in the intertidal zone, and by hydrological factors in the subtidal zone. Thwala (2005) recorded 61 subtidal macrozoobenthic species along the length of the Mngazana Estuary, more than has been recorded from similar habitats in other South African estuaries.

In this study 104 species were recorded along the intertidal to subtidal gradient of the sampling area. However, the number of species fluctuated over the three sampling sessions, with a greater number of species collected from the subtidal compared to the intertidal zone during each of the sampling sessions (Fig 4.10.A-C). Similarly Currie and Small (2005) noted that both macrozoobenthic abundance and richness was significantly lower in intertidal transects compared to the subtidal transects of an Australian subtropical estuary.

This study further indicated that comparatively high numbers of species were collected along the low tide mark, with fewer species collected higher up the intertidal gradient. The transect located along the high shore zone (T6) during June 2004 and January 2005 showed very low species numbers as compared to the other transects. Similar research on Eastern Cape flood-tidal deltas (Bursey 1998) and sandy beaches (Wendt and McLachlan 1985) has shown that macrozoobenthic species richness increased from the high shore to low shore. Macrozoobenthic species richness and adundance in Tasmanian estuaries has also shown similar trends, with faunal density and species richness increasing over three- and five fold ranges down the shore from the high water mark to the shallow sublittoral (Edgar and Barrett 2002). These trends could be explained in terms of more available niches in the low shore

zone resulting from a higher moisture content of the substratum, smaller temperature ranges and increased feeding times for benthic organisms (Bursey 1998).

Polychaetes made up the dominant component (over 70%) of the macrozoobenthic community in relation to number of species and number of ind.m^{-2} during each sampling session in the Mngazana Estuary. Polychaetes also dominated all transects along the subtidal to intertidal gradient, except at the extreme high tide mark (T6). Here, the relatively low number of species were represented by brachyurans, polychaetes and gastropods. Previous studies on the Mngazana Estuary and other Eastern Cape estuaries have recorded similar results with polychaetes clearly dominating subtidal macrozoobenthic communities (Schlacher and Wooldridge 1996a, Thwala 2005). Dittmann (2000) reporting on intertidal macrozoobenthic patterns found that polychaetes and crustaceans were the most species rich taxa within certain Australian tidal mangrove flats.

Shannon diversity (H') and Hill's numbers were high at most subtidal transects during all sampling sessions. These relatively high values found in the majority of subtidal transects is indicative of a suitable physical environment causing most species to flourish (Thwala 2005). Intertidal transects generally exhibited lower Shannon diversity and Hill's numbers, decreasing from the low shore to the high shore during June 2004 and January 2005. The trends in decreasing diversity with increasing shore height and therefore greater environmental harshness, agree with similar results recorded on Eastern Cape sandy beaches (McLachlan 1974).

During November 2004 Shannon diversity and Hill's numbers increased with increasing shore height resulting from a larger number of species being collected at mid to high shore. Many of these species were characterised by relatively few individuals, leading to high unevenness. Bursey (1998) noted a similar pattern on the flood tidal delta of the Nahoon Estuary in the Eastern Cape. Larval migrations of certain macrozoobenthic species up into the high shore may also have increased species abundance and richness in the high shore. For example, a large number of unidentified gastropod spat were collected in the low shore (T4) and subtidal regions of the study area. In November 2004 gastropod species richness for the high shore transects (T5 and 6) was much higher than was recorded for the same transects during the other two sampling sessions (Fig 4.10.A-C). It was noted in the Wadden Sea that for the bivalve, *Macoma balthica,* abundance strongly decreased in the lower intertidal and increased

in the upper intertidal due to immigration of newly settled spat from lower transects (Armonies and Hellwig-Armonies 1992).

The zonation of macrozoobenthic fauna in other intertidal habitats such as sandy beaches, salt marshes and tropical tidal flats are well documented (Kneib 1984, Wendt and McLachlan 1985, Bursey 1998, Dittmann 2000). Previous research has also shown that subtidal and intertidal communities are dissimilar from one another in terms of relative species composition (Bazaïri *et al.* 2003, Bursey and Wooldridge 2003). As with Branch and Grindley (1979) this study recorded a relatively diverse community of polychaetes, bivalves and gastropods in the subtidal region of the Mngazana Estuary's middle reaches. Similarly, it was found that at the low tide mark there was an abrupt change in community structure along the intertidal gradient with species diversity being much lower for the high shore areas.

Branch and Grindley (1979) collected large numbers of *Upogebia africana* in the intertidal zone of the middle reaches of the Mngazana Estuary, in addition to different *Uca* species. Although these species were all recorded in this study, their abundance was lower compared to results recorded by Branch and Grindley (1979). By contrast more polychaete species were recorded in the intertidal region in this study. Recent research by Pillay *et al.* (2007a) has shown that extensive bioturbation by the sandprawn, *Callianassa kraussi,* resulted in an associated decrease in the abundance of *Nassarius kraussianus, Prionospio sexoculata* and *Dosinia hepatica*. If local bait collecting activities on Mngazana mudbanks during this study resulted in reduced *U. africana* abundance levels and consequently reduced bioturbation, it is possible that other species increased, following the pattern recorded by Pillay *et al.* (2007a). However, it is also possible that the burrows of these species extended deeper than the depth sampled by the grab used for sampling the benthos in this study. A maximum burrow depth of 15cm has been recorded for *Uca puqnax* in a North American salt marsh (Katz 1980). Although the burrows of *U. africana* can extend to 40-50cm below the surface of the substratum, previous studies indicate that most prawns occur within the top 25cm of sediment (Dubula and Lasiak 2003).

The effects of bait collecting and trampling may also have impacted on the intertidal macrozoobenthos as evidence of trampling was evident during the second and third sampling sessions. In Australian magrove swamps the effects of trampling on intertidal benthic assemblages has lead to increase polychaete numbers, while gastropod and crustacean abundance showed an associated decrease (Kelaher *et al.* 1998). Similarly, bait collecting

impacts on other components of the biota apart from the target species, with modal body sizes of the target species such as the sandprawn, *Callianassa kraussi* often decreasing in areas of intense bait collecting (Wynberg and Branch 1994).

5.2. Physico-chemical variables

Physico-chemical variables including salinity, temperature, oxygen content, and pH showed very little vertical change in the water column, especially in the subtidal zone. Salinity stratification can have a significant impact on fauna in the water column, while the benthic infauna is buffered due to the ability of the sediments to maintain a relatively constant salinity even when salinity changes in the overlying waters (Reid 1930 as quoted by Branch and Grindley 1979). The sediment above the high tide mark and in the high shore region is usually very saline as a result of desiccation (Branch and Grindley 1979). Temperature emerged as an important variable in November 2004, while depth influenced community structure in November 2004 and in January 2005 (Table 4.2). The BIOENV results for January 2005 reflected extremely weak correlations and as a result it is possible that other variables or combinations of variables influenced the separation and clustering of transects. However, no clear trends as to how the above-mentioned physical variables influenced the communities emerged.

Composition and distribution of the estuarine macrozoobenthos are usually the result of the combined effects of numerous factors. However, sediment composition has an overriding influence on infaunal distribution, while salinity tolerance of a species is also important (De Villiers *et al.* 1999). Variable salinity is a characteristic feature of estuarine systems although this variable is more often associated with the axial zonation of species along the estuarine gradient. However, seasonal fluctuations in salinity are probably important in structuring intertidal and subtidal estuarine communities, as population densities of marine species change according to salinity (Furota and Emmett 1993). Although Thwala (2005) observed no seasonal patterns in the subtidal macrozoobenthic community of the Mngazana Estuary, local shifts in dominance, changes in abundance and distribution of species were observed indicating that short-term fluctuations in the abiotic conditions could be significant.

In this study salinity was relatively stable across the tidal gradient with only small fluctuations (Table 4.1), although intertidal transects did have slightly higher salinity values on average. Temperature had a small, but steady increase from Transect 1 to Transect 4 during June and

November 2004. However, there was little change in temperature along the subtidal-intertidal gradient during January 2005. This may have been related to overcast and cool weather conditions during January 2005. Sampling during the previous two sessions occurred on sunny days, leading to higher temperatures and increased desiccation in the intertidal. For burrowing intertidal animals such as the bivalve *Solen cylindraceus* exposure to one single temperature is unlikely and this species will instead demonstrate responses to short-term fluctuations within the tidal period, reflecting the difference between estuarine and seawater temperatures (De Villiers *et al.* 1999).

In Chesapeake Bay estuarine endemic and euryhaline marine species decreased in abundance upshore, while the abundance of opportunist species had the opposite response to increasing salinity and declining oxygen levels (Holland *et al.* 1987). Similarly, high species richness of polychaetes observed in the high shore area during November 2004 may have been a response to particularly high salinity values at that time. Although oxygen levels were also relatively high, Dye (1983b) found that oxygen was not present below a few millimetres in the intertidal substrates near the entrance of 2nd Creek. According to Dye (1983b), oxygen diffusing from the overlying water or air was rapidly utilized at the surface and its uptake rate did not give any measure of metabolic activity in deeper layers, although oxygen content of the water at high tide could possibly decrease to relatively low levels as a result of this demand. Burrows are however, known to cause the extension of oxidised zones deeper into the sediments (Katz 1980).

5.3. Sedimentary characteristics

In Eastern Cape estuaries the distribution of 'true estuarine species' is independent of the salinity found in the adjacent water as such species can tolerate a wide range of salinity values (Teske and Wooldridge 2001, 2003). Instead, research by Teske and Wooldridge (2001) concluded that mud content was the most important variable for the biotic patterns observed in several Eastern Cape estuaries. Similarly, Thwala (2005) found that organic matter and mud content were important physical variables regulating benthic faunal communities in the Mngazana Estuary.

Organic content and mud content of the sediments were found to influence macrozoobenthic community patterns throughout all sampling sessions in this study. Sediment compactness and the water content of the sediments in the intertidal zone were also found to influence the

intertidal biotic communities. Branch and Grindley (1979) and Thwala (2005) recorded similar results for sediment samples from the Mngazana Estuary's middle reaches. Samples from this study area contained relatively high proportions of both organic content and mud fractions. Organic content was on average higher at subtidal transects than at intertidal transects and was positively correlated with mud content for all the intertidal transects during combined sampling sessions. The mangroves are undoubtedly the major contributor to the organic matter pool in the estuary (Thwala 2005) as subtropical estuaries often receive a large organic input in the form of mangrove leaves (De Villiers *et al.* 1999).

