Infaunal Communities in South Australian Temperate Mangrove Systems

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Declaration

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Abstract

South Australian mangroves consist of only one single species *Avicennia marina* (Fosk.) Vierh.var *australasica* (Walp) Moldenke, 1960. They are distributed discontinuously within St. Vincent Gulf and Spencer Gulf and provide significant valuable habitat both in economical and ecological terms. The Fisheries Act 1971-1982 protected the existence of mangroves and the Harbour Act 1936-1981 controlled removal of mangrove areas in coastal development. To date very few ecological studies have been conducted in the South Australian mangroves, particularly on the infaunal organisms that have an important role in maintaining the ecological dynamic within the estuaries systems. As this is the first study on infaunal mangrove communities in the inverse estuaries of South Australia, there was no prior data for ecological comparison. The study was conducted at three mangroves location (Garden Island, Middle Beach and Saint Kilda) close to Adelaide in May 2000 and 2001.

Overall the study has reported that the infaunal mangrove assemblages of South Australian mangroves were comparable to other temperate mangroves. The infaunal communities were characterised by lower diversity and abundance compared to the tropical or subtropical mangroves. The infaunal zonation related to the tidal gradient and habitat variation was detected. Most infauna organisms occupied the surface layers and substantially decreased towards the deeper layers. The study also suggested that sediment structure of mangrove systems were complex and infaunal communities responded differently to the change of environmental conditions both in small scale and larger scale. Thus, assessing the infaunal communities structure in mangrove systems should be based on ecological characteristics rather than geographical positions. The examination of dominant polychaetes families showed that different species have different responses to the environmental cues within mangrove systems. The study did not find that any polychaete species was restricted to mangroves only as they all were also found in the habitat adjacent mangrove forest.

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In the sunny, beautiful spring,

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Chapter 1 The Status of South Australian Mangrove Estuaries

1. Introduction

Mangrove systems are one of the most productive marine habitats. They have several functions including acting as nurseries for some commercial fish species, protection of the land from sea erosion, provision of habitat for biodiversity and also sustaining biogeochemical cycles within the coastal ecosystem. Situated between sea and land, mangroves act as a filtration, stabilizer and buffer zone. South Australia has approximately 3700 km of coastal line, and mangroves represent about 8 % (210 km) of the coastal habitat (Bucher and Saenger, 1994.). The mangroves are distributed discontinuously within St. Vincent Gulf and Spencer Gulf, which collectively represent one of the largest sheltered coastal wetlands in temperate Australia (Edyvane, 1999).
About 80% of South Australian commercial fisheries rely on the sustainability of shore ecosystems (Edyvane, 1995), thus preserving the existence of mangroves is important. The Fisheries Act 1982 has included mangroves as a protected marine species and together with the Harbours Act 1936-1981, controls the removal of mangroves areas in coastal development. Currently, there are 7 separate mangrove habitat reserves which cover almost 56% of the total mangrove areas in South Australia (Edyvane, 1999).

Like other estuarine habitats in the world, South Australian mangroves face considerable threats with significant potential for losses of mangrove forests. Increasing urban and industrial developments have affected the landward and seaward progradations of mangroves in the Port River estuary (Burton, 1982). Trampling by recreational fishers has damaged seedlings and pneumatophores in the Barker Inlet and Port Gawler region. The effect of an oil spill in upper Spencer Gulf has compromised physiological processes in mangrove systems due to hydrocarbon toxicity (Edyvane, 1999). Finally, drift seaweed and seagrass material such as *Ulva sp* smother young seedlings and limit the recruitment of young plants (Fairhead, 1995). This present study also noticed that some pneumatophores have been found covered by *Ulva sp.* at Garden Island and Saint Kilda mangroves.

Plate 1.1. Drift *Ulva sp.* has detrimental effects on mangrove by smothering pneumatophores and young seedlings

As habitat provider mangroves are one of the most important natural resources in maintaining coastal productivity (e.g.Alongi, 1998; Hutchings and Recher, 1981). However, little research has been conducted in South Australian mangroves in assessing the ecological status, dynamics and function of mangrove habitats and relationship mangrove with other adjoining coastal habitats.

2. Ecosystem dynamic of the South Australian mangrove systems

2.1. Habitat characteristics

The word mangrove is a functional classification not a taxonomic one. Mangroves can be defined as woody plants with canopy cover of greater than 50%. They usually grow in the upper part of the intertidal zone between mean sea level and mean high water spring tide, from tropical to temperate sheltered coast lines (Lear and Turner, 1977; Bucher and Saenger, 1994; Chapman and Underwood, 1995). Duke (1995) claimed that 70 species from 20 quite different angiosperm families worldwide are defined as mangroves. Av*icennia, Rhizophora* and *Bruguiera* are the most widespread genera, which are characterized by extensive modification of root systems. In New South Wales, species mangrove plant of *Avicennia marina* and *Aegiceras corniculatum* are dominated the temperate mangroves (Clarke and Hannonn 1970; Hutchings and Recher, 1982). Nevertheless, only one single species *Avicennia marina* (Fosk.) Vierh.var *australasica* (Walp.) Moldenke (1960), exists in South Australia (Duke, 1991).

In Australia, mangroves are distributed from latitude around 12° 15' S and reach their southern limit at 38° 55'S at the Corner Inlet, Victoria as the southernmost mangrove in the world (Ball, 1998). Mangrove species diversity decrease with minimum temperature along the latitudinal gradient and with increasing aridity from east to west (Hutchings and Saenger, 1987; Duke, 1991). Moreover Oliver (1982) stated that variation of climate has indirect affect upon the physiography complexity, which in turn contribute to the structure and distribution of mangrove communities.

Figure 1.1. Interrelationship of environmental factors and a mangrove community (after Oliver, 1982 which adapted from Clarke and Hannon, 1970)

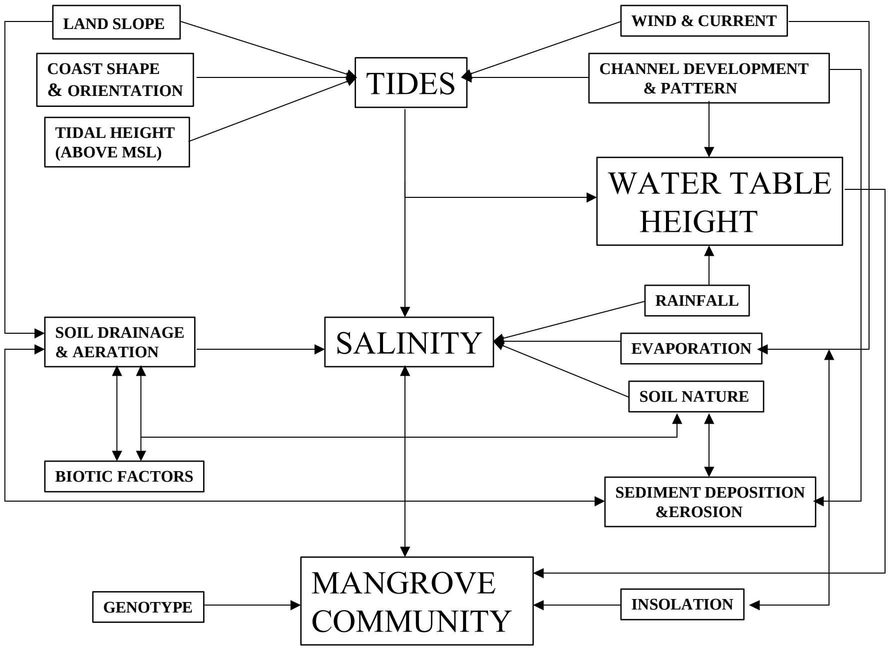


Figure 1.1.illustrates a schematic of interconnection both abiotic and biotic factors as environmental variables that contribute to the characteristics and composition of mangrove communities. Clarke and Hannon (1970) stated that physiography was important factor in determining the zonation of mangroves and salt marshes communities in temperate Sydney districts. They emphasized the role of tidal

fluctuation, salinity of the soil solution and water table together with aeration and drainage in governing the characteristics of mangrove communities in this area. Accordingly, tidal water is the major source of salinity level in the sediment but other factors such as rainfall, evaporation, and wind action also contribute to the salt balance in the systems. Tidal elevation also relate to the fluctuation of water table. During inundation the water table rises above the surface in the mangrove zone as a result of soil ability in water trapping, reducing the salinity level and increase the aeration within soil particles. Possibly, these physiographic factors influence the range of tolerances of mangrove inhabitants in temperate South Australia, even though degree of each variable would be various depend on the local attribute where the mangrove colonises.

The South Australian temperate mangroves are present in the inverse estuaries, where fresh water input is minimal. To date no study has been conducted in mangroves associated with the inverse estuaries which could be used for ecological comparison. Recently, Loo (2001) conducted an infaunal study related to the effluent discharges in a South Australian gulf in which inverse estuarine conditions were taken into account. In these temperate estuaries the salinity regimes range typically from 33 to 66 parts per thousand (ppt) and depend mostly on the input of salt water rather than fresh water (Morrisey, 1995). It has been suggested that around 25 ppt is the optimum salinity level for most mangrove species to grow (English *et al.*, 1994).

Mangrove stands generally occur in low energy estuaries or coastal embayments. In South Australian mangrove areas, the tide is semi diurnal with high tide possibly occur during the night, result a prolong exposure of the habitat during the day. The dodge tide, where there is no net tide movement during 24 hours happens almost every fortnight and produces water lodged sediments due to prolonged reduction of water movement. Consequently the sediment becomes anoxic and nutrients are depleted. It has been reported that the wide range of diurnal variation influenced several important chemical parameters such as dissolved oxygen, salinity, temperature and redox potential in Barker Inlet (Harbison, 1986b). During heavy rainfall, salinity of surface water will drop drastically from 40 ppt to 20 ppt in a few minutes resulting in increasing sediment solubility and rapid ion exchange within the sediment (Harbison, 1986b). When the rain flushing is infrequent or short-lived, salts may remain below the sub surface layer due to the short time for water to infiltrate (Oliver, 1982). The way that rainfall relates to the fluctuation of water table height in the subsurface ground mangrove systems remains questionable. Several factors may be involved in addressing these issues, including the permeability of soils, tidal characteristics and vegetation structures (Clarke and Hannon, 1970).

Being in temperate areas, the mangroves experience a wide range of temperature (0-40 C), moderate rainfall during winter and a dry summer resulting in high evaporation, fluctuations in the height of the water table and salinity level in the sediments.

To be able to thrive in such conditions, the mangrove plants have several recognizable structural and physiological adaptations (Lear and Turner, 1977; Hutchings, 1985):

1. The mangrove communities consist of one single species plant *Avicennia marina* var. *australasica* that constantly grow in climatic areas with lower winter temperature and low rainfall.
2. The forests exhibit fairly narrow open-scrublands with a simple canopy and mature trees reaching a height up to 8 meters.
3. Root systems are extensive, produce the branching aerial roots and breathing roots (pneumatophores), which provide benefits such as facilitation of gas exchange, nutrient and water absorption in the root and below the surface sediment and provide support to anchor the tree in soft substrate.
4. The leaf is succulent in character, having hair and waxy-thick walls, complete salt glands and well develop water tissue storages as adaptation to the dry climate and saline condition.
5. Their adaptation mechanisms to salinity are via accumulation, exclusion and secretion of salts.

South Australian mangroves are part of a continuum of intertidal communities together with salt marshes on the landward side and mudflats or seagrass on the seaward side. The boundary between them depends on the height of their substratum in relation to the tidal height, soil salinities and the degree of water logging, as found in other subtropical Australian mangroves (Bucher and Saenger, 1994). Thus produces a narrow strip distribution of mangroves in this area compared with other tropical mangroves. Subsequently, the characteristics of temperate mangrove environment may give the impression that the habitats are far from ideal for providing a rich diversity of infauna assemblages.

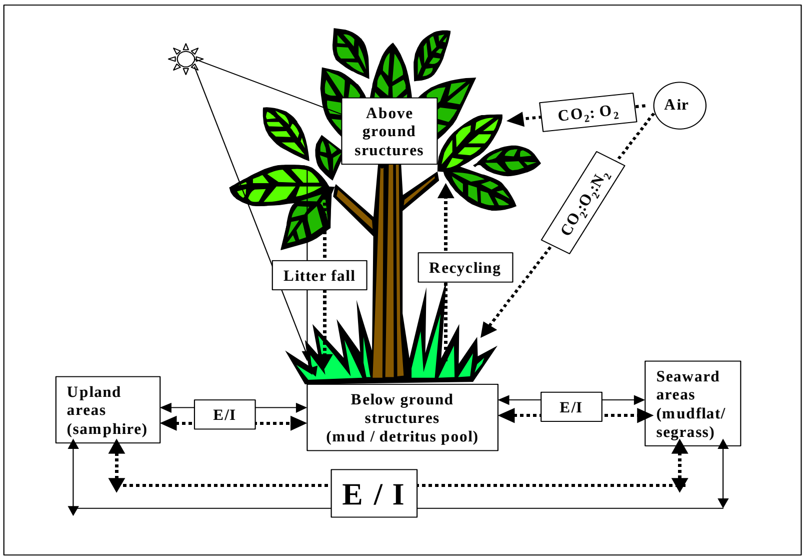
2.2. Energy flow within the mangrove systems

The mangrove ecosystem can be described as an open system in terms of energy and nutrient flows (Butler *et al.*, 1975). It receives energy from the terrestrial habitat and also from the sea as a result of frequent tidal inundation. Eugene Odum has described the energy pathway in this system in 1968 in terms of the out-welling hypothesis, which were the process of transport detritus and other organic material from estuaries to other ecosystems (Alongi, 1998). More over, Odum claimed that mangrove and salt marsh habitats are fertile estuaries and export nutrient to support the productivity of coastal areas (Alongi, 1998). The gross productivity of mangrove detritus is expressed in term of mangal leaf litter, additional benthic cyanobacteria, diatoms and micro algae that fix on the mangrove roots.

Several factors were identified as contributing to the potential of mangroves to act as exporters of organic matter. These include tidal range, pore water concentration, the frequency of rainfall and storms, volume of water exchange, the ratio of the areal extent of mangroves to that of the watershed and the types of mangrove systems (Lee, 1995; Tanaka and Choo, 2000; Dittmar and Lara, 2001). Globally, carbon exported from mangrove is estimated at 210 g carbon / m^2 / year. Comparable figures from Missionary Bay and Hichinbrook Channel in Australia were 325 g carbon/m^2/year (Alongi, 1998) and 560 gr carbon/m^2/year (Wolanski *et al.*, 1998) respectively. There was no data were available about the carbon export from South Australian mangrove areas.

The energy and nutrient pathway models developed so far are more meaningful for tropical mangrove systems where they receive substantial freshwater run-off (Odum, 1971; Lugo and Snedaker, 1974; Wolf *et al.*, 2000). Notwithstanding these differences between tropical and temperate mangroves, Butler *et al.* (1975) drew up a scheme of energy and nutrient flows of South Australian mangroves based on the assumption that the ecological process in the mangroves and the lack of freshwater input (Fig. 1.2.).

Figure 1.2. Schematic of nutrient (---) and energy (—) flows (E=export, I= import) and storages in South Australian mangroves estuaries (After Butler *et.al.*, 1975).



Basically, mangroves comprise two passive storages; above-ground structures and below-ground structures. The above ground structures include leaves, trunks, branches, organisms living in the trees and also dead litter. The below ground structures consist of the roots and the micro and macro organisms associated with sediments. Nutrient recycling and respiration processes fuelled photosynthesis link these passive storages. When primary products from mangrove or samphire are not directly used, they subsequently enter the detritus pools in below ground structures. Detritus is recycled by microorganisms and produces nutrients that are directly consumed by benthic fauna. A recent study in Amazon mangroves, the world second largest tropical mangrove estuaries, reported that 99% of the total system biomass was made up of mangroves and the remaining material was distributed among benthic and pelagic components in proportion 90% to 10% respectively (Wolf *et al.*, 2000) emphasizing the importance of the mangrove forest and of the benthic ecosystem.

The domination of the benthic systems over the pelagic may indicate that some of energy and matter produced remain within the mangrove system. During the spring tides the ground surface is inundated, together with currents and waves, the nutrients are exported to the open sea as out-welling. In contrast, mangroves also receive nutrients from other adjoining systems such as samphire and seagrass. To date there have been no quantitative studies on the net export or energy exchange in South Australian mangroves and adjoining habitats. Not withstanding, it could be expected that nutrient export from salt marshes would be small due to the lack of freshwater input and the smaller area covered by salt marshes due to the landward intrusion of mangrove plants and land use development. From the seaward side, mangroves may also receive low input of nutrients, particularly if they are located in sheltered lagoonal areas where the water circulation is restricted, such as Garden Island. Butler *et al.* (1975) highlighted the energy exchange at the seaward sides between mangroves and seagrass. They noted the position of mangroves that grow along the edge of estuaries while seagrasses are more central. Beside areas of mangroves are less extensive compared with seagrass meadow. This might suggest that mangroves are not the sole important source of organic material for commercial harvests such as fish, prawns and crabs. However, a recent study in tropical mangrove areas found that seagrass habitats adjacent to mangrove fringes have greater nutrient content than other seagrass located further away (Koch and Madden, 2001), suggesting nutrient export. Locally, this is supported by the report that greater diversity and density of fish assemblages were found in seagrass adjacent to a South Australian mangrove (Bloomfield, 2002). Thus, it might suggest that there is a net export of nutrient from mangrove to seagrass systems.

A recent review indicated that the coastal boundary layer will limit the distribution of nutrients off shore (Lee, 1995). Out-welling probably only occurs from a mangrove forest when the availability of nutrients within the forest exceeds the demands of the benthic communities and trees due to a positive sedimentation balance and nitrogen fixation (Dittmar and Lara, 2001). Odum and Heald (1972) undertook trophic analyses of the biological pathways in energy exchange of some invertebrates and fish in mangroves in Florida. Gut contents analysis of the major fauna indicated significant amounts of mangrove detritus.

However, the proportion of carbon utilised within the system is still debatable. It depends on the vegetation structure of the mangroves and the types of local organisms that inhabit the mangrove systems.

2.3. Dynamic of mangrove sediment

On average the sediment of South Australian mangroves typically consist predominantly of quartz, carbonate clay and shell fragments of Foraminifera and diatoms that contribute to the detrital pool, although some local variation does occur (Butler *et al.*, 1977). Generally, mangrove soils are characterised by highly anoxic, sulfidic mud due to predominance of clay and silt with high total organic carbon from the decomposition of litter. Most biochemical processes in mangrove sediments occur under anaerobic conditions which result in less efficient break down of organic matter (Machiwa, 1998) and result in excessive production of sulphides. The reduction of sulphide compounds is important in making sediment suitable habitat for infauna, because sulphide ions are toxic to most aerobic species. Some of the bacteria which are responsible in reduction of sulphide are the filamentous *Beggiota*, sulphur bacterium *Chlorobium* and *Chromatium* (Alongi, 1998). The concentration of sulphide correlates with seasonal changes, the rate of benthic activities and physical transport process within the sediment (Kristensen *et al.*, 2000)

Mangrove sediment is predominantly clay and silt. Clay and silt have the capacity to bind other material through electron exchange. This makes mangrove effective for filtering heavy metal and nutrient pollution (Harbison, 1986b; Tam and Wong, 2000). Yet, Mackey and Mackay (1995) studied the bioavailability of toxic metals within sediment by examining acid volatile sulphide (AVS), as a measure of metal concentration in mangrove sediments. They found that AVS concentration was not correlated with the proportion of clay and silt in mangrove sediment.

Vertical examination of mangrove sediment shows a grey transition layer between the oxygenated and the anoxygenated black layer. The grey layer area marks rapid change of redox potential over depth. This has been called the redox potential discontinuity layer or RPD (Gray, 1981). In fine sediments, like most mangrove sediments, the RPD lies close to the surface and may change seasonally, depending on the accumulation of sediments (Rosenberg *et al.*, 2001). The redox potential in mangrove forest will range from -200 mV to +100mV due to biotic activities within sediments (Machiwa, 1998) such as bioturbation by infauna and translocation of oxygen to plant breathing roots (Boto and Wellington, 1984). This claim was supported by Mackey (1993) that reported the role of aerial root in modification of Eh pattern in the soils of *Avicennia germinans* and *Rhizophora mangle* mangrove forests.

Mangrove sediments contain a rich mix of particulate and dissolved organic material derived from various autochthonous (original inhabitants) and allochtonous (inhabitants from out side) sources, which provide habitat for macrobenthic invertebrates (Alongi, 1998). Most organic material is concentrated in the top several centimetres and is gradually depleted at depths. This has resulted a homogenous distribution of particulate matter due to recycling processes by benthic organisms and rapid bacterial colonisation (Johnson, 1977). This vertical change may be disrupted by erosion, suspension and redeposition of sediment (Johnson, 1967; Rhoads and Young, 1970; Machiwa, 1998). The amount of dissolved organic carbon in mangrove sediment shows a zonation in pattern with lower concentrations toward the seaward side (Machiwa, 1998). This might suggest that particulate matter increases with increasing protection from current and wind. A study reported that dissolved organic carbon in mangrove sediments were lower compared to that found in salt marshes sediments (Holmboe *et al.*, 2001). However other variables also determine the amount of organic material including; above ground biomass, the rate of litter fall and litter flush out, which is regulated by wave and tidal action and also the microbial decomposition activities within the mangrove systems.

Sediments have an important role in determining the type of infanual assemblages. They serve as food source for deposit feeders and may act as a structuring agent in soft- substratum communities that affect the complexity of density dependent species within infaunal communities (Briggs *et al.*, 1979; Whitlatch, 1980). Other aspects contributing to habitat complexity such as geomorphology and vegetation structure are also critical factors, in determining the diversity and density of infauna communities from one place to another.

3. Infauna associated with mangrove systems

3.1. Definition

Benthic infauna includes animals which live in or are associated with sediments for part or all of their life. They may be sedentary or mobile, and often are restricted to the upper part of the sediments profile (Sasekumar, 1974; Hutchings and Saenger, 1987). The commonest animal groups are annelids (polychaetes and oligochaetes), arthropods (insects and crustaceans) and molluscs (gastropods and bivalves). Their body forms are robust to allow burrowing behaviour. They have remarkable adaptations to the wide range of environmental changes that often take place in just a few mm (Snelgrove, 2000). Considering body size, benthic infauna can be separated into macrofauna (> 300 µm), meiofauna (44-300 µm) and microfauna (<44 µm) (Snelgrove, 1999), although there is some controversy around the definition of these size categories. For this study, infauna were defined as those animals retained on 0.5 mm mesh, which is effective in retaining the common mangrove animals including the juveniles which may dominate some sampling seasons (Table 1.1).

Table 1.1. Percentage of various animals retained on graded mesh screen sieve.

Taxon	Screen diameter1 mm	Screen diameter 0.5 mm	Residue
Nematoda	0	1.5	98.5
Nemertea	69.2	100	0
Polychaeta	51	94.3	5.7
Crustacea	17.6	52.9	47.1
Mollusca	87.5	100	0

After Gray (1981)

Functionally, Wildish and Kristmanson (1997) differentiated benthic infauna based on their feeding behaviour. Their categories are :

1. Suspension feeders are benthic infauna, which feed by capturing seston that is suspended in and transported by seawater flow. Seston may contain detritus, micro algae, bacteria, small animals and sediment particles. Animals can be passive suspension feeders if they capture the food

directly form the surface, or active suspension feeders if the seston is pumped by a ciliary or muscular pump to the capture surface.

2. Deposit feeders are benthic animals, which ingest the seston that have already been deposited after transport by seawater.
3. Carnivores are benthic animals that feed other small invertebrates.
4. Omnivores are benthic animals which feed on plant material such as micro algae and bacteria and also other small benthic animals where they abundant.
5. Algal scrapers feed on sacrificial algal material.

3.2. The role of benthic infauna

Benthic infauna assemblages are known to have an important role in term of energy utilisation in the mangrove systems through the decomposition process. This process is critical, involving bacteria, fungi and benthic invertebrates. The decomposition process in mangrove sediment systems involves transformation, assimilation and conversion of chemical materials, as follows (Alongi, 1998):

1. Transformation of dead plant materials from mangrove trees into dissolved organic material via the desiccation process by leaching of soluble compounds such as sugars and simple tannins.
2. Assimilation of organic material by microbial agents such as bacteria, algae, fungi and protozoa via hydrolysis from their extracellular enzymes.
3. Conversion of soluble compounds into microbial growth produces rich nutritious particles that are then grazed by nematodes and other small invertebrates.

The process of decomposition is dependant upon several factors, including rate of primary productivity, climate, detritus composition, species composition of decomposer and abundance of consumers (Hutchings and Saenger, 1987; Chapman and Underwood, 1995). The rates of bacterial production in Australian mangroves are amongst the highest recorded for aquatic sediments (Alongi, 1998).

Benthic infauna are good indicators for predicting the ecological status and trends in the estuarine environment because they are relatively sedentary within the sediment, the water sediment interface and the deeper sediments (Engle and Summers, 1999). Environmental changes can be related to the structure of benthic infauna communities by assessing the benthic diversity, the ratio of long-lived to short-lived species, the biomass, the abundance of opportunistic species and even examining the trophic and functional structure of the communities. Yet the framework for assessing the healthiness of mangrove systems using benthic infauna would presumably be complicated. This is because natural variations in the systems such as salinity and latitude, which affect the diversity of mangrove distribution, will also, affect the structure of benthic assemblages. According to Hutchings (1985) benthic diversity falls with increasing salinity and increases with decreasing latitudes.

Benthic infauna also have a role in restructuring the sediment and subsequently also reshaping the community of organisms which reside in the mangrove habitat. They have often been called ecosystem engineers (Rhoads and Young, 1970). This change can be observed through their biological activities such as burrowing and feeding behaviour. Burrowing activities can improve sediment aeration which can alter pore water sulphide and ammonium concentration, which in turn provides a positive effect on mangrove growth and other heterotrophs (Snelgrove and Butman, 1994; Smith, 1996). Unfortunately, their burrowing may also result in the sediment becoming unstable and easily eroded, increasing the rate of water logging within the sediment (Rhoads and Young, 1970) and a reduction in particle size leading to finer sediment particles as a result of material recycling (Johnson, 1977). The faecal pellet of deposit feeders may result in compaction of sediment, which in turn reduce the ingestible particles organisms due to reduction of suitable type particles (Rhoads and Young, 1970; Whitlatch, 1981; Hall, 1994; Snelgrove and Butman, 1994).

The structural complexity of sediments within mangrove systems makes this habitat unfavourable for many benthic species because of variability in salinity, temperature, exposure and oxygenation. Hence, the diversity of the infauna community in mangrove areas is often less that in adjacent non vegetated areas (Snelgrove, 2000). Previous works (Hutchings and Saenger, 1987; Reise, 1991; Sheridan, 1997) had found that infaunal communities from mudflat areas were richer when compared to the infauna from mangrove sediments. Alongi (1998) confirmed that most mangrove sediment has a lower density of protozoan, meiobenthos and macrobenthos compared to salt marsh and tidal flats due to competition in oxygen demand between aerobic bacteria and other aerobic organisms.

The structure of infaunal communities in mangrove systems is dictated by several biological and physical factors, for instance mangrove species diversity (Wells, 1983; Schrijvers *et al.*, 1998), tidal heights (Clarke and Hannon, 1970), elevation and plant cover (Netto and Lana, 1997; Sasekumar and Chong, 1998) and sediment grain size (e.g. Macfarlene and Booth, 2001). Although infaunal studies are most extensive in subtropical and tropical mangrove areas, and therefore are not directly comparable to South Australian temperate mangroves, they do provide a good comparison in the general assessment of environmental factors relating to characteristics of infaunal assemblages.

4. Aims and objectives

The South Australian mangrove estuaries are relatively unique and different from other Australian temperate mangroves or other temperate mangrove in the world. The mangroves in South Australia form a continuum of intertidal communities with only a single mangrove species *Avicennia marina* var *australasica*, growing in the harsh conditions typical of Mediterranean temperate environment, located in inverse estuaries, having semi diurnal tide cycles. These environmental characteristics are likely to affect the ecological process of organisms inhabiting these systems including the benthic infauna. To date however, research in South Australian mangrove system has been less extensive compared with other marine habitats (e.g. seagrasses). Importantly, there has been no comprehensive research on infauna of these mangrove systems.

To overcome the lack of infauna data, a study has been conducted to understand the nature of benthic infaunal communities in South Australian mangrove estuaries. This study included an examination of the assemblages and also the biological function of infauna. In particular, the objective of the study were :

1. To quantify the structure of infaunal communities through an analysis of the spatial and temporal variation in the community structure as well as the distribution patterns of dominant taxa.
2. To observe the possible effect of the geomorphological factors such as tidal height and sediment characteristics on the infauna assemblages.
3. To examine to what extent the sediment characteristics regulate the distribution of benthic infauna.
4. To compare the characteristics of infaunal of the mangrove habitats with infaunal communities of adjoining habitats including both mudflat and samphire systems.
5. To make a taxonomic assessment of common infauna, particularly polychaetes, in order to gain a knowledge of the biological features of the infauna of the mangrove systems.

Understanding the dynamic of infaunal assemblages within the mangrove ecosystem is essential to conserve and manage the existence of mangroves and maintaining the sustainability of their important role in coastal production.

Chapter 2 The Biology of Benthic Infauna

1. Introduction

Infauna benthic assemblages in mangrove systems are made up of several taxa such as polychaetes, molluscs, crustaceans, sipunculans, nematodes and insects. Their individual number is approximately proportional in order to maintain the biological balance and inter relationship within the communities. They are restricted to the upper layer of sediment and their occurrence within sediment mangrove may be limited by fibrous root structure. They have different lengths of periods in their life cycles. They also have various feeding behaviours ranging from grazers (crustaceans and molluscs), deposit feeders and suspension feeders (polychaetes and certain bivalves), herbivores (such as crabs) and predators. Their burrowing behaviour penetrates the substrate and increase oxygen level within the substrate, which in turn promotes the microbial process to produce food for resident organisms. As they are detritus dependant, they have a critical role in the decomposition process and sustaining trophic function. Certain infaunal taxa can be considered as environmental indicators through their defaunistic or opportunistic life style. Hutchings and Recher (1981) noted about the lack of research on the infauna of mangroves and suggested a well planned and long term collection system throughout Australian mangroves.

The research focuses on mangrove with a comparison to the mangrove edge habitat of samphire and mudflat as typical of South Australian mangrove environments. Due to that the next paragraphs the biology of common taxa will will be briefly addressed in mangrove environments rather than common temperate wetlands.

2. Polychaeta

Among the marine benthic infauna, polychaete worms are usually numerically dominant. They are widely distributed across marine sediment habitats and can be found in deep sea, supra-tidal to intertidal habitats and even in freshwater. Hutchings and Saenger (1987) reported that polychaetes were abundant and diverse across Australian mangrove sediments and may contribute significantly to structuring infaunal communities. Several characteristics which contribute to the high population build up of polychaetes are low dispersal ability, a prolonged reproduction season, being simultaneously hermaphrodite and self fertilised and rapid development rate (Glasby *et.al.*, 2000). Polychaetes are also widely used as an indicator of marine environmental quality and as a model in marine invertebrate toxicology, such as organic contamination (Reish and Gerlinger, 1997). Currently 11 members of common polychaetes species have classified as being bioindicators of anthropogenic pollution. They include, members of the families Capitellidae, Spionidae and Cirratulidae (Fielman *et al.*, 2001).

In the infaunal community, the position of polychaetes is central. As they are detritus dependent organisms, their behaviour influences distribution of sediments through their feeding and burrowing activities. This process leads to restructuring sediment to become more favourable for other organisms to live in, or alternatively become unfavorable for certain larvae to settle because the sediment becomes unstable and easily eroded. Considering the importance of polychaetes as substrate organisms, Woodin (1999) characterized the role of polychaetes as defaunistic organisms, because they can inhabit a habitat or substrate which can not be inhabited by other infauna organisms. She suggested that their behaviour could maintain the biogeochemical processes within sediment, making the habitat more favourable for other organisms.

Polychaetes exhibit a variety of lifestyles, such as the symbiosis between Siboglinids and bacteria, the parasitism of the Nautiliniellidae, or the obligate commensalisms between Serpulidae with living coral (Rouse and Pleijel, 2001) and free living forms. Feeding modes can be grouped into selective deposit feeders, non-selective deposit feeders, raptorial feeders and filter feeders. They also have various forms of feeding apparatus and these structures are used as a basic criterion for polychaete identification and also feeding behaviour is also useful for ecological assessment (Dauer *et al.*, 1981; Rouse and Pleijel, 2001).

Polychaetes are an important part of the trophic system in mangrove sediment communities, and their existence must be taken into account in determining the community energy budget. Examination of the gut content of several polychaetes specimens revealed quantities of mangrove detritus (Odum, 1971; George, 1984). Fauchald and Jumars (1979) studied the polychetes feeding guild based on food type, feeding habits and locomotory pattern in an effort to evaluate the biological function of polychaetes**.** Several polychaetes, such as Spionidae, are capable of switching their feeding behaviour from suspension feeding to filter feeding. This is considered as an opportunistic strategy when they live in polluted systems in which food availabity is unpredictable (Ferner and Jumars, 1999)**.**

Polychaetes exhibit both sexual and asexual reproduction with various reproduction strategies. Asexual reproduction of polychaetes involves subdivision of the body, which is capable of regenerating the missing part of their body in a process called schizotomy. The process of schizotomy consists of paratomy and architomy. If the separations from parent stocks produce a complete and recognizable individual this can be called paratomy, while architomi is simple fission or fragmentation of the body without prior cephalization (Rouse and Pleijel, 2001).

Sexual reproduction of polychaetes shows a wide range of reproductive and development modes. Wilson (*in* Rouse and Pleijel, 2001) identified 17 modes of sexual reproduction based on type of larva and development. They could be dioecious where male and female are separate individuals, but some of them are hermaphroditic. Generally, the life cycle of polychaetes begins with spawning of fertilized eggs by mature animals into the water column. The eggs then develop into planktotrophic larvae in the pelagic environment for weeks or months. Certain species can remain in the larval stage for a long time, while others have short larval stage. Where suitable substrates are found, the larvae then settle and metamorphose into juveniles.

Finding a suitable susbstrate is critical because this will affect the recruitment process of certain polychetes, which in turn determines the population dynamics of polychaetes. Adult polychaetes often create unstable substrates as a consequence of their burrowing behaviour which makes it more difficult for larvae to settle (Rhoads and Young, 1970). Periodic disturbances can lead to a restructuring of the community because of the effect on larval settlement and recruitment (Farnsworth and Ellison, 1996). Thus larvae settlement, sediment grain size and the presence of adults will contribute to the nature of the polychaete communities. While recruitment process of polychaetes in mangroves has not been substantiated yet, Hutchings (1984) worked in Australian coral reefs reported that recruitment success of polychaetes was determined by variation in fecundity, the supply of larvae, number of successful larval settlements on substrate and post settlement mortality which varies considerably between years and sites.

In mangrove habitats, polychaetes regularly experience periods of hypoxia, particularly during low tide. (Warren, 1984) reported that intertidal polychaetes, cope with this situation by a combination of behavioral, physiological and biochemical adapations which include:

1. aerial respiration which is effectively facilitated by branchia during inundation time.
2. burrowing behavior resulting in an irrigatory current and retention of burrow water, so oxygen can be maintained where supply by natural flow is lacking.
3. facultative anerobiosis using the respiratory pigment erythrocruorin which has high oxygen affinity and may function as an oxygen storage pigment.

In laboratory conditions *Capitella capitata* (Capitellidae) showed more than 50% survival after 35 days at a dissolved oxygen of 0.8 ppm (Warren, 1976), *Terebella lapidora* (Terebellidae) was able to survive for 6 days and *Cirriformia tentaculata* (Cirratulidae) survived 3 days under hypoxic condition (Warren, 1984). This adapatation may also be found in temperate mangrove as Hutchings and Recher (1982) stated that most of species polychaetes occurring in temperate mangroves also occur in other estuarine habitats.

