SPATIAL AND TEMPORAL PATTERNS IN THE HYPERBENTHIC COMMUNITY STRUCTURE IN A PERMANENTLY OPEN EASTERN CAPE ESTUARY, SOUTH AFRICA.

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By
Elodie R. Heyns

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ABSTRACT

The spatial and temporal (seasonal and diel) patterns in the hyperbenthic community structure (>500 µm) was investigated in the warm temperate, permanently open Kariega Estuary situated along the south-eastern coastline of South Africa. Spatial and seasonal patterns in the hyperbenthic community structure were assessed monthly at six stations along the length of the estuary over a period of twelve months. Data were collected using a modified hyperbenthic sledge, comprising two super-imposed nets. Physico-chemical data indicate the presence of a constant reverse salinity gradient, with highest salinities measured in the upper reaches and lowest at the mouth of the estuary. Strong seasonal patterns in temperature, dissolved oxygen and total chlorophyll-*a* (chl-*a*) concentrations were evident. Total average hyperbenthic densities ranged between 0.04 and 166 ind.m^{-3} in the lower net and between 0.12 and 225 ind.m^{-3} in the upper net. Hyperbenthic biomass values ranged between 0.02 and 11.9 mg.dry weight.m^{-3} in the lower net and between 0.02 and 17.4 mg.dry weight.m^{-3} in the upper net. A spatial and temporal pattern in total densities was detected with an increase in abundance over the period of September to October 2008 particularly in the middle reaches (Stations 3 and 4). Both the lower and upper nets were numerically dominated by decapods (mainly brachyuran crab zoeae) with the exception of June and July 2008 when mysids (mainly *Mesopodopsis wooldridgei*) dominated, making up 72.4 ± 58.14% of the total abundance in the lower net. A redundancy analysis (RDA) indicated that 99.2% of the variance in the hyperbenthic community structure could be explained by the first two canonical axes. Axis one, which accounted for 96.8% of the total variation detected in the ordination plot was highly correlated with sedimentary organic content and to a lesser extent the chl-*a* concentration within the Kariega Estuary. The correlations with the second canonical axis (2.4%) were less obvious, however, salinity and seston concentration were weakly correlated with this axis. Diel variability in the hyperbenthic community structure was assessed during March 2009. Samples were collected during the day and night (*n* = 6 for each period) using sampling gear described above. Total average hyperbenthic densities during the day (497.9 ± 254.1 ind.m^{-3}) were significantly higher than night-time estimates (129.9 ± 38.5 ind.m^{-3}; $p<0.05$). There were no significant differences in the average day- and night-time estimates of hyperbenthic biomass ($p>0.05$). A hierarchical cluster analysis identified two significantly distinct groupings, designated the day and night samples. Results from the SIMPER procedure indicated that the high densities of crab zoeae recorded during the day-time accounted for the majority of the dissimilarity between the day and night groupings (44.7%). In addition, it is apparent that several benthic species, especially from the cumacean and isopod orders, were absent from the hyperbenthos during the day-time and emerged into the water column at night.

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PREFACE

This study comprises two distinct components:

1. A study on the spatial and temporal patterns of the hyperbenthic community within the permanently open Kariega Estuary.
2. An investigation of the diel patterns of the hyperbenthos within the Kariega Estuary.

Work from the first study has been submitted for publication in the journal, *Estuarine and Coastal Shelf Science*.

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The work from the first section has also been presented at the following international conference:

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DECLARATION

The following thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author.

CHAPTER 1

INTRODUCTION

1.1. GENERAL INTRODUCTION

1.1.1. THE HYPERBENTHOS

The macrofauna found in the waters in close proximity to the bottom of the sea and estuaries have been an important resource for commercial exploitation (Mees and Jones 1997). However, relatively little is known about the smaller organisms that inhabit the same biotope (Mees and Jones 1997; Carleton and Hamner 2007). This association of smaller animals is collectively known as the hyperbenthos (Mees and Jones 1997; Beyst *et al*. 1999).

The term benthos is generally used to describe the entire community of organisms found inhabiting the ocean floor environment, whereas the term benthic boundary layer is used to describe their physical environment (Mees and Jones 1997; Carleton and Hamner 2007). The benthic community may be divided into three major components, distinguished by their distribution related to the benthic substratum. Endobenthic animals are found living within the substratum, epibenthic animals are found living on the substratum and hyperbenthic animals inhabit the water column directly above the ocean floor. The term hyperbenthos was first introduced by Beyer (1958, as cited in Mees and Hamerlynck 1992) to describe the fauna which lives in the water column but has some association with the substratum. The hyperbenthos is thus the association of small, bottom dependant animals, mainly crustaceans, which usually show some degree of seasonal or vertical migration (Mees and Hamerlynck 1992; Mees and Jones 1997; Koulouri 2002).

There is a general lack of synthesis with regards to the information and studies conducted on the hyperbenthos. This may be attributed to the differences in terminology within different fields of study. In the tropics, demersal, swarming or resident zooplankton are common terms, whereas the terms, “bentho-pelagic plankton” and “benthic boundary layer macrofauna” are often used for the fauna from deep-sea studies (Smith 1992; Mees and Jones 1997; Cartes 1998; Sorbe 1999). The term “suprabenthos” is also a widely employed term, especially in the higher latitudes. However, due to etymological reasons, a noun derived from Greek (benthos) should be preceded by a Greek prefix, rather that by its Latin equivalents (supra-, super-), thus the term hyperbenthos is preferred (Mees and Jones, 1997). Nonetheless, the term suprabenthos is still widely employed by various authors. See for example Brandt 1997; Azeiteiro and Marques 1999; San Vicente and Sorbe 1999; Cartes *et al.* 2007.

Hamerlynck and Mees (1991, as cited in Mees and Jones 1997) introduced the terms merohyperbenthos and holohyperbenthos to classify the animals found in the benthos in relation to the time spent within the hyperbenthal region. Merohyperbenthos include the fauna that spend only part of their early life history in association with the ocean or estuarine bottom (Hamerlynck and Mees 1991, In: Mees and Jones 1997). Holohyperbenthos are fauna that spend variable periods of their adult life in the hyperbenthal and include species such as harpacticoid copepods, mysids, amphipods, isopods and cumaceans (Wooldridge and Erasmus 1980; Hamerlynck and Mees 1991, as cited in Mees and Jones 1997). Alternatively, the hyperbenthos can be classified according to size classes. The meiohyperbenthos includes all the animals in the size class 32 µm to 500 µm while the macrohyperbenthos includes all animals larger than 500 µm (Mees and Jones 1997). This suggests that the hyperbenthos encompasses a large and diverse assemblage of organisms, which are linked by their distribution in space and time, rather than by phylogeny or individual functional attributes (Day *et al*. 1989; Mees and Jones 1997). The large array of organisms that make up the hyperbenthos share a unifying factor, in that all spend some time, although a variable amount, in the hyperbenthal. Some species move position very erratically but others show regular diel or seasonal migrations which can be related either to their ecology or life history stages (Mees and Jones 1997). The hyperbenthic community structure is subject to large fluctuations because the flexible diet of hyperbenthic organisms allows them to change their position in the food web seasonally and ontogenetically (Mees and Jones 1997). Despite the unpredictable distribution and position of the hyperbenthos, it may still be considered a true community (Mees and Jones 1997).