Thwala (2005) found that the subtidal benthos in the same area investigated in this study had the highest species richness of all sites along the channel of Mngazana Estuary. As with this study, Thwala (2005) found that depth and organic matter content was relatively high at this site. However, it was noted that environmental variables could not adequately explain the high species diversity observed, as most variables were relatively uniform in comparison to other sites from the middle reaches, which reflected lower species numbers. Possible reasons given by Thwala (2005) for the higher species richness found in the subtidal benthos near the entrance to 2nd Creek included:

- Tidal action resulting in vigorous mixing of different bodies of water (i.e. sea, creeks and river channel) resulting to greater amounts of particulate organic matter maintained in suspension and therefore available to suspension feeders,
- Organic matter export from creeks and middle reaches resulting in increased food resources,
- The deep channel at this site increases residence time of the sediment, which favours decomposition of plant detritus and this creates diverse nutritional sources,
- Additionally, plant debris provides shelter to infauna and favours deposit feeders.

The abundance of certain species such as amphipods, isopods, small brachyurans and some molluscs are known to increase with an increase in organic content (Day 1981a), further explaining the greater species richness and abundance of species in the subtidal zone. Similarly, nutrient concentrations of organic matter have also been shown to be of importance for the reproduction of specific invertebrates. Linton and Taghon (2000) for example, found that certain *Capitella* species had decreased fecundity and longer generation times in sediments with lower protein concentrations and did not reproduce in sediments containing <1 to 2 mg/g.

Roots from *Avicennia marina* trees extend into the intertidal zone and have a marked influence on the substrata. In these intertidal areas the sediment is more consolidated and finer with a higher organic content wherever pneumatophores appear (Branch and Grindley 1979). The area sampled in this study was specifically chosen, as it was largely un-vegetated, although *Avicennia* pneumatophores were still present albeit in relatively lower densities. Branch and Grindley (1979) noted that around the high water spring tide mark in the region of the study site, sesarmid crabs made deep burrows down to the water table and it was the only organism that could tolerate the consolidated substrata. The presence of these crabs may have altered, to some extent, the sediment organic content in the intertidal zone as Emmerson and McGwynne (1992) calculated that sesarmid crabs in the Mngazana Estuary consumed about 44% of the leaf fall.

Water content, sediment grain size, beach exposure and sediment stability are recognised as important factors influencing zonation patterns of sandy beaches (Bursey and Wooldridge 2003). Wendt and McLachlan (1985) found that macrofaunal zonation patterns on the Sundays River beach indicated a correlation with sand moisture content. Wharfe (1977) showed that fine-grained substrates have a larger water retention efficiency than coarse-grained sediments and that the penetrability of bare sediments decreases more rapidly than vegetated sediments, presumably as a result of differences in water retention efficiency. In contrast, results found for this study indicated that water content of the intertidal sediments at low tide was negatively correlated with mud content, indicating that muddier sediments retained less water. It is possible that high shore sediments absorbed less water during a tidal inundation, as they were generally more compact and exposed to the hot sun during a low tide. The water content of intertidal sediments at low tide was also positively correlated with the water content during high tide. This meant that intertidal sediments containing a lower percentage of water during low tide could be expected to contain a lower percentage of water during high tide as compared to an intertidal sediment type with a high water percentage during low tide. In addition, the burrows of fiddler crabs could possibly result in the drying out of tidal flats during extended low tides (Daiber 1977). As few *Uca* species were collected in this study it is possible that the substratum experienced less desiccation as a result of water loss from crab burrows compared to other studies (e.g. Daiber 1977).

Multivariate analyses indicated that sediment compactness separated the high shore infauna community from communities lower down the intertidal gradient during both June 2004 and January 2005. High shore sediments contained a greater proportion of mud and therefore

shared an affinity with the sediments from the deep subtidal transects. Shallow subtidal and low intertidal transects had low proportions of mud. De Decker and Bally (1985) noted that for sediments with a higher mud fraction there is less space within the substratum resulting in the physical exclusion of organisms from interstices. The reduction in interstitial space also results in a decrease in porosity of the sediment, thereby reducing interstitial circulation and increasing the tendency of the sediments to become anoxic (De Decker and Bally 1985). As a result of this, De Decker and Bally (1985) commented that larger fauna tend to inhabit such substrata, as organisms have to be big enough to be able to shift particles when burrowing through the sediment.

Both intertidal as well as subtidal habitats are influenced by tidal forces and can be physically altered by such forces. Hanekom *et al.* (1988) showed that *Upogebia africana* abundance decreased in subtidal channels resulting from strong currents that rendered sediments coarse with a subsieve content apparently to low for colonisation by these animals. In this study *U. africana* was shown to have a uniform distribution throughout most of the subtidal and intertidal zone, possibly as a result of the prevalence of weaker currents in the subtidal area.

Research has shown that the low shore portion of a tidal flat is subject to constant re-suspension and deposition, while the upper shore is primarily subject to deposition of particulate matter (Anderson 1976). During June and November 2004 high shore sediments in this study exhibited higher mud and organic matter content compared to low shore sediments. Barnett (1984) recorded lower abundance levels and small differences in species composition in the low shore fauna in the Humber estuary when compared to the 'community' in the upper half of the shore, possibly as a result of the constant re-working of low shore sediments by wave and current action.

In the Mngazana Estuary, an extreme spring high tide experienced during January 2005 may have resulted in the decline of organic matter and mud content from the mid to high shore transects, caused by the re-working of high shore sediments by waves and currents. It is important to note that benthic samples collected from a North American salt marsh indicated that the densities of some organisms could change significantly during the spring tide portion of the tidal cycle (Kneib 1984). Certain sandy beach macrofaunal species are also known to have tidal migrations (Hacking 1996) and it is possible that certain intertidal estuarine species exhibit similar behavioural responses.

During November 2004 and January 2005 the intertidal region of the study area experienced some degree of disturbance from bait collecting and trampling albeit at a low intensity. During November 2004 the effects of the disturbance were especially evident, as high shore substrata exhibited a much lower compactness as compared to the other two sampling sessions. Furota and Emmet (1993) found that tide pools formed in the soft benthos could increase the abundance of certain macrofauna in the high shore. Previous trampling and bait digging activities could aid the temporary formation of such soft sediment tide pools resulting in an increase in local species abundance and richness, as observed in the high shore zone during November 2004.

Sedimentary characteristics are the most likely variables to shape macrozoobenthic assemblages as they diverge on a broader scale compared to hydrodynamically controlled physico-chemical variables (Thwala 2005). However, even if the physical and chemical properties of a substratum are appropriate, it does not necessarily imply that a given species will populate all the areas in which it could survive as biotic interactions may be limiting (Green 1968 as quoted by Bursey 1998).

5.4. Species dominance

Most of the species recorded in this study showed a broad spatial distribution along the subtidal-intertidal gradient with the exception of the mid and high shore transects where species richness and abundance was found to decrease. This was especially noticeable for the dominant species. Most species that were identified exhibited marked shifts in abundance and these shifts were prevalent in the subtidal-intertidal transition zone. Although community structure did vary between sampling sessions there were some common characteristics between the different sessions and it is important to note that Thwala (2005) found no clear seasonal patterns for the subtidal species in the Mngazana Estuary. However, differences between subtidal and intertidal communities seemed more prevalent as local shifts in species dominance were more evident.

Species found in this study that were also recorded by Branch and Grindley (1979) and Thwala (2005) included: *Ceratonereis keiskamma, Timarete tentacualata, Dendronereis arborifera, Orbinia angrapequensis, Glycera tridactyla, Corophium triaenonyx, Grandidierella bonnieroides, Iphinoe truncata, Apseudes digitalis, Paratylodiplax algoense, Thaumastoplax spiralis, Dosinia hepatica, Assiminea bifasciata* and *Nassarius kraussianus.* In this study 16

species that could not be identified to genus level were recorded of which 8 belonged to the class Polychaeta. All unidentified species were found to be rare during the sampling sessions. In this study macrozoobenthic species did exhibit some zonation as was observed by Branch and Grindley (1979) for the intertidal fauna. As indicated by Thwala (2005), the most abundant species collected during this study showed similarities with other estuaries within the region as the Mngazana Estuary conforms to the category of small permanently open estuaries.

The majority of dominant subtidal macrozoobenthic species collected in this study were deposit feeders corresponding to the results documented by Thwala (2005). In this study, intertidal macrozoobenthic species also consisted of deposit feeding species. However, among the dominant species recorded certain *Prionospio* species are recognized as deposit feeding species with an inclination toward suspension feeding.

The polychaetes *Prionospio sexoculata* and *Capitella capitata* were very abundant species and featured amongst the most dominant species collected during each of the three sampling sessions. These two species are known to have a very wide geographical distribution (Day 1967). Both species also exhibited a relatively high level of abundance within the intertidal zone. *P. sexoculata* dominated the subtidal-intertidal transition zone, with abundance for this species peaking at the low shore transect (T4) during two of the sampling sessions, while high densities were also recorded at the shallow subtidal transect (T3) and mid shore transect (T5). Thwala (2005) found that *P. sexoculata* correlated negatively with the mud content of the substrata and noted that this species was relatively abundant in Creek 1 and at the mouth of the Mngazana Estuary, which generally exhibited reduced levels of organic matter. In this study sediments found at Transects 3, 4 and 5 were coarser, while sediments in the high shore transect (T6) and deep subtidal transects (T1 and T2) had a higher mud content and organic matter content. The evidence presented by this study and from Thwala (2005) suggested that the distribution of *P. sexoculata* was dependant on the presence of coarser sediment types (sandy substrata) and that this species was able to exploit such habitats. It is known that the distribution of certain polychaetes is affected by sediment grain size. Large grain size of sediments have significant and negative impacts on the construction of tubes by certain polychaetes and for species such as *Owenia fusiformis*, distribution patterns are influenced by sediment particle size (Pinedo *et al.* 2000). In this study *P.sexoculata* was also positively correlated with sediment water content at low tide indicating that it was dependent

on some soil moisture content, explaining the species relative absence above the mid shore region.

Capitella capitata was present at all subtidal and intertidal transects, with numerical abundance peaking along the mid shore (T5) during two of the sampling sessions. This was also the most numerically abundant species along the mid shore during each sampling session. *Capitalla* species are known to be opportunistic deposit-feeding polychaetes possess life history adaptations that enable them to rapidly colonise disturbed or enriched sites (Linton and Taghon 2000). The high abundance of *C. capitata* in the mid shore region could have been related to disturbance, as there was some evidence of bait digging and trampling in the sampling locale. However, as the extent of the disturbance to the local benthos was not quantified it is impossible to determine the exact effect of such disturbance events on the local benthic communities at the time of sampling. The total impact of human exploitation could be greater than the estimated harvest of the target species (e.g. *Upogebia africana*), because indirect disturbance (trampling, digging, etc.) on mudflats can have a greater impact than the actual harvest (de Boer and Prins 2002).