Polychaetes are also adapted to vary their activity with tidal and seasonal cycles. As such, some polychaetes can eliminate their activity and reduce their metabolic rate so that feeding and reproduction cease. Low tide may be considered as resting phase for polychaetes. The maximum activity, including feeding and mating, will occur during high tide. Being active during inundation is a strategic behaviour for polychaetes to avoid dessication. When the tide recedes polychaetes will burrow into wet sediment aided by the semi liquid nature of the substrate and then cover their bodies with mucus. The mucus, which is excreted by the body wall tissue, will bind sand and other sediment particles, which protect the worms from water loss and desiccation. In addition, their burrowing can also protect them from predators which are the main biological factor in controlling polychaete populations (Rainer, 1984).

Living in temperate mangrove sediment, organisms have to cope with a wide fluctuation of salinity due to extensive evaporation. Polychaetes occur in euryhaline benthos and have a wide range of salinity tolerance. They are usually osmoconformers in that their internal salinity level is adjusted to that of external water (Anderson, 1994). Lana *et al.*, (1997) studied the polychaetes of Paranagua Bay, Brazil and detected a low degree of spatial overlapping with reference to specific haline regimes. They suggested that the pattern was mainly defined by salinity and environmental energy gradients and only secondarily to the ability of polychaetes to discriminate among unvegetated areas, saltmarshes and mangrove swamps. Hence, activity during inundation time could be interpreted as another strategy for coping with increasing salinity during exposed time.

Salinity tolerance varies among polychaetes species. For instance, certain *Capitella* sp. typically found in changeable environments such as mangrove estuaries where salinity is subject to sudden change on a seasonal basis by developing a population equilibrium methods (Glasby *et al.*, 2000). During unfavorable times polychaetes will reduce their population in order to limit intra specific competition and when favorable conditions return the population expands to reach a new equilibrium. Another study reported that the *Capitella* group was the only polychaete found in the saltpans of Portugal where salinity ranges from 29-112 ppm (Amaral and Costa, 1999). From South Australia, it was reported that *Manayunkia athalasica* a small polychaete from the family Sabelidae, can thrive in ephemeral saline lake sediments in the Coorong which have salinity level between 27-95 $^{0}/_{00}$ (Geddes and Butler, 1984). *Manayunkia* is also found as filter feeders in saltmarsh habitats at northern Florida where salinity ranges between 20-30 $^{0}/_{00}$ during inundation time. They make up most of the annelid biomass, together with Capitellidae (Teal, 1971). Salinity apparently effects the population dynamics of polychaetes in various ways through their reproduction pattern (Neuhoff, 1979; Fong, 1991; Hsieh, 1995), growth rate (Pechenick *et al.*, 2000) and recruitment process (Giangrande and Fraschetti, 1993).

The several environmental factors mentioned above will likely dictate the structure of infaunal communities in South Australian temperate mangrove environments. Hutchings and Recher (1982) stated that most species of polychaetes occurring in temperate mangroves also occur in other estuarine habitats, as polychaetes are common taxa in mangrove estuaries. Details of ecology and biology of certain polychaetes will be assessed in a single chapter in this thesis (Chapter 6).

3.Mollusca

Molluscs are another group of benthic fauna which can be found in mangroves, salt marshes, mudflats and seagrass. Hutchings and Saenger (1987) predicted that the infauna in mangroves was possibly more diverse than that in salt marshes considering the variety of molluscs found in mangrove areas. Most of the molluscs that inhabit mangrove forests are epifauna rather than infauna (Wells, 1984; Jiang and Li, 1995). However, they can be considered as epifauna or infaunaand Hutching and Recher (1981) mentioned that certain gastropods thet are substrate epifauna prefer muddy substrates, burying themselves in mud or hiding under debris. This type of epifauna mollusc, when encountered in this study, will be defined as infauna due to degree of association with the mangrove sediments.

Hutchings and Recher (1981) reported large number of bivalves as the major infaunal molluscs in Australian mangroves, even though local species variation and abundance might occur. Possibly the nature of mangrove sediments influence their abundance and distribution. For instance, the density of mangrove roots may limit their burrowing activities, the acidity and anoxic nature of mangrove soil is critical for their physiological processes and the degree of openness of mangrove ground surface make them potential predator targets (Jiang and Li, 1995).

The common classes of molluscs that live in estuaries are gastropods (Prosobranch, Opistobranch) and bivalves (Lamellibranchiata). Most molluscs have shells with calcium carbonate as the dominant materials. Shell dry weight of some gastropods and bivalves may be up to 35 % and 70% of organic material, respectively (Pechenick, 1996). Molluscs are haemocoelomic and burrowing involves a flexible shifting of blood under the control of a complex musculature (Pechenick, 1996). Thus molluscs prefer wet areas or the seaward side where sediments are soft and higher in oxygen.

Reproduction in molluscs can involve protandric hermaphroditism where the sex of a single individual changes from male to female with age, or alternatively is simultaneous hermaphroditic where the gonads (called ovotestis) of single individuals produces egg and sperm simultaneously (Pechenick, 1996). All pulmonate gastropods are simultaneous hermaphrodites.

Gastropods are generally grazers and can consume significant amounts of mangrove detritus, bacteria and fungi which accelerate the decomposition process within mangrove systems. *Rhizophora apiculata* leaves may decay within just a week if subjected to the shredders such as molluscs, crabs and amphipods, but decay will take up to four months if only carried out by micro-organisms (Saenger, 1994). It was reported that the gastropod *Terebralia polustaris* could graze up to 0.22 ton/ha/year of fresh fallen of leaf mangrove material (Saenger, 1994). The decomposition rate will vary with season and mangrove species.

The distribution of molluscs shows a zonation pattern, which is regulated by several biological and physical factors across the intertidal zone. Many studies have revealed that tidal heights and predators were common factors controlling the distribution pattern of molluscs (Jiang and Li, 1995; Roach, 1998; Richards *et al.*, 1999).

The fate of intertidal organisms is determined by tide. The time of immersion may shape the habitat both on a small scale and a regional scale. Molluscs tend to be more abundant in the seaward margin than landward margin of mangrove areas because of several factors. Salinity would be lower due to regular inundation, food would be more abundant because of more organic material settling, and substrates also have higher oxygen content. Wells (1984) found a higher biomass, density, and diversity of molluscs on the seaward margin of mangroves and further suggested that that much of their secondary production may take place outside of the mangrove trees zone.

When the tide ebbs, some gastropods would attach to the pneumatophores or climb up the trunk of the trees to avoid being washed out of the mangroves and be exposed to heat. On the other hand, bivalve molluscs will burrow into the sediment of mangroves to avoid dehydration (Hutchings and Recher, 1981). So selection of soft and wetter sediments at the seaward side of mangrove forest by molluscs and areas with pneumatophores and shade by gastropods can be considered as a selection of less stressful microhabitats. This selection is a behavioural adaptation used by, for instance, temperate snails in order to maintain their internal physiological processes (Jones and Boulding, 1999). Blanco and Cantera (1999) reported there was a different distribution among 5 species of mangrove gastropods which relate to vertical intertidal zonation.

Predation is another biological factor which helps determine the structure of infauna communities, including molluscs. Molluscs are potential prey for other higher trophic organisms such as fish and crabs. Predation can cause reduction in biomass and abundance, changes in the size structure of prey populations and hence changes in the community structure of permanent residents (Raffaelli and Hawkins, 1996), even though the effectiveness of predation may be limited by habitat complexity and prey size structure. A study in NSW mangrove and saltmarhes complexes reported that *Salinator solida* populations varied significantly more with height on shore and with physical complexity in saltmarshes than in mangroves which offered them more opportunity to avoid predators (Roach, 1998). Furthermore, a caging field experiment suggested that the reduction of density of the bivalves *Mytilus balthica* and *Cerastoderma edule* which affected the spatial and temporal variation of these intertidal bivalves, was due to prey size selection by the crab predator *Carcinus maenas* (Richards *et al.*, 1999).

The occurrence of pneumatophores is significant for some species of molluscs. As a hard substrate for attachment, they may protect molluscs from being washed away and from possible predators, besides also providing microhabitats for certain mangrove fauna. Pneumatophores localise fine materials which consist of detritus, algae and other organic substances. The removal of algae from pneumatophores leads to a reduction of gastropods, because algae is a primary food resource for many grazer, including *Salinator solida* (Skilleter and Warren, 2000). An algal mat is also a prefered microhabitat for snails in controlling their internal temperature because its cooler (Jones and Boulding, 1999). Dense algal mats can also cover the snails and provide protection from local predators, such as *Tetractenos hamilton* (toad fish) (Skilleter and Warren, 2000).

Intertidal gastropods spend about 50% of their lifetime in microhabitat refuges and less time in foraging (Jones and Boulding, 1999). This means that there is a trade off between time spent for foraging and time spent in microhabitat refuges. The microhabitat provides a barrier of movement and mediates the interaction of species within the community, even though the age specific response may overlap in determining suitable and unsuitable microhabitate (Crowe, 1996). In ecological terms, selection of microhabitats will create a state dependent behaviour of organisms and the criteria of microhabitat arrangement will differ among species and with age. In turn, microhabitats will dictate the spatial and temporal variation of infauna which will contribute to the degree of complexity of the mangrove systems.

4. Crustacea

Another important infaunal in mangrove systems are crustaceans. Some Crustaceans are mobile benthic euryhaline animals able to survive a wide range of salinity levels. Their osmoregulatory system maintains their internal salinity level constant through passive osmotic mechanisms (Pechenick, 1996). Their role in maintaining energy cycles within the mangrove systems is significant. They can retain nutrients and energy by consuming leaf litter, increasing the leaf degradation and mineralisation rates by shredding the leaves. Their burrowing activity can induce oxygenation within the substrate. The further review will emphasized mainly in infaunal crabs as permanent resident in Australian mangroves which Ocypodidae was the most common crabs family (Hutchings and Recher, 1981)

Unlike molluscs which are rare or absent in the mangrove tree zone, infaunal crustaceans such as crabs may found dominant in tropical mangrove areas and also in mudflats as reported by Wells (1984) and Sasekumar and Chong (1998), although they will be less visible during the day as some species are nocturnal. Wells (1984) studied the distribution of macro-crustaceans in northwestern Australian mangroves and discovered a higher density and diversity of crustaceans in vegetated areas than in unvegetated areas.

Crabs can be considered one of the permanent residents of mangrove systems. This group is responsible for energy exchange in mangrove estuaries. Herbivorous crabs chew significant quantities of leaves while carnivorous or omnivorous crabs feed on detritus and other macro benthic animals. Wolf *et al.* (2000) stated that in mangroves the food intake of herbivorous mangrove crab *Ucides cordatus* was 1120 gr/m$_2$/year while for omnivorous fiddle crabs was 1375 gr/m$_2$/year. Several studies reported crabs as major predators on groups of molluscs and polychaetes (Roach, 1998; Richards *et al.*, 1999). This would suggest that this group are detritus dependent organisms.

Like other intertidal animals, crabs are also sensitive to zonation, as a result of habitat partitioning. Thus habitat modifications may have great influence on the presence of crustacean's assemblages. Kelaher *et al.* (1998 b) and Skilleter and Warren (2000) reported that the removal of pneumatophores to allow boardwalk development reduced the abundance of crabs due to reduction of their potential food.

As infaunal organisms, crabs live in permanent and semi permanent burrows in the mud. Fiddler crabs (common mangrove crabs) may often penetrate sediment to a depth of 30 cm depth. Their burrows are curved to an L shape which efficiently traps oxygen, nutrient and water. Hence substrate type may be another consideration for certain crabs in habitat selection within mangroves. Sasekumar (1974) reported on the role of sediment type, tidal exposure and food availability in regulating fiddler crabs distribution in Malaysian mangroves.

Living in mangrove environments, many crustaceans demonstrate morphological adaptation, such as the presence of a branchial chamber, which can act as lung (Bock, 1980; Raffaelli and Hawkins, 1996). This chamber holds water that crabs regularly pump out to get oxygen. The need to maintain the water in the chamber could explain the zonation of crab distributions on the basis of tidal height. Certain nocturnal species (ghost crabs or ghost shrimps) are active during the night when the tide comes up (Hutchings and Recher, 1974). This is an attempt to maintain a constant source of water in their branchial chamber, for feeding and also for copulation. The releasing of free-swimming larvae of ghost crabs coincides with high tide.

5. Insecta

Insecta is the richest and most diverse taxa in the animal Kingdom, however comparatively few are considered marine inhabitants. Certain species of

Hemiptera (true bugs) Coleoptera (beetle) and Diptera (flies) may spend almost their whole life cycle in a marine environment, while most cannot. Cheng and Frank (1993) defined a marine insect as an insect that spends at least one of its developmental stages habitually in a marine habitat. They dwell in lagoons, rock-pools, tidal marshes and mangrove flats. They may or may not require adaptation. The most common adaptation of marine insects compared to the terrestrial species is that the marine species are wingless.

Most marine insects reproduce sexually, although groups such as Collembola (subclass Apterygota= primitive insect) reproduce by parthenogenesis, which is an unusual method among insects (Greenslade, 1991). The ontogeny of insects fall into two groups. The Apterypota where juveniles resemble miniature adults, and Exopterygota where juveniles bear little resemblance to adult and metamorphose to a pupal stage before becoming adult.

Certain species of marine insect such as dipterans flies are widely distributed among different marine habitats, while others are restricted in certain marine habitats (Table 2.1).

Among estuarine habitats, mangroves provide the most preferable habitat for marine insects followed by saltmarshes. This may be because the regular inundation, vegetation, ground surface contours and pneumatophore networks produce semi permanent ponds as breeding places for certain mangrove insects.

This study was limited to South Australian temperate mangroves in particular and this review consists only of relevant information about insects encountered in the study which include collembolans (spring tails) and dipterans. Australian mangrove insects have received little attention in mangrove ecology research projects (Hutchings and Saenger, 1987). Studies have concentrated more on insects which have economical or medical significance, such as mosquitoes, bees or termites.

Table 2.1. The occurrence of insect marine by taxonomic grouping and habitat (P=Pelagic, C= Coastal water, I= Intertidal, M= Mangrove, S= Saltmarsh).

Taxonomic group	Common name	P	C	I	M	S
Subclass Apterygota :						
Collembola	Springtails	-	+	+	+	+
Microcoryphia	Jumping bristletails	-	-	+	+	+
Thysanura	Bristletails	-	-	+	+	+
Subclass Pterygota :						
Odonata	Dragonflies	-	-	+	+	+
Phasmotodea	Stick insects	-	-	-	+	-
Orthoptera	Grasshopper, crickets	-	-	+	+	+
Mallophaga	Chewing flies	+	+	+	+	+
Anoplura	Sucking flies	+	+	+	+	+
Hemiptera	True bugs	+	+	+	+	+
Homoptera	Cicadas, aphids	-	-	+	+	+
Coleoptera	Beetles	-	-	+	+	+
Trichoptera	Caddisflies	-	-	+	+	+
Diptera	Flies	+	+	+	+	+
Hymenoptera	Bees, wasp, ants	-	-	+	+	+

After Cheng and Frank (1993)

Dipterans are one of the insect groups that have wide distribution compared with other marine insects. A few species of Diptera have submarine tube building larvae but surface dwelling adults (Cheng and Frank, 1993). One family which is commonly found in Australian mangrove and the larval stage of which can be considered as infauna is Ceratopogonidae or biting midges (Hutchings and Saenger, 1987). They occur exclusively above mid tidal level. The factors that control their zonation are tidal heights, substrate composition, water movement and ancillary flora and fauna (Reye pers. com. *In* Hutchings and Saenger, 1987).

Another littoral insect group frequently encountered in mangrove areas are Collembola or springtails. Collembola are tiny insects with their body size rarely exceeding 5 mm. They are a group of primitive insects with no wings and no larval stage (Greenslade, 1991). They have a worldwide distribution and may be extremely abundant in places where other invertebrates are hardly able to survive. In Australia, the number of individual Collembola can range from 2000 to 30,000 per m^2, depending on habitat, season and climate. Harsh arid environments produce the lowest density of collembolans (Greenslade, 1991). Dealing with intertidal environments, marine collembolans are able to avoid desiccation because of the impermeability of their integument and can obtain water by everting the ventral tube vesicle into soil water (Witteveen and Joose, 1987).

In terms of diversity, it was predicted that from 132 genera of Collembola currently identified, only 27 are Australian endemics (Greenslade, 1991). The number may alter since generic revisions were found in some families. One genus, which is restricted to the intertidal zone is the genus *Pseudanurida* (Family Neanuridae). They are pseudomorph collembolans and can be easily recognised by the combination of long furcula and styliform mouth parts which are not found in other collembolans (Murphy, 1971). In mangrove forests, *Pseudanurida* may be found aggregated, possibly hiding inside air bubbles among the roots when the tide washes in. The air bubbles may act not only as an oxygen store but also as a compressible of external gas gill which lasts three time longer than the of oxygen the insects could be stored (Zinkler *et al.*, 1999). When the tide recedes, the insects will move progressively into the lower part and start feeding. The foraging behaviour and circa- tidal rhythm orientation allow them to migrate from the up-shore to the down-shore horizon (Manica *et al.*, 2000).

As collembolans are littoral foragers, their distributions are likely to be limited not only by tidal height, but also salinity and food availability. Witteven and Jones (1987) noted that the salinity level dictated the distribution of *Anurida maritima* (Neanuridae), *Isotoma viridis* (Isotomidae) and *Hypogastura sp.* (Hypogasturidae). Notwithstanding bias with the site selections, e Sterzynka and Ehrnsberger (2000) reported the distribution of *Archisotoma sp.* (Neanuridae) within saltmarsh habitats in German North Sea were related to the distribution of organic material.

6. Predictions

Mangrove infauna assemblages are made up by several taxa. Their abundance, the structure of their communities, their distribution patterns and their adaptation explain the way they utilise mangrove systems as a result of interaction between organisms and abiotic factors. As the mangroves are a transition habitat between terrestrial and estuarine mudflat, the infauna which are found in mangrove forests may also be found in other habitats adjacent to mangrove forests.

In South Australia, mangroves which are located in semidiurnal estuaries where high and low tides occur every 12 hours, tidal cycles may modify the behaviour the infauna. During inundation some species may seek refuge to the landward side of the mangrove, the saltmarsh habitats, while others may move to the seaward side to spawn or to feed. When the tide recedes foraging infauna may be found in the lower part, while others will burrow into the sediment to avoid desiccation. Morphological and behaviour adaptation to minimize water loss can be assumed as a life strategy for infauna in the mangrove habitat.

South Australian mangroves are situated in inverse estuaries where the salinity levels are mostly determined by seawater rather than freshwater influx. Prolonged inundation can reduce the salinity level in sediments. It is likely that salinity influences the infaunal zonation within the mangrove systems. Higher salinity within sediments may be found in the higher part of mangrove areas as a result of less inundation which in turn may regulate the distribution pattern of infauna. It is predicted that the low density and diversity may characterise the infaunal communites in the upper part of mangrove areas.

As mangroves are intertidal forests, tides may have a major influence in regulating the physical and chemical processes in mangrove sediments, including increasing air circulation within sediment which enhances nitrification and reduces harmful sulphate. Aggregation of the sediment particles and softer sediment provide access for infauna to burrow and modify drainage patterns within sediment which protect the burrowing infauna from dessication during sediment exposure. It is not clear whether similar infaunal community structure and distribution patterns exist in other temperate mangroves, as the information of infaunal ecology in South Australian mangrove systems is sketchy. The following chapters will examine the infaunal assemblages in South Australian temperate mangroves and consider how the heterogeneity of sediment conditions and biological interaction affect the infaunal communities.

Chapter 3 Response of Benthic Infaunal Assemblages to Spatial and Geomorphological Differences between three South Australian Mangrove Systems

Synopsis : The aim of this chapter is to quantify the community structure of infaunal organisms and how to examine the response of the infaunal communities to several environmental variables such as tidal gradients and sediment characteristics. Furthermore, it considers to what extent the pattern of community structure and the distribution of the infauna are maintained in relation to geographical differences of mangrove locations.

1. Introduction.

Infaunal organisms are involved in physical, chemical and biological processes in mangrove ecosystems. In most cases previous work has been conducted in tropical and subtropical mangrove areas, where mangroves form either open or closed forests made up of several species. Sasekumar and Chong (1998) for example, reported that several ecological parameters such as canopy cover and water content in sediments affected the density and composition of infaunal assemblages in Malaysian mangroves. Similarly, a study in Taiwan found that interactions between suspension feeders, deposit feeders and other organisms could maintain the structure of infaunal communities in mangrove systems (I-Jiunn, 1995). In addition, Dittmann (2001) and Sheridan (1997) suggested that the structure of infaunal assemblages was related to habitat characteristics which are regulated by tidal elevation, sediment type and vegetation structure. In subtropical mangroves, there was suggested that these environmental factors also control the infaunal distribution patterns (Netto and Lana, 1997; Roth and Wilson, 1998). A study of temperate mangroves in East Africa (*Ceriops tagal*) reported that biological interactions such as predation and competion for resources were important in structuring benthic assemblages (Schrijvers *et.al.*, 1998).

In tropical Australia, Wells (1983) found different characteristics of invertebrate assemblages associated with different species of mangrove plants such as *Rhizopora stylosa* and *Avicennia marina.* In temperate Australian mangroves, Chapman (1998) studied the spatial patterns of infaunal distribution related to the level of taxonomical resolution. Several studies have been conducted to study the changes in macrobenthic structures resulting from anthropogenic disturbances (Kelaher *et. al*., 1998a; Lindegarth and Hoskin, 2001; Macfarlene and Booth, 2001).

There have been some studies on the infauna associated with the grey mangroves *Avicennia marina* in temperate Australia. However, most of the research has focussed on certain individual taxa including barnacles (Michinton and Ross, 1999; Satumantpan and Keough, 1999), gastropods (Roach, 1998) and crabs (Kelaher *et al*., 1998b) . The focus on these taxa is likely to have been influenced by the perception that crustaceans and molluscs are dominant benthic taxa in mangrove forests in tropical, subtropical and temperate zones. At the level of community structure, Hutchings and Recher (1974) conducted research on the fauna of a temperate mangrove forest (Careel Bay, NSW) and commented that faunal communities in mangrove zones (which consisted of *Avicennia marina* var. *australasica* and A*egiceras corniculatum*), were richer in terms of species and individuals compared with salt marshes.

South Australian mangrove systems are typical of temperate Australian mangroves (Cann and Gostin, 1985) where extensive mudflats with patches of seagrasses can be observed on the seaward side. On the landward side mangrove fringes are backed up by salt marsh communities, low growing fleshy halophyte plants, commonly found in temperate regions as a result of climate factors that lead to accumulation of salt. This pattern in the distribution of vegetation is closely related to the tidal flooding pattern, soil salinity and water table fluctuation (Clarke and Hannon, 1970). South Australian mangrove forests form a fairly open forest with a simple canopy and consist of a single species *Avicennia marina* var. *australasica.* Most of the mangrove plants stand on calcareous substrates (Butler *et al*., 1975; I-Jiunn, 1995; Ferguson, 1986). The type of substrate in the mangrove forests maybe determined by several environmental factors such as the effectiveness of the roots of the vegetation in trapping sediment, hydrological factors, climate and nature of the local marine fauna.

The aims of the work presented in this chapter were to test the following hypotheses:

1. Geographical location is likely to affect benthic community structure.
2. There would be a zonation of infauna across the system which relates to the different habitat types such as mudflats, the mangrove forest itself and salt marshes.
3. Tidal height would have a major role in determining the infaunal zonation and lower tidal areas are likely have a high abundance and diversity compared with the upper intertidal areas.
4. Substrate characteristics are important in determining the distribution of benthic infauna in the mangrove ecosystems.

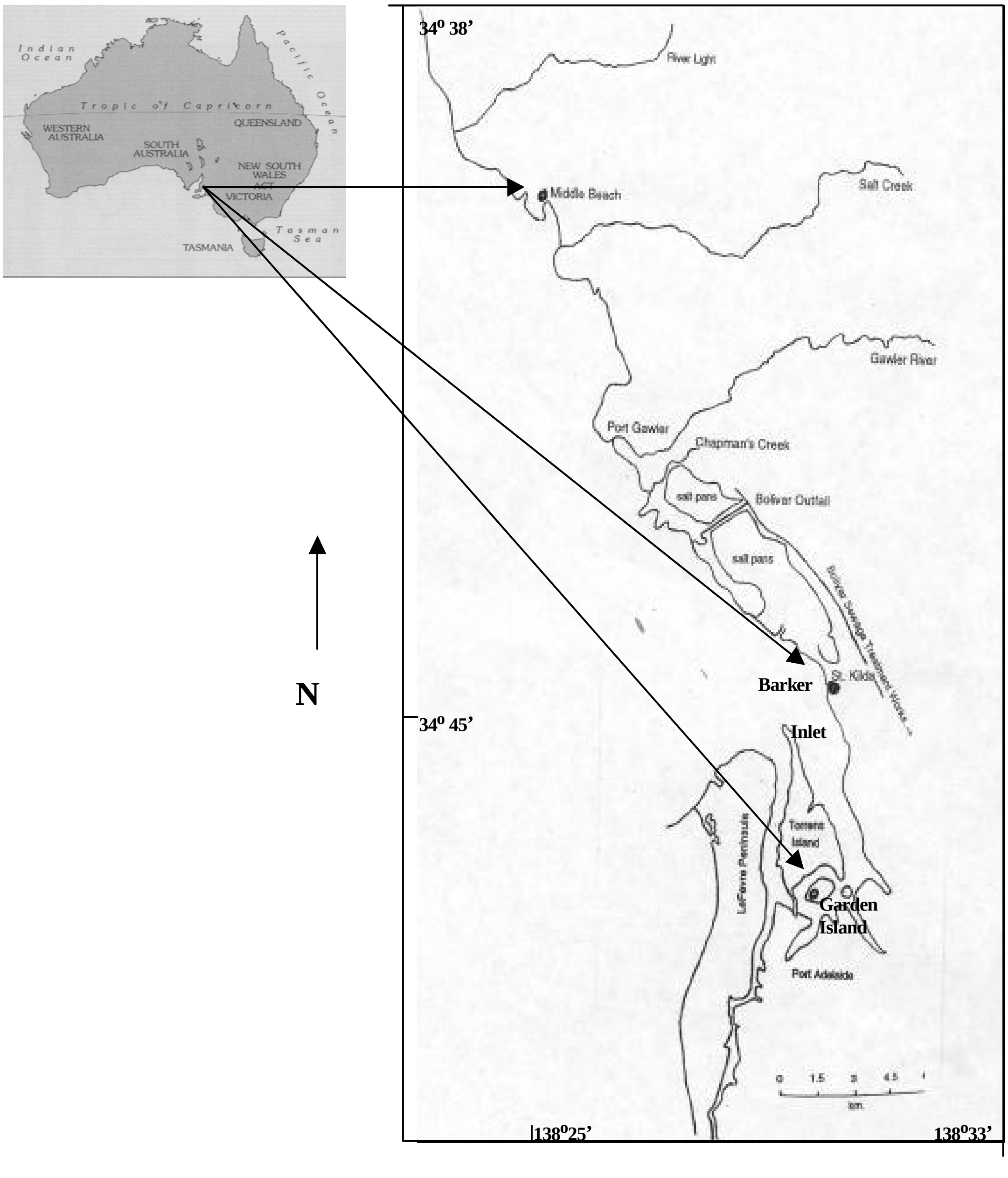
2. Materials and Methods

2.1. Study sites

Garden Island, Saint Kilda and Middle Beach were chosen as representative sites of South Australian temperate mangroves (Fig. 3.1)**.** These locations are situated on the eastern coast of the Gulf St. Vincent. This region of South Australia experiences a Mediterranean climate which is mostly hot and dry in summer, often reaching 40° C, and mild in winter with minimum temperatures around 5°C. The annual rainfall is 420 mm; there are occasional thunderstorms and heavy rain. The estimated evaporation is 1800 mm per year (Cann and Gostin, 1985). The tide is generally semi-diurnal with a mean spring tidal range of 0.6-3.5 meters (Burton, 1982).

Geographically, both Saint Kilda and Garden Island are located in the Barker Inlet Aquatic Reserve, while Middle Beach is located further north. Even though only a single mangrove species *Avicennia marina* var *australasica* (Duke, 1991) grows in these areas it shows morphological variation in size between different sites.

Figure 3.1. The study sites, showing the 3 locations of mangrove forests (Garden Island, Middle Beach and Saint Kilda).



Garden Island, 15 km north of the city of Adelaide, is located on the southern side of Barker Inlet Aquatic Reserve and is surrounded by a network of tidal channels. At the highest tide the mangroves and saltmarsh areas are submerged, while in the low spring tide the mudflats are exposed. The mangroves comprise an extensive mature forest with old mature trees being 5 to 6 meter high with dense cover. The area covers about 1200 hectares and it was suggested that landward expansion of *Avicennia marina* var *australasica* has produced a 2/3 reduction of adjacent saltmarsh habitats over the period 1979-1993 (Coleman, 1998). On the landward side, the mangrove forest is backed up by mixed samphire species, *Halosarcia flabelliformis, Sarcocornia quinqueflora* and *Sclerostegia arbuscula*. A causeway has been established in the middle of the mangrove areas to construct support structures for power lines. Industrial and sanitary landfill take place on Garden Island but there is no evidence that leachate from landfill operations has affected mangrove or samphire communities (Clyde, 1995). Torrens Island, another dense mangrove forest is close to Garden Island. Other human activities in the area of Garden Island include the Torrens Island Power Station, storm water drains, embankments and boat launcing ramps. It was reported that thermal effluent from the Torrens Island Power Station affected the growth of mangrove seedlings (De Guia, 1982) and the invertebrate assemblages (Thomas *et al.*, 1986) in surrouding areas.

The Saint Kilda mangrove area is located at St. Kilda Bay, 27 km north of Adelaide at the northern end of the Barker Inlet complex. The forest forms an almost continous expanse of well developed mangroves with trees reaching up to 7 m high (Butler *et al.*, 1975). The landward side is backed up by saltmarsh communities dominated by *Sclerostegia arbuscula* and *Halosarcia halochemoides* near the causeway (Gravier and Robinson, 1983). The seaward side is barely exposed at the lowest tide and filled with dead seagrasses and algal fragments, which are washed into the mangrove zone by the tide. The Saint Kilda mangrove forest has suffered degradation due to changes of drainage pattern surrounding the bay and eutrophication due to sewage discharge from the Bolivar Sewage Treatment Plant (Fairhead, 1995; Coleman and Coleman, 2001). Dead seaweed and seagrasses cover much of the tidal flat and forest floor resulting in black, soft and smelly sediments. A recent study reported that the concentration of hydrogen sulphide (H_2S) in the interstitial water ranged from 9 mg/l to 42.5 mg/l. This concentration is well beyond (2100 to 4500 times) the ANZECC guidelines for freshwater and marine water quality (recommended ambient level is 2 parts per billion) (Coleman and Coleman, 2001).

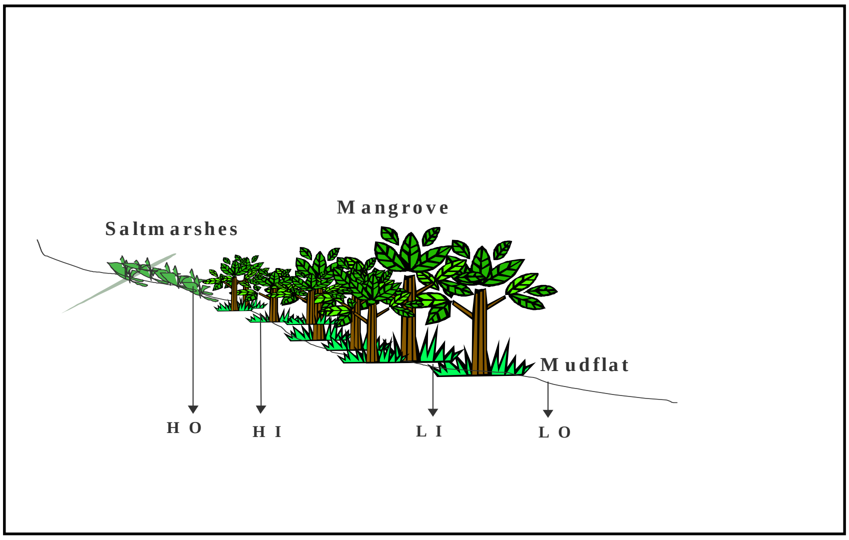
The mangrove community at Middle Beach has a different form compared with the two previous mangrove areas. The beach has been cut-off from the sea due to mangrove colonisation. Like the other two mangrove areas, during low spring tides extensive mudflats are exposed with sparse cover of seagrasses (*Zostera* *spp.*) at the seaward side of the mangrove fringe and salt marsh plants of *Sclerostegia arbuscula* and *Halosarcia halochemoides* backing onto the mangroves from the landward side. The mangrove community grows in a viscous semi-liquid sediment and has colonised the area since 1976 (Bayard, 1995). As a result, trees are only 3-4 m tall and a high number of trees have smaller trunks (Butler *et al.*, 1975; Fairhead, 1995). This mangrove area is relatively free from human intervention and a lot of young seedlings were observed. Burton (1982), using GIS techniques mapped these areas and found that mangroves colonised seaward at approximately 18m per annum at Middle Beach. From St. Kilda to Swan Alley Creek where Garden Island is situated, colonisation was 17 m per annum toward the landward side. Edyvane (1999) noted that both Garden Island and Saint Kilda have been considerably affected by human activities, while at Middle Beach human impacts may be considered as moderate.

2.2. Sample collection

Sampling was carried out in May 2000 (autumn) for 5 days, in the same tidal cycle. Samples were taken during daytime at low spring tide when the mangrove systems were exposed. At each location, two different tidal heights were determined, low and high 40 m transect lines were then established inside and out side the mangrove forest at the low and high tide levels. The execution of the transect lines base on assumption that the lower transects have longer immersion than the transects which located in the higher tidal parts.Thus there were four transect lines parallel to the water's edge. The first was mudflat seaward of the mangrove forest, the second was inside the lower tidal areas of mangrove forest, the third was inside the higher tidal areas of mangrove forest and the fourth was in the salt marshes landward of the mangrove forest (Fig. 3.2). The reason behind this design was to observe the consistency of community structures relative to physical factors such as tidal heights and habitats (mudflats, mangrove forest, saltmarshes) between the 3 different locations.

Five sites were established at 10 meter intervals along each transect. At every site, four replicate samples were randomly collected within a 1 m quadrat (both for infauna and soil) with a PVC hand operated corer (diameter 6.0 cm, surface area 5.2 cm) to 20 cm depth, reaching the nutritive layer, so that the consistency of the infaunal habitat sampling was maintained (as suggested by Kelaher *et.al.* ,1998a). Each soil sample then was put in an airtight jar and infauna samples were preserved in 10% buffered formalin. In total there were 20 infauna samples and 20 soil samples collected from each transect. The decision to sample during the day may affect the number of some fauna collected including Ocypodidae (crabs), as some of the species are nocturnal.

Figure 3.2. Schematic sampling design at each location showing a cross section of the four transects (HO=Higher Outer, HI=Higher Inner, LI=Lower Inner, LO=Lower Outer)



Core samples could not be collected from the lower outer station at Saint Kilda, because a mat of dead seagrasses permanently covered it. Similarly no samples could be collected from the lower inner station at Middle Beach because the area was permanently covered by seawater. It was not expected that the lower inner of Middle Beach sites were actually lower than lower outer sites. At Garden Island samples were collected from all of four sites. This resulted in an unbalanced design that needs to be considered in relation to the data analyses, particularly univariate analyses.

2.3. Sample processing

Infaunal samples

In the laboratory, infauna samples were washed through 0.5-mm mesh sieve in order to achieve a maximum number of infauna retained. Animals retained on the sieve were sorted to the phylum level. Each animal was subsequently identified to family level for the purpose of this study, except for Nemerteans. During identification, several references have been used. Polychaeta samples were identified using Glasby *et al.*, (2000), Fauchald (1977) and Hutchings and Murray (1984) references and have been confirmed with Dr. Greg Rouse, invertebrates curator from South Australian Museum. Insecta samples were identified using Nauman (1993) and Greenslade (1991). Collembola samples have been confirmed with Dr Penny Greenslade from CSIRO, Entomology Division, Canberra while larvae and pupae insect samples were confirmed by Dr. Peter Hudson from Environmental Biology, The University of Adelaide. Crustecean samples were identified using Hale (1976) and Mollusca samples were identified based on Shepherd and Thomas (1989). All infauna were then recorded and counted before placing in a bottle containing 70% alcohol for preservation.