1.1.2. HISTORY OF THE RESEARCH ON HYPERBENTHOS

Research on the ecological significance of the hyperbenthos is relatively new and started in the late 1950s (Bossanyi 1957). Prior to the work done by Bossanyi (1951; 1957), Russell (1925, 1926, 1928) identified a region of increased zooplankton abundance and biomass in close proximity to the bottom. This finding triggered the resultant research interest in the fauna associated with the substratum and led to the construction of the first hyperbenthic sampler (Mees and Jones 1997). From the early hyperbenthic samplers (Russell 1928; Colman and Segrove 1955), more elaborate trawls with opening and closing devices were constructed (Bossanyi 1951; Wickstead 1953). During this time the "small natant fauna immediately above the sea floor" was first recognised as an ecological entity and the importance of this community in the economy of the ocean was recognised (Bossanyi 1957). In Oslofjord (Norway), Beyer (1958, as cited in Mees and Jones 1997) studied the bottom plankton and found that there was a distinct increase in the concentration of plankton near the substratum. Following this observation, Beyer (1958) stated that this near bottom plankton community must be seen as part of the benthos and accordingly named it the hyperbenthos. Subsequent to the work done by Beyer (1958, as cited in Mees and Hamerlynck 1992), several other studies on the 'hyperbenthos' were conducted, but differences both in sampling methods and the manner in which densities were expressed resulted in a general lack of synthesis in knowledge concerning the hyperbenthic community (Mees and Jones 1997).

Later studies on estuarine hyperbenthos include the work by Dodson *et al.* (1989) and Dauvin and Dodson (1990), which were concerned with the vertical distribution of the larval rainbow smelt (*Osmerus mordox*) in the St. Lawrence Estuary (Québec, Canada). Many studies on the hyperbenthic community structure related to environmental variables are centred on Western European estuaries. In the Netherlands, especially the Westerschelde, Eems and Gironde estuaries, intensive studies concerning the hyperbenthos community structure and distribution have been conducted (Mees & Hamerlynck 1992; Mees *et al*. 1993; Mees *et al*. 1995). These studies suggest that the hyperbenthic communities are structured along unidirectional salinity, dissolved oxygen and turbidity gradients (Table 1.1). In shallower estuaries, such as the Mondego (Portugal), species richness, biomass and abundance were also shown to be positively correlated with the salinity gradient (Azeiteiro and Marques 1999) (Table 1.1). Most studies also agree that diversity is consistently highest at the mouth of the estuary, which coincides with the lowest densities and biomass of the hyperbenthos (Mees & Hamerlynck 1992; Mees *et al*. 1993; Mees *et al*. 1995; Azeiteiro and Marques 1999). Estimates of the total abundance and biomass of the hyperbenthos are highly variable and range from ≈ 4 to 3330 ind.m^{-3} and from ≈ 1 to 618 mg.dry weight.m^{-3}, respectively (Azeiteiro and Marques 1999; Drake *et al*. 2002; Carleton and Hamner 2007) (Table 1.1). Seasonal changes within the hyperbenthic community structure found in the Mondego Estuary (Portugal) and the Ebro Delta (Spain) indicate a peak in densities in early summer (Azeiteiro and Marques 1999; Cartes *et al*. 2007). This peak can mostly be related to environmental factors such as river discharge and food availability. Azeiteiro and Marques (1999) indicated that during winter months in the Mondego Estuary, the upper reaches were species poor because increased freshwater discharge limited the number of species that could penetrate the brackish upper reaches. The hyperbenthic community structure consists largely of crustaceans, dominated by mysids (Mees and Hamerlynck 1992; Mees *et al*. 1993; 1995; Drake *et al*. 2002; Morgado *et al*. 2003). Other important taxonomic groups include amphipods, isopods, cumaceans, brachyuran crab larvae and also post larval fish species (Mees and Hamerlynck 1992; Mees *et al*. 1993; 1995; Cunha *et al*. 1997; Mees and Jones 1997; Azeiteiro and Marques 1999; Cartes *et al*. 2007).

Table 1.1. Summary of basic results and conclusions of published hyperbenthic studies conducted globally. SSD indicates Secchi Disk Depth, dO_2 indicates dissolved oxygen concentrations, ND indicates no data available, N/A indicates parameters that are not applicable to the study and values in brackets are converted to allow comparison with present study.

System	Type of system	Freshwater discharge	Salinity gradient	Densities	Biomass	Environmental variables structuring the hyperbenthos	Reference
European systems							
Portugal							
Mondego Estuary	Shallow estuary	8.5 x 109$m^3.s^{-1}$	Yes	≈ 4 - 132 $ind.m^{-3}$	≈ 1 - 28 mg $AFDW.m^{-3}$	Salinity, SDD and dO_2	Azeiteiro and Marques 1999
				12.7 - 385 $ind.m^{-3}$	ND	Salinity	Morgado *et al* . 2003
Continental margin	Deep system	N/A	No	700 - 13591.7 $100m^{-2}$	ND	Sediment type, depth and associated environmental factors	Cunha *et al.* 1997
Belgium							
Sandy beaches	Surf zone	N/A	No	0 - 3430 $ind.m^{-2}$	0 - 15 000 mg $AFDW.m^{-2}$	Water temperature, wave height and turbidity	Beyst *et al* . 2001
Spain							
Ebro River Delta	River delta (47 - 61m deep)	≈ 100 - 2450 $m^3.s^{-1}$	Unknown	740 - 8048 $100m^{-2}$	ND	River discharge (salinity and temperature)	Cartes *et al.* 2007
Guadalquivir Estuary	Deep estuary (Sample depth: 3m)	Unknown	Yes	403 - 6005 $ind.100m^{-3}$ (4.03 - 60.05 $ind.m^{-3}$)	3.8 - 61.8 $g.100m^{-3}$ (0.038 - 0.618 $g.m^{-3}$)	Salinity	Drake *et al* . 2002
Creixell Beach	Surf zone	N/A	N/A	11.1 - 117 $ind.5m^{-2}$	ND	Wave action and currents	San Vicente and Sorbe 1999
Hendaya Beach	Surf zone	N/A	N/A	25.4 - 488.4 $ind.5m^{-2}$	ND		San Vicente and Sorbe 2001
Netherlands							
Dutch Delta:							
Westerschelde (WS)	Deep estuary	105 $m^3.s^{-1}$	Yes	> 12 $ind.m^{-2}$	5 - 50g $AFDW.1000m^{-2}$	WS: Salinity, turbidity and dO_2	Mees and Hamerlynck 1992
				≈ 0.1 - 53 $ind.m^{-2}$	≈ 0.2 - 35 mg $AFDW.m^{-2}$	WS:Salinity, dO_2 and turbidity	Mees *et al* . 1993
				0 - 250 $ind.m^{-2}$	0 - 555 mg $AFDW.m^{-2}$	WS:Salinity, SSD, temperature	Mees *et al* . 1995
Oosterschelde (OS)	Deep estuary	10 $m^3.s^{-1}$	No	< 0.05 $ind.m^{-2}$	< 0.004g $AFDW.m^{-2}$	OS: SDD, dO_2, mud content	Mees and Hamerlynck 1992
Voordelta (VD)	Shallow coastal area	N/A		Intermediate of above	< 0.5g $AFDW.m^{-2}$	VD: Temperatuer and salinity	Mees and Hamerlynck 1992
Eems	Deep estuary	5.1 - 390 $m^3.s^{-1}$	Yes	5 - 20 $ind.m^{-2}$	10 - 66 mg $AFDW.m^{-2}$	Salinity, SSD, temperature	Mees *et al* . 1995
France							
Gironde	Deep estuary	200 - 1500 $m^3.s^{-1}$	Yes	0 - 50 $ind.m^{-2}$	0 - 114 mg $AFDW.m^{-2}$	Salinity, SSD, temperature	Mees *et al* . 1995
England							
English Channel	Deep system	N/A	N/A	1 - 10 000 $ind.100m^{-3}$ (0.01 - 100 $ind.m^{-3}$)	ND	Temperature, salinity, nutrients	Vallet and Dauvin 2004
Southern Hemisphere							
Australia							
Great Barrier Reef	Coral reef lagoon	N/A	N/A	750 - 3330 $ind.m^{-3}$	ND	Detritus	Carleton and Hamner 2007