Other species that were found to have a relatively high numerical abundance along the mid shore included *Prionospio sexoculata, Nassarius kraussianus* and Nematode sp. As previously mentioned the relatively higher abundance of these species in the intertidal may have been an indication to the effects of bait digging activities resulting in lower *Upogebia africana* abundance. *N. kraussianus* is a soft-sediment surface-grazing gastropod and is reported by Day (1981b) to be relatively common in Southern Africa. Pillay *et al.* (2007b) observed that *N. kraussianus* could withstand low levels of bioturbation caused by burrowing anomurans due to the animal's mobility, although it incurs metabolic costs resulting from increased energy expenditure and lost feeding time. If such bioturbation activities are sustained it could lead to diminished growth, reproduction and survival of *N. kraussianus* or lead to emigration to avoid area of bioturbation (Pillay *et al.* 2007b).

Uca species exhibited a relatively high abundance in the high shore region compared to the few other species inhabiting this zone. Katz (1980) found that the fiddler crab, *Uca pugnax* could turn over approximately 18% of the upper 15cm of sediment in a salt marsh per annum and thereby significantly affected the composition and chemistry of salt marsh sediments. Apart from changing the physical and chemical composition of sediments the effects of bioturbation caused by these species may affect other infaunal species, similar to the

burrowing activities of anomurans (Pillay *et al.* 2007a). Pearse (1914) as quoted by Daiber (1977) observed that fiddler crab species displayed a substratum specificity, which gave rise to zonation. *Uca* species are also capable of avoiding dessication during low tide as their burrows can extend down to the low-tide water level (Daiber 1977).

Although most nematode species are mainly classified as meiofauna, one unidentified species was collected in relatively high numbers along the subtidal to mid shore level. As with certain C*apitella* species, nematode communities can be sensitive indicators of change, responding to physical disturbance activities of the substratum (Boyd *et al.* 2000). Abundance of the nematode species collected during this study was positively correlated with water content of mid and high shore sediments during low tide. During November 2004 the sediment water content at low tide and at Transect 6 was higher when compared to the other two sampling sessions. This was also the only session during which this particular species was collected along the high shore, indicating that this species may have been limited by relatively low substratum water content during low tides. Highest abundance of this species was typically limited to the subtidal and low intertidal zone where moisture content of the sediment would always be saturated or close to saturation levels. Similarly, Teal and Wieser (1966) as quoted by Daiber (1977) found that for Sapelo Island intertidal nematodes, greatest vertical distribution was closest to the low tide level. Organic content was also suggested as a major variable limiting distribution and abundance, as the low tide area was reported to harbour the greatest amount of detritus.

The polychaetes *Timarete tentaculata* and *Paraonides lyra capensis* together with the bivalve *Dosinia hepatica* were highly abundant along the subtidal to low shore, intertidal gradient. The densities of these animals were generally much lower along the mid shore and high shore transects during all three sessions. On occasions, species were absent at these upper intertidal levels. During January 2005, the distribution of *T. tentaculata* and *P. lyra capensis* was positively correlated with depth, while *D. hepatica* was positively correlated with depth and negatively correlated with temperature in November 2004. Similar to Thwala (2005), *Heteromastus* sp. was recorded in comparatively high numbers along the subtidal to low shore intertidal level at the study site. Data collected from the present study does not provide clear answers as to the reasons for the prevalence of these species in the subtidal zone, with lower abundance levels in the intertidal zone. Previous research has however, connected decreased abundance of *D. hepatica* with increased bioturbation activities of anomurans

(Pillay *et al.* 2007a). Similar biological interactions between the polychaetes *T. tentaculata*, *P. lyra capensis* and other species can not be ruled out.

Of all physico-chemical parameters measured during this study, community patterns in relation to sedimentary characteristics presented the strongest relationships. Thwala (2005) also stated that for the Mngazana Estuary's subtidal benthos, physico-chemical variables did not adequately explain observed distribution patterns of macrozoobenthic communities. In this study, the subtidal community shared greater similarities within a session compared to between sessions. These observed trends indicate the importance of variability within subtidal benthic communities. Although Thwala (2005) found no clear seasonal patterns in community structure along the length of the estuary it is possible that at reduced spatial scales, seasonal effects become more prominent (Findlay 1981). The effects of environmental factors are further complicated by biological interactions that can vary according to the presence of particular species (Edgar and Barrett 2002).

In the intertidal zone community patterns were shown to have some dependence on sediment characteristics, as was shown by both analytical and visual methods of analysis. However, as discussed in previous sections, the impact of biological interactions in the intertidal zone must not be ruled out. Additionally, anthropogenic activities in the intertidal zone also have the potential to alter both the physical and biological components of the estuary.

5.5. Directions for future research

Observations made during this study led to the formulation of additional questions relating to the dynamics of the Mngazana Estuary's macrozoobenthos. Although these questions were not included in the objectives of this study, future attempts at understanding intertidal-subtidal macrozoobenthic community patterns in the estuary should address the following interactions:

- The impacts of human activities on macrozoobenthic community structure (e.g. bait collecting, trampling),
- The temporal and spatial influence of larval and post-larval migration patterns (between the subtidal and intertidal zone) on macrozoobenthic community structure,
- Small-scale patch effects together with seasonal impacts on the subtidal and intertidal macrozoobenthic communities,
- Community fluxes in relation to tidal fluxes (i.e. spring tide, neap tide).

Human disturbance may have had a significant impact on the benthic communities present at the study site, especially in the intertidal zone. Although it was not the aim of this study to investigate the effects of human activities on the benthic communities present at the study site, it was evident that bait collecting as well as trampling by humans and livestock may have resulted in significant alterations to the macrozoobenthic communities and their habitat. Such impacts on infauna could be as a direct result from disturbance activities, as with the removal of *Upogebia africana*. Indirect impacts could be as a result of tidal pools created in the soft substrata resulting in an increase in abundance of certain macrofauna in the high shore (Furota and Emmet 1993). The removal of certain burrowing anomuran species has also shown to have an associated increase in the relative abundance of some polychaete, gastropod and bivalve species (Pillay *et al.* 2007a). Furthermore, impacts on sediment characteristics such as sediment compactness and water content will be important factors in regulating the macrozoobenthic community structure of the intertidal benthos.

Larval migration patterns between the subtidal and intertidal zone were not examined in this study, but evidence supporting the existence of such events was collected. During June 2004 gastropod spat was found to be relatively abundant in the subtidal and low intertidal zone with larval spat and adults mostly absent in the mid to high shore region. During the subsequent sampling session (November 2004) gastropod adults/juveniles were found to be relatively abundant in the mid shore to high shore, compared to the previous sampling session. Similarly, the abundance of bivalves in the Wadden Sea strongly decreased in the lower intertidal and increased in the upper intertidal due to immigration of newly settled spat from lower transects (Armonies and Hellwig-Armonies 1992). Composition of macrozoobenthic communities may also be affected by dispersal and deposition (active or passive) of postlarvae or adults (Bursey 1998).

The existence of small-scale temporal variation in the distribution of the fauna of marine soft sediments has long been recognised (Morrisey *et al.* 1992b). In addition, the variation (patchiness) in the distribution of organisms and other environmental variables exists at different spatial scales (Morrisey et al. 1992a). In this study subtidal communities sampled during the same session shared greater similarity with each other than with subtidal transects sampled during different sessions. These trends indicate the potential importance of variability (including seasonal effects) in physico-chemical variables or some other resource (e.g. food availability) on subtidal benthic communities. Thwala (2005) found no clear seasonal patterns in community structure along the length of the Mngazana Estuary, but it

could be that at a reduced spatial scale, seasonal effects may become more prominent (Findlay 1981). In addition, Rainer (1981) found that benthic species composition of intertidal and shallow-water transects in a small Australian estuary was more stable than that of the deeper transects, due to the presence of short-lived opportunistic species at the deeper transects after periods of de-oxygenation. Rainer (1981) concluded that the relatively stable community structure and species composition at intertidal and shallow water transects suggested that greater environmental harshness does not necessarily imply less faunal stability.

Although each sampling session during this study took place during spring tide, small differences in the extent of the high tide were still noted between sessions. It is possible that differences in tidal heights during different sampling sessions may have influenced the distribution of certain intertidal species and that intertidal species composition may have fluctuated with different tidal states (e.g. spring tide, neap tide). Kneib (1984) noted that benthic samples collected from a North American salt marsh indicated that the densities of some organisms at a particular level could change significantly during the spring tide portion of the tidal cycle. Similarly, some sandy beach macrofaunal species undergo tidal migrations (Hacking 1996) and it is possible that certain intertidal estuarine species exhibit similar behavioural responses. The extent of these tidal migrations may depend on the tidal state as well as the extent of the tide. Furthermore, tidal forces have shown to affect intertidal communities by altering certain substrate characteristics according to tidal elevation (Barnett 1984). It is possible that different tidal states and the differences in tidal amplitude experienced during such states may be responsible for different substrate characteristics. This could help explain the sedimentary characteristics observed for this study during January 2005 when an extreme spring high tide was experienced.

Chapter 6. Conclusion

This study served as the first comparison between macrozoobenthic communities across the subtidal and intertidal zone in the Mngazana Estuary. To date, research has largely focused on intertidal macrozoobenthic communities of Southern African estuaries, but comparatively few studies have concentrated on the subtidal component. The objectives addressed in this study were:

1. To investigate and compare macrozoobenthic invertebrate community structure and composition of the intertidal and subtidal fauna in muddy substrata.
2. To identify the physical variables responsible for macrozoobenthic community structure across the intertidal-subtidal gradient.

Three sampling trips were undertaken and a total of 104 macrozoobenthic species were recorded, using a 500 µm mesh net. Polychaetes made up the dominant component of the macrozoobenthic community in terms of the number of species and number of ind.m^{-2} during all sampling sessions and at most transects along the gradient. At high shore transects the community was characterised by fewer species, consisting mostly of brachyurans, polychaetes and gastropods. Species richness was higher in the subtidal zone than in the intertidal zone and species richness decreased from the subtidal zone along the intertidal gradient to the high tide mark.

Shannon diversity (H') was higher for subtidal communities than for intertidal communities, indicating that the distribution of individuals among species in the intertidal zone experienced greater variability. Shannon diversity also decreased from the low shore to the high shore during both June 2004 and January 2005, but the opposite trend was recorded in November 2004. The results for Hill's numbers followed the same trend as was found for Shannon diversity during each sampling session. Generally, subtidal communities contained abundant species followed by very abundant species. The majority of intertidal species that were recorded were rare.