Soil samples

Before further analysis, soil samples were oven dried at 60° C to avoid damage to volatile substances. Every soil sample was ground and sieved and put in an air-tight plastic bag for further analysis. Substrates were carbonate rich, so analysis of carbonate content in sediment from the 3 different places was necessary. The carbonate content was measured by a volumetric calcimeter. The principal of this method was to measure the volume of CO_2 in the burette produced by chemical reaction between carbonate and acid solution in a closed system. For precise work, the system must be placed in a thermostat and the calibration has to be done using the solubility of CO_2 in the acid used (Page, 1982).

Total organic carbon, the nutrient most likely affect the distribution of infauna was measured. The total organic carbon was assayed using the Walkley and Black rapid titration method (introduced in 1946) by calculating the chromic acid that is consumed by organic material (Allison, 1965). This method has been examined by Gaudette *et al.* (1974) by comparing the Walkley-Black method and the LECO combustion apparatus applied to carbonate clay shallow marine sediments. The result demonstrated an excellent agreement between these two methods.

In addition, sediment type was determined by calculating the percentage of clay and silt in the soil using a hydrometer method (Bouyoucos, 1962). This method provides faster processing of samples than pipet methods with acceptable accuracy (English *et al.*, 1994). The principle of the hydrometer method is that the settling time of individual soil particles is based on their size. The International Society of Soil Science has defined fine sands as having a particle size range of < 2000-20 μm, silts as <20-2 μm and clays as <2 μm (Gee and Bauder, 1986). Prior to dispersion and sedimentation, some preliminary procedures were applied. Organic content was removed using 1N hydrogen peroxide, carbonate content with 1M hydrogen chloride and soluble salt by washing with distilled water and centrifuging until salt concentration dropped below a reasonable value (in the present study this was 500 ppm on average, to avoid further destruction of clay/silt particle).

Salt content of the sediments were obtained by measuring the electrical conductivity of a 1:5 soil water suspension. The reading was converted to mS/cm (the Australian standard unit for electrical conductivity). Salt content of the sediment is referred to as “salinity” in the text below. Thus salinity in this study is the salt content in the sediment which includes NaCl and other ions. The conductivity of the overlaying seawater in the Port River, where Garden Island Saint Kilda located, was 53.0 mS/cm on May 2000. It would possibly vary from 50 to 60 mS/cm.

2.4. Data analyses

Shannon-Wiener diversity indices (H’), taxa abundances and species richness were used to determine the characteristics of the benthic infaunal assemblages at each site. Due to the unbalanced design (missing samples), univariate analyses to detect the responses of infauna to the environmental conditions were only applied for the upper part of mangrove forests. Subsequently, the differences between the 3 locations were assessed using a two-way ANOVA with an *a-priori* probability level of 0.05. *Post-hoc* comparisons among locations were tested using Tukey’s multiple comparison. In essence, the experimental design comprised a nesting of replicate cores within quadrats which were then replicated along the transect line. A nested ANOVA was run to test the extent of variation at quadrat scale. All the univariate analyses were done using the JMP® (version 3.01) statistical software.

Due to the some variables involved in structuring the mangrove infaunal communities, the application of multivariate statistical techniques were useful. Various multivariate analytical tools were employed to assess the extent to which community structure differed between sites (locations and/or transects) and how these differences were related to the defined environmental factors of the sites. These analyses were performed using the PCORD (version 4) software package. An NMS (Non-metric Multidimensional Scaling) analysis was used to examine how the environmental variables correlated with the structure of the infauna community across the sites. NMS is used to illustrate the relationship between objects based on the degree to which they have similar attributes. A Bray Curtis similarity measure was calculated and used to provide the basis for comparison between samples. Because the association measure is calculated in relation to pairs of samples the lack of balance in the survey design does not affect the utility of this method. Outputs from the NMS analysis were used to produce two dimensional ordination plots that illustrate the degree of similarity between samples. Ordinations in three dimensions were used to achieve a minimum stress (which is a measure of the goodness of fit of a NMS ordination). The resultant ordination illustrates the relationships between samples. This can then be considered in conjunction with information about the taxa, sample location and environmental factors. In the resultant plot taxa which are arrayed together are considered to have similar assemblages (Jongman *et al.*, 1987).

In conjunction with ordination and to test the hypothesis that there were no differences between the 3 locations, Multiple Response Permutation Procedure (MRPP) was utilized. MRPP is a non parametric procedure which is recommended by McCune and Grace (2002) to be used if the set of data lacks a linear relationship or has a skewed frequency distribution (as observed in this present study). Basically, MRPP is a method to observe the effect of treatments on groups of entities. This study intended to observe the effect of geographical differences (locations) on the pattern of infaunal communities based on the Bray-Curtis dissimilarity of the taxa abundance. Distance measures were calculated using the Bray Curtis formula to maintain consistency with the previous analysis. MRPP provides the “chance corrected within group agreement” or A. The A value ranges between –1 to +1. If A =1 it means that the samples are homogenous, but if

A=0 the heterogeneity within groups equals expectation by chance. It was stated that A<0.1 are common in ecological data and A>0.3 indicates a fairly high level of correlation between sample groups as a signal of homogeneity of data sets (McCune and Grace, 2002). The signficance (p-value) of the differences between groups can be assessed using the value for A and the sample size.

Another way to characterise infaunal assemblages is using a classification (or cluster) analysis. The most common technique is a hierarchical agglomerative method. Samples are combined into groups based on Bray Curtis dissimilarities method between each pair of entities. The level of grouping is measured by percentage of the information lost as a function of dissimilarities between samples (taxa abundance) during the grouping process. A dendrogram can then be produced with two defining axes. One axis consists of an array of the samples, while the other axis represents the scale of information lost at each step. The lower percentage of information lost during grouping process indicates higher degrees of similarities among the entities.

An Indicator Species Analysis was then employed to assess the contribution of each taxon to the characterization of the community structure. If a species cannot be predicted to exist in all sites but contributed to the habitat specificity then it is called an asymmetrical indicator. However, if a species that can be predicted to occur in all sites of the group but its abundance contributed to the specificity of species assemblages then its called a true symmetrical indicator (Dufrene and Legendre, 1997). The basis of this approach is the index that is calculated from the combination of relative abundance and relative frequency of occurrence of taxa in the group. The index ranged from 1 (no indication) to 100 (perfect indication). Furthermore, the statistical significance was obtained based on a randomization procedure using Monte Carlo methods.

In order to find out the level of species response to environmental variables, Canonical Correspondence Analysis was used. Correspondence analysis is a useful tool to examine the interaction of population and environmental factors because the assumption of linearity between the abundance of taxa and gradient of environmental variables can be avoided and a unimodal relationship between species and environmental variables is possible to detect (Jongman *et al.*, 1987). Biplot vectors can be drawn to illustrate the relationship from the centre of ordination. The vectors indicate the degree of influence of the environmental variables on the structure of the community.

All statistical analysis used untransformed data as infauna assemblages were made up by the contribution of individual taxa as suggested by Chapman (1998).

3. Results

3.1. Taxa composition

In total, across all locations and transects, 24 families (include unidentified insect, insect pupa, and insect larvae) of infaunal taxa were found during this survey, which recovered a total of 1506 animals. They were unevenly distributed across the mangrove areas. Notwithstanding bias due to non-orthogonal sampling procedure, Garden Island was the habitat with highest abundance with 900 individuals from 17 taxa, followed by Middle Beach (352 individuals and 22 taxa), and Saint Kilda (254 individuals in only 14 taxa). This suggested that Saint Kilda was the less favourable mangrove habitat. The mean abundance of taxa per core varied between, Garden Island (5.1 ± 7.2(sd) individuals or 2105 ± 3031 individuals/m^2), Middle Beach (2.4 ± 5.0 or 1010 ± 2105 individuals/m^2) and Saint Kilda (2.2 ± 2.4 or 926 ± 1010 individuals/m^2). The high values for the standard deviation indicated the patchiness in the distribution of taxa across sites. Certain polychaete taxa, for instance, were plentiful at several sites at a location but were absent at other sites. Also the insect, Neanuridae, which was abundant in certain sites of Middle Beach and Garden Island was relatively rare at Saint Kilda.

Polychaete groups were numerically the most dominant taxon and contributed 56% to the total infaunal numbers. Insecta (28%) were the next most frequently encountered taxon, then molluscs (including gastropods and bivalves) comprised 10% and crustaceans contributed a further 6% of the total numbers infauna.

Table 3.1. List of taxa collected during the study from 3 difference locations.

	GARDEN ISLAND				MIDDLE BEACH			SAINT KILDA			
FAMILY	HI	HO	LI	LO	HI	HO	LO	HI	HO	LI	SUM
AMPHIBOLIDAE	1	0	1	0	1	2	0	10	14	0	29
ARACHNIDAE	0	1	0	0	0	0	0	0	0	0	1
CAPITELLIDAE	53	89	0	110	9	2	10	35	34	17	359
EUNICIDAE	0	0	0	0	0	0	1	0	0	0	1
FLABELLIGERIDAE	6	2	0	0	3	0	0	0	0	0	11
GAMMARIDAE	6	13	1	2	2	0	6	4	1	6	41
GLYCERIDAE	0	0	0	0	0	0	2	0	0	0	2
INSECT LARVAE	3	1	0	1	2	0	0	6	0	0	13
INSECT PUPAE	3	9	10	7	3	7	0	9	4	3	55
INSECTA	0	0	1	1	2	0	0	1	0	0	5
MYSIDACAE	0	0	0	0	0	0	2	0	0	0	2
MYTILIDAE	0	0	0	0	5	9	28	0	0	0	42
NEANURIDAE	2	1	87	145	1	130	0	5	2	26	399
NEMERTEA	3	0	0	5	2	0	4	0	0	0	14
NEPHTYIDAE	0	0	0	0	0	0	4	0	0	0	4
NEREIDIDAE	3	2	41	0	21	31	16	2	4	15	135
OCYPODIDAE	0	0	0	0	1	2	6	0	1	0	10
PARAONIDAE	0	0	0	4	6	1	9	0	0	0	20
SPIONIDAE	0	0	0	252	0	0	2	0	0	0	254
SYLLIDAE	15	0	0	0	7	0	1	1	0	1	25
TRACHIDIDAE	0	0	0	0	0	0	0	0	5	0	5
TUBIFICIDAE	0	4	0	1	1	0	0	2	1	0	9
TURBINIDAE	0	0	1	4	0	0	1	1	0	2	9
VENERIDAE	3	0	0	6	2	4	4	2	0	40	61
Grand Total	98	122	142	538	68	188	96	78	66	110	1506
Percentage	6.51	8.1	9.43	35.72	4.515	12.48	6.375	5.179	4.3825	7.304	100
Number of taxa	11	9	7	12	16	9	15	12	9	8	

Table 3.1. shows that among the polychaete taxa, Capitellidae were the most abundant (359 individuals or 44%) and were frequently found at Saint Kilda and Garden Island. Nereididae, comprised 17% of the total polychaete abundance or 135 individuals and were most commonly found at Middle Beach. Spionidae had a restricted distribution being found only from the lower-outer transect at Garden Island. Not withstanding this restricted distribution, they made a significant contribution to the overall numbers of polychaetes (31% or 254 individuals).

Insects were dominated by the family Neanuridae, the springtails which comprised 95% (or 399 individuals) of the total number of insects across all samples and were most commonly found at Garden Island. During sample collection, a variety of other insects were caught with individuals at different stages of metamorphosis, including larvae, pupae and adults. They most likely belonged to different families of Dipterans (Peter Hudson, pers.com., 2002), but they were definitely not springtails, because this taxa does not have a larval stage. Due to the difficulty in identification of insect larvae, the pupa and larvae no attempt was made to identify them beyond this level of classification.

Mollusca were distributed spatially among the 3 locations but most of them existed in the lower areas of mangrove forests where the substrates were associated with seagrass. The bivalve Mytilidae characterised the infaunal assemblages of Middle Beach and contributed almost 12 % (42 individuals) of the total infauna caught in these mangroves, while Veneridae was frequently found at Saint Kilda mangroves making 17% (or 61 individuals) of their total infaunal assemblages.

3.2. Benthic distribution patterns within the systems.

The collection of samples either at Middle Beach or Saint Kilda were incomplete. At Saint Kilda, the sites were covered by dead seagrass, while at Middle Beach the sites were permanently covered by seawater which made these sites inaccessible. However, it was still useful to examine the spatial distribution of infauna in these systems and how their occurrence related to the measured environmental mangrove systems, Garden Island with Saint Kilda and Garden Island with Middle Beach. To balance the design, some samples from Garden Island were excluded parallel with the missing samples from each of the other locations.

Infauna was variably distributed across the sites in the upper part of the mangrove forest (Fig.3.3). A nested ANOVA detected that variation of infaunal abundance within quadrat ($p<0.02$) significantly affected the infaunal distribution between the higher inner transects (mangroves) and higher outer transects (saltmarshes) ($p<0.01$). Infaunal assemblages in samphires adjacent to the mangrove forest showed greater abundance (average 1388 and 1759 individuals / m^2) compared to the infauna in the mangrove itself, except for Saint Kilda (mean 731 individuals/m^2). On the other hand, the variation of infaunal diversity showed no significant influence (quadrat [transect *location] p>0.37) on the infaunal diversity at the higher level (transect [location] p>0.45transect) Infaunal assemblages in mangroves were made up of a greater variety of taxa compared with those in saltmarsh habitats. Mean diversity (H') of the mangrove areas was 0.6 while in samphire areas the mean diversity was 0.47.

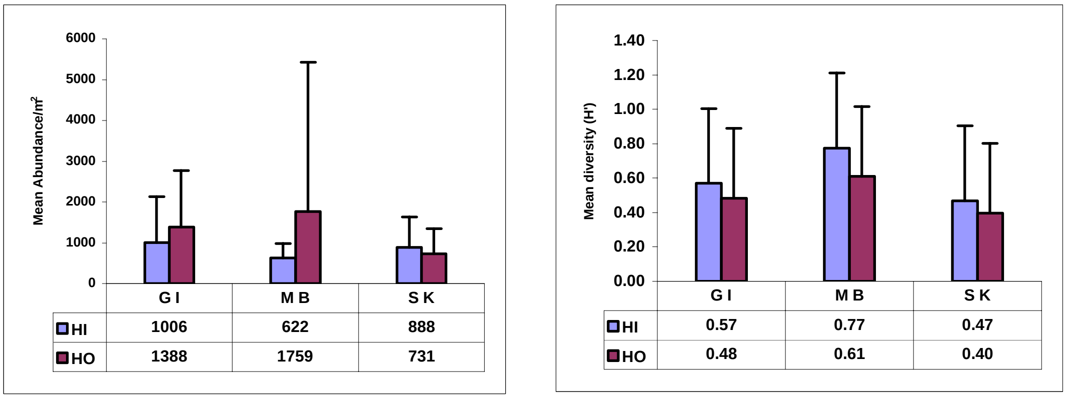
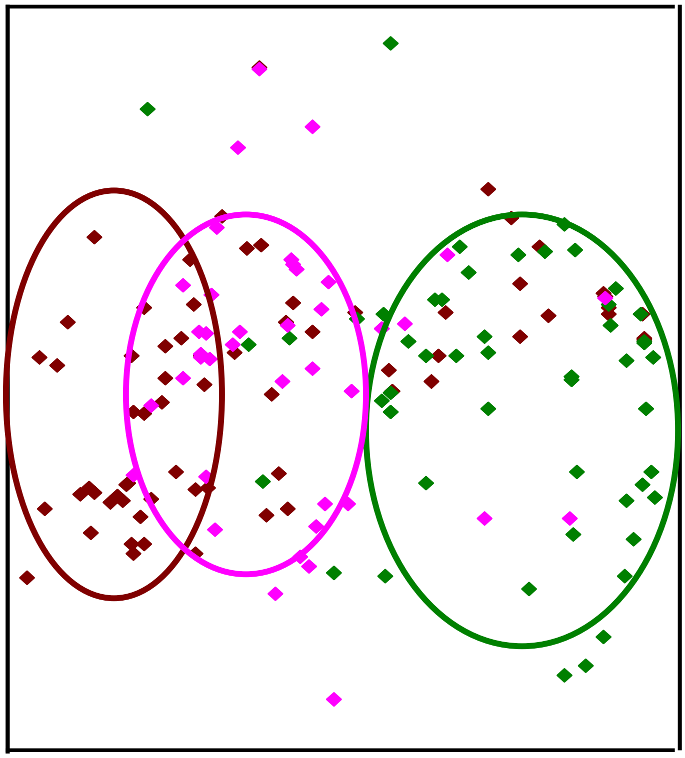


Figure 3.3. Mean abundance and diversity index (± SD) in the upper part of the 3 mangrove systems showing a spatial trend between saltmarsh and inside the mangroves.

In addition, a comparison of abundances of infauna at single locations revealed that there was a highly significant difference between Garden Island and Middle Beach (p <0.001), while between Garden Island and Saint Kilda the difference was smaller but still significant (p <0.05). However most differences between the locations were due to the abundance of certain polychaete taxa and Neanuridae insects.

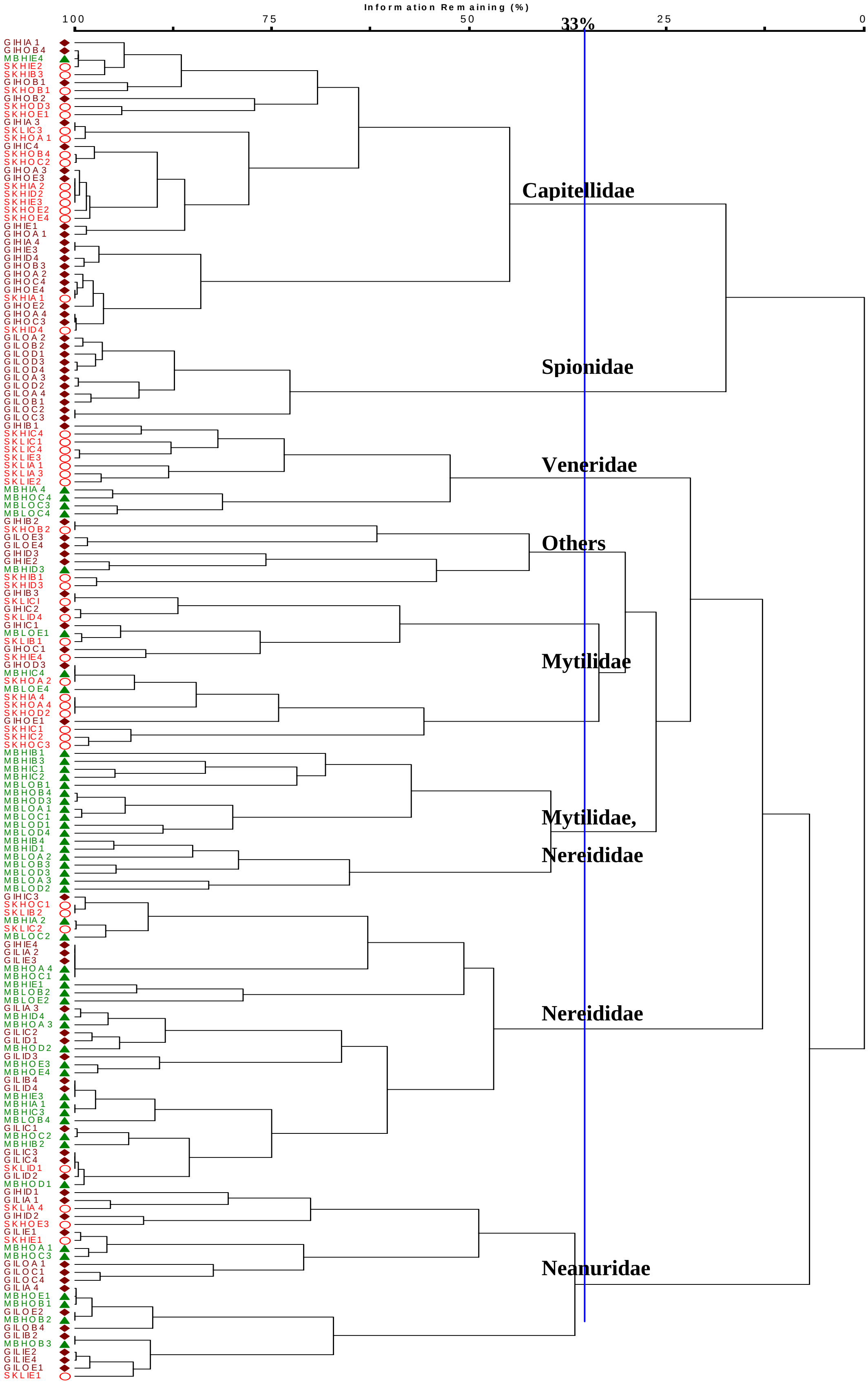
Multivariate analysis was employed in conjunction with univariate analysis to detect the spatial pattern of infauna among the 3 locations. A species matrix data set consisting of 168 samples and 24 identified taxa was compiled for all samples from the three geographic locations of the mangrove forests. An NMS ordination showed that there was a geographical separation among the three mangrove forests, even though a small number of samples from each location overlapped (Fig. 3.4). The samples from Garden Island and Saint Kilda, which are situated in the Barker Inlet reserve, were clumped together, while samples from Middle Beach, located further north of these two locations, were completely separated.

Figure 3.4. A two dimensional ordination based on raw abundance of taxa per sample (stress=0.18) showing a distinct separation between locations. Distance between symbols approximate dissimilarities between infaunal composition (♦: Garden Island, ♦: Middle Beach and ♦ : Saint Kilda).



Subsequently, the MRPP was carried out to test the hypothesis that there were no differences between the infaunal communities at the three locations. To maintain the consistency, the Bray Curtis dissimilarity measure was used in calculating the distance matrix. The result showed that that there were significance differences between the three locations as indicated by p = 0.0000. More-over the samples reached a relatively good level of agreement of A=0.12 indicating that samples size was ideal and achieved a fairly homogenous level among samples. This result was also in agreement with univariate analysis for location differentiation.

Figure 3.5. Dendrogram (using flexible beta=-0.25) based on family raw abundance per sample showed that with about 33% Bray-Curties similarities information remaining, infauna was grouped into 8. (♦: Garden Island, ♠: Middle Beach and o : Saint Kilda).



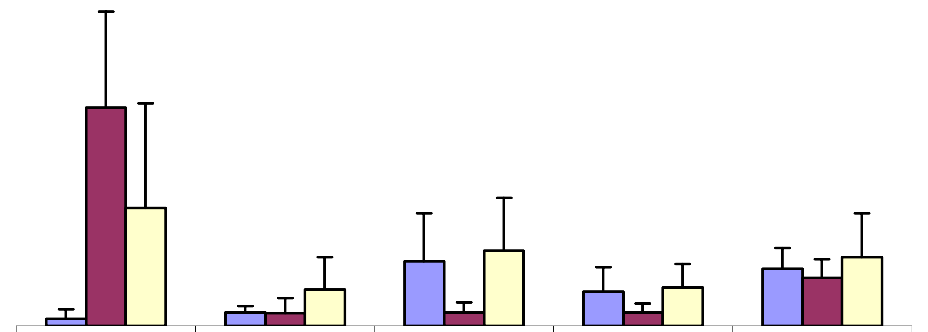
To evaluate to what extent the infaunal organisms are grouped, a hierarchal cluster analysis using Bray Curtis dissimilarities was carried out. This resulted in a dendrogram, which shows that infaunal assemblages showed only modest grouping (Fig. 3.5). This indicated that infaunal organisms were patchy and unevenly distributed across the mangrove areas, and also that the infaunal community was strongly influenced by contributions from individual family, which increase the heterogeneity of samples. Nevertheless, at the 33 % dissimilarities level, groupings relating to the influence of dominant infaunal taxa could be detected, even though the grouping was not perfect. There were eight different groups each characterised by a dominance of infauna inhabiting the mangrove systems. There were communities that were dominated by the polychaetes Capitellidae, Spionidae, Veneridae, Mytilidae, Nereididae, a combination of Mytilidae and Nereididae, Neanuridae and others (less common taxa).

Capitellidae and Nereididae were shown to have wide distributions compared with other taxa. Interestingly, the distribution of taxa tended to follow small scale variations within each system, rather than following the common characteristics of temperate mangrove systems. For instance, the mudflat habitat adjacent to Garden Island mangrove forest is strongly dominated by the polychaetes Spionidae, while the bivalve Mytilidae occupied the mudflat at Middle Beach. Samples from the Garden Island mangroves were most dominated by Spionidae, Capitellidae, Nereididae and Neanuridae. Samples from Middle Beach were characterised by high abundances of Nereididae and Mytilidae, while Capitellidae and bivalves (Veneridae) were commonly found in the infauna communities at Saint Kilda.

3.3. Abiotic characteristics

Environmental variables of the sediments that were used to quantify the edaphic characteristics of these temperate mangrove systems were carbonate content, total organic carbon, clay and silt percentage and salinity. In general, there was a local variation of these environmental parameters, which has shaped the habitat characteristics of these mangrove systems (Fig. 3.6).

Figure 3.6. Mean abiotic parameters (± SD) of the three location of mangrove systems



	% Carbonate	% TOC	% Clay	% Silt	Salinity (mS/cm)
🟦 G I	1.61	2.95	14.58	7.66	12.87
🟪 M B	49.10	2.84	3.04	2.97	10.82
🟨 S K	26.60	8.19	16.89	8.67	15.45

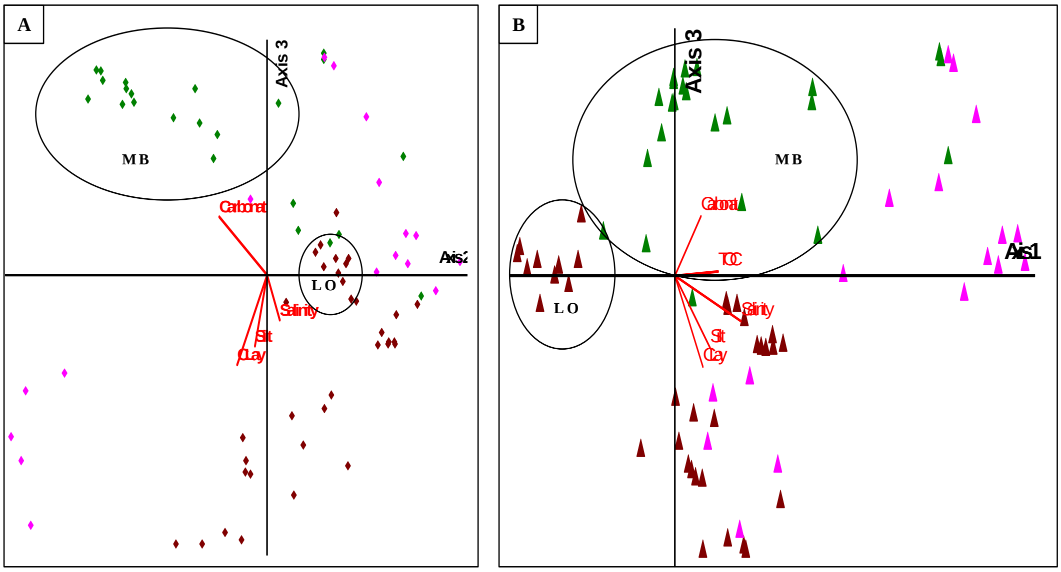
For instance, Middle Beach had significantly different sediment characteristics compared to the two other mangrove areas by having less TOC, clay and silt and a low salinity but high carbonate content. Garden Island had similarities in clay/silt percentage and low salinity with Saint Kilda, but significant differences in carbonate content and TOC.

Two-way correlation showed that salinity correlated with sediment type (r=0.67). Middle Beach and Saint Kilda could be characterised as having calcareous sediments, with carbonate content of 49 % and 27 % respectively, which were significantly different to Garden Island ($p < 0.0001$) where the carbonate content was 1.6%. High TOC’s were found at Saint Kilda, while Garden Island and Middle Beach sediment contained less TOC.

3.4. Linking biotic and abiotic factors

There is a growing understanding that invertebrate assemblages are shaped not only by biological factors such as predation, competition and recruitment, but also by environmental variables with which they are associated. In order to observe the extent to which the measured environmental parameters (carbonate, clay/silt, TOC and salinity) correlate with the structure of infauna communities in the three mangrove locations, Canonical Correspondence Analysis (CCA) was used. The data matrix was standardised by centering and normalising with $\alpha = 0.5$ as a compromise way in configuration of both species and sites in the ordination. The solution of this analysis was an ordination where environmental variables represented by vectors. Axis 2 and 3 were pragmatically chosen to give a good display in term of community structures. Axis one was not chosen as this axis was more closely linked to absolute abundance rather than community structure even though the information content of axis 1 (as a percent of variance) was 5.8%. Axis 2 which refers to tidal level, covers 4.7% of information and axis 3 which refers to inside/out side mangrove forests, covers 2.0% of information.

Figure 3.7. CCA ordination showing the effect of environmental variables on the distribution pattern of infauna across the 3 locations (♦: Garden Island, ♦: Middle Beach, ♦: Saint Kilda) A. Ordination with axis 2 and axis 3 : B. Ordination with axis 1 and axis 3



A two dimensional ordination demonstrated that the infauna distribution patterns were related to certain environmental variables with p = 0.001 (Fig. 3.7). Samples from Middle Beach appeared to be separated on the basis of the carbonate content in the sediment, while between Saint Kilda and Garden Island the basis of the separation was more complex. In detail, salinity seemed related to the separation of some samples according to the tidal height (r = 0.725), while clay and silt drove separation of samples from inside and outside of mangrove forests (r_{clay}=0.860 and r_{silt}=0.655). TOC differences influenced the samples from vegetated areas (r=0.531). It was detected that the samples from the mudflat adjacent to the Garden Island mangrove forest (GILO) were distributed and clumped together against the distribution of TOC, salinity, carbonate as well as sediment grain size.

3.5. Indicator Species Analysis

Sites or habitat can also be described by assessing the occurrence of taxa in a given place at a given time. In order to examine which taxa may have a major role in characterising the infaunal assemblages of these mangrove forests, Indicator Species Analysis was employed. The indicator value can be calculated from the absence or presence of certain taxa and also their frequency of occurrence.

Table 3.2. Summary of Indicator Species Analysis when samples were grouped into; A.different locations B. different tidal height (high and low). List of taxa only includes those that make significant contribution.

A.

Taxa	**Indicator Value**			**Monte Carlo Test (p)**
	Garden Island	**Middle Beach**	**Saint Kilda**	
Amphibolidae(Gastropoda)	0	1	19	0.001
Capitellidae (Polychaeta)	35	2	24	0.003
Mytilidae (Bivalve)	0	37	0	0.001
Nereididae (Polychaete)	8	37	5	0.001
Ocypodidae (Crustacea)	0	14	0	0.001
Paraonidae (Polichaeta)	0	15	0	0.001
Spionidae (Polychaeta)	25	0	0	0.001
Trachididae (Grastopoda)	0	0	7	0.001
Veneridae (Bivalve)	1	2	15	0.001

B.

Taxa	**Indicator taxa**		**Monte Carlo test (p)**
	High	**Low**	
Amphibolidae	14	0	0.03
Neanuridae	4	24	0.02
Nereididae	14	29	0.05
Spionidae	0	27	0.01
Veneridae	1	20	0.01

Table 3.2. indicates that most taxa prefer lower areas in the mangrove forests, rather than higher areas. Middle Beach appeared to be the preferred habitat for most indicator taxa rather than Garden Island and Saint Kilda. Another finding revealed that the tube building polychaete worms mostly made up infaunal assemblages in these mangrove systems. They have wide ranging distribution

from low tide to high tidal levels. This was expected, as polychaetes were diverse as well as numerically dominant.

The polychaete Spionidae was an asymmetrical indicator both for locations and tide. Spionidae was a good indicator taxa for Garden Island and they contributed 25% to the infaunal assemblages. Their occurrence was restricted to low tide areas. Conversely, the polychaetes Capitellidae and Nereididae were true symmetrical indicator taxa, because their preponderances can be predicted for almost all the sites of the mangrove forests. However, the abundance of Capitellidae was more useful as an indicator for Garden Island and Saint Kilda while abundances of Nereididae were better indicators at Middle Beach (where they can be found mostly in the lower part of mangrove forests).

Molluscs were also another group of indicator taxa in these mangrove systems. For instance, the bivalve Mytlidae was an asymmetrical taxa, as their occurrence was restricted to Middle Beach, and this contributes to the habitat specificity of Middle Beach. They made up 37% of the infaunal assemblages at that site. The gastropods Amphibolidae were commonly found in the higher part of mangrove areas as opposed to the bivalves Veneridae, which were most frequently encountered in the lower part of the mangroves. In both cases they were more abundant at Saint Kilda.

4. Discussion

4.1. Infaunal characteristics

In general, the structure of infaunal communities in these South Australian temperate mangroves showed no distinctive characteristics compared with other temperate mangroves. Polychaetes tended to dominate the sites across the mangrove areas, followed by insects and molluscs. This composition can be found in other Australian temperate mangroves such as those in NSW temperate mangroves (Kelaher *et al.*, 1998a; Hutchings and Recher, 1974; Macfarlene and Booth, 2001). The result was also in agreement with Butler *et al.* (1975) who stated that no specific infauna assemblages were characteristic of SA mangrove forest. This is possibly due to some taxa being favoured in certain locations of mangroves but being rarely distributed or even absent in another location. Sasekumar and Chong (1998) also discussed the difficulties of characterising the benthic infaunal community of mangroves as some species probably exist in habitats beyond the mangrove forest.

Although only a few species were common to all 3 locations, several taxa occurred in at least two of them. Their occurrence could be related to the different biological and physical settings of the mangrove systems. For instance Capitellidae, which are found in disturbed environments (e.g. Pearson and Pearson, 1991) like Saint Kilda and Garden Island, were hardly found at Middle Beach. In addition Nereididae preferred the wetter areas such as the lower part of the mangrove forest which receive prolonged inundation. Hutchings and Recher (1974) also found certain nereidids such as *Nereis diversicolor* and *Neanthes vaalii* close to the channel and creek which flowthrough the temperate Careel Bay mangrove forest. Bivalves, including Veneridae and Mytilidae, were variously distributed at all locations, although their number was far lower than Capitellidae. Nevertheless, most of the bivalves were more commonly caught at the lower part of the mangroves often associated with seagrasses.

4.2. Infaunal zonation

The distribution of infauna in temperate South Australia appeared to be affected by tidal heights. There was a distinct zonation between the higher part of mangrove forests which was occupied by less diverse and less abundant infauna relatively to the lower part of the mangrove forests. This situation in accordance with other studies (Evink, 1974; Netto and Lana, 1997; Roth and Wilson, 1998) which showed that tide has a major role in dividing the infaunal assemblages. The prolonged inundation of the lower part of the mangrove forest gives several advantages such as aeration of sediment which helps reduce the concentration of sulphide, gives enough time for particulate matter settlement which increases the nutrient content in sediment, enhanced decomposition of mangrove litter and chemical processes within sediments (Alongi, 1998). These, in turn, produce the favourable substrate for infauna to live and grow. On the other hand, this also gives a chance for predators to prey on the infauna. In that case, certain animals will then seek refuge in the higher part of mangrove or samphire. Kneib (1984) reported the value of *Spartina* saltmarsh communities as refuge for small invertebrates, because the structure of stems reduced the predation rates on certain prawn crustaceans by two of the four species of predatory fish (Minello and Zimmerman, 1983).

Saltmarsh transects were found to be less rich in taxa but with relatively high abundances when compared with the adjacent mangrove sites, especially at the Garden Island and Middle Beach sites. This was probably a result of the extreme saline conditions that infauna experience and the competition with other successful members of communities (Rader, 1984; Hutchings and Saenger, 1987; Packham and Willis, 1999), even though the effect would be varied and could be happening on a small scale (Rader, 1984).