1.1.3. ECOLOGICAL ROLE OF THE HYPERBENTHOS

The hyperbenthos plays a vital role in marine trophodynamics (Morgado *et al*. 2003) by linking the benthic and pelagic food webs (Perissinotto and McQuaid 1990). Perissinotto and McQuaid (1990) suggest that the high concentration of phytoplankton blooms associated with the waters within immediate vicinity of the Prince Edward Islands is seldom directly consumed by pelagic zooplankton. However, a large concentration of benthic suspension feeders consumes this source of unutilised phytoplankton. The benthos in turn is preyed on by the shrimp *Nauticaris marionis*, which undergoes diel and diurnal vertical migrations and thereby indirectly makes the settled phytoplankton available to pelagic predators, thus linking the benthic and pelagic food webs (Perissinotto and McQuaid 1990). Knowledge of the interactions of bentho-pelagic food webs aids in the development of carbon flux models, although these models often exclude samples from the hyperbenthal, which can underestimate the flux of particulate matter (Mees and Jones 1997).

Mysids, which are prominent components of the hyperbenthal, are omnivorous and feed on detritus, phytoplankton and zooplankton (Mees and Jones 1997; Winkler and Greve 2004). Mysids thus influence the population structure and composition of their prey items (Mees and Jones 1997). Furthermore, the mysids and the other components of the hyperbenthos feed on refractile detritus, thus contributing to the remineralisation of nutrients (Mees and Jones 1997; Carleton and Hamner 2007). Mysids in turn represent an important prey item in the diets of many important commercially exploited fish species such as cod, herring, and flatfishes as well as gobies and shrimp (Winkler and Greve 2004).

1.1.4. ESTUARIES

According to Costanza *et al*. (1997) marine systems globally contribute to about 63% of the total world's ecosystem services with a value of US$ 20.9 trillion yr^{-1}. Most of this is contributed by coastal systems (US$ 10.6 trillion yr^{-1}; Costanza *et al*. 1997). When measured by the hectare, estuaries are by far the most important ecosystem service globally, with a total value per hectare of US$ 22 832 (Costanza *et al*. 1997). Approximately 60% of the world's human population live within 100 km of the world's coastline (Vitousek *et al*. 1997). Coastal wetlands, which are important in mediating interactions between terrestrial and coastal systems, have been greatly altered over large areas and over 50% of the world's mangroves have been destroyed by human activities (Vitousek *et al*. 1997). These facts indicate that estuaries are globally under pressure from human activities, and thus information on the functioning of this important ecosystem is critical.

The definition of an estuary can be as simple as "the meeting place of terrestrial drainage systems with the coast" (Cooper *et al*. 1999) or as descriptive as that by Pritchard (1967) "an estuary is a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with freshwater derived from land drainage". Day (1980) pointed out that Pritchard's definition does not hold true when considering most South African and Australian estuaries. According to Day (1980) two phases in Pritchard's definition cause difficulty, the first "a free connection with open sea" and the second "diluted by freshwater". Many of the estuaries in southern Africa are temporarily closed by sandbars, especially during the dry season and therefore do not show a free connection with the open sea (Day 1980; Day 1981; Whitfield 1998). Furthermore many of these systems, including the St Lucia, Milnerton, Mhlanga (Day 1980) and Kariega estuaries, often demonstrate the absence of a horizontal gradient in salinity, and indeed hypersaline conditions (>40 practical salinity units) may predominate in the upper reaches (Whitfield 1998). Thus Day (1980) modified Pritchard's definition to: "An estuary is a partially enclosed coastal body of water which is either permanently or periodically open to the sea, and within which there is a measurable variation of salinity due to the mixing of sea water with fresh water derived from land drainage"

Whitfield (1998) devised a classification system for South African estuaries based on the physiographic, hydrographic and salinity characteristics of individual systems (Table 1.2). From this classification system 258 estuaries were identified along the southern African coastline and include permanently open estuaries (POEs), river mouth and temporarily open/closed estuaries, estuarine lakes and estuarine bays (Table 1.2) (Whitfield 1998, 2000).

Table 1.2. Estuarine classification system, based on the hydrographical, physiographical and salinity characteristics of estuaries (after Whitfield 1998).

System type	Spring tidal prism	Mixing process	Mean salinity
Estuarine bay	Large (>10 x 106 m^3)	Tidal	25 - 35
Permanently open estuary	Moderate (1-10 x 106 m^3)	Tidal/Riverine	15 - 40
River mouth	Small (<1 x 106 m^3)	Riverine	1 - 15
Estuarine lake	Negligible (<0.1 x 10 6 m^3)	Wind	1 - >35
Temporarily closed estuary	Absent	Wind	1 - >35

Permanently open estuaries show typical estuarine characteristics with a moderate tidal prism, a horizontal salinity and a vertical salinity gradient which depend on the bathymetry, the tidal cycle and river flow of an individual estuary (Whitfield 1998). Also according to Day (1981) ‘normal’ estuaries, which include permanently open estuaries (POEs), show a net flow seaward (over a full tidal cycle), and are defined by the degree of salt and fresh water mixing that occurs in individual systems. From this Day (1981) divided permanently open estuaries into four groups: estuaries that exhibit a salt-wedge, estuaries that show high stratification, partially mixed estuaries and lastly vertically homogenous estuaries. MacKay and Schumann (1990) indicated that the degree of stratification is dependent on the river flow, tidal range and mouth condition. During neap tides, the Sundays River Estuary, Eastern Cape, South Africa was highly stratified, but during spring tide the estuary was completely mixed (MacKay and Schumann 1990).