Mutivariate methods for analysing species abundances, cluster analyses and MDS plots produced comparable patterns as well as dissimilarities between transects. Cluster dendrograms used in conjunction with MDS ordination mapping revealed that macrozoobenthic communities were generally distinct between the high shore and subtidal zone. Subtidal community structure was dependant on the time of sampling as subtidal

transects sampled during the same session shared greater similarity than with subtidal transects that were sampled during different sessions. Intertidal transects shared greater similarity with transects situated at the same location along the intertidal gradient irrespective of sampling time.

The multivariate analysis of the environmental data showed similar patterns as was found with the multivariate analysis for biota, although differences between the clustering of transects were observed. Several techniques were employed to analyse the impact of various environmental variables and their importance for structuring different macrozoobenthic communities as well as the distribution of dominant species. However, no clear trends emerged that indicated the influence of the physico-chemical variables on the various biotic communities.

Sedimentary variables appeared to have a greater influence on structuring macrozoobenthic communities than other measured physico-chemical variables. Organic content and mud content of the sediments were found to have an influence on community patterns along the subtidal to intertidal gradient during all sampling sessions. Additionally, sediment compactness together with water content of the sediments in the intertidal zone was found to influence intertidal macrozoobenthic community structure. Multivariate analyses suggested that sediment compactness separated the high shore macrozoobenthic community from communities lower down the intertidal gradient for both June 2004 and January 2005. High shore transects were also shown to have sediments characterised by a higher percentage mud content and shared a greater affinity with the sediments from the deep subtidal transects than with shallow subtidal and low-intertidal transects.

Most of the species recorded in this study showed a broad spatial distribution along the subtidal-intertidal gradient with the exception of the mid and high shore transects where species richness and abundance was found to generally exhibit a rapid decline. This effect was found to be especially visible for the dominant species identified. Most of the species recorded exhibited marked shifts in abundance and this was especially noticeable in the transition zone between the subtidal and intertidal habitat. Although community structure varied between sampling sessions there were common characteristics between the different sessions with the majority of species being deposit feeders. Two polychaete species, *Prionospio sexoculata* and *Capitella capitata,* were very abundant species and were amongst the most dominant species collected during all sessions. Both species appeared at relatively

high frequencies within the intertidal zone. *P. sexoculata* dominated the subtidal-intertidal transition zone at the low shore and was positively correlated with sediment water content at low tide. *C. capitata* was found numerically abundant in the mid shore zone.

Environmental variables measured did not adequately explain all of the observed macrozoobenthic community patterns, but instead raised questions as to the role that certain biological relationships may play in structuring the various benthic assemblages. Aspects such as interactions between trophic groups, recruitment and migration patterns of larvae, human disturbance, seasonality, and community fluxes in relation to tidal fluxes may all have had an impact on the results obtained by this study.

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Appendix A: Mean abundance (m^{-2}) for each macrozoobenthic species found at the six transects along the subtidal and intertidal gradient in the Mngazana Estuary.

	June 2004					
	Transect 1	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**	**Transect 6**
Polychaeta						
Boccardia polybranchia	23.3	18.3	101.7	43.3	8.3	0.0
Capitella capitata	970.0	523.3	248.3	308.3	765.0	0.0
Ceratonereis erythraeensis	0.0	0.0	0.0	1.7	1.7	0.0
Ceratonereis keiskama	0.0	0.0	0.0	6.7	11.7	0.0
Timarete tentaculata	986.7	506.7	821.7	500.0	0.0	0.0
Cossura sp.	371.7	308.3	208.3	186.7	0.0	0.0
Dendronereis arborifera	0.0	0.0	1.7	11.7	0.0	0.0
Desdemona ornata	26.7	13.3	10.0	10.0	5.0	0.0
Dorvillea sp.	0.0	0.0	6.7	0.0	0.0	0.0
Onuphis sp.	3.3	1.7	1.7	0.0	0.0	0.0
Eunicidae sp.	0.0	0.0	1.7	5.0	0.0	0.0
Exogone normalis	13.3	1.7	60.0	28.3	5.0	0.0
Glycera tridactyla	0.0	0.0	0.0	5.0	0.0	0.0
Lamellisyllis sp.	3.3	1.7	0.0	0.0	1.7	0.0
Lumbrinereis tetraura	238.3	151.7	128.3	55.0	0.0	0.0
Magelona cincta	0.0	1.7	0.0	3.3	0.0	0.0
Heteromastus sp.	485.0	476.7	380.0	130.0	3.3	0.0
Nephtys capensis	3.3	3.3	3.3	1.7	0.0	0.0
Nicomache sp.	285.0	251.7	398.3	240.0	0.0	0.0
Orbinia angrapequensis	11.7	5.0	31.7	3.3	0.0	0.0
Paraonides lyra capensis	435.0	345.0	505.0	158.3	0.0	0.0
Perinereis falsovariegata	0.0	0.0	3.3	1.7	13.3	0.0
Phyllodoce malmgreni	43.3	35.0	61.7	100.0	71.7	0.0
Potamilla reniformis	8.3	3.3	0.0	0.0	0.0	0.0
Prionospio sexoculata	78.3	96.7	820.0	2348.3	750.0	0.0
Pygospio elegans	8.3	0.0	0.0	0.0	0.0	0.0
Syllidae sp. A	1.7	0.0	0.0	1.7	0.0	0.0
Polychaete sp. A	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. B	0.0	0.0	3.3	0.0	0.0	0.0
Polychaete sp. C	10.0	8.3	1.7	5.0	0.0	0.0
Polychaete sp. D	1.7	0.0	13.3	1.7	0.0	0.0
Nematoda						
Nematode sp.	1198.3	418.3	355.0	116.7	5.0	0.0
Nemertea						
Nemertea sp.	8.3	6.7	13.3	5.0	0.0	0.0
Hirudinae						
Hirudinae sp.	0.0	1.7	0.0	0.0	0.0	0.0
Mysidacea						
Gastrosaccus psammodytes	0.0	0.0	0.0	0.0	3.3	0.0
Mesopodopsis wooldridgei	0.0	0.0	73.3	30.0	0.0	0.0
Rhopalophthalmus terranatalis	0.0	3.3	0.0	0.0	0.0	0.0
Cumacea						
Cumacean sp.	43.3	16.7	110.0	68.3	0.0	0.0
Iphinoe truncata	10.0	0.0	28.3	10.0	0.0	0.0
Tanaidacea						
Apseudes digitalis	0.0	0.0	0.0	0.0	16.7	0.0
Tanaid sp.	0.0	0.0	1.7	0.0	80.0	0.0
Isopoda						
Cirolana hirtipes	0.0	0.0	3.3	0.0	0.0	0.0

Appendix A: continued

	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
Cyathura carinata	43.3	16.7	11.7	8.3	5.0	0.0
Amphipoda						
Afrochiltonia capensis	6.7	0.0	0.0	0.0	0.0	0.0
Corophium triaenonyx	0.0	0.0	1.7	0.0	0.0	0.0
Gammaropsis sp.	0.0	1.7	1.7	1.7	0.0	0.0
Grandidierella bonnieroides	58.3	16.7	65.0	43.3	0.0	0.0
Melita zeylanica	0.0	0.0	0.0	0.0	0.0	0.0
Perioculodes longimanus	3.3	0.0	5.0	0.0	0.0	0.0
Seba sp.	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda						
Corycaeus subtilis	1.7	1.7	5.0	0.0	0.0	0.0
Pseudodiaptomus charteri	35.0	1.7	23.3	48.3	3.3	0.0
Acartia negligans	0.0	1.7	0.0	73.3	0.0	0.0
Caridea						
Macrobrachium rudis	0.0	0.0	0.0	0.0	0.0	0.0
Anomura						
Upogebia africana	45.0	32.5	3.3	1.7	16.7	0.0
Brachyura						
Brachyuran larvae	0.0	0.0	8.3	3.3	0.0	0.0
Brachyuran juvenile sp.	8.3	0.0	0.0	0.0	0.0	0.0
Cleistostoma algoense	40.0	31.7	0.0	0.0	0.0	0.0
Cleistostoma edwardsii	1.7	5.0	3.3	3.3	3.3	0.0
Hymenosoma orbiculare	1.7	0.0	1.7	0.0	0.0	0.0
Metopograpsus thukuhar	0.0	0.0	0.0	0.0	0.0	0.0
Rhynchoplax bovis	68.3	38.3	8.3	5.0	1.7	0.0
Thaumastoplax spiralis	23.3	13.3	1.7	1.7	1.7	0.0
Paratylodiplax blephariskios	3.3	3.3	0.0	0.0	0.0	0.0
Uca annulipes	0.0	0.0	0.0	0.0	6.7	5.0
Cirripedia						
Balanus elizabethae	5.0	11.7	0.0	3.3	1.7	0.0
Balanus venustus	5.0	0.0	0.0	0.0	0.0	0.0
Tetraclita sp.	1.7	0.0	0.0	0.0	0.0	0.0
Pygnogonidae						
Tanystylum sp.	5.0	1.7	0.0	1.7	0.0	0.0
Mollusca						
Assiminea bifasciata	8.3	1.7	5.0	3.3	0.0	0.0
Bivalve spat	1.7	1.7	1.7	1.7	0.0	1.7
Dosinia hepatica	235.0	188.3	515.0	123.3	1.7	0.0
Gastropod spat A	153.3	193.3	330.0	263.3	0.0	0.0
Gastropod spat B	5.0	0.0	0.0	1.7	0.0	0.0
Macoma litoralis	1.7	1.7	0.0	0.0	0.0	0.0
Nassarius kraussianus	56.7	36.7	85.0	40.0	1.7	10.0
Nassarius speciosus	5.0	3.3	5.0	0.0	0.0	0.0
Natica tecta	0.0	0.0	1.7	0.0	0.0	0.0
Sanguinolaria capensis	3.3	0.0	8.3	0.0	1.7	0.0
Solen cylindraceus	16.7	13.3	41.7	26.7	6.7	0.0
Telina gilchristi	0.0	0.0	3.3	0.0	0.0	0.0
Echinodermata						
Amphipholis sp.	5.0	5.0	0.0	0.0	0.0	0.0

Appendix B: Mean abundance (m^{-2}) for each macrozoobenthic species found at the six transects along the subtidal and intertidal gradient in the Mngazana Estuary.