Mudflats were favourable habitats for infauna and the greater diversity (up to 21 taxa) and density (2187 individuals/m^2 on average) was observed at Garden Island as well as Middle Beach, even though most of this abundance at Garden Island resulted from greater numbers of the polychaetes Spionidae and Neanuridae insects. Higher numbers of taxa have also been found on temperate mudflats North Sea (55 species and 4,500-200,000 individuals/m2) and Chile (43 taxa) as shown by (Reise, 1991). The mudflats were mostly dominated by burrowing infauna that acted as “ecosystem engineers” (Rhoads and Young, 1970). They can modify the structure of the substrate and nutrients, which make habitats more or less favourable for other organisms. Ditmann (2002) hypothesised that the occurrence of ecosystem engineers would determine the site-specific variation in tropical tidal flats, and in turn would regulate the structure of benthic assemblages. This situation could be applied to the present study where bivalves (Mytilidae) were dominant in the mudflat habitat at Middle Beach, while polychaetes dominated the mudflats at Garden Island. In other words the presence of asymmetrical indicator taxa and true symmetrical indicator taxa that have different ecological functions resulted in site-specific variation between Garden Island, Saint Kilda and Middle Beach.

4.3. Sediment characteristics associated with infauna

Data have shown that sediment characteristics differed between the three locations. These differences would possibly affect the structure of infaunal assemblages. Middle Beach sediments, for instance, were characterised by high carbonate content, less clay, lower salinity, and contained infaunal assemblages which were more diverse with higher abundances. Most of the carbonates in the sediments resulted from organic material such as mollusc shells and benthic Foraminifers (Butler *et al.*, 1977; Cann and Gostin, 1985). Recent study also showed that relatively abundant molluscs occupied high carbonate sites. The mollusc group is one of the common taxa in temperate mangrove areas (Hutchings and Recher, 1981), and they were distributed mostly in the vegetated areas such as those found at Saint Kilda or in mudflats associated with seagrasses such as at Middle Beach. Their occurrence in different sites of mangrove systems was more likely as consequence of habitat preferences. Wells (1983) reported a zonation of mollucs related to the types of vegetation in Australian tropical mangroves. Another study near Sydney on temperate mangroves also detected a tidal height zonation of gastropods in the mangrove areas and adjacent saltmarshes (Kaly, 1988 as cited by Chapman and Underwood, 1995). This pattern of distribution of molluscs might be due to salinity and temperature variations which are inhibitory factors for certain molluscs (Jiang and Li, 1995).

The present study detected the presence of Capitellidae and Spionidae in disturbed areas, such as Garden Island and Saint Kilda. Most Capitellidae were found in muddy areas and in areas with high organic content such as Saint Kilda and Garden Island. A high density of Capitellidae was also observed in other mangroves areas (George, 1984). Capitellidae are widely known as bio indicators for organic pollution (Grassle and Grassle, 1976; Glasby *et al.*, 2000). Spionidae were found to be very abundant in the mudflats of Garden Island where sediment had a lower content of clay and silt, less salinity and less TOC. Two studies in temperate mangrove areas reported the occurrence of Spionidae in relation to environmental disturbances (Thomas *et al.*, 1986; Kelaher *et al.*, 1998a).

This study also observed that variations in infaunal communities were probably affected by small scale habitat differences. Grain size was not the only factor determining the local distribution of infauna. Other proposed causative agents include organic content, microbial content, the rate of food supply and trophic interactions (Snelgrove and Butman, 1994). These differences in the capacity of taxa to utilise the habitat contributes to the heterogeneity of samples which probably reflects the complexity of these temperate mangrove systems.

Chapter 4 Temporal and Spatial Variation of Infaunal Communities : Garden Island Mangrove Case Study

Synopsis: Having demonstrated (chapter 3) that infaunal communities differ between sites in relation to both geographical location and position on the tidal gradient, the work in this chapter aims to develop a better understanding of the distribution patterns within a forest and to quantify the extent to which these patterns vary on both seasonal and inter-annual timescales.

1. Introduction

Garden Island, is located, close to Torrens Island where a power plant has operated since 1967. The warm water discharged from the power plant has increased the water temperature by 8°C to 12°C. The effect of warm water reaches as far as 3.5 km from the outfall; at the entry to Angas inlet the water is typically 2-4°C higher than at the discharge due to the mixing with cooler tidal water and spreading out to the mangrove areas (Thomas *et al.*, 1986). This thermal effluent has affected the dynamics of both mangrove growth and litter decomposition rates in areas adjacent Torrens and Garden Island (De Guia, 1982).

Until recently, most research in these areas related to the management of land-use conflicts and has been conducted by environmental consultants. Only a few studies related to the fauna associated with these mangroves. For instance (Butler *et al.*, 1975) considered conservation issues, Bayliss (1979) examined the behaviour of epifaunal species and Thomas *et al.* (1986) examined invertebrate communities with regard to the water discharged from the Torrens Island Power Station. No research has been conducted on infaunal communities, or particularly in assessing the community structure in different habitats through time.

Infaunal assemblages persist in the extreme environment characteristic of these temperate mangroves where sediments are characterised by low oxygen and nutrients, high silt and clay content due to root trapping, extreme salinity due to extensive evaporation and a wide range of temperatures. Like other faunal communities, their response to extreme environments includes reduction in abundance, changes in functional feeding behaviour, reduction in diversity of species and changes in the relative dominance of certain species that are tolerant to stress.

The infaunal assemblages are made up of various invertebrate organisms, which have different life cycles and feeding strategies. Their community structure depends on their biological interaction within community and the sediment status which they inhabit (Whitlatch, 1981; Giangrande *et al.*, 1994; Hall, 1994).

Considering this, the aims of this study were:

1. To characterize the community structure of infaunal assemblages and the spatial patterns of distribution across the range of tidal height.
2. To observe any inter annual variation in infaunal communities.
3. To correlate the measured abiotic factors such as TOC, salinity and sediment grain size with spatial and temporal variation in the structure of the infaunal communities.

2. Materials and methods

2.1. Study site

Garden Island is just north of Adelaide on the eastern side of the Baker Inlet Aquatic Reserve. It is within the Port River estuary in Gulf St. Vincent, at latitude 34°48’00”- 34°48’45”S (Fig. 4.1). The island is surrounded by a network of tidal channels and has four principal habitats: the mangrove habitat, the saltmarsh habitat, the tidal mudflat habitat and the subtidal habitat (Clyde, 1995).

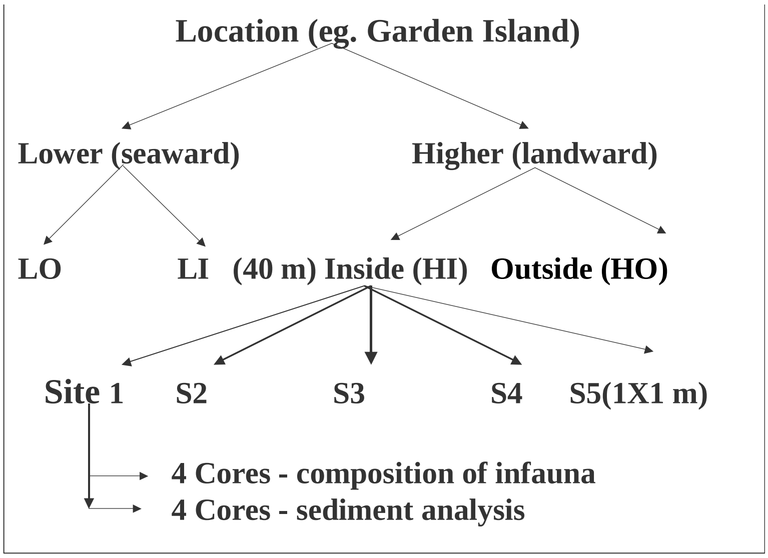
Figure 4.1.Garden Island Mangrove Area, 30 km north of Adelaide, South Australia, shows location of study sites. The tidal channels around the mangrove areas and a causeway blocked the tidal channel in the eastern part of the island. On the landward side (higher part), it was noted that the mangrove was backed up by saltmarsh communities. On the seaward side, it was noted that a narrow band of mudflat backed up the mangrove communities at the lower part. The center of the map shows land use developments that resulted a reduction of the mangrove and samphire areas.

The mangrove habitat occupies the zone between mean high water to mean sea level and covers about 1200 hectares. Old mature stands of *Avicennia marina* (Frost) Vierh. var *australasia* (Duke, 1991) of 3–6 m height appear to be healthy. On the landward side, mixed samphire plants including, *Halosarcia flebelliformis, Sarcocornia quinqueflora* and *Sclerostegia arbuscular* back up the mangrove forest. Local tides are characterized as semi diurnal (Womersley and Thomas, 1976). Land-use activities have resulted in the destruction of some areas of the mangrove andsaltmarsh communities. This includes a causeway development across mangrove areas for servicing three high tension electricity transmission lines. It has been claimed that this development has not adversely affected the mangrove and samphire communities (Rust-PPPK, 1995.). Industrial and sanitary landfill takes place on Garden Island but there is no evidence that leachate from landfill operations have affected mangroves or samphire communities (Clyde, 1995). Other human activities in the area include the Bolivar Sewage Plant, Torrens Island Power Station, storm water drains and embankment. However, little research has been conducted in the mangroves and there are no data on infaunal community structure to evaluate possible impacts.

2.2. Sampling design

Sampling at Garden Island was undertaken on separate occasions. First in May 2000 as part of a broader geographical survey detailed in the previous chapter, and again in May 2001 as part of seasonal samples at Garden Island. The sampling procedure essentially followed that described in the previous chapter for the geographical assessment. Samples were collected from two different tidal heights, low and high, and transect lines were then established inside and outside the, mangrove forest at the high and low tide (Fig. 4.2).

Figure 4.2. Schematic sampling procedure in Garden Island Mangrove sites



Thus there were four transect lines; the fist was in the mudflat seawardto the mangrove forest (lower outside mangrove forest=LO), the second was inside the lower tidal areas of the mangrove forest (lower inside of forest = LI), the third was inside the higher tidal areas of mangrove forest (higher inside of forest= HI) and the fourth was in the salt marshes landward to the mangrove forest (higher outside of forest = HO). The rationale for this design was to observe whether tide and habitat differentiation (mudflat, mangrove and samphire) affected the pattern of infaunal community distributions. Five sites were establish 10 meters apart along each of the transects (over a total distance of 40 m). At these sites four replicate samples of sediment were cored for infaunal and another four for the assessment of physico-chemical properties. In total 20 samples were collected for infauna and 20 samples for soil analysis from each transect at each sampling period.

2.3. Samples processing

Both infaunal samples and sediment samples were processed according to the methods detailed in Chapter 3.

2.4. Data analysis

Ecological indices including species richness (number of taxa), taxa density and taxa index of diversity (H’) were calculated using raw abundance data. Spatial variation was then investigated by grouping the samples into the different transects, while temporal variation was analysed by pooling the samples into sample period. Since the infaunal assemblages appeared to be made up by contributions from a few individual taxa within communities, abundance data were left untransformed as suggested by Chapman(1998).

The first step in the statistical analysis was to compare several series of data using a one-way analysis of variance (ANOVA) both for times and transects. When a difference was found between sample groupings then the HSD Tukey-Kramer was applied to identify the source of the variation. However, since the experimental design comprises nesting replicate cores within quadrats which then are replicated along the transect line, a nested ANOVA was used to test the extent of variation at the quadrat scale. Secondly, a multi factorial-ANOVA was employed to investigate the effect of treatments on infaunal distribution such as time variation, tidal height (tide by pooling upper inside mangrove plus samphire versus inside lower mangrove plus mudflat), inside and outside of forest (in/out by pooling upper plus lower inside mangrove versus samphire plus mudflat) and position into the mangrove forest (transects). When a significant difference was found from the interaction of any combination of treatments, neither the higher order interaction nor the main effects were interpreted.

Subsequently, analysis was done to study the temporal and spatial variation with regard to the structure of infaunal assemblages. In this analysis multivariate techniques including both ordination and classification, were used. Bray-Curtis dissimilarity was computed to examine the magnitude of the dissimilarities within samples. Based on the BC dissimilarities matrix, subsequently the NMS procedure was applied to obtain the ordination. It was found that 3 axes were required to achieve an ordination with minimal stress (goodness of fit) of the NMS ordination plot. Significant differences among groups of samples were obtained through analysis of similarity using the MRPP method. The A statistic was then used to examine the degree of agreement (correlation) among groups of samples (as detailed in Chapter 3).

Indicator Taxa Analysis was used to assess the contribution of taxa to infaunal assemblages in relation to variations in both time and space.

In order to quantify the response of species to environmental variables, Canonical Correspondence Analysis (CCA) was used. CCA is a useful tool for examination of the interaction of population and environmental factors because it avoids the assumption of linearity between the abundance of taxa and the gradient of environmental variables and is able to detect unimodial relationships between species and environmental variables (Palmer, 1993). The relationship can be drawn by biplot vectors from the centre of the ordination. The vectors indicate the degree to which environmental variables correlate with the differences in community structure.

4. Results

4.1. Infaunal composition.

Infaunal assemblages changed between the two sampling periods (May 2000 to May 2001) with both increases and reductions in several taxa and also changes in the presence and absence of certain taxa. In total there was 1605 individuals collected during the study belonging to 17 families. Phylum Annelida, dominated by class of Polychaeta were the most diverse and abundant group at Garden Island. These taxa were found across all sites and during both sampling periods. The next most abundant taxa was class Insecta (with various life cycle stages). In contrast, low numbers of crustaceans and gastropods were collected during both sampling periods (Table 4.1).

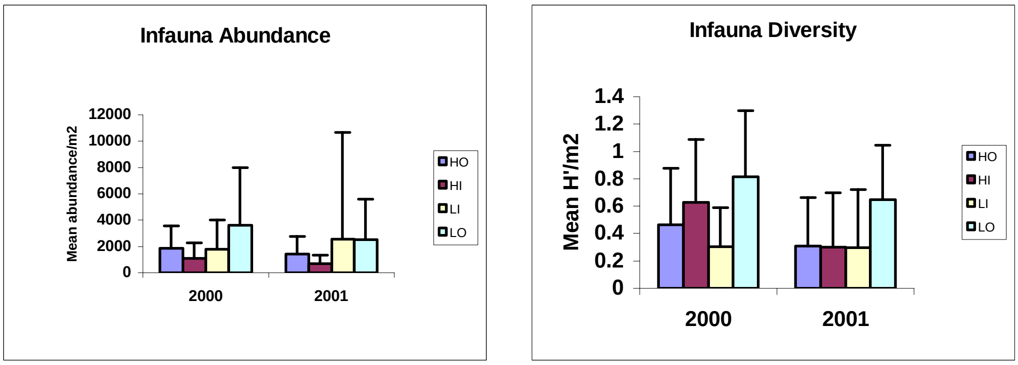
Table 4.1. Infaunal status in Garden Island, regard to spatial and temporal variation.

		Year 2000				Year 2001					
CLASS	FAMILY	H I	H O	L I	L O	H I	H O	L I	L O	Total	%
POLYCHAETA	CAPITELLIDAE	53	89	0	110	32	73	0	10	367	22.87
POLYCHAETA	FLABELLIGERIDAE	6	2	0	0	0	0	0	0	8	0.50
POLYCHAETA	NEREIDIDAE	3	2	41	0	3	1	12	0	62	3.86
POLYCHAETA	PARAONIDAE	0	0	0	4	0	0	0	1	5	0.31
POLYCHAETA	SPIONIDAE	0	0	0	252	0	0	0	102	354	22.06
POLYCHAETA	SYLLIDAE	15	0	0	0	3	0	0	6	24	1.50
OLIGOCHAETA	TUBIFICIDAE	0	4	0	1	0	3	0	0	8	0.50
CRUSTACEA	GAMMARIDAE	6	13	1	2	0	5	0	0	27	1.68
INSECTA	INSECT LARVAE	3	1	0	1	2	2	0	7	16	1.00
INSECTA	INSECT PUPAE	3	9	10	7	4	0	5	8	46	2.87
INSECTA	INSECTA	0	1	1	1	0	2	0	1	6	0.37
INSECTA	COLLEMBOLA	2	1	87	145	0	0	159	249	643	40.06
CRUSTACEA	OCYPODIDAE	0	0	0	0	0	0	2	0	2	0.12
GASTROPODA	AMPHIBOLIDAE	1	0	1	0	3	5	0	0	10	0.62
GASTROPODA	TURBINIDAE	0	0	1	4	0	2	0	0	7	0.44
BIVALVIA	VENERIDAE	3	0	0	6	0	0	1	2	12	0.75
NEMERTEA	NEMERTEA	3	0	0	5	0	0	0	0	8	0.50
	TOTAL	98	122	142	538	47	93	179	386	1605	100
	TAXA RICHNESS	10	9	7	12	6	8	5	9		

Among the polychaetes worms, the family Capitellidae appeared to be the most dominant through time (367 individuals or 23%) and followed by Spionidae (354 individuals or 22%). From the class Insecta, Collembola was the most dominant taxa and contributed 40% or 643 individuals to the infaunal assemblages. Total abundance in May 2000 was 900 individuals and 705 individuals in May 2001. However, variation of infaunal abundance within replicates showed no significant differences and this condition was maintained through the sampling period (quadrat[site (year)] df = 32, F_{rat}1.23; p=0.2). .

Taxa richness also showed only slight differences between years with 16 famiies in 2000 and 15 families in 2001. The nested analysis also found that variation of the index of diversity (H') within quadrats was not significant (quadrat[site(year)] df = 32; F_{rat} = 0.88; p = 0.65). The index of diversity (H') in 2000 was 0.56 and was reduced slightly in May 2001, being 0.40. The index of diversity values combine information on the proportions of abundance as well as taxa richness in every sample.(Fig.4.3).

Figure 4.3 Comparison of mean (± SD) infaunal abundance and diversity (H'*(in italics)*) during two consecutive sampling periods and e summary of nested and multifactorial analysis comparing the year sampling period and transects. Significance: *) $\alpha<0.05$; **) $\alpha<0.01$; *) $\alpha<0.001$**



Effect test	**Df**	**SS**	**F_{ratio}**	**Prob>F**
Year	1 /***1***	237.66/***0.63***	1.86/***4.02***	0.18/***0.05****
Transects [year]	6 /***6* 3**	9961.74/***4.84***	12,99/***5.19***	0.0001***/***0.0001******
Quadrat [transect,year)	32/***32***	5035.70/***4.363***	1.23/***0.88***	0.2/***0.66***
Tide	1/**1**	4796.10 / **0.30**	33.88 / **1.67**	0.0001/**0.16**
In/Out	1/**1**	3830 / **1.21**	19.203 / **6.70**	0.0001/ **0.01**
Year vs Trans	3 / **3**	514.72 / **0.43**	9.31 / **0.88**	0.27 / **0.45**
Year vs Tide	1/**1**	16.90 / **0.29**	0.12 / **1.59**	0.73 / **0.21**
Year vs In/out	1/**1**	21.60 / **0.002**	1.49 / **0.01**	0.22 / **0.90**
Error	152/ **152**	23080.91 / **21.57**		

In contrast, the number of individuals (abundance) and also the diversity of taxa (H') showed significant spatial variations, between heights on the tidal gradient, from inside and outside of the mangrove forest as well as between transects at any given tidal height. These differences were maintained during the two sampling periods (May 2000 vs May 2001). For example, the high tidal areas (HO and HI) were made up by infaunal assemblages that were characterised by lower abundances and diversities when compared with lower tidal areas (LO and LI). A similar situation was also found where the mangrove forest transects (HI and LI) were compared with those transects outside the mangrove habitats (HO and LO). Results showed that infaunal communities in mangrove areas had lower abundances and diversities than habitats outside the mangrove areas.

The mudflat habitat adjacent to the mangrove forest (LO) was consistently the most diverse with the highest total abundance of infauna when compared with any other transect in the Garden Island mangrove system. There was variation between years, in diversity, as H' was 0.9 in 2000 and decreased to 0.6 in 2001, as well as in density where 3,598 individuals/m^2 were observed in 2000 and 2,507 individuals/m^2 in 2001.

The lower inside of the mangrove forest transect (LI) was the least diverse transect. The number of individuals was comparatively higher in 2001 than 2000. The increase in the abundance of Collembolans from 87 to 159 individuals (summed across all samples in the survey) drove this change. At the same time the abundance of Nereididae in LI went down from 41 in 2000 to only 12 individuals in 2001 along this transect.

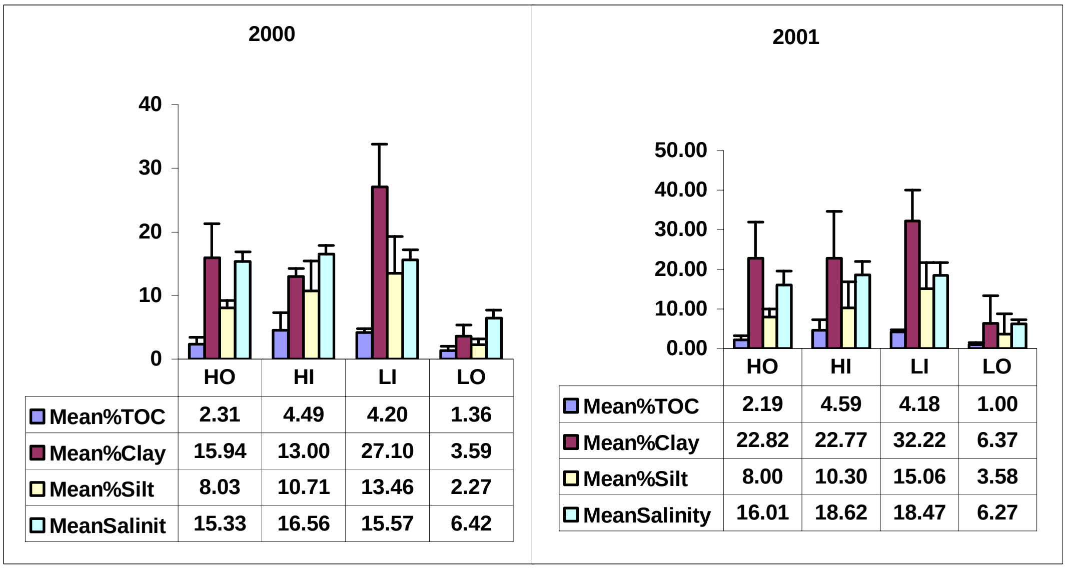
The upper part of the mangrove forest (HI) was quite different from other transects. There was a lower abundance of common taxa such as family Capitellidae inside the forest compared to outside the forest and the absence of certain taxa (such as Spionidae) which demonstrated that this transect was not as favoured as the lower transects (see Table 4.1). Infaunal communities at this location were characterised by assemblages with a lower abundance.

The samphire habitat (HO) was similar to the upper part of the mangrove forest. Infaunal abundance, as well as diversity, was lower during the two consecutive sampling periods indicating that this habitat was relatively unfavourable compared with the other non-mangrove habitat (mudflat) in the Garden Island systems.

4.2. Abiotic characteristics

Abiotic factors such as TOC, clay, silt and salinity appeared to vary consistently with the vegetated areas characterised by higher levels of TOC, salinity, silt and clay. However, multifactorial analysis suggested that all abiotic factors varied between transects as well as between mangrove and non mangrove habitats , while the amounts of clay and salinity levels also changed through time (Fig. 4.4). Salinity seemed to be the most important abiotic factor in this mangrove system. Salinity was generally higher in the samphire areas and in the higher site on the tidal gradient and this was maintained consistently through the time.

Figure 4.4. Mean abiotic parameters (± SD) at Garden Island during two consecutive sampling periods and summary of multifactorial analysis comparing time and spatial treatments. The value of significance level : *) α< 0.05 : **) α<0.01: *) α<0.001**



	HO	HI	LI	LO
■ Mean%TOC	2.31	4.49	4.20	1.36
■ Mean%Clay	15.94	13.00	27.10	3.59
□ Mean%Silt	8.03	10.71	13.46	2.27
□ MeanSalinit	15.33	16.56	15.57	6.42

	HO	HI	LI	LO
■ Mean%TOC	2.19	4.59	4.18	1.00
■ Mean%Clay	22.82	22.77	32.22	6.37
□ Mean%Silt	8.00	10.30	15.06	3.58
□ MeanSalinity	16.01	18.62	18.47	6.27

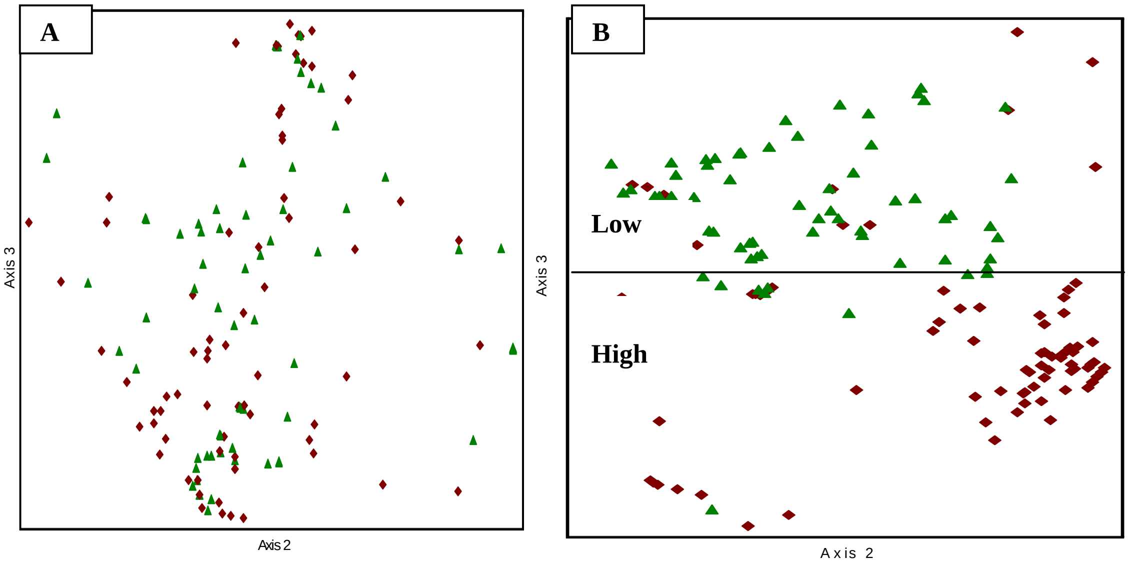
Source	% TOC	Salinity	% Clay	% Silt
Year	0.20	0.03*	0.0001***	0.29
Transects	0.0001***			0.0001***
Tides	0.07	0.0001***	0.95	0.16
In/out	0.0001***			0.0001***
Year vs Transect	0.55	0.005**	0.01*	0.28
Year vs Tide	0.78	0.88	0.007	0.09
Year vs In/Out	0.55	0.05**	0.01*	0.36

Two-way correlation between salinity and infaunal abundance and salinity with other abiotic factors showed a modest correlation ($r_{\text{infaunal-salinity}} = 0.48$; $r_{\text{toc-salinity}}=0.67$; $r_{\text{silt-salinity}} =0.53$; $r_{\text{clay-salinity}}=0.76$).

4.3. Temporal and spatial variation of benthic community structure

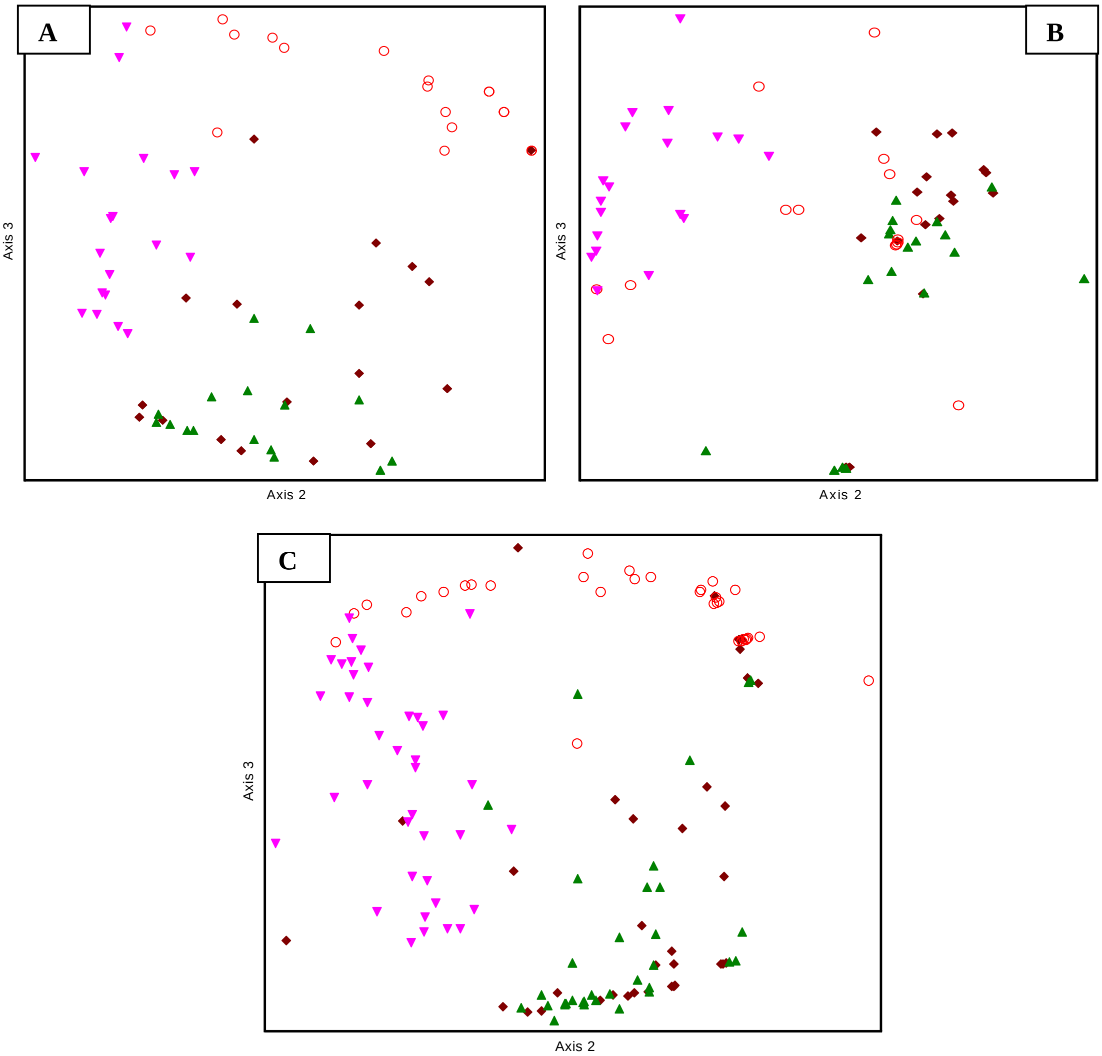
The structure of infaunal communities did not show changes on an inter-annual basis. A Non-metric Multidimensional Scaling (NMS) ordination analysis, based on raw abundances, demonstrated little separation between the samples from 2000 and 2001 (Fig. 4.5 A). This was because there were no significant increases or decreases in the number of individual taxa between the two sampling periods. The increasing number of Neanuridae in 2001 did not have a marked overall effect on the structure of these infaunal assemblages as the communities were dominated by polychaete taxa.

Figure 4.5. NMS ordination showed different results when infaunal samples were pooled into different categories (stress=0.16). A : year category (♦ 2000, ♦ 2001), B:. tidal category (♦ high tidal mark, ♦ low tidal mark)



In contrast, when the samples were pooled on a spatial basis considering tidal height and transects, there was a distinct separation in relation to tide and transect, even though some samples from HI and HO did overlap and some samples from LI were more widely distributed across the ordination (Fig. 4.6). It was shown that samples ordinate based on tidal height and location inside or outside the forest and that these patterns were maintained from year to year. When the 2 sampling periods were pooled, the primary effect was tidal height and location in the forest with little effect attributable to inter-annual changes in community structure.

Figure 4.6. Ordination of infauna when samples were pooled into different transect categories relative to the mangrove forest (stress=0.18) . A: 2000, B: 2001, C: 2000 and 2001, ♦ higher outer (HO), ♦ higher inner (HI), O lower inner, ♦ lower outer (LO)



Subsequently, to test the hypothesis of no differences between groups of samples a rank transformed MRPP was employed. The rank transformation can help the loss of sensitivity of distance measures as community heterogeneity increases (McCune and Grace, 2002). In this process, the distance matrix was calculated using the Bray-Curtis similarities, because the MRPP was used in conjunction with the NMS ordination detailed above.

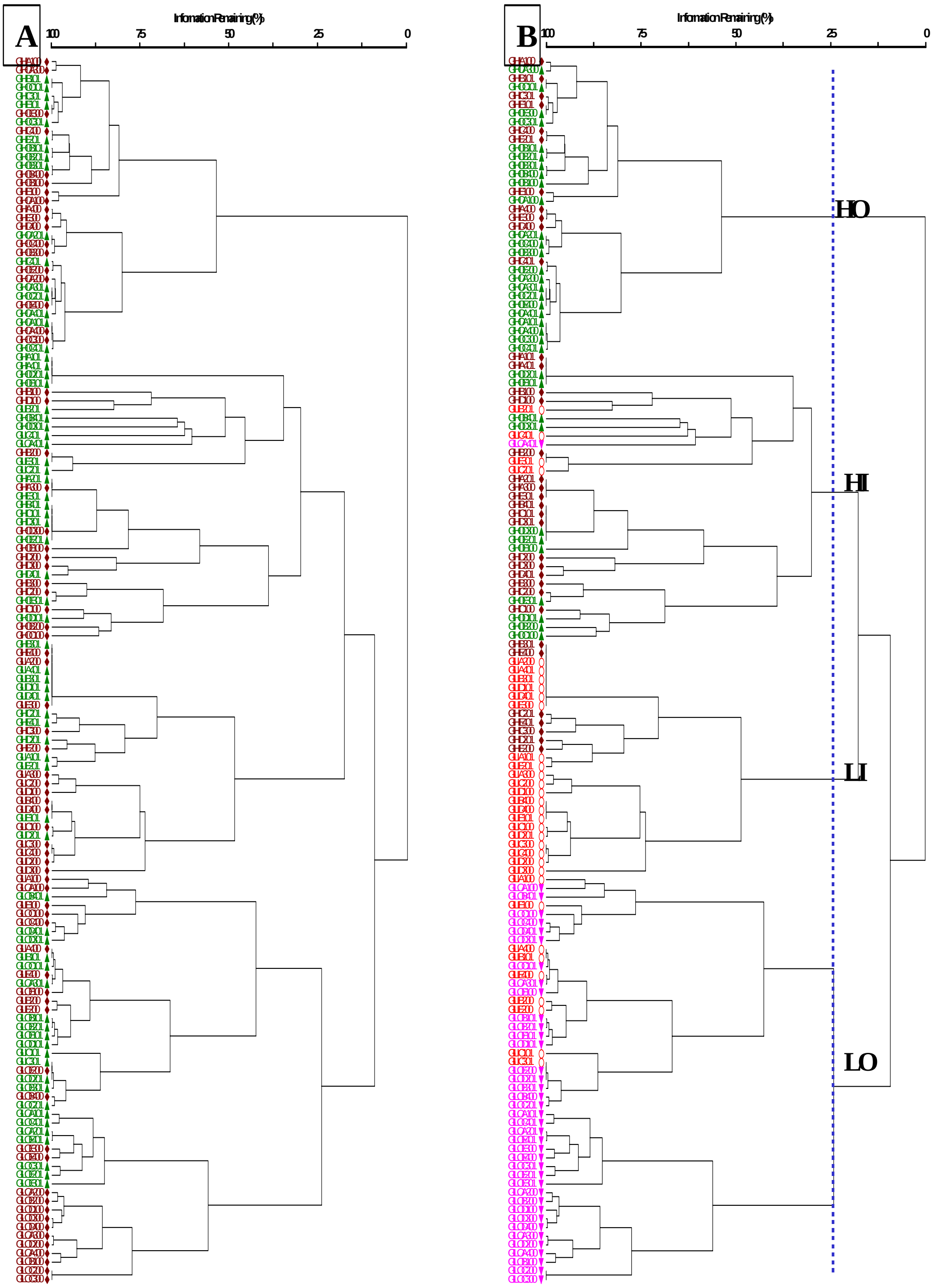
Table 4.2. Summary of statistics for rank-transformed MRPP where the samples were grouped into various categories (year, tidal height, in/out and transsects). A value (range from 0-1) shows the level of homogeneity/correlation within groups, while p is statistical significance. δ value is under null hypothesis

Category	Observe δ	Expected δ	Variance	Skewness	T	A	P
Year	0.496	0.497	0.53E-05	-1.456	-0.297	0.001	0.300
In/Out	0.444	0.497	0.53E-05	-1.455	-22.700	0.1	0.000
Tide	0.396	0.497	0.53E-05	-.1455	-43.782	0.2	0.000
Transects	0.3099	0.497	0.16E-04	-0.329	-46.51	0.3	0.000

The result of the MRPP analysis showed less agreement (correlation) when samples were aggregated into different years (A=0.001, p=0.3), again indicating that the communities were similar in the two years. But when samples were grouped based on spatial differentiation, the value of A was increased. Both in/out of the forest and tidal height were differentiated and resulted in a good level of agreement among samples. Furthermore, there was a significant differentiation when the samples were pooled into transects (A = 0.3; p<0.000).