Under natural conditions, the average salinities of POEs fluctuate between 15 and 25 (Whitfield 1998). Relative to human demands, freshwater is becoming a growing scarcity, especially in the more arid parts of the world (Postel *et al*. 1996; Postel 2000). South Africa is considered an arid country, with a high demand for freshwater used in agriculture, industry and domestic use (Allanson and Read 1987). The high demands on South Africa's freshwater resources result in decreasing amounts of freshwater available for environmental management, especially in estuaries (Allanson and Read 1987). In particular, estuaries in the southern and Eastern Cape regions often become hypersaline due to low freshwater inflow and high summer evaporation rates (Whitfield 1998). The amount of freshwater that enters an estuary plays an important role in the ecological functioning of that system. Under natural conditions, freshwater discharges show predictable timescales, with either diel, seasonal or annual patterns (Gillanders and Kingsford 2002). Man made alterations redirect the natural flow and change the patterns of freshwater discharge (Gillanders and Kingsford 2002). These changes in freshwater discharge may change the water chemistry and sediments, which in turn influence the resident fauna and flora within these systems (Gillanders and Kingsford 2002). As an example, a decrease in freshwater discharge into an estuary would increase salinity, which would allow marine species to colonise and replace the brackish water community within the upper reaches of these systems (Wortmann *et al*. 1998; Gillanders and Kingsford 2002). In contrast, large amounts of freshwater released into a system (opening the floodgates of dams) change a mostly marine system (35 practical salinity units) to fresh (0 psu) and back to marine conditions in a short time frame (Gillander and Kingsford 2002). These changes in freshwater flow could alter the temperature and nutrient regimes, and remove cues for migration; thus human mediated water diversion may have serious ecological implications (Wiens *et al*. 1993; Schlacher and Wooldridge 1996; Gillander and Kingsford 2002).

Freshwater flow influences the amount of primary production which occurs within estuarine systems (Allanson and Read 1987, 1995; Froneman 2000a). Compared to freshwater deprived oligotrophic systems, such as the Kariega Estuary, estuaries with sustained freshwater inflow demonstrate higher nutrient status and consequently higher primary production rates (Grange and Allanson 1995; Froneman 2000a). Minimum and maximum chlorophyll-*a* values in the Kariega Estuary range between 1 and 8 µg L^{-1} and between 0 and 52 µg L^{-1} in the Great Fish River Estuary (Adams *et al*. 1999). The seston in the Great Fish River show seasonal and spatial patterns, which can be related to the changes in freshwater inflow, and show higher phytoplankton production during periods of high freshwater flow rates (Grange and Allanson 1995). The changes in the abundance and biomass of phytoplankton and seston concentrations directly impact zooplankton biomass and densities (Froneman 2006 a). Not surprisingly, permanently open estuaries with sustained freshwater inflow are generally characterised by elevated zooplankton densities and biomass (Grange *et al*. 2000). The increased zooplankton values are sustained by the elevated phytoplankton stocks within these systems (Grange *et al*. 2000).

1.1.5. OBJECTIVES

Most research on the hyperbenthos in southern Africa has been conducted on commercially important species, such as prawns from the family Penaeidae, which include *Penaeus monodon* and *P. indicus* and the mud crab *Scylla serrata* (De Villiers *et al*. 1999). In Algoa Bay, a few studies have been conducted on the feeding, migration and nitrogen regeneration of the mysid, *Mesopodopsis wooldridgei* (previously *M. slabberi*, see Wittmann 1992) (Webb *et al*. 1987; Cockcroft *et al*. 1988; Webb and Wooldridge 1990). More recently, Froneman (2001c) studied the feeding ecology of the mysid, *Mesopodopsis wooldridgei*, and Allan *et al*. (2006) investigated the standard metabolic rate of *Paleamon peringueyi* in the Kariega Estuary (Eastern Cape Province). These studies were mostly conducted on components of the hyperbenthos within the littoral zone of estuaries. To date no studies have been conducted on the hyperbenthic community especially in the channel of South African estuaries. The importance of this largely unstudied community within South African estuaries is unclear.

The main objectives of the study were as follows:

1. To assess the spatial and temporal patterns in the hyperbenthic community structure in a permanently open estuary.

2. Assess the variability in the hyperbenthic community structure.

The study was conducted in the permanently open, freshwater deprived Kariega Estuary, located in the Eastern Cape Province of South Africa.

CHAPTER 2

STUDY AREA

2.1. INTRODUCTION

This study was conducted in the Kariega Estuary (33°40’55’’S, 26°41’15’’E), situated on the eastern seaboard of South Africa. The estuary is located eastward of the small coastal town, Kenton-on-Sea, approximately 30 km west of Port Alfred and 100km east of Port Elizabeth (Figure 2.1). According to Whitfield (2000), the Kariega Estuary is classified as being in fair condition indicating that the estuary is subjected to moderate anthropogenic impact which is mostly due to reduced freshwater input, which in turn can be attributed to urban and agricultural practices. These include housing developments west of the Kariega and the narrowing of its channel due to a bridge which forms part of the main coastal road (R72). The land use in the catchments of the Kariega Estuary includes private game reserves and agricultural practices such as pineapple and beef farming. The mean annual runoff of the Kariega Estuary is estimated at 15 x 10^6 m^3 (Grange and Allanson 1995).