	November 2004					
	Transect 1	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**	**Transect 6**
Polychaeta						
Boccardia polybranchia	5.0	3.3	5.0	0.0	5.0	0.0
Capitella capitata	175.0	125.0	66.7	65.0	571.7	126.7
Ceratonereis erythraeensis	0.0	0.0	0.0	0.0	0.0	0.0
Ceratonereis keiskama	0.0	0.0	0.0	0.0	13.3	1.7
Timarete tentaculata	598.3	508.3	411.7	6.7	0.0	0.0
Cossura sp.	140.0	125.0	76.7	0.0	0.0	0.0
Dendronereis arborifera	0.0	1.7	0.0	5.0	0.0	0.0
Desdemona ornata	15.0	10.0	40.0	20.0	6.7	1.7
Dorvillea sp.	1.7	0.0	0.0	0.0	0.0	0.0
Onuphis sp.	6.7	0.0	0.0	0.0	0.0	0.0
Eunicidae sp.	0.0	0.0	0.0	0.0	0.0	0.0
Exogone normalis	0.0	3.3	1.7	0.0	5.0	0.0
Glycera tridactyla	5.0	0.0	0.0	1.7	0.0	0.0
Lamellisyllis sp.	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrinereis tetraura	93.3	65.0	40.0	3.3	0.0	0.0
Magelona cincta	0.0	0.0	0.0	0.0	0.0	0.0
Heteromastus sp.	168.3	100.0	23.3	5.0	0.0	0.0
Nephtys capensis	3.3	0.0	5.0	0.0	0.0	0.0
Nicomache sp.	5.0	0.0	3.3	0.0	0.0	0.0
Orbinia angrapequensis	1.7	0.0	11.7	0.0	0.0	0.0
Paraonides lyra capensis	118.3	106.7	76.7	1.7	1.7	0.0
Perinereis falsovariegata	0.0	0.0	0.0	0.0	0.0	0.0
Phyllodoce malmgreni	30.0	28.3	23.3	6.7	0.0	0.0
Potamilla reniformis	0.0	0.0	0.0	0.0	0.0	0.0
Prionospio sexoculata	130.0	320.0	980.0	1135.0	531.7	1.7
Pygospio elegans	0.0	0.0	0.0	0.0	0.0	0.0
Syllidae sp. A	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. A	0.0	0.0	0.0	0.0	25.0	13.3
Polychaete sp. B	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. C	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. D	0.0	0.0	0.0	0.0	0.0	0.0
Nematoda						
Nematode sp.	30.0	26.7	16.7	16.7	10.0	8.3
Nemertea						
Nemertea sp.	1.7	0.0	0.0	0.0	0.0	0.0
Hirudinae						
Hirudinae sp.	0.0	0.0	0.0	0.0	3.3	0.0
Mysidacea						
Gastrosaccus psammodytes	0.0	0.0	0.0	0.0	0.0	0.0
Mesopodopsis wooldridgei	0.0	0.0	0.0	0.0	0.0	0.0
Rhopalophthalmus terranatalis	0.0	0.0	0.0	0.0	0.0	0.0
Cumacea						
Cumacean sp.	3.3	5.0	33.3	11.7	0.0	0.0
Iphinoe truncata	0.0	0.0	23.3	0.0	0.0	0.0
Tanaidacea						
Apseudes digitalis	10.0	8.3	1.7	1.7	11.7	0.0
Tanaid sp.	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda						
Cirolana hirtipes	0.0	0.0	1.7	0.0	0.0	0.0

Appendix B: continued	**Transect 1**	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**	**Transect 6**
Cyathura carinata	60.0	68.3	28.3	5.0	0.0	0.0
Amphipoda						
Afrochiltonia capensis	0.0	0.0	0.0	0.0	0.0	0.0
Corophium triaenonyx	10.0	1.7	1.7	0.0	0.0	0.0
Gammaropsis sp.	0.0	0.0	0.0	0.0	0.0	0.0
Grandidierella bonnieroides	48.3	46.7	160.0	35.0	3.3	0.0
Melita zeylanica	30.0	10.0	1.7	0.0	0.0	0.0
Perioculodes longimanus	0.0	0.0	0.0	0.0	0.0	0.0
Seba sp.	0.0	5.0	0.0	0.0	0.0	0.0
Copepoda						
Corycaeus subtilis	0.0	0.0	0.0	0.0	0.0	0.0
Pseudodiaptomus charteri	6.7	11.7	3.3	1.7	1.7	0.0
Acartia negligans	0.0	0.0	0.0	1.7	0.0	0.0
Caridea						
Macrobrachium rudis	0.0	0.0	0.0	0.0	0.0	0.0
Anomura						
Upogebia africana	16.7	21.7	1.7	1.7	8.3	13.3
Brachyura						
Brachyuran larvae	0.0	0.0	0.0	0.0	1.7	0.0
Brachyuran juvenile sp.	63.3	45.0	0.0	0.0	0.0	0.0
Cleistostoma algoense	0.0	0.0	0.0	0.0	0.0	1.7
Cleistostoma edwardsii	1.7	1.7	0.0	0.0	0.0	1.7
Hymenosoma orbiculare	0.0	0.0	0.0	0.0	0.0	0.0
Metopograpsus thukuhar	0.0	0.0	0.0	0.0	0.0	3.3
Rhynchoplax bovis	1.7	1.7	3.3	0.0	0.0	0.0
Thaumastoplax spiralis	18.3	30.0	8.3	3.3	1.7	0.0
Paratylodiplax blephariskios	151.7	100.0	3.3	0.0	0.0	0.0
Uca annulipes	0.0	0.0	0.0	0.0	0.0	1.7
Cirripedia						
Balanus elizabethae	0.0	0.0	0.0	0.0	0.0	0.0
Balanus venustus	0.0	0.0	0.0	0.0	0.0	0.0
Tetraclita sp.	0.0	3.3	0.0	0.0	0.0	0.0
Pygnogonidae						
Tanystylum sp.	1.7	0.0	0.0	0.0	0.0	0.0
Mollusca						
Assiminea bifasciata	0.0	0.0	0.0	0.0	0.0	0.0
Bivalve spat	0.0	0.0	0.0	0.0	0.0	0.0
Dosinia hepatica	208.3	126.7	56.7	8.3	8.3	3.3
Gastropod spat A	16.7	456.7	33.3	26.7	3.3	1.7
Gastropod spat B	0.0	0.0	1.7	0.0	0.0	0.0
Macoma litoralis	0.0	0.0	0.0	0.0	0.0	0.0
Nassarius kraussianus	36.7	31.7	80.0	6.7	15.0	38.3
Nassarius speciosus	0.0	0.0	0.0	0.0	0.0	0.0
Natica tecta	0.0	0.0	0.0	0.0	0.0	0.0
Sanguinolaria capensis	1.7	1.7	6.7	0.0	1.7	0.0
Solen cylindraceus	0.0	0.0	5.0	0.0	3.3	0.0
Telina gilchristi	0.0	0.0	0.0	0.0	0.0	0.0
Echinodermata						
Amphipholis sp.	0.0	0.0	0.0	0.0	0.0	0.0

Appendix C: Mean abundance (m^{-2}) for each macrozoobenthic species found at the six transects along the subtidal and intertidal gradient in the Mngazana Estuary.

	January 2005					
	Transect 1	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**	**Transect 6**
Polychaeta						
Boccardia polybranchia	0.0	0.0	0.0	0.0	3.6	0.0
Capitella capitata	71.7	283.3	250.0	178.3	642.9	0.0
Ceratonereis erythraeensis	0.0	0.0	0.0	0.0	0.0	0.0
Ceratonereis keiskama	0.0	1.7	5.0	3.3	3.6	0.0
Timarete tentaculata	820.0	846.7	46.7	261.7	0.0	3.8
Cossura sp.	38.3	73.3	13.3	40.0	0.0	0.0
Dendronereis arborifera	0.0	0.0	8.3	0.0	1.8	0.0
Desdemona ornata	0.0	0.0	0.0	0.0	1.8	0.0
Dorvillea sp.	0.0	0.0	0.0	0.0	0.0	0.0
Onuphis sp.	0.0	0.0	0.0	1.7	0.0	0.0
Eunicidae sp.	0.0	0.0	0.0	0.0	0.0	0.0
Exogone normalis	0.0	0.0	0.0	0.0	0.0	0.0
Glycera tridactyla	0.0	0.0	0.0	0.0	0.0	0.0
Lamellisyllis sp.	0.0	0.0	0.0	0.0	0.0	0.0
Lumbrinereis tetraura	61.7	56.7	0.0	30.0	0.0	0.0
Magelona cincta	1.7	0.0	0.0	0.0	0.0	0.0
Heteromastus sp.	26.7	48.3	10.0	16.7	0.0	0.0
Nephtys capensis	0.0	0.0	0.0	1.7	0.0	0.0
Nicomache sp.	6.7	6.7	3.3	0.0	0.0	0.0
Orbinia angrapequensis	0.0	0.0	0.0	0.0	0.0	0.0
Paraonides lyra capensis	331.7	286.7	28.3	280.0	0.0	0.0
Perinereis falsovariegata	0.0	0.0	0.0	0.0	0.0	0.0
Phyllodoce malmgreni	33.3	75.0	6.7	26.7	0.0	0.0
Potamilla reniformis	0.0	0.0	0.0	0.0	0.0	0.0
Prionospio sexoculata	36.7	78.3	1261.7	205.0	592.9	0.0
Pygospio elegans	0.0	0.0	0.0	0.0	0.0	0.0
Syllidae sp. A	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. A	0.0	0.0	0.0	0.0	26.8	0.0
Polychaete sp. B	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. C	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete sp. D	0.0	0.0	0.0	0.0	0.0	0.0
Nematoda						
Nematode sp.	26.7	90.0	16.7	20.0	33.9	0.0
Nemertea						
Nemertea sp.	0.0	0.0	0.0	0.0	0.0	0.0
Hirudinae						
Hirudinae sp.	1.7	1.7	0.0	0.0	0.0	0.0
Mysidacea						
Gastrosaccus psammodytes	0.0	0.0	0.0	0.0	0.0	0.0
Mesopodopsis wooldridgei	0.0	0.0	0.0	0.0	0.0	0.0
Rhopalophthalmus terranatalis	0.0	0.0	0.0	0.0	0.0	0.0
Cumacea						
Cumacean sp.	3.3	1.7	1.7	0.0	0.0	0.0
Iphinoe truncata	0.0	0.0	0.0	0.0	0.0	0.0
Tanaidacea						
Apseudes digitalis	0.0	0.0	0.0	1.7	14.3	0.0
Tanaid sp.	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda						
Cirolana hirtipes	0.0	0.0	0.0	0.0	0.0	0.0