Cluster analysis was used to assess temporal and spatial influence on community structure in the system (Fig. 4.7). Inter annual variation was not apparent in the infaunal assemblages between years (Fig. 4.7.A). Meaningful patterns were seen when the samples were grouped based on transect (Fig. 4.7.B). The percentage scale was chosen as a pragmatic compromise to interpret the ecological affinities among infaunal organisms. As groups are fused the amount of information decreases until all group are fused with no information remaining at 0%. With 25% information remaining, the infaunal communities were structured into 4 characteristic groups. This reflected the four transectlocations, where the higher inner transect (HI) was comparatively more variables than the others.

Figure 4.7. **Average-linkage dendrogam based on infaunal raw abundance per sample unit using flexible beta (β=-0.25) as linkage method on Bray-Curtis similarities distance measures. The resulting dendogram was scaled by Whishart's objective function converted to a percentage of information remaining. A: samples was grouped into year (♦ 2000, ♦ 2001) and B: samples were grouped into transects (♦HO, ♦ HI, O LI, ♦LO)**



In detail, group one or HO was characterised by infaunal communities, which were dominated by polychaetes including, Capitellidae. Group two or HI had a community that included Capitellidae with taxa such as Syllidae and Flabelligeridae (Polychaeta), Gammaridae (Crustacea) and Amphibolidae (Gastropoda) which all appeared to contribute to the structure of the community on this transect. The lower number of Capitellidae has meant that other taxa characterise the infaunal community at HI sites. Group three or LI consisted of infaunal communities, which were characterised by Group three or LI consisted of infaunal communities, which were characterised by dominance of the polychaete family Nereididae. The infaunal communities in group four or LO were characterised by 2 types of communities. Sub-group one was dominated by the insect Neanuridae and by the polychaete Spionidae. Samples containing Neanuridae were fused together with several other Neanuridae samples from the lower part of the mangrove forest. The other sub-group was strictly characterised by an abundance of the polychaete Spionidae.

4.4. The role of major taxa

Over the two years of sampling, some taxa were restricted to certain areas. An Indicator Taxa Analysis (with regard to spatial variation) indicated that certain polychaete groups such as Spionidae, Capitellidae and Nereididae, the insect Neanuridae and the bivalve Veneridae might all be considered as good indicator taxa. Their abundances and frequencies of occurrence at a given time and a given place can be analysed by the randomisation of distribution test which showed significant patterns in their distribution ($p=0.01$). Spionidae act as an asymmetrical indicator of mudflat areas with 97 % of Spionidae samples coming from the mudflat sites.

Family Capitellidae were considered to be a true symmetrical indicator taxa because they could be found in almost every site of the mangrove forest, even though they were more frequent in the upper part of mangrove forest (56%). The indicator analysis also detected that the Capitellidae varied inter-annually.

Most Nereididae (68%) inhabited the lower inside of the mangrove forest and their occurrence, was related to the annual variation. Neanuridae insects (Order;

Collembola) dominated in the lower part of the mangrove forest (57%). Another taxon that also contributed to structure of the infaunal assemblages was the bivalve Veneridae which was most common in mudflat areas (69%).

Table 4.3. Summary of two-way factorial analysis for important infaunal taxa in the mangrove system. The stars indicate signifucant : *) $\alpha < 0.05$: **) $\alpha < 0.01$: *) $\alpha < 0.0001$**

Taxa	**Year**	**Site**	**Year vs Site**
Capitellidae	0.001 **	< 0.0001 ***	0.005 **
Collembola	0.20	< 0.0001 ***	0.557
Nereididae	0.001**	< 0.0001 ***	< 0.0001***
Spionidae	0.002 **	< 0.0001 ***	< 0.0001***
Syllidae	0.038	0.0006 **	0.003 *
Veneridae	0.16	0.04 *	0.30

The two-way factorial analysis (Table 4.3) supported the assessment of indicator taxa and supported the proposal that some polychaete worms, such as Capitellidae, Spionidae, Nereididae and Syllidae were important taxa in characterising infaunal communities in this area. Moreover, their local occurrence was also influenced by time.

4.5. Linking abiotic factors with infaunal communities

In order to observe the main factors correlating with the patterns of infaunal distribution, a matrix of infaunal samples (raw abundance) was over-layed with a matrix of abotic data including TOC, salinity, clay and silt percentage. The biplot vectors indicate the degree of influence of the abiotic factors on the distribution of samples, the longer the vector the stronger the relationship is. The Monte Carlo method, to test the null hypothesis, resulted in a rejection of the null hypothesis that there was no relationship between infaunal distribution and the abiotic factors (Table 4.4). Most of the information was correlated with axis one rather than the other two axes (as indicated by the eigenvalue). The result indicates that salinity was strongly correlated with all other abiotic factors (Table 4.5). Furthermore, Figure 4.8.A. shows that samples from the mudflat transect (LO) were clustered together in the upper left hand portion of the plot. None of the vectors representing the abiotic factors runs orthogonal to the line separating this group from the others. This suggests that, apart from a slight influence of salinity, that the separation of the mudflat samples is not correlated with the other abiotic factors. On the other hand, infauna in vegetated transects were ordinated in a manner consistent with the influence of the measured abiotic factors.

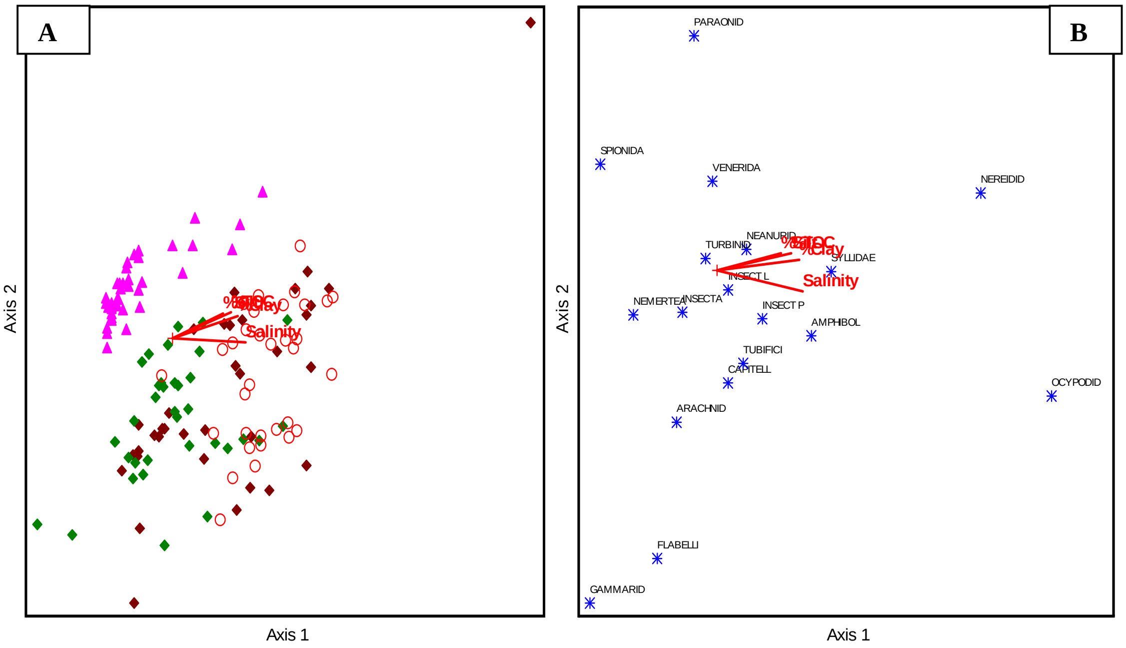
Table 4.4. Summary of Monte Carlo test result to test the null hypothesis and eigen value to evaluate which axis is more connected to the environmental variables

	Real data	**Monte Carlo test**			
Axis	Eigen value	Mean	Minimum	Maximum	P
1	0.240	0.089	0.041	0.181	0.01
2	0.116	0.039	0.016	0.090	0.01
3	0.058	0.021	0.009	0.048	0.01

Table 4.5. Correlation among measured abiotic factors

	% TOC	% Clay	%Silt	Salinity
%TOC	1	0.458	0.355	0.670
%Clay	0.458	1	0.519	0.753
% Silt	0.355	0.519	1	0.531
Salinity	0.670	0.753	0.531	1

Figure 4.8. Ordination of sample unit in environmental space as defined by CCA. The biplot overlay shows vector related to the strongest environmental variables which drove the separation of infaunal distribution in this system. A. Sites; B. Taxa(◆HO, ◆ HI, OLI, ◆LO)



(Fig. 4.8.B) demonstrates that Spionidae and Veneridae were most dominant on the lower part outside of the mangrove forest (LO), prefering sites that had lower salinities with less clay and silt (more sandy). In contrast, Capitellidae occurred in the more saline areas with high TOC and medium levels of clay and silt. Nereididae tended to have a similar relationship with salinity and also followed the distribution of other sediment properties such as TOC, clay and silt concentration.

5. Discussion

5.1. Infaunal charateristics

This study has shown that the Garden Island mangrove system is unlike those considered elsewhere which is reflected in the character and distribution patterns of benthic infauna. The structure of benthic infaunal communities was characterised by a low abundance and very low diversity, being comprised of only 18 families. Richer communities have been found in other temperate mangroves. For instance, at least 22 polychaete families made up benthic assemblages at Careel Bay, NSW (Hutchings and Recher, 1974), 29 taxa of benthic infauna were found in urban temperate mangroves around Botany Bay (Kelaher *et al.*, 1998a). A recent study at NSW temperate estuaries recorded 40 taxa of macroinfauna and 20 taxa alone form the mangrove zones (Lidegrath and Hoskin, 2001). A far greater abundance of infauna were found in an East African temperate mangrove forest where densities were up to 23,058 individuals/m^2 (Schrijvers *et al.*, 1998) compared to the 2,236 individuals/m^{2}found in the present study. The present study also noted that the infauna found in the Garden Island mangrove forest were lower in both density and diversity when compared with the non- mangrove habitats at the same location. This situation may relate to conditions on Garden Island, which is located in the Adelaide urban area and receives considerable anthropogenic impact (Edyvane, 1999), even though Clyde (1995) claimed that mangrove and saltmarsh communities were not affected by the leachaete from the landfill activities at Garden Island. Moreover, detailed data on the heavy metals pollutions or other potential contaminations may have revealed the cause of the lower densisty and diversity of the infaunal assemblages, which was beyond the scope of this study.

5.2. Inter annual diferences

In considering the inter-annual variation in community composition, both univariate and multivariate analyses concluded that infaunal distribution was not substantially different between the two years. This might be due to several common taxa, such as Spionidae, Capitellidae and Nereididae maintaining their dominance within the infaunal assemblages. This result was in agreement with a previous study at a similar location that monitored the effect of the thermal effluent discharge from the Torrens Island power plant from 1972-1985 (Thomas *et al.*, 1986). They reported that the infaunal community was in a stable state from 1982 to 1985 due to the occurrence of opportunistic taxa such as Capitellidae and Spionidae. Moreover Sheridan (1977) found that the variation in density of dominant taxa of benthic communities between mangrove, seagrass and mudflats were more related to habitat then to sampling time.

Benthic infaunal assemblages were made up by some taxa, which have relatively long life spans. In the case of time scale, the length of the life cycle will affect the chance of changes in the number of individual taxa over given time frames. The significant increase in the number of individual Spionids (from 252 to 354 individuals between 2000 and 2001) may indicate that Spionids have an annual breeding cycle. The study observed that in the 2001 samples, some Spionids were in a reproductive condition which was indicated by the body of the worm being much more fragile, being protected by the sand-mucus tube with embryos inside their body (Blake and Woodwick, 1975).[1]

Some infaunal organisms did show changes in the abundances of individual taxa, and there were changes in the presence or absence of certain taxa from the assemblages. For example for Nereididae, the density was reduced by almost 1/3 from the 2000 to 2001. This situation could be explained by two possibilities. First, this was probably related to their life cycle, which, according to Glasby *et.al.* (2000), Australian nereidids can complete their lifecycle between 1-1.5

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[1] Detailed information about the biology of common polychaete taxa, including information about reproductive status and species identification is provided in chapter 6. The information has been included at this point to provide some context for the discussion.

years before they die, as is characteristic of monotelic species in which adults typically die after spawning. Secondly, that salinity may affect the synchronization of reproduction in this habitat. Hsieh (1995) reported that sediment salinities in the range 8-28 mS/cm affected the timing and synchronization of nereidid reproduction. The mean salinity in the lower inside of the mangrove forest was 15-18 mS/cm which is well within this range.

Inter-annual changes were also found in the Capitellidae, mostly dominated by *Capitella* sp. (further detail will be discussed in Chapter 6). This taxa was not only reduced in density but almost disappeared from the mudflat (LO) in 2001. The replacement of Capitellidae by spionids was also detected during the study of Thomas *et al*. (1986). Qian and Chia (1994) reported juvenile mortality of *Capitella* sp. in mudflat areas and suggested that inter specific interactions, such as predation, could be a major process regulating the abundance of this group.

5.3. Abiotic factors and distributions

Clay and silt levels were consistently higher inside the mangrove forest which indicates that *Avicennia marina* is efficient in silt trapping and retaining sediments when compared with saltmarsh vegetation as suggested by Burton (1982). The distribution pattern of clay was correlated with sediment salinity (($r_{\text{sal-toc}}=0.67$; $r_{\text{sal-clay}}=0.756$; $r_{\text{sal-silt}}=0.53$) and this may be a result of clay binding capacity in the cation exchange process. The trend of salinity correlating with clay content was also found in a study on mangroves in Hongkong (Tam and Wong, 2000), even though Machiwa (1998) stated that sediment properties vary within mangrove forests depending on tidal regime and forest types.

5.4. Spatial patterns of infaunal distribution in relation to habitat charateristics

The benthic infauna at Garden Island exhibited spatial variations that were correlated with the geomorphological features as well as sediments properties. This was in agreement with Butler *et.al*. (1997) who suggested that the distribution and abundance of benthic faunal species characteristic of mangroves in South Australia depended primarily on substrate type and sediment height above mean sea level rather than the presence of the mangrove itself. One of the most important geological features was tidal regime and the response of benthic infaunal communities were relatively different. Peterson (1991) stated that in intertidal areas, organisms show a distinct zonation related to elevation on the shore, due to the level of stress experienced. The higher the elevation from sea the more stress the animals face.

The upper part of Garden Island was a more variable place and this was reflected in the infaunal assemblages that were characterized by the less diverse and less abundant communities. On the other hand, the lower part of the mangrove forest was inhabited by infaunal communities that were characteristically more dense and diverse. Prolonged inundation at the lower part may give some advantages to benthic infauna, such as maintaining oxygenated processes in the sediment and increasing food supply. The vertical distribution, which affected the infaunal zonation, was has also been found in subtropical mangrove systems (Kolehmainen and Hildner, 1974; Netto and Lana, 1997). At Garden Island, the contribution of deposit feeders to the structure of infaunal communities changes along the gradient, from the higher intertidal to the low water mark. Capitellidae (56% indicator value) together with Syllidae (67% indicator value), and some of the subsurface deposit feeders, were most common in the upper tidal areas. Meanwhile, Nereididae (68% indicator value) together with Spionidae (97% indicator value) are some surface deposit feeders commonly found at the lower intertidal sites. The vertical changes in the distribution of deposit feeder communities along the tidal gradient was also reported from a northern hemisphere bay (Wilson and Roth, 1998.). Although there are changes in the structure of communities from surface deposit feeders in the lower intertidal to sub-surface deposit feeders higher up on the tidal gradient, Dauer *et al.* (1981) argued that some taxa (e.g. Spionidae) can exclusively change their feeding behaviour (particle preference) to match the availability of food in any given habitat. Furthermore, the food availability is likely to be uncertain through time and may well change, for example, on a seasonal basis.

Benthic organisms have strong associations with sediment. Multivariate analyses detected that the infaunal communities tended to classify consistent with the differences in sediment characteristics which in turn were related to tidal elevation. The distribution pattern of benthic infauna was related mostly to patterns in polychaete taxa which appeared to favour unconsolidated sediments in which burrowing is easier (Hutchings and Saenger, 1987). Garden Island is geologically located within the St. Kilda formation where sediments are unconsolidated with a high organic content (Clyde, 1995).

A distinct spatial pattern of infaunal assemblages was identified between mangrove areas and the adjacent mudflats (LO). The mudflat community was characterized by high abundance and high diversity. The infauna lived within the sediment which was more sandy, having less clay and silt, lower salinities and with lower organic content. This result is consistent with several previous studies on the differences in the structure of infauna in mudflat and mangrove areas (Ditmann, 2001; Hutching and Recher, 1974; Schrijvers *et.al.*, 1998; Sheridan,1997).

Spionidae was the most obvious polychaete taxon at the mudflat site (LO). *Pseudopolydopora paucibranchiata* was dominant in the Spionid community (as will be discussed in Chapter 6). This resulted was consistent with the findings of Thomas *et al*. (1986) who found that *Pseudopolydora sp* continued to dominated the Angas Inlet. Spionidae are benthic polychaetes with a pair of grooved feeding palps (Glasby *et al.*, 2000). Their feeding behaviours include suspension feeding and deposit feeding that depend on environmental condition (Fauchald and Jumars, 1979; Ferner and Jumars, 1999). This feeding behaviour may explain why *Pseudopolydopora paucibranchiata* was restricted to the wetter sediment found on the seaward side of the mangrove forest or near the region of permanent water as suggested by Hutchings and Saenger (1987). This statement was also supported by Hillderbeg and Nateewathana (1991) who claimed that habitat preferences are important in explaining the large numbers of Spionidae within small areas.

The lower inside habitat of the mangrove forest was characterized by sediments with high clay and silt, high salinity and high organic content. These conditions were reflected in the structure of the community with lower diversity and abundances of infauna. Nereididae was the most commonly encountered taxon at this site, which was mostly dominated by the species *Neanthes vaalii*. It seemed possible that the physico-chemical parameters of this site provide a favourable habitat for Nereididae but unfavourable conditions for other taxa. A study conducted at a subtropical mangrove forest where clay in the sediment ranged from 15-60%, showed a positive correlation with abundance of *Neanthes flandicinta* (Hsieh, 1995). That study concluded that clay content would not be the only single factor in maintaining the abundance of this species, which would also depend on the species feeding behaviour and chemical processes within sediment (Vismann, 1990).

The increase in density of Neanuridae (Order: Collembola) from 2000 to 2001, seemed not to affect the pattern of the community as the infaunal community was dominated mostly by polychaetes worms. As Hutchings (1998) and Thomas *et.al.* (1986) stated, polychaete worms are likely to dominate infaunal communities in mangrove systems. However, their occurrence made a greater contribution to the infaunal assemblages at Garden Island. Collembolans or spring-tails inhabited the lower part of the mangrove systems. Many marine collembolan species are very susceptible to desiccation because of a permeable integument and regain water by everting the ventral tube vesicle into soil water (Witteven and Joose,1987). Neanuridae (dominated by *Pseudanuridae sp*. cf. *galuerti* Womersly- Greenslade, pers.com-2001) is a common litoral insect found along the south coast of Australia (Greenslade, 1991). Neanurids are very small insects rarely exceeding 5 mm long. They breed annually without having a larval stage. Their distribution in the mangrove forest was patchy and they were found in aggregations possibly hiding in air bubbles among plant roots when the tide was up. The air bubbles may acts not only as an oxygen store but also as a compressible gas gill (Zinkler *et al.*, 1999) . When the tide recedes, the insect will move progressively in to the lower part and start feeding. (Greenslade, pers.com. 2001). The foraging behaviour and circa tidal rthym orientation allowing this insect to migrate from up-shore to the down shore horizon (Manica *et al.*, 2000 : Mc Meehan *et al.,* 2000). Sterzynka and Ehrnsberger (2000) also noted that the distribution of *Archisotoma* sp. (other species of Neanuridae) in the saltmarsh was influenced by organic content.

The higher area inside the mangrove forest (HI) and the saltmarshes (HO) have similar infaunal assemblages at the Garden Island mangrove system. Sediments comprised high clay and silt content, high salinity and were rich in organic carbon. The infaunal communities on these transects were dominated by *Capitella sp.*(Capitellidae). As a semi-burrowing taxon, their occurrence in mangrove forest is often related to the muddy-rich organic carbon sediment (Pearson and Rosenberg, 1978; Hutchings and Saenger, 1987; Sheridan, 1997; Schrijvers *et al.*, 1998; Dittmann, 2001) which is consistent with sediment properties at Garden Island. *Capitella sp* also exhibit a higher tolerance of hypoxic conditions (Pearson and Rosenberg, 1978), as would be found in sediments from the upper part of the mangrove forest. Increasing salinity probably represents an inhibitory factor for other taxa which showed a marked decrease in density or absence from the infaunal assemblages. In temperate estuaries where salinity is subject to sudden change on a seasonal basis, Capitellidae are typically found (Glasby *et al.*, 2000) and have a major role in balancing competitive equilibria among polychaetes species (Giangrande and Fraschetti, 1993).

Infaunal communities at Garden Island showed spatial variation, and to lesser extent temporal variation. The variation in density of dominant taxa was mostly related to the habitat characteristics, which relate to tidal height and sediment properties.

Chapter 5 Infaunal Distribution within Mangrove Sediments

Synopsis: Infaunal communities at Garden Island vary with respect to position on the tidal gradient and habitat (inside or outside the forest). These variations were maintained between samplings at two times (May 2000 and May 2001) and were related to edaphic characteristics of the sediment at any site. This chapter will extend this through an investigation of the extent to which the vertical distribution of infuana relates to the sediment condition and changes through time.

1. Introduction

Studies of infauna in mangrove systems demonstrate a close relationship between infauna and sediment conditions. The distribution of infauna is shaped by physical, chemical and biological factors that work together forming an ecological complex within the sediments. For infauna, burrowing activities can be adopted as the life strategy to avoid desiccation during sediment exposure, refuge from predators and also as territorial behaviour. However, information about the vertical distribution of benthic invertebrates, relating to the variation of depth within mangrove sediments is very scattered compared with the information concerning distribution patterns of infauna relating to different intertidal habitats (mudflats, mangroves, seagrass, saltmarshes), latitude (tropical, temperate, subtropical) and sediment characteristics (mud, sand).

Mangrove sediments are often anoxic and frequently saturated with hydrogen sulphide (Macnae, 1968 ; Alongi, 1998) and exhibit a low redox potential (Peterson, 1991). Biological activity within the sediment promotes peturbation and sediment reworking and can change the chemical profile of sediments (Johnson, 1977; Machiwa, 1998), although this process is generally limited only to a certain depth. Generally only the surficial sediments are likely to be oxidised and associated aerobic mineralisation processes, which release nutrients, are more prevalent in the surface layer (Kristensen *et al.*, 2000; Rosenberg *et al.*, 2000) and are often related to seasonal fluctuations (Cheng, 1995).

Reports from tropical and subtropical mangroves have confirmed that surface sediments are most favoured for infauna (Kumar, 1997; Stark, 1998; Cheng and Chang, 1999). Some infauna can burrow to a depth of few centimeters while other taxa, such as bivalves and crabs, can penetrate sediments to depths of 30 cm (Hines and Comtois, 1985; Tomascik *et al.*, 1997). The pattern of vertical stratification of infauna may reflect differences in ecological function, such as burrowing ability, feeding behaviour and resource partitioning for food and space (Hines and Comtois, 1985; Kumar, 1997). Hence, the environmental factors, especially organic content, oxygenation, redox potential and associated products of redox reactions, will have a vertical pattern that will challenge the existence of infauna at depth.

In order to understand the patterns of infaunal distribution over depth within the mangrove sediments, this study has quantified:

1. The pattern in the distribution of infauna over depth within the sediment.
2. The abiotic factors which are likely to drive these patterns in the vertical distribution of infauna.
3. The extent to which temporal variations affect the characteristics of community structure and associated abiotic factors including TOC, salinity, redox potential and sediment grain size.

2. Materials and Methods

2.1. Sampling design

Samples were taken from the lower inner site on Garden Island. Sediments in this area were comprised of a high proportion of clay (20 % to 36.25%) and silt (6.25 % to 16.25%), a high salinity (13mS/cm to mS/cm24.1%) and high total organic content (3.2% to 5.5. %).

Sediment samples were collected on 3 occasions (Nov. 2000, Feb. 2001 and May 2001), during low spring tides, along a 40m transect line running parallel to the coast line. A series of five sampling points were established at 10 m intervals along the transects. At each point, four replicate infauna samples and four replicate sediment samples were randomly collected by pushing a pvc hand core device (∅ 6.0 cm, 5.2 cm surface area) to 20 cm depth. To avoid error due to the migration of infauna, the sediment core was cut immediately into 4 different layers (0-5 cm, 5-10 cm, 10-15 cm and 15-20 cm). At the end, there were 80 samples of infauna and 80 samples of sediment collected at every sampling period. Both infauna and soil samples were put into air-tight plastic bags for further treatment in the laboratory. Infauna samples were then preserved in 10 % formalin for identification and soil samples were subjected to textural and chemical analysis. The procedure of infauna identification and soil analysis was similar to that reported for the previous experiments (Allison, 1965; Gee and Bauder, 1986; English *et al.*, 1994). Redox potential (Eh) was measured *in situ* by inserting a redox electrode into a core. The core had small holes drilled at four different locations for measurement of Eh. The Eh reading was taken by placing electrodes through the holes and into the core as soon as the core was removed to minimise the oxidation. The redox potential was measured over six days on a field trip undertaken after the infaunal sample collection was completed.

2.2. Data analysis:

Ideally, in the design where the subject (infauna) was measured repeatedly across time, a univariate/multivariate analysis with repeated measures would be employed. Repeated measure ANOVA would allow an analysis of the effects both within and between subjects (depth and season). Unfortunately, this method cannot be used in this analysis because the infaunal samples over depth, were not spatially independent (samples across depth actually came from the same set of cores). To overcome this problem, the analysis was performed on the delta values which were calculated by subtracting the number of infauna in the bottom layers (10-20cm) from the numbers in the top layers (0-10 cm). To evaluate this value the infaunal number for the top two segments was summed as was the infaunal abundance for the bottom two layers.

To investigate whether there was a difference in abundances between the upper and lower layers of the sediment, the mean value for delta was calculated. If the mean delta is 0, it indicates that on average there was no difference in the numbers in the upper vs lower layers, if the mean delta value is significantly greater than 0 then it can be concluded that most of the infauna were concentrated in the surficial sediments, but if the mean delta was significantly less than zero then it can be assumed that the infauna were mostly concentrated in the deeper layers.

Another analysis was undertaken using a paired (two-sample) t test. A two-sample t test was conducted to test the null hypothesis that there was no difference in infaunal abundance between the top layer and the bottom layer. For the paired t-test the data analyses used absolute abundances except where the absolute numbers resulted in a non normal distribution and the data were transformed using the √√ (double square roots).

Subsequently, univariate analysis of variances (ANOVA) based on abundance difference values (delta) over the three sampling times was carried out to test the null hypothesis that the infaunal abundances between top layer and bottom layers did not vary seasonally. Welch's ANOVA was used to allow for the unequal variances within the sample group. The Welch ANOVA was based on the usual ANOVA F test, but the means have been weighted by the reciprocal of the sample variances. When significance differences were detected in the Welch ANOVA, then the results of the ANOVA F test will be taken. All statistical tests were carried out using JMP statistical software version 3.2.1 (SAS Institute Inc. 1995).

3. Results

3.1. The distribution of benthic orgnisms

A total of 270 individuals from various taxa were recorded during the study (Table.5.1). The average sum abundance per core sample was low, usually 1 (one) individual and higher variation of mean abundance (stdev. = 6), indicating the patchiness of infauna at this site. Across all samples 79.3 % of all infauna were found inhabiting the top 5 cm of the sediment profile. Infaunal abundance decreased with depth with only 9 animals or 3.3 % of the total occupying the lower 15-20 cm section of the cores.

Table 5.1. List of taxa collected at every section of the core (depth) during three consecutive sampling periods

Season	Class	Family	0-5 cm	5-10 cm	10-15 cm	15-20 cm	Total	%
Nov-00	Insecta	NEANURIDAE	1	0	5	0	**6**	**2.2**
Nov-00	Gastropoda	TURBINIDAE	4	0	0	0	**4**	**1.5**
Nov-00	Bivalve	MYTILIDAE	1	0	0	0	**1**	**0.4**
Nov-00	Polychaeta	NEREIDIDAE	13	3	3	2	**21**	**7.8**
Nov-00	Insecta	PUPAE	3	6	4	5	**18**	**6.7**
Nov-00	Bivalve	VENERIDAE	2	1	0	0	**3**	**1.1**
Feb-01	Insecta	NEANURIDAE	9	4	0	0	**13**	**4.8**
Feb-01	Insecta	Un-INSECTA	1	0	0	1	**2**	**0.7**
Feb-01	Polychaeta	NEREIDIDAE	12	5	3	0	**20**	**7.4**
Feb-01	Insecta	PUPAE	1	1	0	1	**3**	**1.1**
May-01	Insecta	NEANURIDAE	156	3	0	0	**159**	**58.9**
May-01	Polychaeta	NEREIDIDAE	11	1	0	0	**12**	**4.4**
May-01	Crustacea	OCYPODIDAE	2	0	0	0	**2**	**0.7**
May-01	Insecta	PUPAE	4	1	0	0	**5**	**1.9**
May-01	Bivalve	VENERIDAE	0	1	0	0	**1**	**0.4**
		TOTAL	**220**	**26**	**15**	**9**	**270**	
			79.3%	**11.1%**	**6.3%**	**3.3%**		

Table 5.1. also shows that infaunal assemblages were dominated by 3 groups, the insect Neanuridae, the polychaete Nereididae and others. In addition, May season appeared to be the time of highest infaunal abundance as more than 70% of animals were collected during this period. Meanwhile infaunal abundance was lowest in February with less than 10% of the total number of infauna collected at that time. The high number of infauna during the May sampling was mainly due to contribution from the insect Neanuridae (Order: Collembola-springtail). The variation in taxa was relatively low with only 8 different taxa across all cores and most of them inhabited the upper sections of the cores. Taxa richness was probably affected by seasonal fluctuations with the greatest number of taxa being caught in November. The least number of taxa were recovered in February.

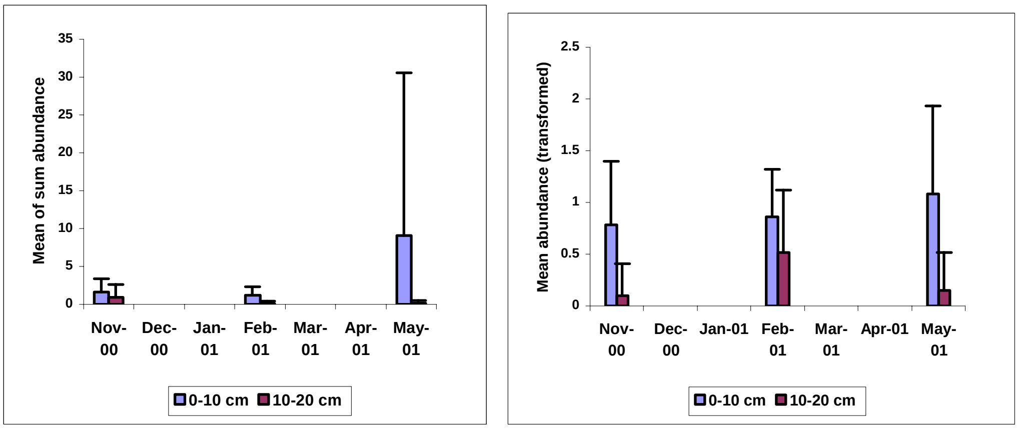
Unlike other sites (Chapter 4) where polychaetes were found to be numerically dominant both in diversity and density, only a single family of polychaete, the

Nereididae, dominated in these samples. The Nereididae contributed 19.6% or 53 individuals to the infaunal assemblages and was found to a depth of 20 cm. Several juvenile Nereidids were found in the surface layer in the May samples. The most abundant taxon was the insect (family Neanuridae). Neanuridae, comprised 177 individuals and made up almost 66% of animals in these infaunal communities. They were limited to the upper layers and their abundance varied substantially across sampling times. They reached a peak abundance in May comprising almost 61.5 % of the total infaunal density or 166 individuals, as opposed to the only 2.2 % or 6 individuals in February.

3.2. Vertical distribution within substrates

Figure 5.1**.** comprises the graphs of transformed and non transformed abundance data. Both measures showed that the maximum aggregation of benthic infauna (90%) was consistently found in the top layer (0-10 cm) of the sediment and abudances at depth were substantially lower.

Figure 5.1. Mean of sum of infaunal abundance (raw and √√ transformed: ± SD) within sediment showing a vertical distribution pattern



Subsequently, as the samples were not independent, the abundance differences (delta) procedure for total infauna was applied. The result revealed that that the mean differences was significantly greater than zero (delta = 3.6; N= 60) which indicated that most of the infauna inhabited the surficial layer. This result was also consistent with the paired t test which demonstrated that there was a significant difference between top and bottom layers (raw abundance t_{value}=2.1; p=0.03; transformed abundance t_{value} = -6.2; $p < 0.0001$; Table 5.2). Transformations to the double square root were undertaken in an effort to improve the normality and homoscedascity of the data and this resulted in an increase in the level of significant differences.

Two taxa contributed strongly to the infaunal assemblages in this study. These were the polychaete Nereididae and the insect Neanuridae. After analysing these taxa separately all other taxa were combined into a single group and analysed collectively

The distribution of these taxa within the infaunal assemblages was examined and analysed using the same procedure and the results are presented in Table 5.2.

Table 5.2. Summary of pair t test statistics for the important taxa in regard to the variation of depth using sum abundances of every depth mentioned (* sign of significance).

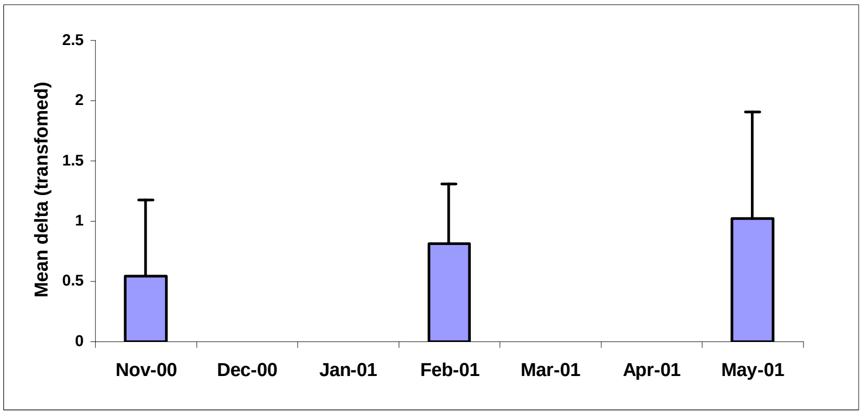
Taxonomic grouping	Source : Depth (0-10 cm vs. 10-20 cm)	T_{value}	Prob >|t |
Nereididae	Raw abundances (N =120)	-5.33	< 0.0001*
	Transformed abundances (N=120)	-6.59	<0.0001 *
Neanuridae	Raw abundances (N =120)	-1.61	0.13
	Transformed abundances (N=120)	-6.507	<0.0001*
Others	Raw abundances (N =120)	1.01	0.03*
	Transformed abundances (N=120)	2.62	0.06

In general, the abundances for all three taxonomic groups were significantly higher in the surficial layer (0-10 cm) than in the bottom layer (10-20 cm). It is worthwhile to note, that the distribution of Neanuridae was somewhat patchy and this affected the analysis of the data when considered collectively. Transformation of the data (double square root) helped to normalise the distribution and this resulted in a general increase in the significance measures (Table 5.2). Hence, it seems that individual taxa made a significant contribution to the infaunal assemblages in this present study.