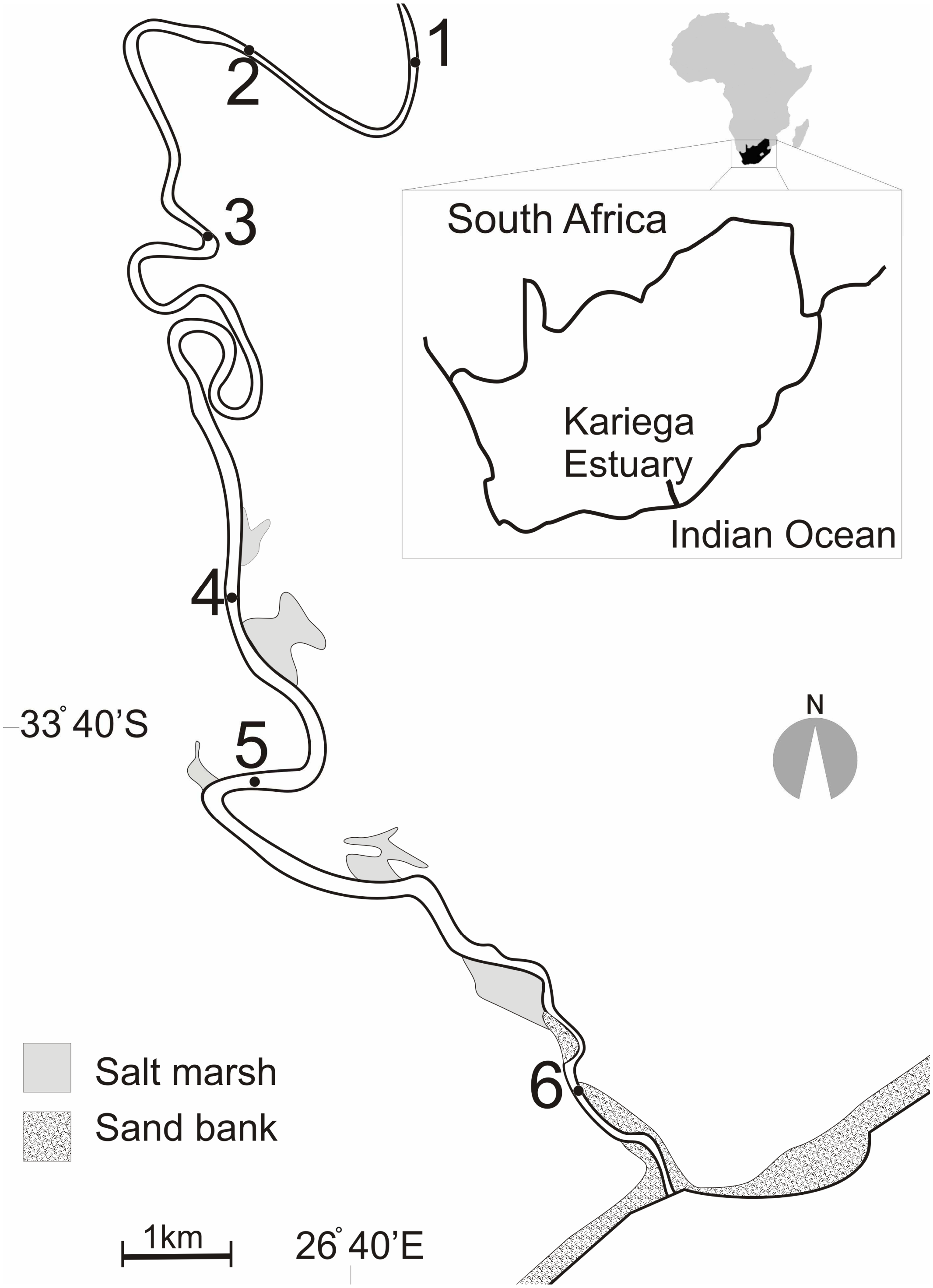


Figure 2.1. The study area showing the location of the Kariega Estuary and the position of the sampling stations along the length of the estuary (adapted from Froneman 2000a).

2.2. CLIMATE

The Kariega Estuary is situated in the Eastern Cape Province of South Africa and, according to the Koppen system of climate classification, is subtropical (Kopke 1988; Lubke 1998). The weather patterns within the region are mostly influenced by the synoptic weather to the south and west of this region, reaching the Eastern Cape about two to three days after landfall on the west coast of South Africa (Stone 1998). The temperatures of the Eastern Cape (air temperatures measured daily in Port Elizabeth between 1961 and 1990) range on average between 13.5 and 22 °C, with the minimum occurring in July and maximum in February (Figure 2.2).

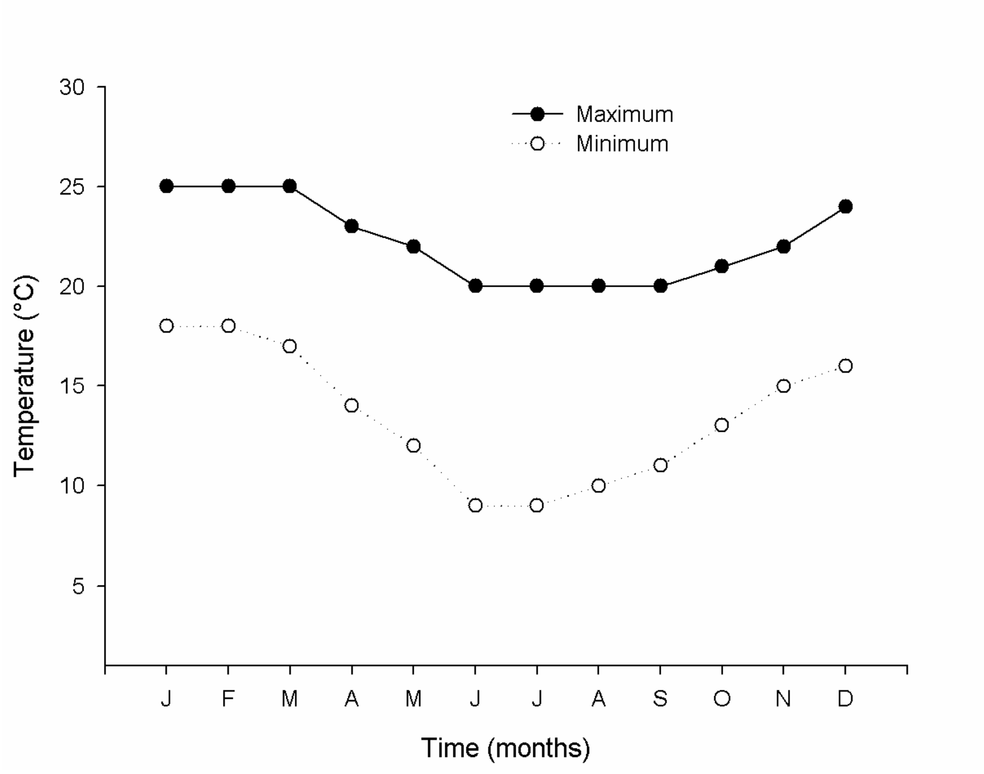


Figure 2.2. The daily average air temperatures measured in Port Elizabeth between 1961 and 1990 (South African Weather Bureau records).

Rainfall in the region of study demonstrates an autumn spring bimodal pattern, with a spring peak (Kopke 1988). The maximum rainfall during the period of study occurred during March (70.33mm) and minimum during July 2008 and January 2009 (0mm) [Figure 2.3; data provided by SAWS (South African Weather Services)].