Appendix C: continued

	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
Cyathura carinata	55.0	16.7	5.0	11.7	1.8	0.0
Amphipoda						
Afrochiltonia capensis	0.0	0.0	0.0	0.0	0.0	0.0
Corophium triaenonyx	0.0	0.0	0.0	0.0	0.0	0.0
Gammaropsis sp.	0.0	0.0	0.0	0.0	0.0	0.0
Grandidierella bonnieroides	3.3	0.0	3.3	0.0	0.0	0.0
Melita zeylanica	5.0	0.0	1.7	0.0	1.8	0.0
Perioculodes longimanus	0.0	0.0	0.0	0.0	0.0	0.0
Seba sp.	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda						
Corycaeus subtilis	0.0	0.0	0.0	1.7	0.0	0.0
Pseudodiaptomus charteri	3.3	1.7	0.0	1.7	0.0	0.0
Acartia negligans	0.0	0.0	0.0	0.0	0.0	0.0
Caridea						
Macrobrachium rudis	0.0	3.3	0.0	0.0	0.0	0.0
Anomura						
Upogebia africana	5.0	1.7	0.0	5.0	5.4	0.0
Brachyura						
Brachyuran larvae	0.0	1.7	1.7	0.0	0.0	0.0
Brachyuran juvenile sp.	1.7	3.3	1.7	0.0	0.0	0.0
Cleistostoma algoense	0.0	3.3	0.0	0.0	0.0	0.0
Cleistostoma edwardsii	0.0	0.0	0.0	0.0	1.8	0.0
Hymenosoma orbiculare	0.0	0.0	0.0	0.0	0.0	0.0
Metopograpsus thukuhar	0.0	0.0	0.0	0.0	0.0	0.0
Rhynchoplax bovis	1.7	0.0	0.0	0.0	0.0	0.0
Thaumastoplax spiralis	6.7	13.3	0.0	8.3	3.6	0.0
Paratylodiplax blephariskios	15.0	13.3	0.0	0.0	0.0	0.0
Uca annulipes	0.0	0.0	0.0	0.0	1.8	1.9
Cirripedia						
Balanus elizabethae	0.0	0.0	0.0	0.0	0.0	0.0
Balanus venustus	0.0	0.0	0.0	0.0	0.0	0.0
Tetraclita sp.	0.0	0.0	0.0	0.0	0.0	0.0
Pygnogonidae						
Tanystylum sp.	0.0	0.0	0.0	0.0	0.0	0.0
Mollusca						
Assiminea bifasciata	0.0	0.0	0.0	0.0	0.0	0.0
Bivalve spat	0.0	0.0	0.0	0.0	0.0	0.0
Dosinia hepatica	46.7	53.3	10.0	76.7	1.8	0.0
Gastropod spat A	8.3	13.3	0.0	13.3	0.0	0.0
Gastropod spat B	1.7	0.0	0.0	0.0	0.0	0.0
Macoma litoralis	0.0	0.0	0.0	0.0	0.0	0.0
Nassarius kraussianus	41.7	40.0	3.3	40.0	0.0	0.0
Nassarius speciosus	0.0	0.0	0.0	0.0	0.0	0.0
Natica tecta	0.0	0.0	0.0	1.7	0.0	0.0
Sanguinolaria capensis	0.0	0.0	0.0	5.0	0.0	0.0
Solen cylindraceus	0.0	0.0	11.7	11.7	1.8	0.0
Telina gilchristi	0.0	0.0	0.0	0.0	0.0	0.0
Echinodermata						
Amphipholis sp.	0.0	0.0	0.0	0.0	0.0	0.0

Appendix D: Species that were found at the Mngazana Estuary, which were not included in the analyses.

Polychaeta
Harmothoe sp.
Lopadorhynchus nationalis
Maldanidae sp.
Nereis unifasciata
Ophiodromus sp.
Syllidae sp. B
Polychaete sp.E
Isopoda
Exosphaeroma hylocoetes
Amphipoda
Amaryllis macropthalma
Amphilochus neapolitanus
Caprella equilibra
Copepoda
Copepod sp. A
Oncaea sp.
Tisbe sp.
Caridea
Palaemon peringueyi
Brachyura
Scylla serrata
Stegocephalidae sp.
Uca vocans
Mollusca
Eumarcia paupercula
Turritella sanguinea
Clionella sp.
Foraminefera
Elphidium sp.
Foram sp.A
Foram sp.B

Appendix E (1-3): Breakdown of average dissimilarity between transects/ and or groups of transects during November 2004.

(1) Group B I (Transects B1, B2, B3)
Group B II (Transects B4, B5)

Average dissimilarity = 52.7%

Species	Group B(I) Av.Abund	Group B(II) Av.Abund	Av.Diss	Contrib%	Cum.%
Prionospio sexoculata	10.2	30.4	10.1	19.1	19.1
Capitella capitata	5.3	17.2	5.9	11.3	30.4
Timarete tentaculata	11.0	1.4	4.8	9.1	39.5
Cossura sp.	5.2	0.0	2.6	4.9	44.4
Paratylodiplax blephariskios	3.8	0.0	1.9	3.6	48.0
Paraonides lyra capensis	4.9	1.5	1.7	3.2	51.2
Gastropod spat A	5.0	3.7	1.7	3.2	54.4
Heteromastus sp.	4.5	1.2	1.6	3.1	57.5
Lumbrinereis tetraura	3.9	0.9	1.5	2.8	60.3
Polychaete sp. A	0.0	2.7	1.4	2.6	62.9
Dosinia hepatica	5.4	3.0	1.2	2.2	65.1
Grandidierella bonnieroides	4.4	4.1	1.2	2.2	67.3
Brachyuran juvenile sp.	2.3	0.0	1.2	2.2	69.5
Cyathura carinata	3.5	1.2	1.1	2.1	71.6
Ceratonereis keiskama	0.0	1.9	1.0	1.8	73.4
Cumacean sp.	1.7	1.8	0.9	1.7	75.2
Desdemona ornata	2.2	3.8	0.9	1.7	76.8
Melita zeylanica	1.6	0.0	0.8	1.5	78.3
Nematode sp.	2.4	3.9	0.7	1.4	79.7
Apseudes digitalis	1.2	2.6	0.7	1.4	81.1
Phyllodoce malmgreni	2.5	1.4	0.7	1.3	82.4
Boccardia polybranchia	1.0	1.2	0.6	1.1	83.6
Exogone normalis	0.5	1.2	0.6	1.1	84.7
Dendronereis arborifera	0.2	1.2	0.6	1.1	85.8
Upogebia africana	1.6	2.2	0.6	1.0	86.9
Hirudinae sp.	0.0	0.9	0.5	0.9	87.8
Solen cylindraceus	0.4	0.9	0.5	0.9	88.7
Nassarius kraussianus	3.4	3.5	0.5	0.9	89.5
Corophium triaenonyx	0.9	0.0	0.5	0.9	90.4

(2) Transect B6 & Group B I (Transects B1, B2, B3)

Average dissimilarity = 74.1%

Species	Group B(I) Av.Abund	Transect B6 Av.Abund	Av.Diss	Contrib%	Cum.%
Capitella capitata	5.3	27.7	11.2	15.2	15.2
Nassarius kraussianus	3.4	15.2	5.9	7.9	23.1
Timarete tentaculata	11.0	0.0	5.5	7.4	30.5
Polychaete sp. A	0.0	8.9	4.4	6.0	36.5
Upogebia africana	1.6	9.0	3.7	5.0	41.5
Prionospio sexoculata	10.2	3.5	3.4	4.5	46.0
Cossura sp.	5.2	0.0	2.6	3.5	49.5
Paraonides lyra capensis	4.9	0.0	2.4	3.3	52.8
Nematode sp.	2.4	7.0	2.3	3.1	55.8

Appendix E: continued

Heteromastus sp.	4.5	0.0	2.2	3.0	58.8
Grandidierella bonnieroides	4.4	0.0	2.2	3.0	61.8
Metopograpsus thukuhar	0.0	4.3	2.1	2.9	64.7
Lumbrinereis tetraura	3.9	0.0	2.0	2.6	67.3
Paratylodiplax blephariskios	3.8	0.0	1.9	2.6	69.9
Ceratonereis keiskama	0.0	3.5	1.7	2.4	72.3
Cyathura carinata	3.5	0.0	1.7	2.3	74.6
Cleistostoma algoense	0.0	3.2	1.6	2.1	76.7
Uca annulipes	0.0	3.2	1.6	2.1	78.9
Cleistostoma edwardsii	0.4	3.5	1.5	2.1	80.9
Gastropod spat A	5.0	3.5	1.4	1.9	82.9
Phyllodoce malmgreni	2.5	0.0	1.3	1.7	84.6
Brachyuran juvenile sp.	2.3	0.0	1.2	1.6	86.1
Thaumastoplax spiralis	2.0	0.0	1.0	1.4	87.5
Cumacean sp.	1.7	0.0	0.8	1.1	88.6
Melita zeylanica	1.6	0.0	0.8	1.1	89.7
Pseudodiaptomus charteri	1.3	0.0	0.6	0.9	90.5

(3) Transect B6 & Group B II (Transects B4, B5)

Average dissimilarity = 56.4%

Species	Group B(II) Av.Abund	Transect B6 Av.Abund	Av.Diss	Contrib%	Cum.%
Prionospio sexoculata	30.4	3.5	13.4	23.8	23.8
Nassarius kraussianus	3.5	15.2	5.8	10.4	34.2
Capitella capitata	17.2	27.7	5.3	9.4	43.5
Upogebia africana	2.2	9.0	3.4	6.0	49.5
Polychaete sp. A	2.7	8.9	3.1	5.5	55.0
Metopograpsus thukuhar	0.0	4.3	2.1	3.8	58.8
Grandidierella bonnieroides	4.1	0.0	2.1	3.7	62.4
Cleistostoma edwardsii	0.0	3.5	1.7	3.1	65.5
Cleistostoma algoense	0.0	3.2	1.6	2.8	68.3
Uca annulipes	0.0	3.2	1.6	2.8	71.1
Nematode sp.	3.9	7.0	1.5	2.7	73.8
Apseudes digitalis	2.6	0.0	1.3	2.3	76.2
Ceratonereis keiskama	1.9	3.5	1.0	1.7	77.9
Gastropod spat A	3.7	3.5	0.9	1.6	79.5
Cumacean sp.	1.8	0.0	0.9	1.6	81.1
Thaumastoplax spiralis	1.7	0.0	0.8	1.5	82.6
Paraonides lyra capensis	1.5	0.0	0.8	1.3	84.0
Timarete tentaculata	1.4	0.0	0.7	1.3	85.2
Phyllodoce malmgreni	1.4	0.0	0.7	1.3	86.4
Pseudodiaptomus charteri	1.4	0.0	0.7	1.2	87.7
Dosinia hepatica	3.0	4.3	0.6	1.1	88.8
Boccardia polybranchia	1.2	0.0	0.6	1.1	89.8
Exogone normalis	1.2	0.0	0.6	1.1	90.9

Appendix F (1-3): Breakdown of average dissimilarity between transects/ and or groups of transects during January 2005.