3.3. Temporal variation of infaunal vertical distribution

The extent of temporal variation in the vertical distribution pattern of infauna was investigated. This analysis used the delta value (differences in abundances between the top layer and the bottom layer) as the response variable. The null hypothesis, was that there was no temporal effect on the vertical distribution pattern of infauna. The analysis of variance (ANOVA) failed to reject the null hypothesis (untransformed delta df =2; F_{ratio}=2.8; p=0.07; transformed delta df =2; F_{ratio}= 1.65; p=0.1). This means that there was no temporal variation in the pattern of infaunal abundances between the top layer (0-10 cm) and the bottom layer (10-20 cm).

Figure 5.2. Mean of infaunal abundance (√√ transformed ±SD) during three consecutive sampling periods.



Even though a significant difference was not found, Figure 5.2 demonstrates that the absolute abundance in May 2001 was higher than in November 2000. The change appears to be due to an increase in the abundance of Neanuridae in the May 2001.

3.4. The dominant taxa

The taxa that contributed to the infaunal communities were also examined to observe the extent to which sampling time affected the distribution within the two layers. Table 5.3 provides the results of a Welch ANOVA. Data were not transformed as this test is able to cope with the unequal variances.

Table 5.3. Summary of Welch ANOVA test of the important taxa using the abundance differences (delta) value (*sign of significance)

Group	Source:sampling time	F_{value}	Prob>F
Nereididae	Raw abundances (N =60)	0.26	0.77
Neanuridae	Raw abundances (N =60)	2.0	0.13
Others	Raw abundances (N =60)	1.2	0.4

The result showed that the differences in abundance of the three infaunal groups between the top layer (0-10 cm) and the bottom layer (10-20 cm) did not change between seasons. This result indicated that the surficial layer was consistently preferred by the taxa present during the study.

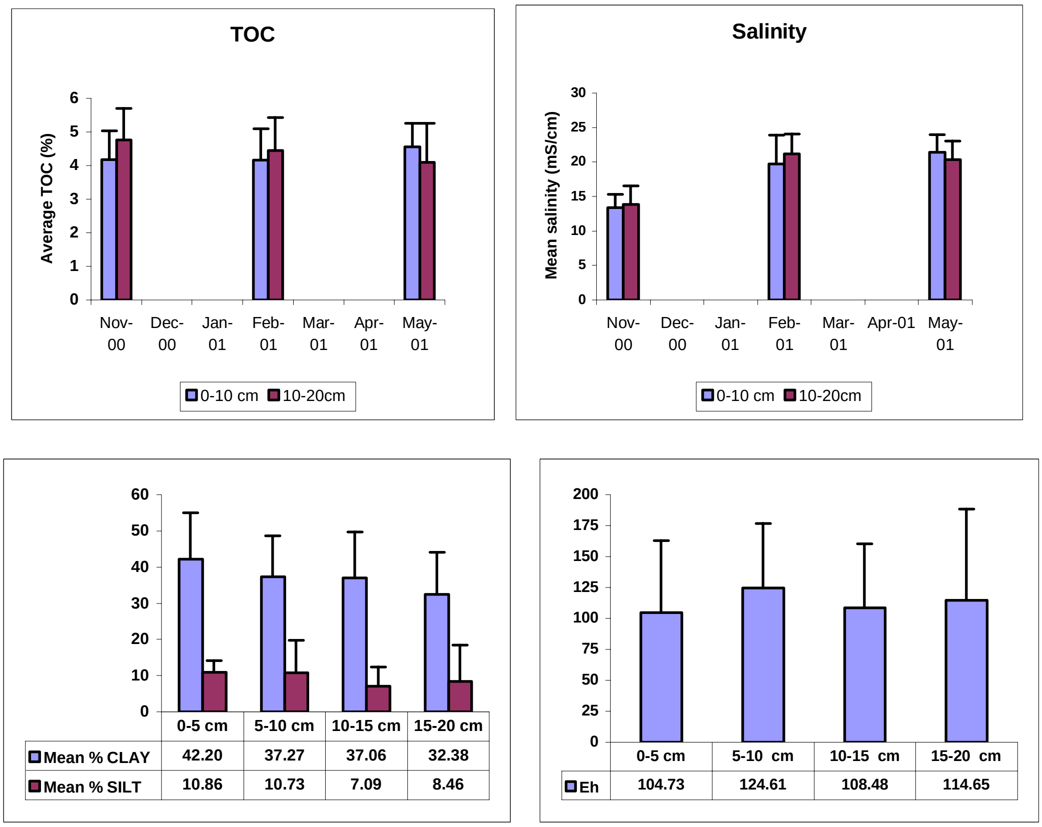
3.5. Abiotic characteristics

Abiotic characteristics of the sediment include %TOC, salinity, sediment grain size (%clay and %silt) and redox potential (Eh). These environmental factors were not consistenly measured during the study due to lack of time and the required extensive labour. Table 5.4 and Figure 5.3 are summaries of the measured environmental factors during the study and the data was not analysed further.

Table 5.4. Mean abiotic characteristics during three consecutive sampling periods.

Source	November 2000	February 2001	May 2001
% TOC	4. 34%	4.33 %	4.32 %
Salinity (mS/cm)	13.34%	20.48%	20.89%
Redox potential (mV)	NA	NA	+ 113.12 mV
% Clay	38.27%	NA	NA
% Silt	9.54 %	NA	NA

Figure 5.3. Mean TOC and salinity at every depths during 3 consecutive sampling periods, clay and silt content in November season and redox potential in May season (bars denote the standard deviation). ***There was no further statistical analysisof the data presented.***



	0-5 cm	5-10 cm	10-15 cm	15-20 cm
Mean % CLAY	42.20	37.27	37.06	32.38
Mean % SILT	10.86	10.73	7.09	8.46

	0-5 cm	5-10 cm	10-15 cm	15-20 cm
Eh	104.73	124.61	108.48	114.65

In general, the edaphic characteristics of the sediment varied considerably across the sampling times, as well as with depth. Salinity was lowest in November 2000 (13 mS/cm on average) and higher in May 2001 reached 21 mS/cm on average. Total organic carbon (TOC) shows less fluctuation over time and depth range of 3.8 % to 4.7 %. On the other hand clay and silt content show a gradual trend relate to variation of depths and was higher in the surface layer (approximately 42 % clay and 11% silt on average). Meanwhile no pattern could be defined for redox potential (Eh).

4. Discussion

4.1. Abiotic characteritics

Patterns of distribution of infauna within the mangrove substrate suggest that their occurrence is dependent on the physical and chemical parameters of the sediments. Sediments at this lower inner site on Garden Island are typical of mangrove sediment with a high content of organic material, moderate salinity and high silt and clay content. Some variations, both spatially and temporally, occurred in the subsurface area (between 0-20 cm depth) probably as a result of the active biological and chemical processes that often take place in these surficial layers. As the site was located close to the lower tidal mark, it may have received benefit from prolonged inundation, as indicated by the relatively high redox potential found within the sediment. Moreover, it has been reported that biological activities, including feeding and burrowing by infauna can result in a homogenous sediment (Johnson, 1977). Notwithstanding this, the sediment parameters measured in this study showed no definite trend in relation to biological processes over depth. For instance, redox potential (Eh) did not show the expected trend of being higher in the top 5 cm and gradually decreasing over depth. Instead the parameters showed no definite trend across the 0-20 cm depth profile.

(Mackey and Mackay, 1995) was of the opinion that the aerial roots of mangroves often modified the redox potential within sediments, making the range of redox potential in an area very large. English *et al.*, (1994) state that the value of redox potential may range from totally anoxic sediments (below –200 mV) to a typical oxygenated sediment (above +300 mV) In a temperate East African mangrove forest the Eh of soils ranging from –200 to +100 mV (Machiwa, 1998), while in Gazi Bay Kenya the Eh of mangrove soils was –284mV to +175mV (Matthijs *et al*., 1999). Vorenhout *et al*. (2004) reported the range of Eh of a satlmarsh soils as large as –400 mV to + 100mV.

The variation of Eh values were related to biotic processes. If light is available the algal communities will be present providing an oxidised layer for benthic infauna and other meiofauna. The redox discontinuity layer is the home for chemosynthetic bacteria such as sulfate reducers, methane bacteria and certain anaerobic protozoan and a few nematodes (Odum, 1971). The oxidised layer may be quite thin in muddy or silty bottoms. Stark (1998) found the redox potential discontinuity (RPD) layer in the mangrove sediments of Sydney estuaries was at 5 – 10 cm depth.

4.2. Infaunal communities

Infauna in the mangrove forest was affected by variations in sediment parameters. It has been shown in the previous chapter (chapter 4) that the richness of the infaunal communities in these mangrove sediments was low, less than in the mudflat sites adjacent to the mangrove forest. The infaunal communities in this study were largely comprised of only 2 families. A single group of polychaetes (Nereididae) and the Neanuridae insect. A range of other taxa were observed to have very low abundances of less than 10 individuals. Similarly, the mean abundance of taxa was very low. Hence the data set obtained was very limited and showed no real pattern, except that most of the taxa were present in the surficial layer (0-5 cm). The marked increase of the Neanuridae insect numbers in May 2001 affected the analysis of the data. Data transformation usingthe double square root increased the relative weighting of the low abundance taxa relative to the higher abundance taxa. However, due to the generally low abundance of most taxa caught during this study it was difficult to make any meaningful analysis of the temporal variation.

4.3.Vertical distribution patterns.

Examination of the vertical distribution pattern of infauna within the mangrove sediment found that abundances were higher in the surficial layer (0-10 cm) and this was also more diverse when compared to the bottom layer (10-20 cm). This result was in agreement with previous research on tropical mangrove systems which found that most macro-invertebrates were concentrated in the top 0-5 cm layer (Kumar, 1997). Gray (1981) stated that the redox potential discontinuity (RPD) layer which extends below 5 cm was beyond the range of most macrobethos. In addition, Cheng and Chang (1999) reported that in a Taiwanese subtropical mangrove 80% of infauna were concentrated in the upper 2-3 cm. It was likely that the upper layers of the substratum (0-10 cm) were more suitable for the infauna.

Most mineral recycling by organisms is found in the surficial regions where the sediments are aerobic and redox potential is high. Cheng (1995) found that organic content was higher in the top 8 cm of a subtropical mangrove system and he suggested that the depth penetration of infauna may be limited to the aerobic layer of sediment. This observation is similar to the finding of Kristensen *et al.* (2000) who stated that anaerobic conditions could be maintained to a deeper layer as a result of organic matter degradation mediated by sulfate reduction pathways.

Variation in the extent to which individual taxa penetrated the sediments was also observed in the present study. Nereididae for instance, can be found across the profile. Since juvenile nereids (indicated by small size and other morphology descriptions) were found only in the top layer of substratum, the occurrence of Nereididae at different depths may reflect the burrowing ability of the taxon to penetrate the sediment which often relates to the body size. Nereididae drill the sediment by circular muscle contractions assisted by their proboscis, which allows them to burrow deeper (Glasby *et al*., 2000). In addition, the nereidids burrow into the deeper layer probably as part of their territorial behaviour (Glasby *et al*., 2000). However the ability of infauna to penetrate sediment is likely to be very much species specific as Hines and Comtois (1985) found in bivalves and Kumar (1997) found in nereidids.

4.3. Temporal variations of infaunal distribution within sediments

The study found that sampling time did not significantly effect the vertical distribution of infauna within sediments. It was consistently observed that infauna mostly occupied the surficial layers. The study was unable to confirm the observations of seasonal changes in taxa as reported by Hines and Comtois (1985) because the duration of the sampling did not extend over a sufficent length of time to observe the complete life cycle of the permanent residents.

In general vertical distribution of infauna within sediment appeared to be more concentrated in the 10 cm of the top substratum and this vertical pattern was maintained consistently across time during the study. Edaphic characteristics showed no definite trend as expected. This may indicate that the infaunal vertical patterns were regulated by additional parameters beyond those measured in this study, such as sulphide. Matthijs *et al*. (1998) found a strong correlation between redox potential (Eh) and sulphide correlation in the Kenyan temperate mangrove forest that determined plant zonation within the mangrove forest. Sulphide is a toxic substance produced as a result of degradation processes and mangrove plants are capable of detoxifying soils via root aeration mechanisms (McKee, 1993). Another possibility was that the animal bioturbations increased the variability within sediment and indicated the complexity of subsurface sediment habitats. Further study with regard to vertical distribution within sediment should pay attention to the sampling methodology e.g. collecting each sample from a separate core at each different depth, so the independency of each sample can be maintained. With regard to redox potential measurement, the readings must take place at the same time within same animal core to avoid any confounding factors during measurement. As redox potential measurements in the soil are fluctuating, single-point measurements will be insufficient in describing redox condition in soil systems as suggested by Vorenhout *et al*. (2004). In other words, greater planning, care and effort needs to be employed to measure this difficult and labile environment.

Chapter 6 Taxonomy and Biology of Important Polychaetes in South Australian Mangroves

Synopsis: Previous chapters have shown that polychaetes were consistently dominant in the infaunal communities in all transects. Certain taxa were distributed widely across the mangrove areas while others were resticted to certain sites. This chapter will assess their occurrence via taxonomical assessment and their biological attributes.

1.Introduction

The present study suggests that polychaetes made a significant contribution to characterizing the infauna assemblages in these temperate mangrove systems. They were found to be numerically dominant and diverse within infaunal assemblages. Rainer (1984) discussed the role of polychaetes in characterizing communities where polychaetes are dominant non-selective deposit feeders in habitats with a high level of organic content, such as mangroves. Being largely dependent on detritus, polychaetes have a vital role in maintaining biological processes within mangrove habitats through their feeding and burrowing activities. These produce accessible sediments for other benthic organisms and sediment bioturbation by polychaetes is known in structuring sediment dependent communities (Whitlatch, 1981). They are known tol affect the recruitment process of suspension feeders, their redistribution of sediment particles affect the population of selective deposit feeders and they prevent larval attachment due to sediment erosion (Rhoads and Young, 1970; Johnson, 1977; Hutching and Turvey, 1982)

Most polychaetes do not have internal fertilization and have a simple reproduction system that develops before breeding (Schroeder and Hermans, 1975). Their reproduction systems are varied between species and habitat characteristics. In stressful environments certain polychaete species are able to reproduce rapidly in the absence of competition and these are called opportunistic species, while others delay the reproduction process (Glasby *et al.*, 2000). The structural morphology of polychaete larvae is determined by the arrangement of cilia bands used for locomotion and feeding. These include prototroch, acrotroch, metatroch and telotroch patterns which can be used in polychaete larvae classification (Schroeder and Hermans, 1975). The developmental stages of polychaete larvae include the trochopore as a presegmental larvae, the metatrochopore that is marked by a segmental arrangement of ciliary bands and the nectochaeta which is a segmented swimming larva. The duration and morphology of a given stage may be species specific (Schroeder and Hermans, 1975). Rouse (2000) reviewed the evolution of feeding larvae and outlined differentiation of feeding mechanisms among polychaete larvae.

To date, in temperate South Australia there are no polychaetes known to be restricted to mangrove areas but rather they also occur more broadly in adjacent non-mangrove areas. In support of this, Hutchings and Saenger(1987) stated that although many polychaetes occupied mangrove areas, this is only part of their normal habitat. Their morphology does not result from adaptation to mangrove environments because similar morphologies can also be found in other polychaetes occupying other marine habitats. However, mangroves are transitional habitats between aquatic and terrestrial environments, thus mangroves have characteristics that are not possessed by other marine habitats. Among these are higher salinity, pulse inundation, richness of organic materials, high sulfide, predominantly fine particle substrate and water-logging which could become limiting factors for other organisms.

The openness of the ground surface exposes polychaetes as potential targets for predators. Several studies have shown that polychaete communities were more diverse and dense in non-mangrove areas than in intertidal mangroves (Hutchings and Recher, 1974; Netto and Lana, 1997; Sheridan, 1997). Moreover, Henandez-Alcantara and Solis-Weiss (1991) stated that salinity regulated the polychaete distribution within mangrove habitats, even though species co-existence could be also mediated by environmental heterogeneities (Whitlatch, 1980). Due to this, only certain groups of polychaetes are able to thrive in the mangrove environment, because they must cope with a variety of challenges not seen in the marine environment. Fauchald (1983) suggested that examination of polychaete distribution patterns based on ecological information is more worthwhile than studies based on geographical position as polychaetes respond to small-scale spatial variation.

The aim of this chapter was to assess the occurrence of polychaetes as the dominant taxon in the infauna community structure, and how this relate to the characteristics of the mangrove habitats. The families Capitellidae, Nereididae and Spionidae were chosen based on the assessment of indicator species analysis as mentioned in the previous chapters (Chapter 3 and Chapter 4) in order to avoid the subjective choice of taxa. Refering the discussion in these chapters, Capitellidae and Nereididae were considered as true symmetrical taxa due to their common presence in the mangrove systems and contribution to the infaunal assemblages. Meanwhile Spionidae was considered as an asymmetrical taxon as its occurrence was restricted to certain sites but showed a significant contribution to characterize the infaunal communities (see, Dufrene and Legendre, 1997). In addition, biological features of each taxon mentioned were also reviewed in order to give a better understanding of their occurrence in characterizing the infauna assemblages of these temperate mangrove systems.

2. Materials and Methods

2.1. Sampling sites

Polychaete samples were collected from three different locations of South Australian mangrove habitats, Garden Island, Saint Kilda and Middle Beach. The sediment characteristics of these mangrove areas are shown in Table 6.1. Salinity in this table is the salt content of sediment as defined in Chapter 3

2.2. Specimen preparations

The polychaete specimens examined here were those that had been collected and studied in Chapter 3 to 5. The infaunal samples had been preserved by 10 % buffered formalin within the sediments cores collected. Then they were sieved, washed under running water, sorted and counted before they were put in 70% alcohol for further indentification. For photography, fresh samples were taken from the same sites in Garden Island. The suspension-decantation method (Rouse and Pleijel, 2001) using 0.5 mm sieve was done *in situ*. Unsorted material was then put in plastic bags filled with seawater. In the laboratory, the unsorted materials were poured into white shallow trays and the worms were collected alive and put in a jar with clean seawater. Before photography, the worms were relaxed using $MgCl_2$ solutions recommended for polychaetes (Rouse and Pleijel, 2001)

Table 6.1. Sediment characteristics where polychaete samples were collected

Parameters	Garden Island	Saint Kilda	Middle Beach
Clay (%)	14.6	16.9	3.0
Silt (%)	7.7	8.7	3.0
Salinity (mS/cm)	12.9	15.4	10.8
TOC (%)	2.9	8.2	2.8
Carbonate (%)	1.6	26.6	49.1

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2.3. Polychaete assessments

The assessment of the three dominant polychaete taxa was based on several approaches:

1. Identification to finer taxonomic levels allow consideration of the occurrence of important species of polychaetes in the mangrove systems.
2. Understanding the characteristics of the important polychaetes by assessing the population dynamics both spatially and temporally.
3. Linking polychaete abundance as a biotic factor with measured environmental parameters to observe the factors driving the population dynamics.
4. Observing the burrowing and feeding activities within sediment.

The identification work was assisted and confirmed by Dr. Greg Rouse, curator of marine invertebrates of the South Australian Museum. Unfortunately, the biological assessment was primarily based on literature, as there no opportunity to conduct my own biological experiments on the polychaete species.

3. Biology and Taxonomy of Capitellidae

Capitellidae is a common family of polychaete worms frequently found in routine benthic sampling. The head is pointed or rounded and lacks appendages. The body is long, cylindrical and resembles a terrestrial oligochaete earthworm. The sizes range from less than 10 mm up to 200 mm (Rouse and Pleijel, 2001). The body is divided into a thorax and abdomen which have various number of segments and carry different types of chaeta, include capillaries and hooks in both notopodia and neuropodia. In some species, the notopodial hooks are replaced by genital spines which have a role during copulation. The arrangement of chaetae and number of thorax segments are often utilized as basic identification tools in Capitellidae. Many capitellids have eye spots and branchia are considered absent in most Capitellidae as they lack of circulatory systems (Glasby *et al.,*2000) The pygidium is highly variable in shape but often a short, blunt cone with a complete ring without appendages (Rouse and Pleijel, 2001).

Among soft sediment marine communities, Capitellidae is often regarded as a bio-indicator of disturbed environments though they also found in many undisturbed habitats. Their temporal adaptation to counter such unpredictable environments is based partly on their dispersal capability and partly their relatively long breeding season (e.g. Grassle and Grassle, 1976).

3.1. Taxonomical assessment

Many Capitellidae have an opportunistic life history this enables them to colonize and reproduce rapidly in environments where high amounts of organic materials occur (Grassle and Grassle, 1976; Warren, 1991). Identification of Capitellidae species is quite confusing as morphological differentiations are often found in one species. Eckelbarger and Grassle (1987) highlighted that genetically distinct sibling species, which have great morphological similarities, could have different biological behavior in the response to environmental cues. Because of this Rouse and Pleijel (2001) suggested the need for a serious taxonomic revision for Capitellidae, because the species definitions so far are based more on a combination of morphological characters than on phylogenetic relationships.

Capitellidae identification is technically difficult. Their size is small, making it hard to distinguish between juvenile and adult worms. Their bodies are fragile, easily damaged or broken during sample sorting. However, certain species can only be recognized from complete specimens. Diagnostic characters of Capitellidae can be obtained via gross morphological differences (Pearson and Pearson, 1991; Warren, 1991), gene flow in life history analysis (Grassle and Grassle, 1976) and karyotype studies (Eckelbarger and Grassle, 1987). The present study, identified the Capitellidae based on morphological attributes that were pragmatically chosen. Limited time and resources did not allow any study of the capitellid specimens based on genetic variations.

From samples sorted, 359 individual Capitellidae were collected. From these, 160 preserved specimens were randomly examined to “species” level. The samples can be considered mature worms as they were retained in the 0.5 mm mesh screen sieve and their body had developed 40 segments and more (George, 1984; Tsutsumi, 1987). The method of identification was based on the number of segments, structure and arrangement of chaetae, thoracic chaetal formulae and location of genital spine as suggested by Fauchald (1977) and Warren (1991). Most of the bodies were shrunken, making it difficult to count the number of segments in order to differentiate between juvenile and adult worms. The form of the prostomium and peristomium, an important part of taxonomical diagnosis to genus (Warren, 1991), was also difficult to observe.

Identification results

In general, there was a variation in the number of segments of adult worms. From 160 specimens judged to be mature worms, 18 % (22 individual) had less than 50 segments, 21% (35 individual) had 50-60 segments and 61% or 103 individual have more than 60 segments. All specimens had 9 chaetigorous segments with capillary chaetae and hooded hooks. The 7 first segments bore capillary chaetae both notopodial and neuropodial (Plate 6.1**).**

Plate 6.1. Main body of *Capitella* sp. A: head with fused prostomium, B: thorax , showing capillary chaetae both notopodial and neuropodial, C: abdomen, showing hooked chaetae D: pygidium

The thoracic formulae were mostly: 1-7C(capillary setae) + 8H (hooded hook) + 9 H (hooded hook), even though eight (8) specimens 7C+ 8M (mixed capillary and hooded hook) + 9H and one (1) specimens showed variations in thoracic formulae being : 1-7C+ 8H + 9 H + 10H. Accordingly these worms were mostly genus *Capitella* Hartman, 1947 as they have 9 thoracic segments. This was also in accordance with Grassle *et. al*,(1987) which stated that most of capitellid genera, including *Capitella,* have 9 thoracic segments.

In addition, genital hooks were observed mostly at the 8th thorax segments (Plate 6.2.), even though a few specimens (8 individuals) were observed having genital hooks at the 8th and 9th thorax segments, while in 31 specimens genital hooks were not obvious.

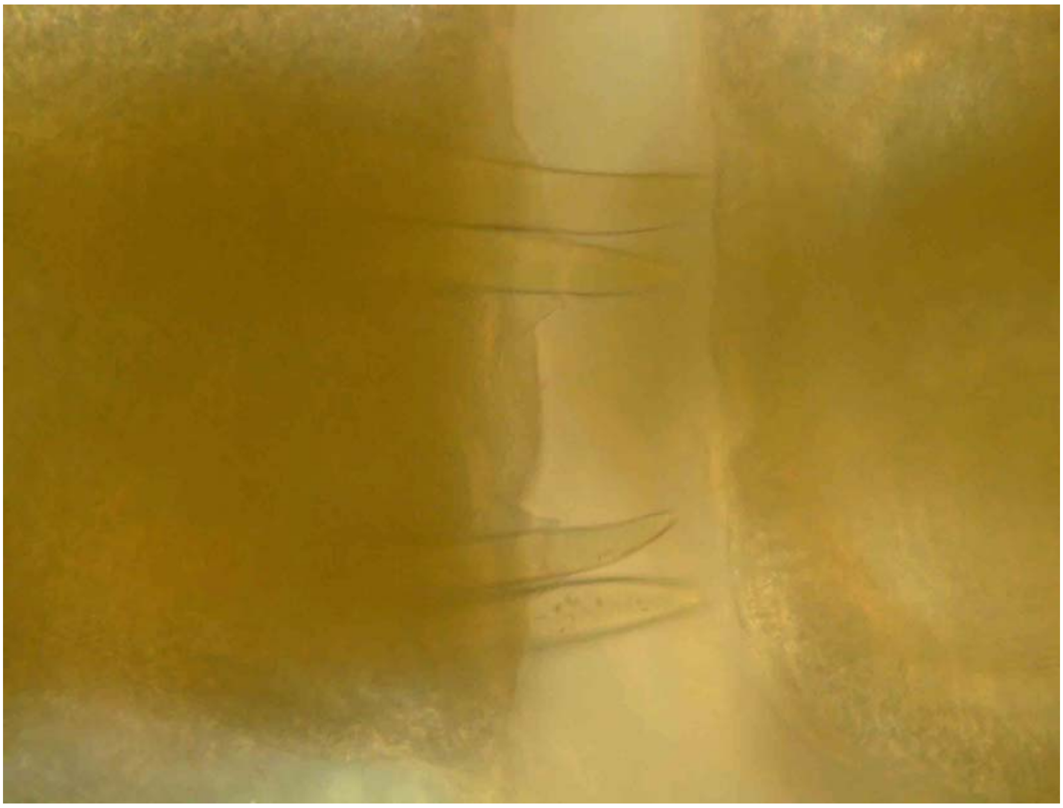


Plate 6.2. Genital spine shows at 8th segments, simple, heavily pointed and slightly recurved. Located dorsally from genital pore have role in copulation.

Possibly the genital hooks were broken during sample collection as is commonly the case for worms (Eckelbarger and Grassle, 1987), or they were in tightly coiled form making the genital spines hard to observe. All abdominal chaetae were hooded hooks. The observation did not note the occurrence of gonads at a given segment. So it cannot be said whether the genital spine was present in male worms only or also in hermaphrodite worms, a feature which is also species specific (Warren, 1991). Based on this morphological feature, the capitellids samples may contain only one species. This is *Capitella sp.* a member of the *Capitella* group. The small number of specimens which were observed to differ from *Capitella* sp. should not be classified as a variant sibling species as there were only 9 variant specimens. *Capitella* sp. in this present study cannot be classified as *Capitella capitata* because of the presence of genital spines generally only on the 8th setiger, while in *Capitella capitata* the genital spines occur in the 8th and 9th setiger in mature worms in place of the hooded hooks (see Warren (1976)

Table 6.2. gives comparative information about certain *Capitella* species which are quite close to the present identification.

Table 6.2. Species of *Capitella* where number of capillary-bearing segment ≥6 and shows the arrangement of thoracic chaetal formula (C=capillary, H= hooded hook, M= mixed cap and hook) (After Warren, 1991).

Species	Thoracic chaetae	Presence of genital hook	Reference:
Capitella caribaeorum (Warren & George, 1986)	1-6C 7M 8-9H	All (hermaphroditic)	George, 1984
Capitella capitata (Fabricius, 1780)	1-6C 7M 8-9H or 1-7C 8-9H	Male	Warren, 1976; Grassel & Grassel 1976
Capitella peramata (Gravier, 1911)	1-7C 8-9M	Male	Warren, 1991
Capitella aciculatus (Hartman, 1959)	1-8C 9H	All	Warren, 1991

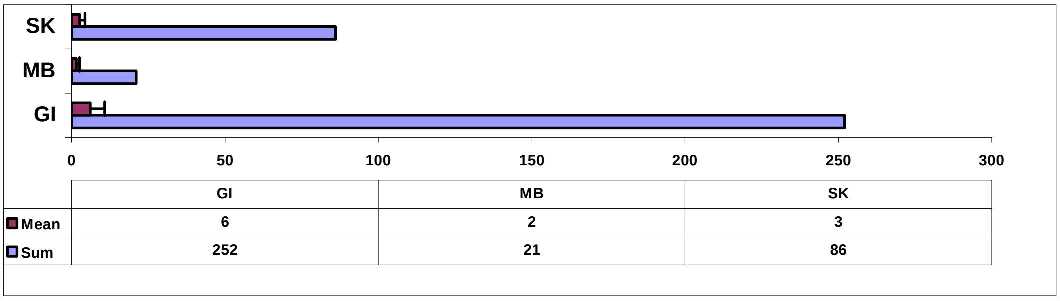
Species of *Capitella* above have 9 thorax chaetigerous segments, genital spines and bearing segments in which capillary chaetae are located. Eckelbarger and Grassel (1987) considered including the variation in number of genital spines into *Capitella* species definition. However, the study showed the degree of complexity of Capitellidae and supports revision of Capitellidae taxonomy as suggested by Rouse and Pleijel (2001) involving more principal characteristics used in identification .

An earlier study identified the capitellid worms from Port River estuary, where Garden Island and Saint Kilda are located, as *Capitella capitata* (Thomas *et al.*, 1986)**.** Nevertheless, there is no diagnostic information of their capitellid samples to compare with this present study. The morphological variations between these capitellid samples might have occurred as these worms inhabited a disturbed region that may promote morphological variability. Realizing that the species distinction within the genus *Capitella* based on the number of segments would overlap considerably, Grassle *et al.* (1987) identified the chromosome number of six *Capitella* species. They found that worms identified as *Capitella capitata* has 18, 20 or 26 diploid chromosomes which were related to different larvae dispersal and reproductive modes. This suggested that *Capitella capitata* is better treated as a species complex and identified as *Capitella* sp. The morphological differences between present study and Thomas *et al*. (1986) study may be a result of adaptation morphological variability related to the local mangrove conditions.

3.2. Spatial variation of Capitellidae

As one of the true symmetrical indicator taxa, Capitellidae were found at almost every site across mangrove habitats with various abundances (Fig. 6.1).

Figure 6.1. Mean abundance/ core (± SD) and total abundance collected of Capitellidae in the three mangrove locations

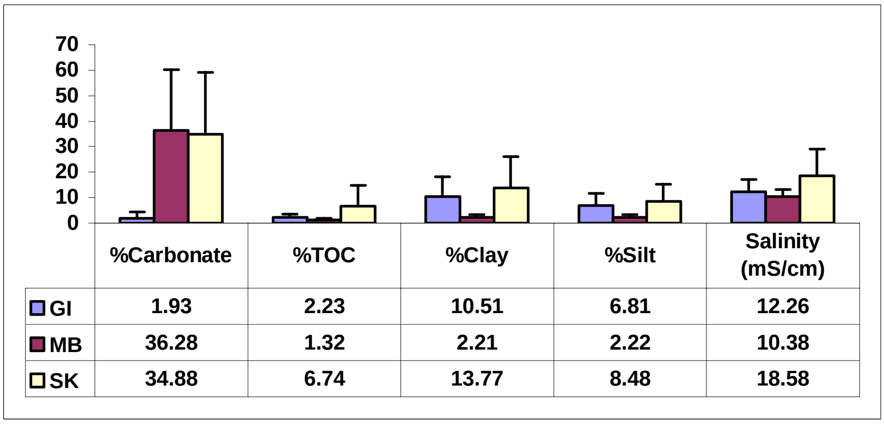


	GI	MB	SK
🟥 Mean	6	2	3
🟦 Sum	252	21	86

Based on the species identification, Capitellidae are best referred to as *Capitella* sp. The statistical ANOVA test resulted that the abundance of *Capitella* sp. in Garden Island was significantly different ($\alpha<0.03$) compared to the other 2 locations. Two hundred and fifty-two (252) individuals were found in Garden Island samples, Saint Kilda had 86 individuals and Middle Beach only 21 individuals. The different abundance of *Capitella* sp. may be related to the environmental conditions of these locations. Capitellidae is commonly known as a polychaete taxon which is able to thrive in degraded habitats like Garden Island and Saint Kilda (Edyvane, 1999). In fact Tsutsumi (1987) predicted that polluted areas are possibly the native habitat of certain species of capitellids, such as *Capitella capitata* which he found in an organically polluted cove in Japan. In organic polluted areas Capitellidae are able to recover rapidly after defaunisation because of their short life cycle and high reproductive rate and rate of utilizing abundant food sources (Pearson and Rosenberg, 1978).

As sediment-dependent organisms, the preponderance of *Capitella* sp. may also be determined by characteristics of the sediment, which varied between locations (Fig. 6.2).

Figure 6.2. **Sediment characteristics (mean ± SD) at the 3 location of SA mangroves**



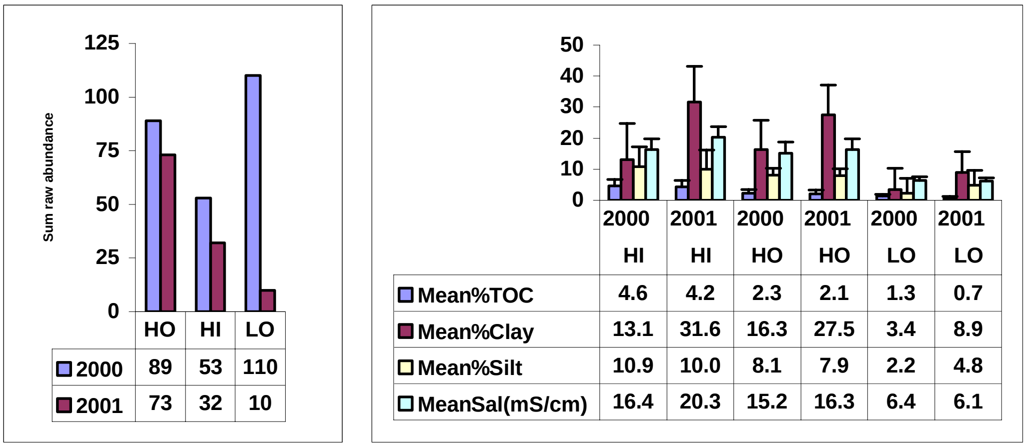
	%Carbonate	%TOC	%Clay	%Silt	Salinity (mS/cm)
🟦 GI	1.93	2.23	10.51	6.81	12.26
🟥 MB	36.28	1.32	2.21	2.22	10.38
🟨 SK	34.88	6.74	13.77	8.48	18.58

It seemed that higher density of the capitellids could be found within sediments which have low carbonate content, such as Garden Island. In addition the abundance of *Capitella* sp. may also be determined by other factors which were not measured in this study such as sulfide concentration and labile organic matter in the sediment. Saint Kilda is a location characterized by having high hydrogen sulphide due to eutrophication (Coleman and Coleman, 2001). Under laboratory conditions, survival rate of *Capitella* sp. were higher in the low sulphide sediment (Tsutsumi *et al.*, 2001). Cheng (1995) suggested that growth of certain *Capitella* spp. was independent of sedimentary organic content, but still correlated with labile organic matter as an instant food source in which the availability of labile organic material varied with season and depth. The study detected that higher abundance of *Capitella* sp. was found in the organic enriched areas. The organic enrichment could be the natural processes such as in mangrove sediments or as a result of organic pollution. *Capitella* sp. seemed well adapted to the enriched organic sediment by utilizing the organic materials to support their metabolism and growth.