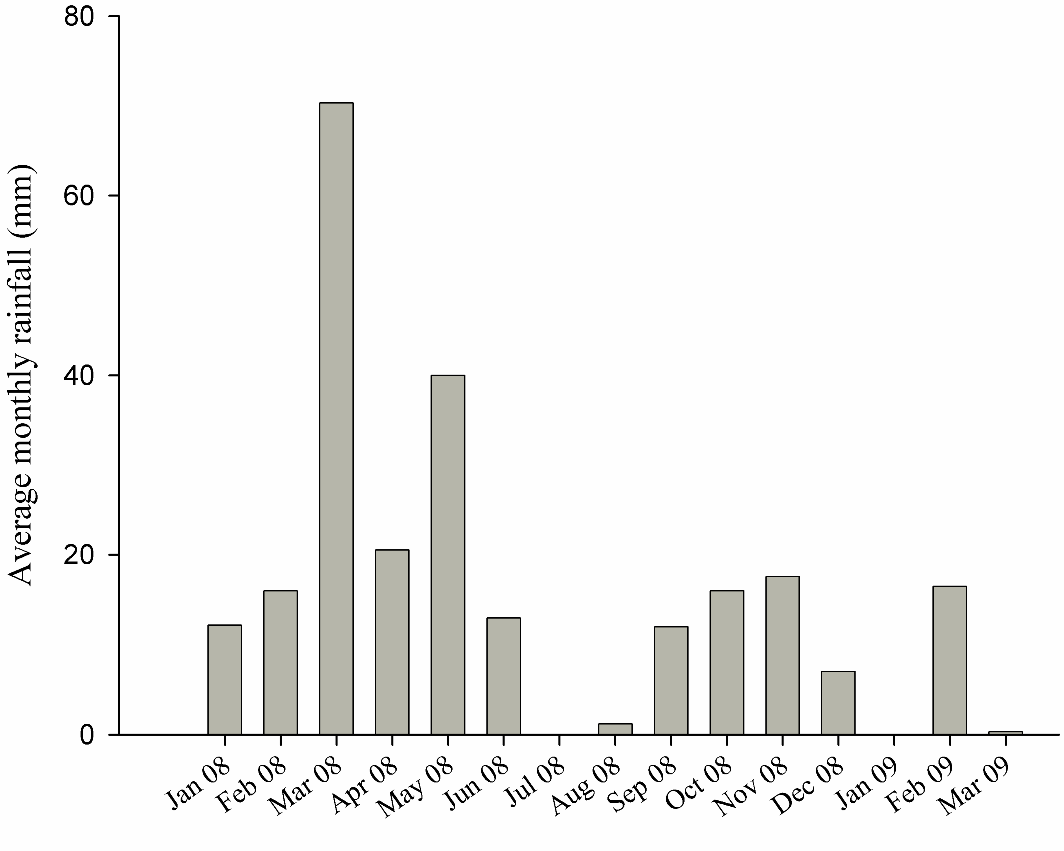


Figure 2.3. The average monthly rainfall recorded in Port Alfred (35km west of Kenton-on-Sea) over the period of study. Data provided by SAWS (South African Weather Services).

2.3. THE COASTAL HYDROGRAPHY

The nearby coastal marine environment in the area of study is mostly influenced by the Agulhus Current. Originating north of Durban, the Agulhus Current follows the narrow continental shelf closely (never exceeding 25 km offshore) and only moves offshore near East London where the shelf broadens (Lutjeharms 2006; Payne and Crawford 1989). Unlike previously thought, this current is not a continuum of the

Mozambique Current, but intermittent and consists mostly of the South West Indian Sub-Gyre, and rings and eddies from the Mozambique and East Madagascan currents (Lutjeharms 2006). The offshore movement of the Agulhus Current near East London causes upwelling of cold nutrient rich waters derived from the upper to middle levels of the South Indian Central Water (Lutjeharms *et al*. 2000). This upwelling is centred at Port Alfred which is situated 25 km north east of the current site. Upwelling has profound effects on the inshore water bodies, altering nutrient concentrations and water temperatures, which in turn influences biological processes such as increased levels of primary production (Lutjeharms *et al*. 2000).

2.4. THE KARIEGA ESTUARY

The Kariega Estuary is classified as a warm temperate system, and due to low freshwater inflow the system is considered homogenous oligotrophic (Grange and Allanson 1995; Froneman 2001a, b, c). The estuary is shallow (<5 m depth), has a mean width of 110 m and is 17.4 km long (Paterson and Whitfield 1997). The low freshwater input into the Kariega Estuary often results in the estuary demonstrating a reverse salinity gradient especially during drier months. The freshwater flow rates into the Kariega Estuary were measured at the Smithfield weir (situated 14km upstream from station 1), and indicate that minimum values were recorded during September 2008 (0.00336 $m^3.s^{-1}$) and maximum flow rates were recorded during March 2008 (0.017 $m^3.s^{-1}$) (Figure 2.4; data provided by DWAF). During these periods hypersaline conditions prevail in the upper reaches of the estuary (Froneman 2000a). Overall the system is a clear-water, well mixed, marine dominated system (Paterson and Whitfield 1997).

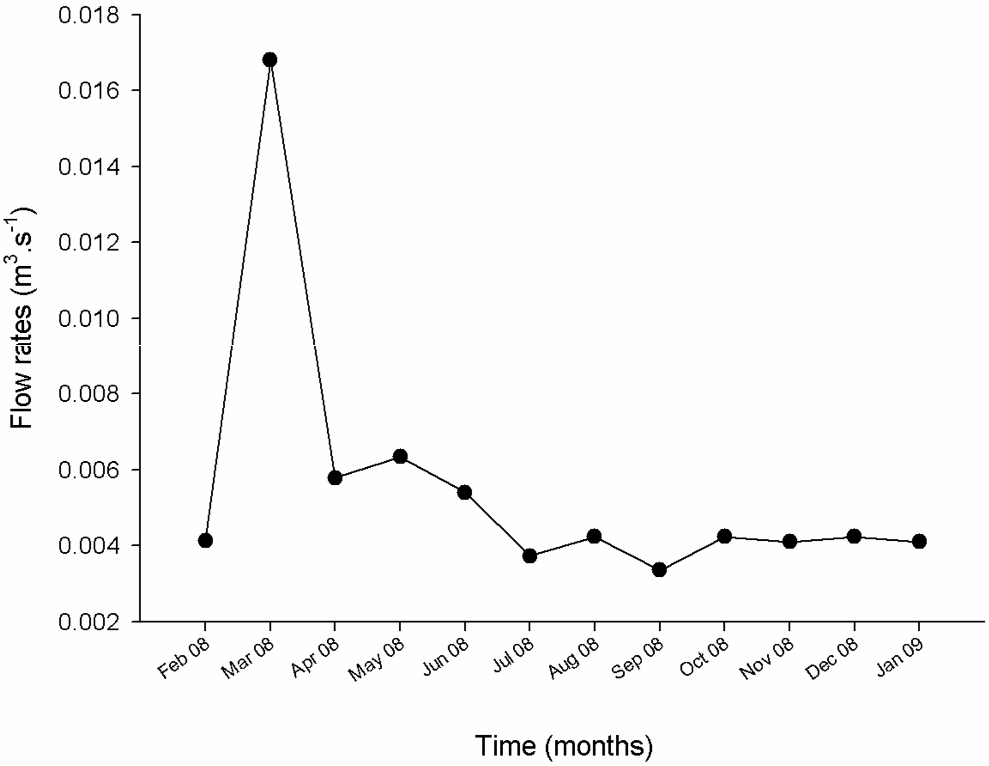


Figure 2.4. Flow rates measured at the Smithfield weir (situated 14km upstream of station 1) from February 2008 to January 2009. Data provided by DWAF.

The Kariega Estuary is characterised by low chlorophyll-*a* (chl-*a*) concentrations (<2 µg l^{-1}) which are dominated by the nano (2–20 µm) and picophytoplankton (0.45–2 µm) size classes (Grange and Allanson 1995; Froneman and McQuaid 1997). The low chl-*a* concentrations recorded in the system are thought to be related to low primary production rates, which are linked to low nutrient availability (Allanson and Read 1995; Grange and Allanson 1995). Low nutrient concentrations in the Kariega Estuary are associated with low freshwater inflow, which is a result of a small catchment area (680 km^2), the presence of several impoundments along the length of the estuary and sporadic rainfall in the region (Allanson and Read 1995; Grange and Allanson 1995; Froneman 2000a). The low nutrient concentrations in the Kariega Estuary may also impact on the zooplankton densities and biomass (Froneman 2000b). Compared to the freshwater dominated Great Fish River Estuary within the same geographic region, which records zooplankton densities ranging from 256 to 4253 mg.m^{-3}, the fresh water deprived Kariega Estuary consistently shows zooplankton densities below 50 mg.m^{-3} (Grange *et al*. 2000).