(1) Group C I (Transects C1, C2, C4)
Group C II (Transects C3, C5)

Average dissimilarity = 59%

Species	Group C(I) Av.Abund	Group C(II) Av.Abund	Av.Diss	Contrib%	Cum.%
Prionospio sexoculata	6.9	31.6	12.3	20.9	20.9
Capitella capitata	8.9	22.6	6.9	11.6	32.5
Timarete tentaculata	16.8	3.3	6.7	11.4	43.9
Paraonides lyra capensis	12.0	2.6	4.7	8.0	51.8
Lumbrinereis tetraura	4.8	0.0	2.4	4.0	55.9
Nassarius kraussianus	4.4	0.8	1.8	3.0	58.9
Phyllodoce malmgreni	4.5	1.3	1.6	2.7	61.6
Cossura sp.	4.8	1.8	1.5	2.6	64.2
Polychaete sp. A	0.0	3.1	1.5	2.6	66.8
Dosinia hepatica	5.3	2.4	1.5	2.5	69.3
Gastropod spat A	2.3	0.0	1.2	2.0	71.2
Dendronereis arborifera	0.0	2.2	1.1	1.9	73.1
Apseudes digitalis	0.4	2.2	1.1	1.9	75.0
Heteromastus sp.	3.7	1.5	1.1	1.8	76.8
Solen cylindraceus	0.9	2.5	1.0	1.7	78.4
Nematode sp.	4.3	5.4	0.9	1.5	79.9
Cyathura carinata	3.4	1.9	0.8	1.3	81.2
Ceratonereis keiskama	0.7	2.3	0.8	1.3	82.5
Paratylodiplax blephariskios	1.4	0.0	0.7	1.2	83.7
Boccardia polybranchia	0.0	1.2	0.6	1.0	84.7
Upogebia africana	0.8	1.2	0.6	1.0	85.7
Thaumastoplax spiralis	2.1	1.2	0.6	1.0	86.7
Melita zeylanica	0.5	1.5	0.5	0.9	87.6
Pseudodiaptomus charteri	1.0	0.0	0.5	0.8	88.4
Nicomache sp.	1.2	0.8	0.4	0.8	89.1
Desdemona ornata	0.0	0.8	0.4	0.7	89.8
Upogebia africana	1.0	0.8	0.4	0.7	90.5

(2) Transect C6 & Group C I (Transects C1, C2, C4)

Average dissimilarity = 83.3%

Species	Group C(I) Av.Abund	Transect C6 Av.Abund	Av.Diss	Contrib%	Cum.%
Timarete tentaculata	16.8	58.6	20.9	25.1	25.1
Uca annulipes	0.0	41.4	20.7	24.9	50.0
Paraonides lyra capensis	12.0	0.0	6.0	7.2	57.2
Capitella capitata	8.9	0.0	4.4	5.3	62.5
Prionospio sexoculata	6.9	0.0	3.5	4.1	66.7
Dosinia hepatica	5.3	0.0	2.7	3.2	69.9
Cossura sp.	4.8	0.0	2.4	2.9	72.7
Lumbrinereis tetraura	4.8	0.0	2.4	2.9	75.6
Phyllodoce malmgreni	4.5	0.0	2.2	2.7	78.3
Nassarius kraussianus	4.4	0.0	2.2	2.7	80.9
Nematode sp.	4.3	0.0	2.2	2.6	83.5

Appendix F: continued

Heteromastus sp.	3.7	0.0	1.8	2.2	85.7
Cyathura carinata	3.4	0.0	1.7	2.1	87.8
Gastropod spat A	2.3	0.0	1.2	1.4	89.2
Thaumastoplax spiralis	2.1	0.0	1.0	1.2	90.4

(3) Transect C6 & Group C II (Transects C3, C5)

Average dissimilarity = 96.7%

Species	Group C(II) Av.Abund	Transect C6 Av.Abund	Av.Diss	Contrib%	Cum.%
Timarete tentaculata	3.3	58.6	27.6	28.6	28.6
Uca annulipes	0.0	41.4	20.7	21.4	50.0
Prionospio sexoculata	31.6	0.0	15.8	16.3	66.3
Capitella capitata	22.6	0.0	11.3	11.7	78.0
Nematode sp.	5.4	0.0	2.7	2.8	80.8
Polychaete sp. A	3.1	0.0	1.5	1.6	82.4
Paraonides lyra capensis	2.6	0.0	1.3	1.3	83.7
Solen cylindraceus	2.5	0.0	1.3	1.3	85.0
Dosinia hepatica	2.4	0.0	1.2	1.2	86.2
Ceratonereis keiskama	2.3	0.0	1.1	1.2	87.4
Dendronereis arborifera	2.2	0.0	1.1	1.1	88.5
Apseudes digitalis	2.2	0.0	1.1	1.1	89.7
Cyathura carinata	1.9	0.0	1.0	1.0	90.7

Appendix G (1-3): Breakdown of average dissimilarity between intertidal transects/ and or groups of intertidal transects for the three sampling sessions combined.

(1) Group I (Transects A4, B4, C4)
Group II (Transects A5, B5, B6, C5)

Average dissimilarity = 58.8%

Species	Group I Av.Abund	Group II Av.Abund	Av.Diss	Contrib%	Cum.%
Capitella capitata	8.2	26.5	9.2	15.6	15.6
Prionospio sexoculata	20.9	19.9	6.5	11.0	26.6
Timarete tentaculata	7.5	0.0	3.8	6.4	33.0
Paraonides lyra capensis	6.2	0.4	2.9	4.9	38.0
Polychaete sp. A	0.0	5.1	2.6	4.4	42.3
Nassarius kraussianus	3.3	5.1	2.3	4.0	46.3
Phyllodoce malmgreni	3.4	1.7	1.7	2.9	49.2
Upogebia africana	1.2	4.5	1.7	2.9	52.1
Gastropod spat A	4.5	1.3	1.7	2.8	54.9
Cossura sp.	3.1	0.0	1.6	2.7	57.5
Lumbrinereis tetraura	2.8	0.0	1.4	2.4	59.9
Heteromastus sp.	3.1	0.4	1.4	2.3	62.3
Grandidierella bonnieroides	2.8	0.5	1.3	2.3	64.5
Apseudes digitalis	0.9	2.9	1.2	2.1	66.6
Ceratonereis keiskama	0.7	3.1	1.2	2.1	68.6
Dosinia hepatica	4.5	2.5	1.1	1.9	70.6
Nematode sp.	3.8	4.8	1.1	1.9	72.4
Cumacean sp.	2.1	0.0	1.1	1.8	74.2
Desdemona ornata	1.9	2.5	1.0	1.8	76.0
Tanaid sp.	0.0	1.8	0.9	1.6	77.5
Uca annulipes	0.0	1.7	0.9	1.5	79.0
Nicomache sp.	1.7	0.0	0.8	1.4	80.4
Cleistostoma edwardsii	0.2	1.6	0.8	1.3	81.7
Boccardia polybranchia	0.7	1.8	0.7	1.2	82.9
Cyathura carinata	2.0	0.9	0.7	1.2	84.1
Acartia negligans	1.4	0.0	0.7	1.2	85.3
Dendronereis arborifera	1.2	0.4	0.6	1.0	86.2
Solen cylindraceus	1.5	1.4	0.5	0.9	87.2
Metopograpsus thukuhar	0.0	1.1	0.5	0.9	88.1
Exogone normalis	0.6	1.1	0.5	0.9	89.0
Pseudodiaptomus charteri	1.5	0.7	0.5	0.8	89.8
Thaumastoplax spiralis	1.5	1.3	0.5	0.8	90.6

(2) Group I (Transects A4, B4, C4)
Group III (Transects A6, C6)

Average dissimilarity = 94.5%

Species	Group I Av.Abund	Group III Av.Abund	Av.Diss	Contrib%	Cum.%
Uca annulipes	0.0	36.9	18.4	19.5	19.5
Timarete tentaculata	7.5	29.5	14.8	15.6	35.1
Nassarius kraussianus	3.3	23.2	11.6	12.3	47.4
Prionospio sexoculata	20.9	0.0	10.4	11.1	58.5
Bivalve spat	0.2	10.4	5.2	5.5	63.9
Capitella capitata	8.2	0.0	4.1	4.3	68.3
Paraonides lyra capensis	6.2	0.0	3.1	3.3	71.5
Gastropod spat A	4.5	0.0	2.3	2.4	73.9
Dosinia hepatica	4.5	0.0	2.2	2.4	76.3

Appendix G: continued

Nematode sp.	3.8	0.0	1.9	2.0	78.3
Phyllodoce malmgreni	3.4	0.0	1.7	1.8	80.1
Cossura sp.	3.1	0.0	1.6	1.6	81.7
Heteromastus sp.	3.1	0.0	1.5	1.6	83.4
Lumbrinereis tetraura	2.8	0.0	1.4	1.5	84.9
Grandidierella bonnieroides	2.8	0.0	1.4	1.5	86.3
Cumacean sp.	2.1	0.0	1.1	1.1	87.5
Cyathura carinata	2.0	0.0	1.0	1.1	88.5
Desdemona ornata	1.9	0.0	1.0	1.0	89.5
Nicomache sp.	1.7	0.0	0.8	0.9	90.4

(3) Group II (Transects A5, B5, B6, C5)
Group III (Transects A6, C6)

Average dissimilarity = 95.7%

Species	Group II Av.Abund	Group III Av.Abund	Av.Diss	Contrib%	Cum.%
Uca annulipes	1.7	36.9	17.6	18.4	18.4
Timarete tentaculata	0.0	29.5	14.8	15.4	33.8
Capitella capitata	26.5	0.0	13.3	13.9	47.7
Nassarius kraussianus	5.1	23.2	11.6	12.1	59.8
Prionospio sexoculata	19.9	0.0	10.0	10.4	70.2
Bivalve spat	0.0	10.4	5.2	5.4	75.6
Polychaete sp. A	5.1	0.0	2.6	2.7	78.3
Nematode sp.	4.8	0.0	2.4	2.5	80.8
Upogebia africana	4.5	0.0	2.3	2.4	83.1
Ceratonereis keiskama	3.1	0.0	1.6	1.6	84.8
Apseudes digitalis	2.9	0.0	1.4	1.5	86.3
Dosinia hepatica	2.5	0.0	1.3	1.3	87.6
Desdemona ornata	2.5	0.0	1.2	1.3	88.9
Tanaid sp.	1.8	0.0	0.9	1.0	89.8
Boccardia polybranchia	1.8	0.0	0.9	0.9	90.8

Appendix H (1-2): Breakdown of average similarity within groups of transects during November 2004.