3.3. Inter-annual variations of Capitellidae

As an opportunistic taxon, the Capitellidae has a short life cycle and breed continuously, thus their abundance may possibly vary widely with time. Inter-annaul assessment of *Capitella* sp. in the present study was conducted on the Garden Island samples where higher number of *Capitella* sp. were collected.

Figure 6.3. The sum abundance of *Capitella* sp. density and variation of sediment parameters (mean ± SD) where *Capitella* sp. were caught (HO: samphire, HI : mangrove upper part, LO; mudflat) in Garden Island.



	HO	HI	LO
■ 2000	89	53	110
■ 2001	73	32	10

	2000 HI	2001 HI	2000 HO	2001 HO	2000 LO	2001 LO
■ Mean%TOC	4.6	4.2	2.3	2.1	1.3	0.7
■ Mean%Clay	13.1	31.6	16.3	27.5	3.4	8.9
□ Mean%Silt	10.9	10.0	8.1	7.9	2.2	4.8
□ MeanSal(mS/cm)	16.4	20.3	15.2	16.3	6.4	6.1

Two-way analyses of variances where sites and times were fixed variables showed that the density of *Capitella* sp. varied significantly with time at every site (time vs site $\alpha = 0.002$), while sediment parameters showed no significant variation with a combination of site and time (time vs site $p = 0.09$). The greatest drop of *Capitella* sp. abundance was in the mudflat site (LO) from 110 individuals in 2000 to 10 individuals in 2001 (Fig. 6.3). The reduction in the number *Capitella* sp. maybe related to failed reproduction or to biological interaction such as predation. It was found that in a Taiwanese mudflat, Qian and Chia (1994) reported a high mortality of *Capitella* sp. and pointed to the role of predators in determining the population dynamics of the *Capitella* sp. Another factor that may influence the density of *Capitella* sp. is increasing salinity. Increasing salinity may reduce their growth rate and fecundity, and delay reproduction of *Capitella sp*. (Pechenick *et al.*, 2000).

Several *Capitella* species are able to self fertilize producing viable eggs under certain conditions in order to maintain the continuation of species (Warren, 1976). This type of reproduction is genetically based (Qian and Chia, 1994). Capitellidae have an iteroporous life cycle in which they are able to breed several times in their lifetime. Capitellidae protect their larvae to ensure that young worms develop under optimum conditions and that a high proportion of them reach the planktonic stage (Warren, 1976). When the tide is high, the metatrochophore larvae are released from the adult tube and enter the water column to be distributed for some distance from the parental burrows. This behaviour would be particularly useful for larval dispersal to colonize new areas, even though Tsutsumi (1987) argued that *Capitella* species in polluted areas have poor larval dispersal. This condition may be explained that *Capitella* sp. are able to metamorphose in the plankton within 15-30 minutes or possibly they are under less pressure to find organic materials as they often inhabit the rich organic sediments. Alternatively it may be possible that they are different subspecies. Grassle and Grassle (1976) and Grassle *et al.* (1987) found a variation of karyotypes in siblings of *Capitella* species related to larval dispersal and reproductive modes.

As mentioned the arrangement of ciliary bands is species specific and can be used for classification. The *Capitella* group has highly visible prototrochral and telotrochal ciliary bands which may reflect different behaviour in feeding (Cohen and Pechenick, 1999). It was suggested that Capitellidae with prototrochal lobes preferred to feed on the smaller size food such as diatoms and dinoflagellates (Yokouchi, 1991).. A study found that larvae of one species of *Capitella* did not always settle and metamorphose in highly organic sediments (Cohen and Pechenick, 1999) or in other words, *Capitella sp* settlement were independent of organic sediment content (Tsutsumi *et al.*, 1990; Tsutsumi *et al.*, 2001). This is contrary to the general expectation that suitable substrate will improve the performance and fitness of post larval development (Qian and Chia, 1994).

Organic material in sediment may not be the single factor affecting the population dynamics of *Capitella* sp. especially in the larval stage. Temperature, salinity and tidal frequency are also believed to be responsible factors regulating the duration of larval life (Tsutsumi, 1987; Giangrande and Fraschetti, 1993; Pechenick *et al.*, 2000). In a few cases a sudden freshwater influx may possibly regulate reproduction of certain polychaete species on a seasonal basis due to reduction of salinity. Harbison(1986a) found a sudden drop of salinity during heavy rainfall in Barker Inlet, Port River estuary, which possibly influenced the shallow benthic microorganisms distribution and the infauna, like *Capitella* sp.. Indeed, more information is needed in the physiological tolerance of larvae to salinity as it may differ in populations which live under extreme condition (Schroeder and Hermans, 1975) such as South Australian temperate mangroves.

3.4. Feeding behavior of Capitellidae

Generally the Capitellidae group are categorized as sub-surface deposit feeders (Glasby *et al*., 2000; Fauchald and Jumars, 1979). They ingest particles by everting their proboscis and feed throughout the tidal cycle. They lack feeding/sensory appendages on the prostomium and are often relatively unselective during feeding.

However Horng and Taghon (1999) found that *Capitella* sp.1 is a selective particle feeder but that the body size may not affect particle selection. The *Capitella* spp. prefer to ingest the smallest particles in sediments and the preferable particle size is 17 μm which is categorized as fine particles which include very fine sand, silt and clay (Woodin, 1974), typical of mangrove sediments. A gut content study revealed that mangrove *Capitella* sp. nov. consumed significant amounts of mangrove detritus (George, 1984).

3.5. Burrowing behaviour of Capitellidae

Capitellidae is a sedentary polychaete group with limited mobility. The worm burrows slowly through sediments by strong muscular peristaltic waves. If they meet an excessively resistant substrate, the proboscis may then forcefully evert to assist sediment penetration. The burrows are lined with mucus secreted by epidermal glands.

In the mangrove sediments *Capitella* sp. can be found in the shallow sediments approximately 5 cm deep (Cheng and Chang, 1999) where most available labile organic material is concentrated. *Capitella* sp. at this present study may be categorised as deposit feeders. They prefer to ingest the finer sediments, which contain rich organic materials. They could be found in the shallow depths of sediments, possibly as a strategic adaptation to maintain contact with the surface especially during exposed time.

This current study suggests that *Capitella* sp. could be found in mangrove areas that are not characterised by organic rich sediment. Even though their distribution was not dictated only by total organic content, it appeared that typical mangrove sediments may accommodate their biological characteristics including reproduction, larvae dispersal, burrowing and feeding activities.

4. Taxonomy and Biology of Nereididae

Nereididae was a well-represented group of marine invertebrates in Australia and New Zealand (Hartman, 1954). They are conspicuous and usually occupy littoral habitats. Curiously she gave the opinion that in the southern Australian bays, the Nereididae group was less diversified but this may have been due to less extensive surveys and incidental collections there.

The Australian Nereididae can be large, reaching up to 300 segments; most of them have 150 segments and are 10 cm long or less. Most body segments are similar with a lack of regionalisation. Generally the prostomium is triangular in shape; it usually has 2 pairs of antennae with a pair of biarticulte palps. In certain species of Nereididae, the prostomium and the first segment are fused, while in others they are not.

Jaws are a distinguishing characteristic of Nereididae. The eversible pharynx is often armed by a chitinous paragnath or papillae. The details of pharyngeal structure such as jaws, teeth and other chitinized forms are the principal taxonomy features in characterising the species of Nereididae (Fauchald, 1977; Glasby *et al.*, 2000). Parapodia are biramous, generally with no gills. Chaetae are compound in both falcigers, spinegers and capillaries. Other characteristics in species determination are variation in the form of parapodia and chaetae from the anterior to the posterior segments, the number and form of parapodia lobes present, type and number of chaetae and the segment in which these chaetae are present (Glasby *et al.*, 2000).

Nereididae is the polychaete family group with a tremendous range of reproductive strategies. Some species of nereidid have complete epigamous metamorphosis in their reproductive system (Glasby *et al.*, 2000). Upon sexual maturity, some Nereididae undergo morphological modifications such as eye enlargement, the development of large flattened parapodial lobes and compound chaetae into epitokous forms, in order to leave the bottom for the purposes of reproduction (Schroeder and Hermans, 1975). Regionalisation is often visible in the epitokous form as reduction of the posterior most segments while anterior segments remain unmodified (Glasby *et al.*, 2000). Rouse (pers.comm., 2002) suggested avoiding identification of Nereididae in spawning forms as some morphological changes could confound indentification work.

Most nereidids have separate sexes and asexual reproduction so far has not been reported (Glasby *et al.*, 2000). Reproduction is typically monolitic and the adult will die after spawning. Generally adult worms will mature in one year but certain species can live until they are six years old. Australian nereidids such as *Australonereis ehlersi* can complete their life cycles in 1-1.5 years. Reproduction of nereidids is variable both between taxa and habitat and is regulated by a combination of environmental parameters such as temperature, lunar cycle, salinity and secondary day length (Neuhoff, 1979; Fong, 1991). The pelagic lecithotrophic larvae are dispersed by currents and develop into juveniles in 4-40 days and most of the larvae when released to the open environment are in the trochophore stage (Ben-Eliahu, 1991; Glasby *et al.*, 2000).

4.1. Taxonomical assessment

Identification of Nereididae to species level in this study is based on Hutchings and Turvey (1982) and Hutchings (1997) who suggested a careful check against the descriptions during identification as some species were very similar. This includes checking notopodial homogomph falciger for *Nereis* species, and the pattern of paragnaths for *Neanthes* species.

From 130 specimens of Nereididae collected, two (2) different genera were identified. They were *Namanereis* where there were only two specimens collected, while the rest were *Neanthes.* These two genera are similar in having a peristomium with frontal antennae and palps with palpostyle as well as two pairs of eyes at base of prostomium with four pairs of tentacular cirri extending to posterior margin of setiger 1. Parapodia are biramous with two thick acicula which are not protruding. Notochaetae are present in all spinigers, while neurochaetae consist of homogomph spinigers and falcigers. The obvious differences were the pharyngeal armaments in which *Namanereis*'s pharynx have no paragnaths while in *Neanthes* the arrangement of paragnaths is the main characteristic in species identification. The genus description was in agreement with (Hutchings, 1997).

Plate 6.3. Anterior end of dorsal view of head of *Neanthes vaalii* (Nereididae), showing that prostomium and first segment fused. A: pair of palps with palpostyle B : Pair of antennae, C: Four pairs of tentacular cirri, D: prostomium, E: parapodium F: two pairs of eyes

Further identification suggested that the *Namanereis* was *Namanereis littoralis*, Hutchings 1982, with the pharynx lacking paragnath and papillae and with pair of chitinised jaws. Notopodial lobes were absent. The neurochaetae have 2 spinigers and 6-7 falcigers. The two *Namanereis littoralis* specimens were found in Middle Beach mangroves and agreed with the description of Hutchings and Turvey (1982).

Species identification of genus *Neanthes* is based on paragnath arrangements. Chitinous paragnaths were observed in several mature specimens. In the dissected pharynx the characteristics of the pharynx areas, which are species specific, were not completely clear. After discussions with Dr. Greg Rouse, it was decided that the species should be referred to *Neanthes vaalii,* Kinberg 1866. Accordingly, *Neanthes vaalii* can be differentiated from *Neanthes uniseriata* by the arrangement of the oral paragnaths (Plate 6.4, 6.5 and Table 6.3.) and reduction of the ventral neuropodial lobe.

Plate 6.4. Anterior end of *Neanthes vaalii* with proboscis erected showing a continuous paragnath in oral ring. A: maxilla ring showing area I and II, B: oral ring showing area V and VI, C : Jaws

Plate 6.5. Ventral view of *Neanthes vaalii* showing irregular rows of chitinous paragnath band A: maxilla ring showing area III and IV , B: oral ring showing area VII

Plate 6.6. Biramous parapodia 10th setiger of *Neanthes vaalii*. A: aciculum, B: neuropodium with neurochaetae B1: ventral neuropodial heterogomph falciger, B2: ventral neuropodial heterogomph spiniger, C: notopodium with notochaetae homogomph spiniger.

Parapodia consist of neuropodia and notopodia with various chaetael types. Homogomph spinigers in notopodia, while neuropodial dorsally has homogomph spinigers and heterogomph falcigers, ventrally has heterogomph spinigers and falcigers (Plate 6.6.). Hutchings and Turvey (1982) identified *Neanthes vaalii* from a specimen collected at mudflats in front of mangroves with patchy *Zostera* at South Australian estuaries.

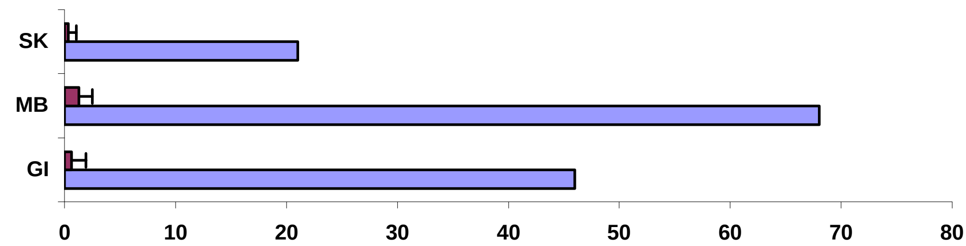
4.2. Spatial variation of Nereididae

Nereididae, in this case the species *Neanthes vaalii*, is another taxon which can be considered a true symmetrical taxon because they can be found in the three mangrove system locations and make a significant contribution to the infauna assemblages (Fig. 6.4).

Table 6.3. Comparison of paragnath arrangement in species *Neanthes* which are considered close to the present collected specimens; I-VIII refer to pharyngeal areas (after Hutchings and Turvey, 1982)

Species	**Area I**	**Area II**	**III**	**IV**	**V**	**VI**	**VII-VIII**	**Habitat**
Neanthes uniseriata (Hutchings & Turvey, 1982)	3	8	4	12-15	4	9-12 large cones are continous with V & VII	38 small cones, rare and scattered through the band	Algal holdfasts, coralline alge, crevice fauna and sand
Neanthes vaalii (Kinberg, 1986)	1-4	7-8	17-34	24-41	3	3-5 (isolated)	50-70 in 2 or 3 irregular rows	Seagrass, sand, mud and intertidal clumps of mussels
Neanthes cricognatha (Ehlers, 1904)	13-16	26-34	28-63	29-47	Continous band, 5 deeply ventrally, 2 deeply dorsally			Seagrass, mudflat
Neanthes isolata (Hutchings & Turvey, 1982)	1-2	6-10	8-12	8-16	2-3	6-11	37-55 arranged as holotype	Algal holdfasts, coralline alge, sand, crevice fauna

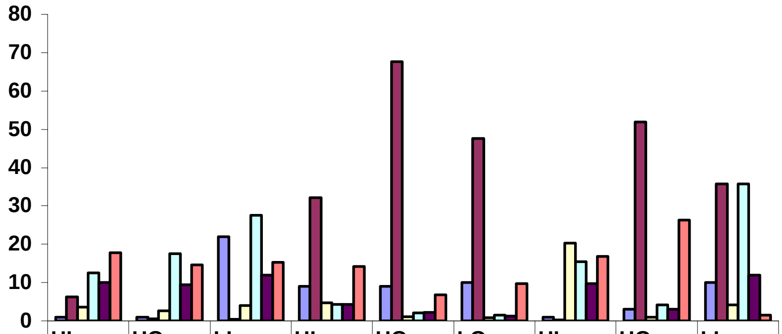
Figure 6.4. Mean abundance (± SD) and total abundance of *Neanthes vaalii* in the 3 location of mangrove systems showing a spatial variation.



	GI	MB	SK
Mean	0.65	1.31	0.34
Sum	46	68	21

One-way analysis of variance revealed that Middle Beach, the location with the highest number of *Neanthes vaalii,* was significantly different (p< 0.0001) from the other two locations (Saint Kilda and Garden Island) (Fig. 6.4). Even though the two-way correlation analysis between abundance of *Neanthes vaalii* with measured environmental parameters (carbonate, TOC, salinity, clay and silt, Fig. 6.5), resulted a weak inference which did not expose the causal relationship.

Figure 6.5. Edaphic characteristics where Nereididae occur in the 3 mangrove locations (HI=higher inner (mangrove), HO : higher outer (samphire), LI=lower inner (mangrove), LO=lower outer mudflat), GI=Garden Island, MB=Middle Beach, SK=Saint Kilda).



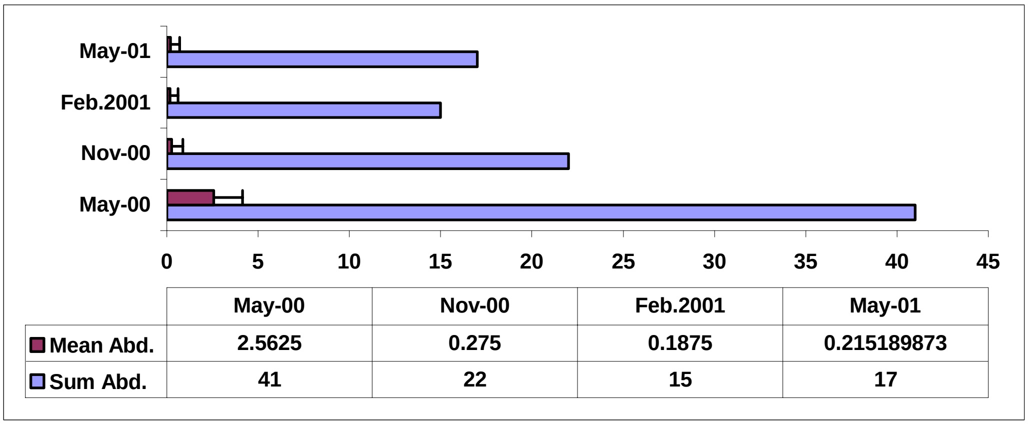
	HI GI	HO GI	LI GI	HI MB	HO MB	LO MB	HI SK	HO SK	LI SK
Sum Abundc.	1	1	22	9	9	10	1	3	10
Mean % Carbonate	6.24	0.54	0.48	32.18	67.55	47.56	0.30	51.88	35.74
Mean %TOC	3.67	2.68	4.03	4.71	1.17	0.90	20.25	1.00	4.19
Mean %Clay	12.50	17.50	27.50	4.36	2.13	1.54	15.50	4.11	35.72
Mean %Silt	10	9.50	12.03	4.33	2.29	1.24	9.80	3.03	11.96
Mean Salinity (mS/cm)	17.80	14.60	15.29	14.20	6.83	9.76	16.80	26.30	1.56

Other factors beyond those measured here were probably important in determining their distribution and abundance.This result was in agreement with Woodin (1974) who reported that no correlation was found between the abundance of *Platynereis armandia* and physical sediment characteristics in a mudflat habitat. The extent of inundation may possibly influence nereidid distribution as most of them were caught at the lower sites, especially in Middle Beach. Geologically, the Middle Beach mangrove was located in sloppy sediments where the position between the lower and the higher parts were not obvious. Abrantes *et al*. (1999) found that not only varying tidal level but also salinity and nature of substratum regulated the distribution of nereidids in mangrove habitats.

4.3. Seasonal variations of Nereididae

The distribution of *Neanthes vaalii* showed a spatial variation and lower sites were the most favourable sites for this species. Seasonal variation in abundance was measured in the lower inner area of Garden Island mangroves across four times (Fig. 6.6).

Figure 6.6. Mean abundance/core (± SD) and total abundances collected of *Neanthes vaalii* at lower inner Garden Island mangroves showing a temporal variation



	May-00	Nov-00	Feb.2001	May-01
🟥 Mean Abd.	2.5625	0.275	0.1875	0.215189873
🟪 Sum Abd.	41	22	15	17

In general, statistical test (ANOVA) resulted in a significant difference (p=0.03) in individual numbers of the nereidids within season with samples in May 2000 (late autumn) yielding the highest members compared with other times. Seasonal fluctuation was found in *Nereis diversicolor*, a common species in Portuguese estuaries, with peak numbers during spring and summer and low abundance in winter (Abrantes *et al*., 1999). This temporal fluctuation may be a result of reproductive events such as adult mortality after spawning as found at *Platinereis bicanaliculatio* (Glasby *et al.*, 2000), or due to poor settlement success or poor larval survival in the plankton (Woodin, 1974). It may also be due to the impact of predators as observed for *Ceratonereis pseudoerythraensis* in the intertidal mudflats of Victoria (Kent and Day, 1983)

4.4. Feeding Behaviour

The feeding apparatus of nereidids is an eversible pharynx armed with a pair of strong jaws. An eversible pharynx as part of the anterior digestive tract is common to most polychaetes. There are two different constructions of the pharynx, namely a ventral plate-muscle pharynx and an axial symmetrical muscle pharynx which often assists during burrowing. Glasby *et al.*, (2000) stated that the morphology of jaws was considered as poor guidance to the feeding strategy because jaws are used for gathering fine particle in surface sediment, for ingestion and for scavenging plants and other worms. As selective deposit feeders, the tentacles are used for capturing particles in the water column. Gut analysis of *Neanthes japonica* showed that the percentage of decomposed materials was higher than undecomposed material suggesting the role of bacterial organisms as a direct source of food and as food preparators (Tsuchiya and Kurihara, 1979). These might be considered as the fact that considerably numbers of *Neanthes vaalii* in the present study were caught in the lower sites or in the sites where prolonged inundation occur and bacterial organisms were more abundant. As surface deposit feeders, *Neanthes vaalii* might emerge from the burrow to scavenge or to capture food particles in the water column during high tide.

4.5. Burrowing behaviour

As motile worms, nereidids can burrow to a certain depth and may reach 20 cm or deeper as found in this present study. Kumar (1997) observed that certain nereidids, such as *Nereis glandicinta* and *Ceratonereis coastae* which occur in the deeper 10-15 cm layer of mangrove sediment have well developed characteristic gills coupled with high oxygen affinity haemoglobin in the blood and include burrow irrigation which enabled the nereidids to survive in anaerobic intertidal sediments. Kristensen *et al.* (2000) developed an experiment using sediment microcosms and reported that *Nereis diversicolor* burrows could induce oxygenation of the upper layer to a depth of 10 cm. Their burrowing activity can cause reworking of sediments by head down deposit feeding and water movement via irrigation which reduce sulfate compounds, increase re-oxidation and lowered anaerobic decomposition (Banta *et al.*, 1999).

Their burrowing can also serve as protection from predators and also territorial behavior as they are aggressive toward each other (Glasby *et al.*, 2000). It was reported there was a positive correlation among the density of three species of tube builders suggesting that they defend their burrows as a territory from others (Woodin, 1974). The present study suggested that the occurrence of *Neanthes vaalii* in the lower part of the mangrove habitat probably was supported by their morphological apparatus. This includes a well developed blood vessel along the length of the body and the gills, strong pharynx and jaws which make it possible to burrow deeper to avoid predator and desiccation during exposed time. However, this morphological apparatus may not be a particular adaptation to the mangrove habitats.

5. Taxonomy and Biology of Spionidae

One of the most abundant polychaete taxa occuring in sediments of the marine temperate zone is Spionidae (Fauchald, 1977). Spionidae is most well known as obligate tube-dwelling worms. Their prostomium may be blunt or pointed with a pair of lateral horns. Rising from the prostomium are a pair of long grooved palps which make them different from other polychaete worms (Glasby *et al.*, 2000). These palps are easily lost during sample processing or damaged due to predator browsing behaviour (Woodin, 1982). Certain species have occipital tentacles while others do not. The parapodia are biramous with various types of simple capillaries and hooded hooks with apical teeth. Certain species may lack notochaetae in their first segment. Unlike Nereididae, Spionidae do not have dorsal and ventral cirri (Glasby *et al.*, 2000), but their dorsal digitate branchiae are often present on different number and different part of the body.

Spionids are ubiquitous in marine habitas. In Australia, spionids are typically marine surface deposit feeders, occupying various substrates such as sandy-muddy sediments, coralline algae and barnacles, oysters, crevices, shells and stones, coral and sponge habitats (Blake and Kudenov, 1978). Certain species of genus *Polydora* even live in the collumella of hermit crab shell (Sato-Okoshi, 1999). They can be found in large numbers and encountered in the intertidal and shallow subtidal sediments. For example, *Orthoprionospio cirriforma* occurs widely and is considered an endemic species for southern Australian estuaries (Glasby *et al.*, 2000).

5.1. Taxonomy assessment

Globally, 38 genera of Spionidae have been recognized, with 24 of them occurring in Australian waters. Spionids are a morphologically diverse group in which species can be compared based on the morphological differences without crossing familial boundaries (Woodin, 1982). Blake and Kudenov (1978) reviewed the taxonomy of Spionidae from intertidal and subtidal waters and adjacent areas of southeastern Australian. They identified 68 species and 19 genera of spionids, and included some revision of certain genera. In this study, species identification of spionid was based on Blake and Kudenov (1978) and Hutchings and Murray (1984).

The identification work used mostly preserved specimens from the outer sites of the lower part of the Garden Island mangrove location. As some worms were preserved in 10% buffered formalin while they were within sediments, damage resulted to the specimens when they were pulled out from the tube. Other specimens had lost their palps due to poor sample handling. Hence, only complete specimens have been chosen for spionids taxonomic work.

From 354 collected individuals of Spionids, about 196 individuals were identified. Only one species could be recognized among the samples. After discussion with Greg Rouse (South Australian Museum), the spionid was identified as *Pseudopolydora paucibranchiata,* Okuda 1937, and specimens were largely in agreement with the description of Blake and Kudenov (1978).

Plate 6.7. *Pseudopolydora paucibranchiata* showing the feeding palp and pygidium like disc.

The characteristics of *Pseudopolydora paucibranchiata* (Plate 6.7) are as follows : the worms have up to 45 segments and about 25 mm length. Prostomium is entire in which it differs from *Pseudoplydora kempii* where the prostomium is incised with two flaring anterior lobes. The caruncles which extend to chaetiger 3 may be recognized by gently pushing the head under a stereo microscope using the highest magnification. It is sometimes difficult to observe due to the small size, and most of the preserved worms were flat with palps positioned underneath their head. In addition, two pair of eyes were always present with the occipital tentacle at the posterior. Palps were long, extending about half the length of the worms. Branchiae were noticeable and started from setiger 7 continuing to more than half of their body Branchiae lacked glands which was different from *Pseudopolydora glandulosa*. The arrangement of setigers are as follows. The first setiger was without notochaetae. The major spine of the fifth setiger (5th) was arranged in a U-shaped line while in *Pseudopolydora kempii* this is in a J row (plate 6.8),

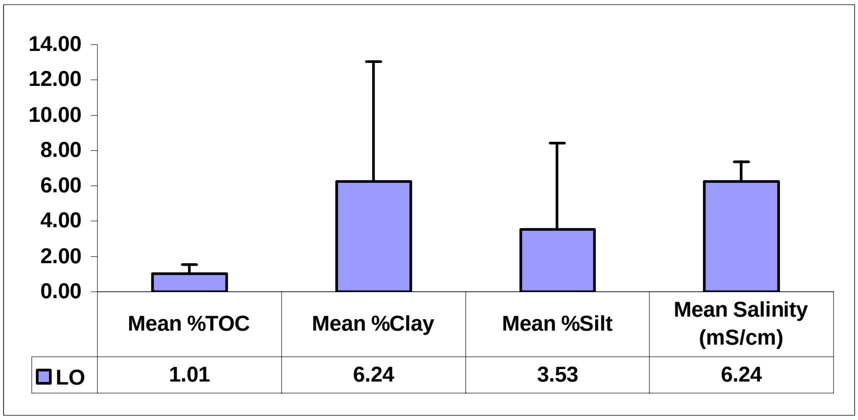
Plate 6.8. ***Pseudopolydora paucibranchiata*** **showing setiger 5th with specialized spine arranged in U shaped line.**

Setiger five was relatively unmodified. The pygidium was disc-like with a large dorsal gap. Hutchings and Murray (1984) mentioned that *Pseudopolydora paucibranchiata* was commonly found at Torrens Island and Port Lincoln, South Australia, inhabiting fine mud to shelly sand both high content of detritus and salinity around 32-35 $^{0}/_{00}$. Thomas *et al*. (1986) also reported the occurrence of spionids in the Angas Inlet and identified the spionids as *Pseudopolydora sp.*

5.2. Spatial and temporal variation of Spionidae

In the previous chapter, it was mentioned that spionids contributed strongly to the structure of infauna assemblages at Garden Island. Their occurrence was restricted to the lower level outside the mangrove zone where prolonged inundation may be favourable for spionids. This is in accordance with another field study using reciprocal transplant experiments with several spionid species in False Bay, USA, which reported that vertical distribution pattern of spionids within intertidal sites could be attributed to physical stress associated with prolong exposure (Wilson, 1984). The frequency of tidal inundation will affect the physico-chemical structure of sediment such as particle grain size, salinity and organic materials. Sediment characteristics where the spionids occur in this study were 1 % total organic carbon (TOC), 6.2 % clay, 3.5 % silt and salinity 6.2 mS/cm (Fig. 6.7).

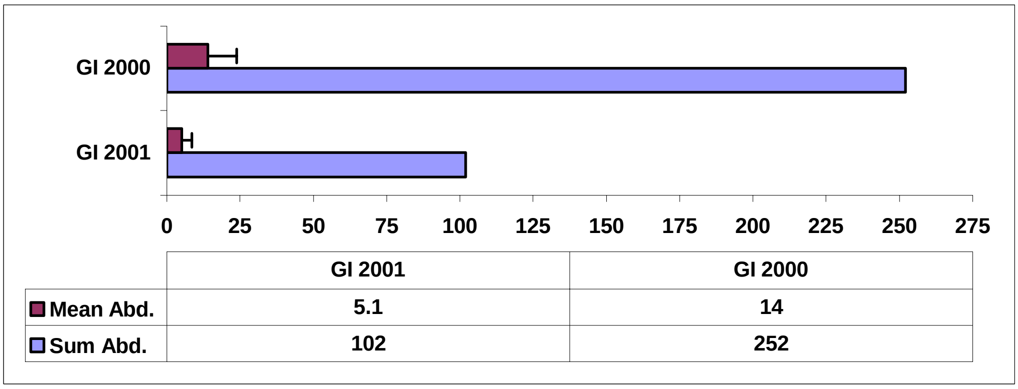
Figure 6.7. Mean abiotic parameters (± SD) at lower outer (LO=mudflat) of Garden Island



The measured environmental factors were, in fact, relatively low when compared to other sites within the Garden Island mangrove. These characteristics possibly favored the occurrence and growth of *Pseudopolydora paucibranchiata*. It was claimed by Hillderbeg and Nateewathana (1991) that habitat preference is important in explaining large numbers of Spionids within small areas. Blake and Woodwick (1975) found *Pseudopolydora paucibranchiata* in mixed sand-mud sediment on tidal flats of Tomales Bay, California associated with other polychaetes, include *Capitella* sp. which is in concordance with the present study. Moreover, Weinberg (1979) suggested that stations dominated by tubicolous deposit feeding polychaetes, were more sandy in texture with low organic content.

The density of *Pseudopolydora paucibranchiata* in these sites showed annual fluctuation (Fig. 6.8).

Figure 6.8. The mean abundance/core (± SD) and total abundance of *Pseudopolydora paucibranchiata* showing an inter annual variation



Statistical analysis revealed that abundance in May 2000 was significantly different from May 2001 (p=0.03). The fluctuation of the spionid density may relate to the timing of biological functions of spionid, such as reproduction events or biological interactions such as predation. Woodin (1982) studied the effect of predator browsing by flatfish on spionids which resulted in loss of feeding palps or damage to the tissue at the upper part of their body where the vital organs are located. The damage to tissue or loss the feeding apparatus will have a major impact on their activity such as reducing feeding rate, growth and reproduction (Lindsay and Woodin, 1995; Lindsay and Woodin, 1996) which leads to a reduction in the competitive interaction between surface deposit feeders. On the other hand, the lost of palps will result in a reduction of sediment bioturbation which would increase the chance of larvae settlement of other species, although this may be objected to as certain larvae have preferential sites to settle (Tamaki, 1985).

The reproduction and larval development of *Pseudopolydora paucibranchiata* has been observed in the laboratory (Blake and Woodwick, 1975). They compared the development of two species *Pseudopolydora kempii* and *Pseudopolydora paucibranchiata*, and revealed a different pattern of reproduction modes from an early stage. For instance, *P. paucibranchiata* has small eggs attached to the lining tube of the adult worm, but it does not have nurse cells, so that they only a have short time in brood protection and are released when the worms reach the 3-setiger stage and spend a long time as pelagic larvae. After development of 13-17 segments they settle and begin a benthic life. The study noticed some *P.paucibranchiata* contained embryos within the adult worm. In contrast, the egg size of *P. kempii* is bigger and attached to the lining of the tube of the adult worms. They are accompanied by nurse cells, that are utilized during growth and development, allowing them have longer size within the adult tube. Larvae are released from the capsule when they reach 15 setigers and settle reasonably close to the parent (Wilson, 1984). The juvenile stage involves reduction and development of certain organs essential for the next live cycle stage. For instance development of feeding palps which do not function during the larval stage, elongation of prostomium and loss of larval cilia, perceptible of internal formation of spines in setiger 5th and changing in pygidium into a simple cup shape (Blake and Kudenov, 1978).

5.3. Feeding behaviour

Commonly spionids are surface deposit feeders which capture food particles from the water column. Certain spionids have ability to switch from suspension feeder into deposit feeders depending on the type of food availability and hydrodynamic regimes (Fauchald and Jumars, 1979; Taghon, 1982).

Pseudopolydora paucibranchiata is a facultative surface deposit-feeder capturing the organic material by opening the tube to erect the feeding palps. During feeding they rarely expose their head into the surface except for fecal pellet release (Ferner and Jumars, 1999). When spionids become deposit feeder their main food is diatoms which is also a food preference for Capitellidae (Yokouchi, 1991). In limited food supply this will create interspecific competition with other deposit feeders. Weinberg (1979) studied the effect of depletion of organic material aggregates (OMA) due to burrowing and feeding activities of tube dwelling *Axiothella rubrocinta* (Maldanidae) on spionids. He found a higher mortality and lower larval recruitment of *P. kempii* and a reduction in the number of adult worms and the tube building rate of *P. paucibranchiata.* Also the accumulation of fecal pellets which contain less chemical cues required will influence the distribution of spionids, as found by Miller and Jumars (1986) in *Pseudopolydora kempii japonica*.

The genus *Pseudopolydora* has a strong preference for low specific gravity particles (Self and Jumars, 1988) a selection based on particle size, surface texture and organic coating (Weinberg, 1979; Taghon, 1982). During suspension feeding their feeding areas only cover 0.04 cm^2, but when they become deposit feeders the feeding areas will increase to 3.2-7.7 cm^2 (Taghon, 1992). When the flow speed (velocity) is less than 2 cm/second they use their palps to disturb and feed on the surface sediment within a circular area centred on the tube opening (active suspension feeding mode). When the flow was increased beyond 6 cm/second the palps form into helical coils and are held parallel to and 0.5 cm above sediment surface, trailing in the down stream direction (passive suspension feeding mode).

When water flow is reduced or tentacles are lost due to predator browsing, the spionids will switch to deposit feeding (Taghon, 1992). There was a correlation between velocity, width of palps, food supply and the rate of feeding in a study of *Pseudopolydora paucibranchiata* (Shimeta, 1996). It was reported that palps movement patterns were species specific (Dauer *et al.*, 1981).

Pseudopolydora pauchibranchiata may represent as surface deposit feeding spionid and with a pair of palps to collect food particle from the sediment surface in which influenced by water flow and velocity. Some aspects that may influence their feeding rates include temperature, particle size and particle species gravity, palp diameter, flow velocity, sediment transport and protein content of sediment, even though the level of sensitivity and response may be species dependent.