Floristically the Kariega can be described as dominated by macrophytes. Salt marshes situated in the middle and lower reaches of the systems are dominated by *Spartina maritima*, *Sarcocornia perennis* and *Chenolea diffusa* (Paterson and Whitfield, 1997). The eelgrass, *Zostera capensis*, has extended its distribution almost the entire length of the estuary due to the Kariega Estuary being a clear-water, marine dominated system (Allanson and Read 1995).

CHAPTER 3

THE HYPERBENTHIC COMMUNITY STRUCTURE

3.1. INTRODUCTION

The association of smaller, bottom dependent animals, consisting mainly of crustaceans that usually show some degree of seasonal or diel vertical migrations are collectively known as the hyperbenthos (Mees and Hamerlynck 1992; Mees and Jones 1997; Beyst *et al*. 1999; Koulouri 2002). Many pelagic fish species have been shown to feed on several of the components of the hyperbenthos (Blaber 1979; Mauchline and Gordon 1991; Winkler and Greve 2004). The hyperbenthos thus plays a vital role in marine trophodynamics by linking the benthic and pelagic food webs (Perissinotto and McQuaid 1990; Morgado *et al*. 2003). Mysids, which are prominent components of the hyperbenthal, are omnivorous and feed on detritus, phytoplankton and zooplankton (Mees and Jones 1997; Winkler and Greve 2004). They thus influence the population structure and composition of their prey items (Mees and Jones 1997). Furthermore mysids and other components of the hyperbenthos feed on refractile detritus, contributing to the remineralisation of nutrients (Mees and Jones 1997; Carleton and Hamner 2007).

Comprehensive studies on estuarine hyperbenthic community structure are presently restricted to European systems, mainly in France (Mees *et al.* 1995) and The Netherlands (Mees and Hamerlynck 1992, Mees *et al.* 1993, 1995). Crustaceans, including isopods, amphipods, decapods and mysids, have been identified as the numerically dominant components of the hyperbenthos, although ichthyofauna may at times also make a considerable contribution (Mees and Hamerlynck 1992; De Villiers *et* *al*. 1999). The taxonomically numerous inhabitants of the hyperbenthal are either permanently or temporarily associated with the hyperbenthos. The permanent inhabitants include mysids, amphipods and isopods, all of which spend their entire life history within the hyperbenthal (Mees and Hamerlynck 1992). The temporary inhabitants enter the hyperbenthal either to feed or escape predation, or only enter the hyperbenthal during certain developmental stages of their life-history (Mees and Jones 1997). Shifts in the hyperbenthic community structure and biomass within permanently open European estuaries have largely been linked to salinity gradients and to a lesser extent oxygen concentrations and sediment characteristics (Mees *et al*. 1993, 1995; Dewicke *et al*. 2002).

Studies on the hyperbenthos in southern African estuaries have either been restricted to a single species (Webb *et al*. 1987; Cockcroft *et al*. 1988; Webb and Wooldridge 1990; Froneman 2006 b; Allan *et al*. 2006) or have been limited to species of economic importance, including penaeid prawns and portunid crabs (Forbes and Cyrus 1991; Demetriades and Forbes 1993). Furthermore, the majority of these studies have been conducted within the littoral zone of the estuaries (Webb and Wooldridge 1990; Froneman 2006 b; Allan *et al*. 2006). There is thus a paucity of information on the hyperbenthic community structure within the channel of South African estuaries. The main objective of this study was to identify the main components that make up the hyperbenthos and how their distribution (spatial and temporal) is influenced by environmental gradients found in the estuarine environment.

3.2. MATERIALS AND METHODS

Sampling was conducted monthly at 6 stations along the length of the Kariega Estuary from February 2008 to January 2009 (Figure 2.1). Samples were collected with a modified hyperbenthic sledge (Bossanyi 1951; Colman and Segrove 1955; Macer 1967) which consisted of two nets (mouth opening: 0.15 x 0.70 m) superimposed on each other, with a mesh size of 500 µm (Figure 3.1). The lower net sampled the water column between 10 and 25 cm, and the upper net from 25 cm to 40 cm. This allowed for analysis of small scale vertical zonation within the hyperbenthal (Vallet and Dauvin 2004). At each station the net was deployed and towed behind a boat at approximately 1.5 knots for 2 minutes (which constitutes to ind.m^{-3} or mg.dry weight.m^{-3}). Three parallel replicate tows were conducted at each station. Samples were collected during the early morning, always following the same sampling sequence. Environmental variables were recorded at each station and water samples were collected to determine chlorophyll-*a* (chl-*a*) and seston content. After collection, samples were fixed in 10% formalin and stored for 24 hours, before rinsing and subsequent identification.

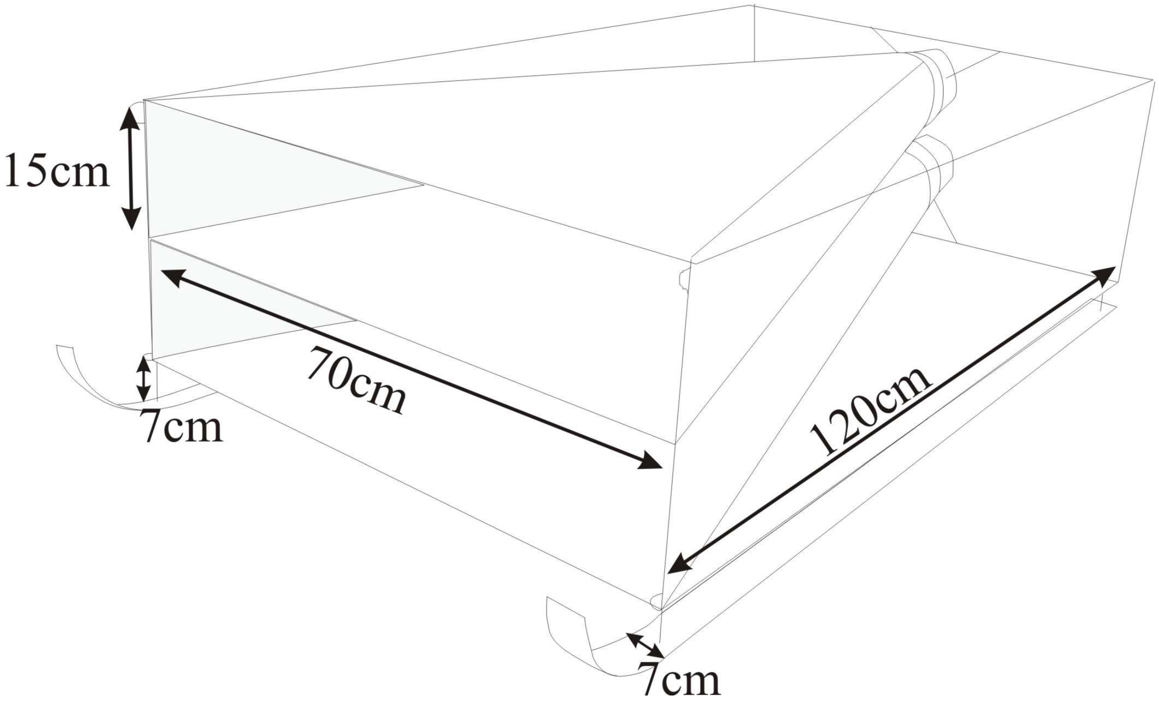


Figure 3.1. Schematic representation of the modified hyperbenthic sledge employed to assess vertical zonation of the hyperbenthic community in the permanently open Kariega Estuary