(1) Group B I (Transects B1, B2, B3)
Average similarity: 74.6%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Timarete tentaculata	11.0	10.7	14.4	14.4
Prionospio sexoculata	10.2	6.4	8.5	22.9
Cossura sp.	5.2	4.9	6.6	29.5
Paraonides lyra capensis	4.9	4.8	6.4	35.9
Capitella capitata	5.3	4.7	6.3	42.2
Dosinia hepatica	5.4	4.5	6.0	48.2
Lumbrinereis tetraura	3.9	3.5	4.7	52.9
Heteromastus sp.	4.5	3.3	4.4	57.3
Grandidierella bonnieroides	4.4	3.2	4.3	61.6
Cyathura carinata	3.5	3.1	4.2	65.8
Nassarius kraussianus	3.4	2.7	3.7	69.5
Phyllodoce malmgreni	2.5	2.5	3.4	72.8
Gastropod spat A	5.0	2.3	3.1	75.9
Nematode sp.	2.4	2.3	3.1	79.0
Paratylodiplax blephariskios	3.8	2.2	3.0	82.0
Thaumastoplax spiralis	2.0	1.7	2.2	84.2
Desdemona ornata	2.2	1.6	2.2	86.4
Upogebia africana	1.6	1.1	1.5	87.8
Brachyuran juvenile sp.	2.3	1.1	1.4	89.3
Pseudodiaptomus charteri	1.3	1.1	1.4	90.7

(2) Group B II (Transects B4, B5)
Average similarity: 56.6%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Prionospio sexoculata	30.4	24.8	43.9	43.9
Capitella capitata	17.2	8.6	15.2	59.0
Nematode sp.	3.9	3.4	6.0	65.0
Dosinia hepatica	3.0	3.0	5.3	70.4
Desdemona ornata	3.8	2.9	5.0	75.4
Nassarius kraussianus	3.5	2.8	5.0	80.4
Grandidierella bonnieroides	4.1	2.0	3.5	83.8
Gastropod spat A	3.7	1.9	3.3	87.1
Thaumastoplax spiralis	1.7	1.5	2.7	89.8
Paraonides lyra capensis	1.5	1.5	2.7	92.5

Appendix I (1-2): Breakdown of average similarity within groups of transects during January 2005.

(1) Group C I (Transects C1, C2, C4)
Average similarity: 78.2%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Timarete tentaculata	17.1	14.5	18.6	18.6
Paraonides lyra capensis	12.2	11.5	14.7	33.2
Capitella capitata	9.0	7.4	9.5	42.8
Prionospio sexoculata	7.0	4.7	6.1	48.8
Dosinia hepatica	5.4	4.7	6.0	54.8
Cossura sp.	4.9	4.5	5.8	60.7
Lumbrinereis tetraura	4.9	4.4	5.7	66.3
Nassarius kraussianus	4.5	4.2	5.4	71.7
Phyllodoce malmgreni	4.5	4.0	5.2	76.9
Nematode sp.	4.4	3.5	4.5	81.4
Heteromastus sp.	3.8	3.4	4.3	85.7
Cyathura carinata	3.5	2.6	3.4	89.0
Gastropod spat A	2.4	2.1	2.7	91.7

(2) Group C II (Transects C3, C5)
Average similarity: 58.8%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Prionospio sexoculata	32.0	29.0	49.3	49.3
Capitella capitata	22.9	15.6	26.4	75.8
Nematode sp.	5.5	4.1	6.9	82.7
Ceratonereis keiskama	2.3	2.2	3.7	86.4
Dendronereis arborifera	2.2	1.7	2.9	89.3
Cyathura carinata	1.9	1.7	2.9	92.1

Appendix J (1-3): Breakdown of average similarity within intertidal groups of transects during all sampling sessions combined.

(1) Group I (Transects A4, B4, C4)
Average similarity: 56.2%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Prionospio sexoculata	20.9	12.6	22.5	22.5
Capitella capitata	8.2	6.7	11.8	34.3
Timarete tentaculata	7.5	4.3	7.6	41.9
Gastropod spat A	4.5	3.6	6.4	48.4
Nematode sp.	3.8	3.5	6.2	54.5
Dosinia hepatica	4.5	3.2	5.7	60.2
Phyllodoce malmgreni	3.4	3.0	5.3	65.5
Heteromastus sp.	3.1	2.7	4.7	70.2
Paraonides lyra capensis	6.2	2.4	4.2	74.4
Nassarius kraussianus	3.3	2.3	4.1	78.5
Lumbrinereis tetraura	2.8	2.0	3.6	82.1
Cossura sp.	3.1	1.5	2.6	84.8
Cyathura carinata	2.0	1.4	2.5	87.3
Pseudodiaptomus charteri	1.5	1.1	2.0	89.3
Thaumastoplax spiralis	1.5	0.9	1.6	90.9

(2) Group II (Transects A5, B5, C5, B6)
Average similarity: 61.4%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Capitella capitata	26.5	24.4	39.8	39.8
Prionospio sexoculata	19.9	13.3	21.6	61.4
Nematode sp.	4.8	3.2	5.2	66.6
Upogebia africana	4.5	3.0	4.8	71.5
Polychaete sp.A	5.1	2.8	4.6	76.1
Ceratonereis keiskama	3.1	2.7	4.4	80.5
Desdemona ornata	2.5	1.9	3.1	83.6
Apseudes digitalis	2.9	1.7	2.8	86.4
Dosinia hepatica	2.5	1.6	2.7	89.1
Boccardia polybranchia	1.8	1.2	1.9	91.0

(3) Group III (Transects A6, C6)
Average similarity: 32.8%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Uca annulipes	36.9	32.8	100	100

Appendix K (1-3): Breakdown of average similarity of all six transects during each sampling session.

(1) June 2004
Average similarity: 40.1%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Capitella capitata	8.1	3.9	9.7	9.7
Prionospio sexoculata	8.6	3.4	8.5	18.2
Timarete tentaculata	5.2	3.0	7.5	25.7
Nematode sp.	4.5	2.3	5.8	31.5
Heteromastus sp.	4.0	2.2	5.5	37.1
Paraonides lyra capensis	3.7	2.0	4.9	42.0
Nicomache sp.	3.4	1.9	4.8	46.8
Dosinia hepatica	3.3	1.9	4.7	51.5
Nassarius kraussianus	9.4	1.8	4.4	55.9
Cossura sp.	3.3	1.7	4.3	60.2
Gastropod spat A	3.1	1.6	4.1	64.3
Phyllodoce malmgreni	2.7	1.4	3.4	67.7
Lumbrinereis tetraura	2.3	1.2	2.9	70.6
Boccardia polybranchia	1.7	1.1	2.7	73.3
Solen cylindraceus	1.3	0.9	2.2	75.5
Cyathura carinata	1.1	0.7	1.9	77.4
Grandidierella bonnieroides	1.3	0.7	1.7	79.1
Cumacean sp.	1.5	0.7	1.7	80.8
Desdemona ornata	1.1	0.7	1.7	82.6
Pseudodiaptomus charteri	1.2	0.7	1.7	84.3
Exogone normalis	1.2	0.7	1.7	86.0
Rhynchoplax bovis	1.2	0.6	1.6	87.6
Upogebia africana	1.3	0.6	1.5	89.0
Thaumastoplax spiralis	0.8	0.4	1.1	90.1

(2) November 2004
Average similarity: 48.6%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Prionospio sexoculata	15.8	8.2	16.8	16.8
Capitella capitata	13.0	7.0	14.3	31.1
Dosinia hepatica	4.4	3.6	7.3	38.4
Nassarius kraussianus	5.4	3.1	6.4	44.8
Timarete tentaculata	6.0	2.7	5.6	50.4
Nematode sp.	3.7	2.7	5.5	55.8
Gastropod spat A	4.3	2.6	5.3	61.1
Desdemona ornata	3.0	2.2	4.6	65.7
Grandidierella bonnieroides	3.6	2.0	4.2	69.9
Paraonides lyra capensis	3.0	1.7	3.4	73.3
Upogebia africana	3.0	1.5	3.0	76.4
Heteromastus sp.	2.6	1.1	2.3	78.7
Cyathura carinata	2.1	1.1	2.3	81.0
Thaumastoplax spiralis	1.6	1.1	2.2	83.2
Lumbrinereis tetraura	2.3	1.1	2.2	85.4
Phyllodoce malmgreni	1.7	1.0	2.1	87.5
Cossura sp.	2.6	1.0	2.0	89.5
Pseudodiaptomus charteri	1.1	0.8	1.6	91.1

Appendix K: continued

(3) January 2005
Average similarity: 40.1%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Timarete tentaculata	19.5	8.1	20.3	20.3
Capitella capitata	12.1	6.1	15.3	35.6
Prionospio sexoculata	14.2	5.7	14.2	49.7
Paraonides lyra capensis	7.0	3.3	8.3	58.1
Nematode sp.	4.0	2.6	6.5	64.5
Dosinia hepatica	3.5	2.0	5.0	69.6
Cossura sp.	3.0	1.6	4.0	73.6
Cyathura carinata	2.4	1.4	3.5	77.1
Phyllodoce malmgreni	2.7	1.3	3.3	80.4
Heteromastus sp.	2.4	1.3	3.2	83.7
Nassarius kraussianus	2.5	1.2	3.0	86.6
Lumbrinereis tetraura	2.4	0.9	2.2	88.8
Thaumastoplax spiralis	1.5	0.8	2.0	90.9

Appendix L: Breakdown of average similarity for all intertidal transects during all sampling sessions combined.

Average similarity: 31.4%

Species	Av.Abund	Av.Sim	Contrib%	Cum.%
Prionospio sexoculata	15.8	7.9	25.1	25.1
Capitella capitata	14.5	7.4	23.4	48.6
Nematode sp.	3.4	1.9	6.0	54.6
Nassarius kraussianus	8.5	1.8	5.8	60.4
Uca annulipes	9.0	1.4	4.6	65.0
Dosinia hepatica	2.6	1.3	4.2	69.2
Timarete tentaculata	9.1	1.0	3.1	72.3
Upogebia africana	2.4	1.0	3.0	75.3
Gastropod spat A	2.1	0.8	2.5	77.8
Desdemona ornata	1.7	0.7	2.3	80.2
Ceratonereis keiskama	1.6	0.7	2.3	82.4
Apseudes digitalis	1.6	0.5	1.7	84.2
Phyllodoce malmgreni	1.9	0.5	1.7	85.8
Solen cylindraceus	1.1	0.5	1.6	87.4
Thaumastoplax spiralis	1.1	0.5	1.5	88.9
Polychaete sp.A	2.3	0.5	1.5	90.4