5.4. Burrowing behaviour

Spionids construct a vertically oriented tube from silt and mucus with the outer layer coated by coarser sand grains (Blake and Woodwick, 1975; Ferner and Jumars, 1999). It had been reported that there was independent selection between sediment particles for feeding and for tube construction (Self and Jumars, 1988), even though Weinberg (1979) argued that he found the organic material favoured as spionid food also incorporated in their tubes. As surface deposit feeders, spionids only penetrate the sediment to a shallow depth because they have to maintain their position close to the surface. *Pseudoplydora paucibranchita* is found protruding only a few mm above the sediment surface, even though the palps can be up to 6 cm long. Ferner and Jumars (1999) reported that *P. kempii* often build up their tubes above the sediment water interface which may aid in separating egested material from the active feeding areas. Dauer *et. al.* (1981) presented more detailed egestion modes in several spionid species from Chesapeake Bay, Florida. Density dependent effects are found in spionids, they will frequently encounter neighbours and competitively inferior individuals will migrate (Taghon, 1992).

6. Discussion

The infaunal assemblages in the South Australian mangrove system were characterized by numerically dominant and diverse polychaetes. Certain species of polychaetes can be found widely in the mangrove systems, such as *Capitella* sp. and *Neanthes* while others may be restricted to certain sites on the seaward edge of mangrove forests such as *Pseudopolydora paucibranchiata*. The distribution pattern of polychaete communities in these mangrove systems is probably dictated by several physical, chemical and biological factors which work together forming different characteristic infauna assemblages either between and within the locations. As polychaetes inhabit the water sediment interface, the variation of environmental factors often takes place on a very small scale.

South Australian mangrove systems provide a unique habitat which is reflected by the characteristics of infauna assemblages which have low diversity and low density compare with studies conducted in Australian temperate mangrove estuaries (Hutchings and Recher 1974, Lindegarth and Hoskin, 2001). Even though there is low diversity at the taxonomic level, their assemblages still provide a complete set of functional feeding modes, which is often also found in other marine habitats. The polychaete communities were represented by suspension feeders and deposit feeders, surface deposit feeder and subsurface deposit feeders, herbivores and carnivores, providing a wide range of particle selection which increases the effectiveness of mangrove habitat utilization by their permanent residents. Thus mangroves provide important habitat for polychaetes.

Tides become one of the major issues controlling the inhabitants living in mangrove environments. The frequency of inundation will affect the physical and chemical properties of sediment such as quantity of silt and clay, organic carbon, and salinity. Prolonged inundation will enhance the oxidation, increase mineral recycling and help sediments become fragmented, unconsolidated and soft so they are accesible for polychaetes to feed and burrow. Moreover, the variety of tidal levels not only correlates with the extent of inundation but also to salinity and the nature of mangrove substratum. The present study has observed that the higher sites of the mangrove forest have high sediment salinity.

The variety of these environmental conditions may alter the nature of biological interaction within the mangrove systems, which in turn could produce an alternative distribution pattern. Woodin (1976) stated that a single infaunal species is commonly dominant in a dense soft substrate community. In the present study, a single species of polychaete dominated infaunal community structure in certain sites, such as *Pseudopolydora paucibranchiata* in the lower part outside of Garden Island mangrove, while other polychaetes contributed to the dissimilarities of community patterns among locations, such as the domination of *Neanthes vaalii* in Middle Beach mangrove.

Sediment reworking by polychaetes via their feeding behaviour and burrowing activities leads to the restructuring of infaunal communites (Whitlatch, 1981). A variety of feeding modes was found within polychaete assemblages of these mangrove habitats. *Capitella* sp. was found in rich organic sites such as Garden Island and Saint Kilda. As non-selective deposit feeders, the abundance of detritus in these sites probably stimulates their growth and enhance their dominance of the infaunal assemblages in these areas. The surface deposit feeders of *Neanthes vaalii* and *Namanereis littoralis* were mostly found in the sites where prolonged inundation occurs. This might satisfy the nereidids in terms of particle supply and adequate time for capturing food particles within water column. On the other hand, the spionid *Pseudopolydora paucibranchiata* was only found and was numerically dominant in the outer lower part of Garden Island mangroves. This site may fit with the nature of their feeding behaviour. As selective particle surface deposit feeders, the sediment type at this site may consist of suitable particle types and sizes, and the hydrodynamic regime such as water flow and velocity assist them during feeding and other biological activities. However, the role of feeding modes in determining the distribution pattern of polychaete communities within mangrove systems has been challenged. There are other environmental variables in temperate mangrove systems, such as salinity level, which do not correlate the feeding modes but play a significant role in mapping of infaunal distribution patterns.

Changes in abundance of polychaete population were detected during the study. The reduction of the number of individual polychaetes between May 2000 to May 2001, probably relates to limited reproductive success, low larval settlement success and predation. The sediment surface of the mangroves is open space in which polychaetes may become a potential predator target. The random effects of predators sometimes mask (as sampling errors) the effect of reproductive events which are often regulated by environmental condition. Certain nereidid species are monoletic i.e. the adults die after spawning, and salinity level and temperature were probable factors influencing the reproductive event (Neuhoff, 1979; Fong, 1991). Certain species of Capitellidae will reproduce rapidly when living in an unpredictable environment such as an organically enriched habitat while others will delay their reproduction (Tsutsumi *et al.*, 1990; Pechenick *et al.*, 2000).

Sediment reworking by polychaete burrowing is another factor in forming the distribution pattern of the 3 dominant polychaete species (*Capitella* sp., *Neanthes vaali* and *Pseudopolydora paucibranchiata*). Their burrowing behaviour and feeding activities may restructure infaunal communities, redistributing particles which affect changes in vertical layers within sediment. The building-tube rate of tube builders such as spionids will affect the adult and larvae relationship, while accumulation of faecal pellets will reduce the particles ingestible by selective deposit feeders (Miller and Jumars, 1986; Taghon, 1992). These biological relationships together with environmental conditions may influence the distribution patterns of the three dominant polychaetes within these mangrove locations which are quite different from one to another (i.e. Garden Island, Saint Kilda and Middle Beach).

The finer taxonomical work at this study did not detect any species as obligate mangrove polychaetes. Some researchers predicted that mangrove areas are considered to be the extension of marine habitat (e.g. Hutchings and Recher, 1981). If this is so, the special morphological adaptations would not be required to inhabit the mangroves.

Chapter 7 Research Synthesis

1. Introduction

The South Australian mangrove forests consist of only one single mangrove plant *Avicennia marina* var. *australasica* that grows within the Mediterranean climate which has wide variation in temperature. The mangroves are situated in inverse estuaries where salinity in the sediments is almost entirely influenced by the ambient salinity of the overlying water column during high tide. Combined with the arid environment where evaporation is high, these environmental conditions are quite challenging for the infaunal organisms and far from ideal for providing a rich diversity of infaunal assemblages. To date however there has no comprehensive research on infauna in these mangrove systems.

This present study was conducted to overcome the lack of infaunal data by examination of the community structure and the biological function of infaunal organisms. In particular, this study addressed the five main objectives:

1. To review the status of South Australian mangroves and the role of infaunal organisms in mangrove ecosystem (Chapter 1 and 2).
2. To observe the response of infaunal organisms to temperate environmental conditions by examining the structure of infaunal communities relating to geomorphological factors and sediment characteristics (Chapter 3).
3. To examine the infaunal distribution pattern within mangrove habitats and other adjoining habitats and to quantify the extent to which these patterns vary on both seasonal and inter-annual time scales (Chapter 4).
4. To investigate the behaviour of infauna within the sediments by examining the vertical distribution pattern through time (Chapter 5).
5. To observe the biological features of contributor taxa via taxonomical assessment and to reviewe their existence in the mangrove systems (Chapter 6).

Achievement of these objectives allowed a better understanding of the important role of infaunal assemblages in maintaining the ecological function of mangroves as part of a coastal system.

2. Summary of findings

The study has found that infaunal communities that live in these temperate mangroves were typified by lower abundance and poor diversity compared with other temperate Australian mangroves. However, the infaunal taxa compositions were comparable to other Australian temperate mangroves by being dominated by the polychaetous annelids, insects and molluscs. The numerically dominant polychaete taxa were; Capitellidae, Nereididae and Spionidae, there was a single dominant insect, a collembolan, in the family Neanuridae, whilst Veneridae and Mytilidae dominated the infaunal molluscs.

The South Australian temperate mangroves extend from the lower tidal level to the high tide mark resulting in a different periods of inundation between the lower part and the high part of mangroves. In addition, living under semi diurnal tides results in prolonged exposure of the habitats during the day to produce a distinct infaunal zonation. The infaunal communities at the low tidal transects were characterised by more abundance and diverse of taxa, as opposed to the higher transects where infaunal assemblages were less diverse and with lower abundance. It was suggested that prolonged inundation may give some benefits which increase the occupancy level of mangrove sediment because sediment becomes aerated, nutrients become abundant, the sediments become more accessible for burrowers and permanent dwellers.

South Australian mangrove habitats cannot be seen as a habitat *per se* due to their specific characteristics. The mangroves are part of a continuum of habitats within the estuary systems joined with other habitats such as mudflats or sea grass and saltmarsh. These inter connections between habitats influence, directly and indirectly, the benthic community within the mangrove habitats. Their association can be explained via organic materials exchanged during inundation time, refugee sites for certain species to avoid predators or desiccation. The study has found that mudflat sites and salt marshes were characterised by higher taxa diversity and higher abundance of individual taxa compared to the mangrove habitats. This might indicate that more secondary production takes place outside the mangrove zone and further suggest that the mangroves act as nutrient exporters to the adjacent habitats. However the mangrove outwelling process in these temperate estuaries are still questionable as some factors outside of the outwelling process possibly mask the nutrient exchange within the systems, such as the position of the mangrove within the estuaries relative to other habitats and extent of use of mangrove detritus by permanent residents.

Infauna has various responses to the sediment conditions. This assumption has been exercised in the variation of the infaunal community structure of the 3 different mangrove locations. Infaunal structures of Middle Beach were dissimilar to Garden Island and Saint Kilda. Moreover, infaunal organisms live near the surface of sediments where a wide gradient of environmental changes often takes place in just a few centimetres. This in turn produces a small-scale variation within the mangrove system. Dendrograms supported the claim that small-scale variations were more influential in structuring the infauna assemblages and subsequently contributing to the differentiation of infauna assemblages in larger scale. In addition, the study also suggested that information based on geomorphologic differences was not as useful as information based on ecological information in observing the infaunal communities, even though the result was not conclusive due to the inaccessibility of certain sites such as in Middle Beach Mangrove and Saint Kilda Mangrove. Indeed the spatial variation of infauna structure found at Garden Island should also be found at Middle Beach and Saint Kilda if similar a method was applied.

Naturally, mangrove sediments are anoxic as a result of organic matter degradation mediated by sulphate reduction pathways. Biological activities such as bioturbation by infauna and translocation of oxygen by aerial mangrove roots can modify the chemical and physical processes within sediment resulting in an oxygenated layer in the surface and increase the redox potential. Vertical examination of infaunal distribution during this study detected that the top layer of substratum (0-10 cm) was the most favourable for infauna. The vertical distribution was maintained during the whole sampling periods. Besides the physical and chemical properties of sediments, the infaunal distribution within sediments may also depend on the biological function of the taxa such as life style, age-size and structural morphology.

Mangrove sediments contain a rich mix of particulate organic material. As deposit dependent feeders, infauna satisfy their nutritional requirements from this organic fraction of ingested sediments. The effect of deposit feeders on the physical and chemical properties of sediment may strongly influence sediment characteristics by resuspension and redeposititition which then will determine the site specific variation because the sediment will become favourable or unfavourable, which in turn will regulate the type of infaunal assemblages. Functionally, the study noticed a systematic change of deposit feeder communities from subsurface deposit feeders to surface deposit feeders along the gradient from the high shore to the low shore. Possibly this was a characteristic of infaunal communities occupying the mangrove systems.

The polychaete taxa dominated the infaunal assemblages. They contributed significantly to both density and diversity of the infaunal communities in the South Australian temperate mangroves. Capitelidae and Nereididae were found widely in the mangrove systems and this were true symmetrical indicator taxa, while another such as Spionidae was restricted to certain sites and thus are asymmetrical indicator taxa. The study noted that the distribution pattern in the mangrove systems was dictated by physical and chemical characteristics of sediments which showed variation both between transects and locations. The variety of sediment condition might produce an alternative distribution pattern due to alteration of natural biological interactions and microhabitat selections. The finer taxonomical assessment revealed that spionids, *Pseudopolydora pauciabranchiata,* dominated the Garden Island mudflat habitat while nereidids, *Neanthes vaalii*, was dominated the mudflat at Middle Beach. On the other hand *Capitella* sp. was mostly found in the rich organic sediment which were typical of mangroves sediment.

The study also noted the population dynamics of the dominant species of polychaetes, *Capitella* sp., *Neanthes vaalii* and *Pseudopolydora paucibranchiata*, through time. The review of biological assessment of dominant polychaete species suggested that local environment condition such as physico chemical sediment characteristics, site positions relative to the tidal height and mangrove forest, might support their ecological behaviour including feeding and burrowing activities, reproduction events and larvae dispersals and settlements.

Like other estuarine habitats elsewhere, South Australian mangrove also suffer degradation due to anthropogenic pollution. It was noticed that infaunal assemblages were dominated by certain opportunistic taxa such as *Capitella* sp. and *Pseudopolydora paucibranchiata*. In the unpredictable environment, certain species of capitellids and spionids may reproduce rapidly by utilising the abundance of food resources while nereids may delay the reproduction process.

3. Recommendation for future research

The study observed that larger areas of mangrove in South Australia have suffered environmental degradation at various levels. The mangroves, such as Garden Island and Saint Kilda are located in urban areas where coastal development activities are high. The impact would, directly and indirectly influence the mangrove habitats, including mangrove dependent organisms. The study has reviewed the mangrove distribution both at the landward and seaward sides and also noted that infaunal assemblages were mostly dominated by opportunistic taxa. Considering possible impact, a buffer zone between mangrove areas and development areas could be considered to protect the mangrove habitat from further degradation.

The study has not yet demonstrated the seasonal shifts, habitat overlapping or resources partitioning among inhabitants as the number of individual taxa was very limited and duration of sampling was not long enough to observe the complete life cycles of the resident taxa. Additional research would be recommended to cover larger areas with sampling on a monthly basis. In addition, it is also suggested that sampling be carried out to at night. As mangroves are located in semi diurnal tide areas, when the low tide occurs during the night, it would be possible to observe the nocturnal behaviour of infauna. Certain taxa that are commonly found in mangrove habitats such as the Oxypodidae crabs are typically nocturnal taxa. Also certain species of Nereididae is often more abundant during the periods of the full moon. The present studies noted a very small number of Oxypodidae (crabs) as common taxa that permanently occupy the mangrove habitat. The crab communities are probably very mobile species, that may burrow deeply and certain species may have nocturnal activities. Regarding the infaunal sampling practice there would be different methods of sample collection for sedentary infauna and mobile infauna such as crabs, including type of sampling devices and depth of penetration of sampling devices.

The mangrove sediments are chemically and physically different with other marine sediments. It would be worthwhile if biological experiments were conducted using laboratory mesocosms which mimic the mangrove sediments to observe to what extent the mangrove sediment influences their biological performance. It is further recommended also to study genetic variances within polychaete taxa to examine if there are any differences in physiological adaptation of infauna between mangrove and non mangrove habitats.

To date most mangrove research in Australia has beene concentrated on plant communities. Studies of infaunal communities in mangrove can be considered rare especially in South Australian mangroves. However to understand the mangrove ecosystems, information about the biological activities of infaunal communities within the mangrove habitats and how infaunal communities interact with other habitats adjacent to mangrove forests is important. This will enable us to construct a food web and allow estimates of secondary productivity to be made. The claim that mangroves are important in Australian estuarine ecosystems can be substantiated.

Lastly, this present study noted how the distribution pattern of sediment dependent organisms, infauna, varied in terms of time scale and spatial scale. Due to this variation, it is important to use similar research design and methods in comparing the structure of benthic infaunal communities in mangrove ecosystems throughout other mangrove forests in the subtropics and tropics. The global features of infaunal distribution in mangrove systems can then be quantified.

4. Conclusion

The study of infaunal communities in South Australian temperate mangrove concluded that infaunal structures were mostly defined by the local environmental variations which influence their biological function. Even though the infaunal assemblages were represented by poor density and diversity within communities, they still provide a complete array of functional feeding modes. The below ground structure of mangroves act as a detritus pool and provide a wide range of particle selection that benefits detritus dependent organisms. The infaunal communities were represented by suspension feeders and deposit feeders, surface and subsurface deposit feeders, herbivores and carnivores reflecting the effectiveness of mangrove habitat utilization by the permanent residents. This suggests that mangroves provide a valuable habitat for other organisms. Therefore their existence has to be protected and other human activities and coastal development plans that can manipulate inshore marine systems must to be carefully controlled and the decisions must be made on the basis of ecological principals hand in hand with economic consideration.

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Appendix I Sediment Analysis

1.Total Organic Carbon

The procedure based on Walkley – Black Method using rapid titration procedure. The soils is digested with chromic and sulphuric acid. A known quantity of dichromate is the source of the chromic acid and the excess of chromic acid not reduced by the organic matter is determined by subsequent titration with standard ferrous sulphate using o- phenanthroline as indicator. It has to be noted that for calcareous sediments the carbonates have to be removed prior analysis using sulphuric acid. The Soil and Water Department of Adelaide University have developed the procedure for total organic carbon as bellow:

Reagents:

1. Potassium dichromate made from 98.08 kg $K_2Cr_2O_7$ in deionised water and dilute to 2000 cm^3.
2. 0.5 Ferrous sulphate made by dissolving 278 g $FeSO_4.7H_2O$ in deionised water, add 30 cm^3 concentrated H_2SO_4 and dilute to 2000 cm^3.
3. Concentrated sulphuric acids, 2000 cm^3
4. Concentrated orthophosphoric acid, 2000 cm^3
5. σ-phenanthroline indicator

Procedure :

1. Carried out the blank determination. As the ferrous sulphate is unstable and must be standardised by titration with potassium chromate regularly.
2. Weight out in duplicate 1.0 gram lots of each of the finely ground dry soils and transfer into 500 cm3 conical flask. The sample should contain about 10-20 mg carbons. Adjust the weight of the soils accordingly. In this study approximately 0.3 gram or 300 mg dried soils were used.
3. Pipette into each flask 10 cm3 of the 1N potassium dichromate solution and then carefully add 20 cm3 of concentration sulphuric acid
4. Shake for about one minute vigorously and then allow the flask to stand on the fume hood for half an hour to digest completely.

5. Add about 200 cm^3 of distilled water, 10 cm^3 of concentrated orthophosphoric acid and 0.5 cm^3 of σ-phenanthroline solution.
6. Cool the flask. Do not titrate the hot solution as the end point (when the solution turn into red) would be difficult to determine.
7. Titrate the excess of chromic acid by adding ferrous sulphate solution from a burette until the solution turn from green into red. If the end point of the titration occurs bellow 2-3 cm^3 of the 0.5 N ferrous sulphate have been added, too much soils have been used, as this also found in this study. Repeating the titration using the smaller amount of soils is recommended.
8. Calculate **the content of organic carbon** in the soils by calculating : **(blank titre – actual titre) X 0.3. M / weight of oven dry soil in mg , where M is the concentration of ferro sulphate solutions.** Given that each cm^3 of 1N potassium dichromate used is equal to 3 mg of carbon. The result can be expressed as per cent organic carbon (Walkley-Black, uncorrected).

2. Determination of CaCO3 in the sediment

As the South Australian mangrove sediments considered as calcareous sediment, which presumably influence the infauna assemblages, the carbonate content in sediment then analysed using Volumetric Calcimeter that treated the acid in a close systems. The increase of the volume in the system is direct measure of CO_2 if no other gases are evolved. Soil and Water Department of Adelaide University had developed the procedure bellow.

Reagents:

1. Hiydrochloric acid (HCl), approximately 4 N
2. Hydrochloric acid (HCl) – ferrous chloride ($FeCl_2.4H_2O$) reagent : dissolve 3 grams $FeCl_2.4H_2O$ in 100 ml of 4N HCl immediately before use
3. Sodium carbonate (Na_2CO_3), primary standard

Procedure :

1. With tap open to atmosphere adjust burette levels to zero.

2. Add oven dried soil to reaction vessel plus vial of $FeCl_2/HCl$ and connect to calcimeter.
3. Close tap to seal calcimeter from atmosphere and lower levelling bulb a few centimetres to create a negative pressure.
4. Connect to wrist shaker and shake moderately to spill $FeCl_2/HCl$ mixture. Shake for 1 to 2 minutes
5. When reaction complete raise levelling bulb to bring the left-hand burette (open to atmosphere) back to zero.
6. Read volume displaced in the other burette.
7. Open burette to atmosphere and repeat.
8. Calibrate with $CaCO_3$ (5 mg in 1 ml CO_2).
9. Calculation of per cent carbonate in soil as follow :

From standard 50 mg $CaCO_3$ = X ml CO_2, then 1 ml CO_2 = 50/X mg $CaCO_3$

Let volume of CO_2 from soil = Y ml

Let weight of soil sample = M grams

Then % $CaCO_3$ = $50 . Y . 10^{-3} .100 / X. M$ or $5Y/ X.M$

3. Particle size analysis

Sediment mangroves generally cover different main combination of sand, silt and clay. The proportion of sand, silt and clay determined the permeability of soil to water that then influence the salinity and water content. A number of different classification for particle size have been devised in the following size fraction :

Fraction	Equivalent spherical diameter (esd)
Gravel	> 2.0 mm
Coarse sand	2.0 – 0.2
Fine sand	0.2 – 0.02
Silt	0.02-0.002
Clay	<0.002 (or <2 µm)

International Society of Soil Science, 1986

In particle size analysis the coarse particle usually separated by sieving and the finer particles by sedimentation using Stokes' Law which gives the relation between the radius of spherical particles and its rate on fall in liquid. There was two common methods used for marine sediment analysis, they are Buchanan methods (1984) and Bouyoucos (1962). The last one has been chosen for this study to speed up the process, using simple equipment but still the result is acceptable. The hydrometer is design to measure the density of the suspension. Sandy particle will settle out more rapidly than smaller particle such as silt and clay. The procedure bellow has developed by the Soil and Water Department of Adelaide University and modified using procedure mentioned in English *et al.*, (1994) for mangrove sediments.

Reagents:

1. 10 % Calgon ($NaPO_3 + Na_2CO_3$) . Dissolve 200 gr of calgon in distilled water and dilute to 2000 ml.
2. 0.6M NaOH. Dissolve 24 g in distilled water and dilute to 1000 ml.
3. Amyl alcohol.

Procedure :

1. Calibrate the hydrometer by taking a blank reading using this solution : 50 ml Calgon solution (1N sodium hexametaphosphate) and 5 ml 0.6 M NaOH and make up to 1 litre by adding distilled water. Put the hydrometer gentle into the solution and read the scale and note the temperature of solution.
2. Place the 40-gr samples into a 1000 ml baker. Prior particle analysis, organic and carbonate content were removed using acid solutions. Then add 150 ml distilled water, 50 ml Calgon solution and 5 ml 0.6 M NaOH. Put the solution into 1 l bottle, put the lid on. Shake using electrical shaker for one night to achieve a maximum dispersion of particles.
3. Transfer the solution into 1 litre-measuring cylinder. Wash out the remaining using distilled and then make up the volume to exactly 1 litre by adding deionised water. Mix the suspension well using the stirrer until the sediment is evenly suspended through water column. Place the cylinder

carefully on a solid, level table and carefully noted the time of commencement of sedimentation.

4. At 5 minutes recommended as time settling for sand, put the hydrometer gently into the cylinder and immediately take a hydrometer reading. Note the temperature of the soil suspension. If froth obscures the scale, add drops of amyl alcohol. Removed the hydrometer, washed it and dried it. Each time reading the hydrometer must be clean and dry.
5. Take another reading after 5 hours since the sedimentation begun and note the temperature of the soil suspension. The 5 hours is recommended time for clay settling (2μm based on) in a clay predominantly soil.
6. Note: as temperature affects the hydrometer reading it was preferable to maintain the temperature around 20^0C by using a water bath.

4. Salinity measurement

Sediment salinity was measured using conductivity meter from the 1: 5 soil suspension. Department of Soil and Water, Adelaide University has developed the procedure as follow:

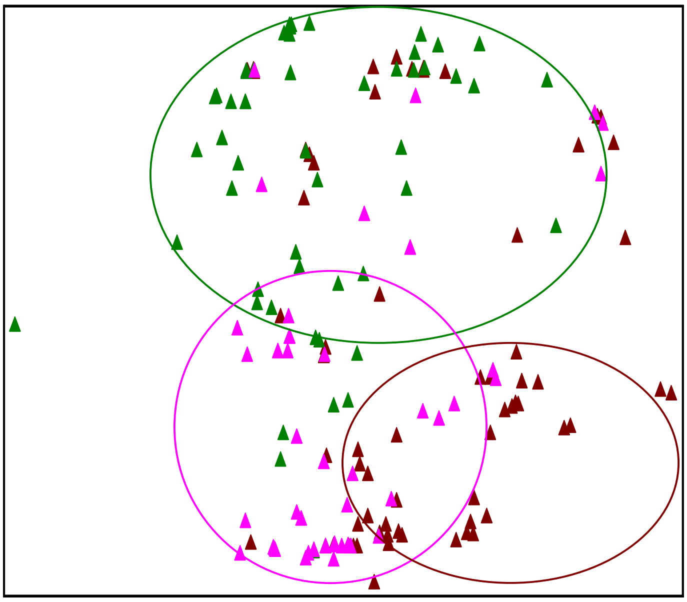
1. Weight 20 mg of fine grain dried soil and pour into the volumetric tube.
2. Add distilled water until the volume of suspension reach 100 ml, put the lid on tightly.
3. Shake vigorously the soil suspension using electrical sample for two hours to make sure that all particulate mater were aggregated.
4. Leave for two hours until all particulate settle before the reading take place.
5. Wash the electrode with distilled water before and after measurement.

Appendix 2 Data Transformation

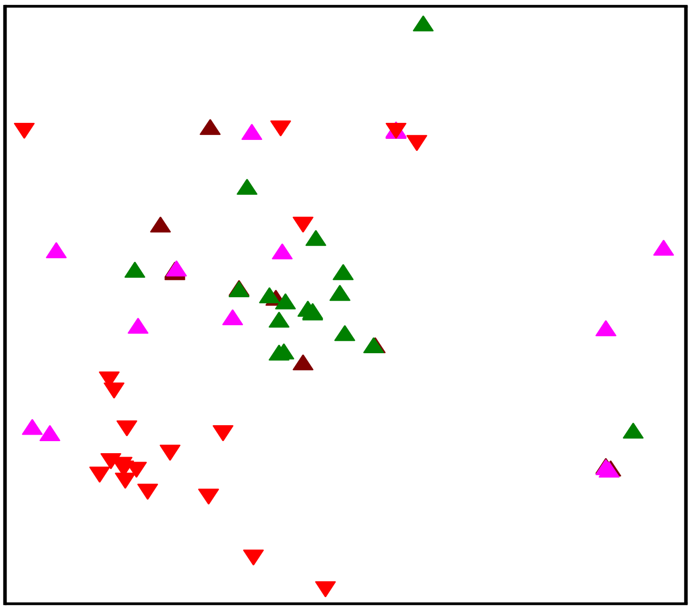
1. Fourth roots transformation.

When the rare taxa are weighted as heavy as the common taxa.

A. Three mangrove locations (♦: Middle Beach ; ♦: Saint Kilda, ♦: Garden Island).



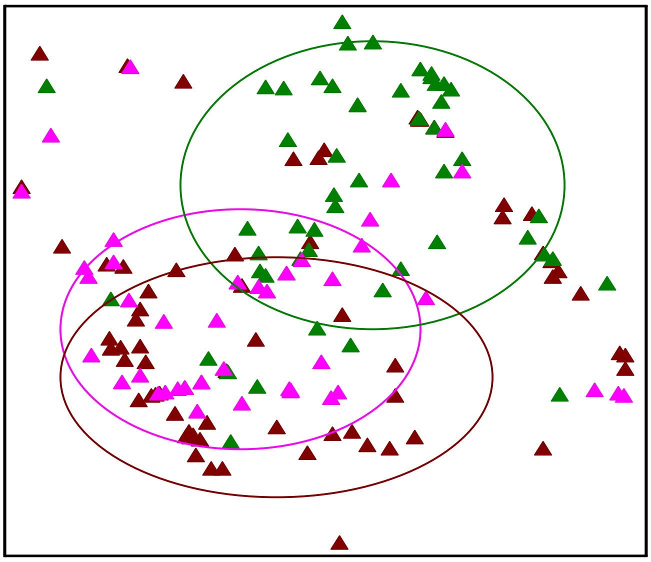
B. Garden Island (♦: HO, ♦: HI, ♦: LI, ♦: LO).



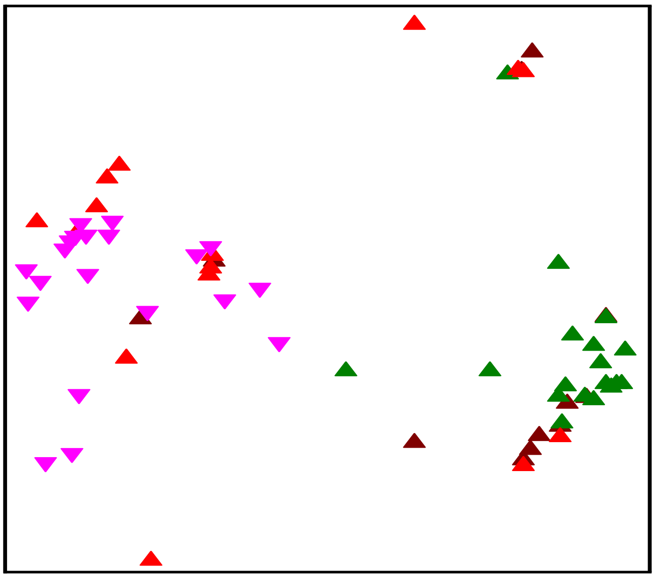
2. Log (x +1) transformation

This transformation was preferable when the infaunal data are consist of many small number or zero

A. Three mangrove locations (♦: Middle Beach ; ♦: Saint Kilda, ♦: Garden Island).



B. Garden Island (♦: HO, ♦: HI, ♦: LI, ♦: LO).

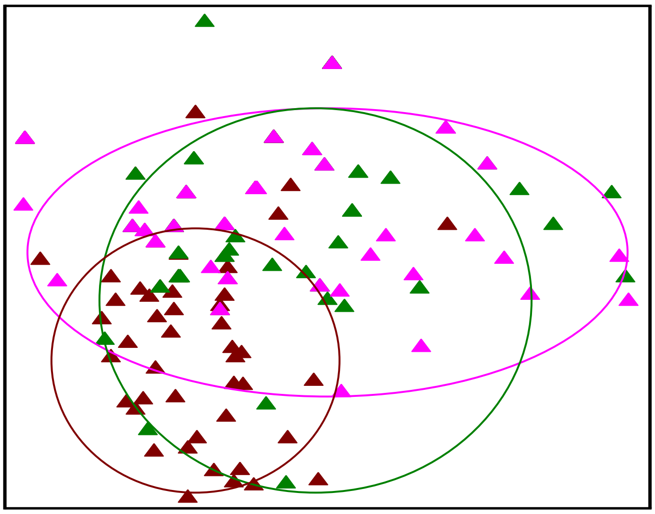


In this study, the data transformation has reduced the contribution of common taxa relative to rare taxa in dissimilarities of measurement. Hence spatial variation was failed to detect.

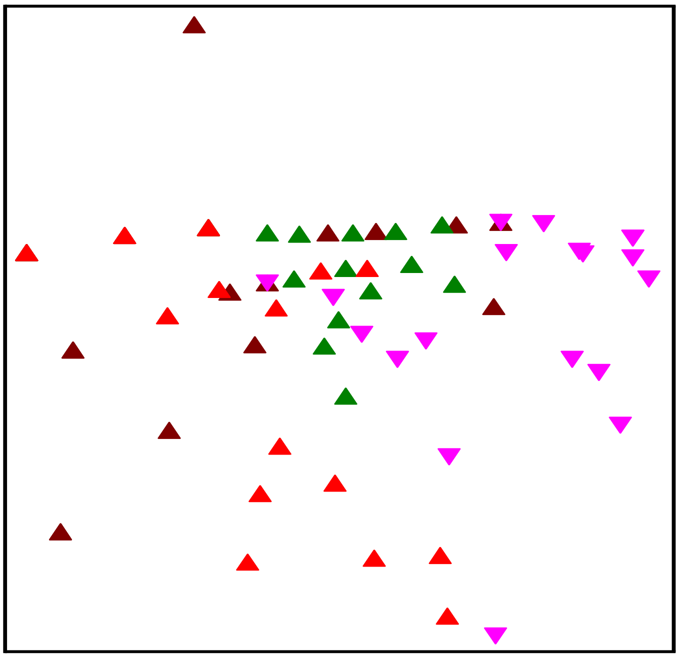
Appendix 3 Taxonomy resolution

1. Phylum

A. Three mangrove locations (◆: Middle Beach ; ◆: Saint Kilda, ◆: Garden Island)

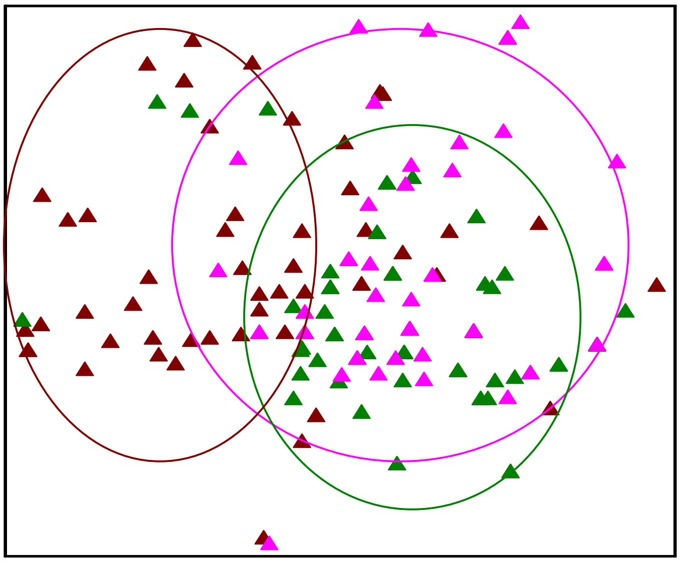


B. Garden Island (◆: HO, ◆: HI, ◆: LI, ◆: LO).

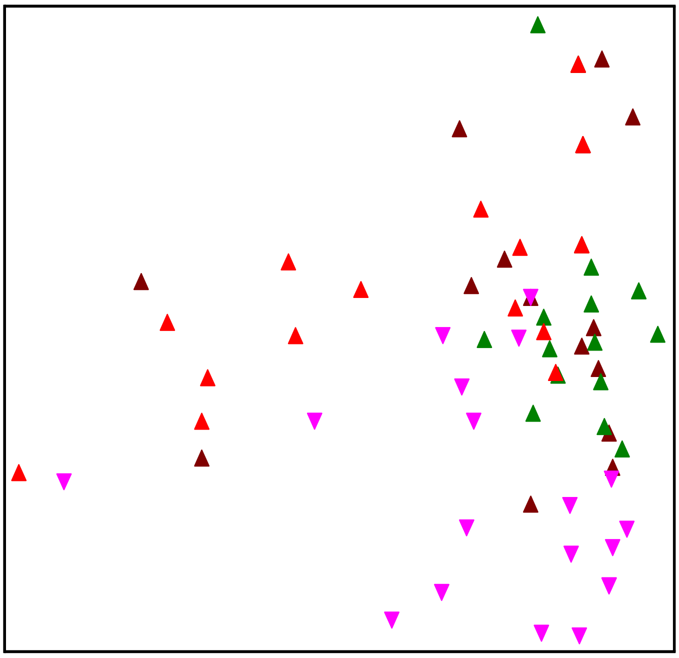


2. Class

A. Three mangrove locations (♦: Middle Beach ; ♦: Saint Kilda, ♦: Garden Island).



B. Garden Island (♦: HO, ♦: HI, ♦: LI, ♦: LO).



Discrimination between mangrove locations and habitat within mangrove decreased at higher taxonomic level (Phylum and Class). Spatial patterns of infaunal assemblages were preserved at the family level.