3.2.1. PHYSICO-CHEMICAL VARIABLES

Temperature, dissolved oxygen (dO_2), salinity (salinity was measured using the Practical Salinity Scale) and secchi disk depth were all measured *in situ*. Temperature and dO_2 were measured using an YSI 550 DO probe (precision of 0.1) and salinity with a hand-held Artigo refractometer.

3.2.2. CHLOROPHYLL-*a* AND SESTON

Total chl-*a* concentration were determined from a 200 ml surface water sample collected at each station. Only surface samples were collected as a previous study demonstrated that there were no significant vertical patterns in total chl-*a* concentration evident in the Kariega Estuary (Froneman 2000a). The samples were gently filtered (Hg<5 cm) through 47 mm Glass Fibre Filters (Scheicher and Schuell) and extracted in 10 ml of 90% acetone for 24 hours at -20 °C. Extracted samples were centrifuged (5000 rpm) for five minutes and the total chl-*a* determined employing a Turner Designs 10AU Fluorometer following the method of Holm-Hansen and Riemann (1978). Chl-*a* concentrations were expressed as milligrams of chl-*a* per unit volume (mg.chl-*a*.m^{-3}).

To determine the seston concentration at each station, a 200 ml surface water sample was gently filtered (Hg<5 cm) through pre-weighed 47 mm Glass Fibre Filter (Scheicher and Schuell). The filtered papers were oven dried overnight at 40 °C and reweighed. The difference in the weight of the filter was assumed to be the seston concentration and results were expressed as mg.L^{-1}. Only a single measurement was made at each station as previous studies indicate that in the absence of freshwater inflow there were no significant spatial differences in the total chl-*a* and seston concentrations within the Kariega Estuary (Froneman 2000a).

3.2.3. ORGANIC CONTENT

Orr *et al*. (2008) indicated that due to the low freshwater inflow into the Kariega Estuary, no seasonality in sedimentary organic content was found within the system. Thus, during the present study the organic content of the sediment in the Kariega Estuary was only determined on one occasion. To determine the organic content of the sediment at each station, three replicate samples of bottom sediment were collected by free diving.

Each sample was collected in a separate 250ml sampling bottle and subsequently frozen until further analysis. Organic content was determined following the loss of ignition technique (LOI) of Beaudoin (2003). LOI technique is often used to determine organic content of sediments especially so in paleolimnological and pollen analytical studies (Beaudoin 2003). The technique is simple and straight forward and shows similar results to wet oxidation which requires specialised equipment and skills (Beaudoin 2003). Collected samples were transferred into foil boats and oven dried at 60 °C for 48 hours. Subsequent to drying, the weight of each sample was recorded and LOI performed by igniting samples in a muffle furnace for 16 hours at 375 °C. The percentage loss of ignition (%LOI), which is a reflection of organic content in the sediment, was calculated from the weight loss as a percentage of the oven-dried sample weight (Beaudoin 2003).

3.2.4. DENSITY AND BIOMASS

From the identified samples the numerical contribution of each species was determined. To determine the contribution per m^3, all samples (counts) were divided by 8.4 [which constitute the area of a single net's mouth (0.105 m^2) and the approximate distance of each tow (80 m), which was calculated employing a Garmin GPS 60]. Data were expressed as individuals per meter cube ($ind.m^{-3}$).

The total average biomass of each net at each station was determined by filtering all the identified samples onto pre-weighed 47 mm Glass Fibre Filters (Scheicher and Schuell). Samples were oven dried for 24 hours at 60 °C and weighed using a Sauter AR 100 microbalance with a precision of 0.0001 mg. Biomass was calculated by subtracting the initial weight from the final weight of the filter papers. Results were expressed as $mg.dry\ weight.m^{-3}$.

3.2.5. IDENTIFICATION & COMMUNITY COMPOSITION

In the laboratory, fixed samples (10% formalin) were washed through a 500 µm mesh sieve and stored in 70% ethanol. Under a stereomicroscope (× 60 magnification), animals were identified, if possible to species level, and counted. Amphipods were identified using the key of Griffiths (1978), isopods were identified from the key of Kensley (1978), and mysid species were identified from Branch *et al*. (2005) and Wittmann (1992).

3.2.6. DIVERSITY

Diversity of the hyperbenthic community was determined from Hill's diversity indices (N_1, N_2 and N_{inf}) (Hill, 1973) in the software package PRIMER 5.
Where:
N_0 = the number of species
N_1 = the inverse natural logarithm of the Shannon–Weiner diversity index
N_2 = reciprocal of Simpson's dominance index (gives more weight to the abundance of common species)
N_{inf} = reciprocal of the proportional abundance of the commonest species

Hill's diversity indices differ in their tendencies to ignore or include rarer species. The higher the diversity number, the great the impact of dominant species and the less important rare species and species richness becomes.

3.2.7. STATISTICAL ANALYSIS

Both total density and biomass data did not conform to the assumptions of normality and homogeneity, thus to test for significance between the upper and lower net, a non-parametric Mann Whitney U test was performed in the statistical package STATISTICA 8.1. Spatial and temporal patterns in total average hyperbenthic abundance were identified with a two way crossed analysis of similarity (ANOSIM) from the statistical package PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick, 1994). Prior to analyses, samples were square root transformed and a Bray Curtis similarity measure was performed (Clarke and Warwick, 1994). To test for significance between stations, a pairwise comparison between each station using Mann-Whitney U test with Bonferroni Adjustments (adjusted level of significance = 0.003) was employed. Density data were separated into the major taxonomic groups (i.e. isopods, amphipods, copepods). To test if the upper and lower nets were significantly different in the respective taxonomic groups a Mann-Whitney U test was performed (STATISTCA 8.1) on each taxonomic group.

Diversity data did not conform to the assumptions of normality and homogeneity and could therefore not be tested for significance employing non parametric tests. A Mann-Whitney U test was performed to determine differences between nets, and a Kruskal-Wallis ANOVA was employed to determine significance for both the stations and month diversity data. These tests were performed in the software package STATISTICA 8.1. A Spearman’s rank order correlation in the software package STATISTICA 8.1, were performed on the total density, biomass, diversity and environmental variables.

Finally, because the density data demonstrated a linear distribution, a Redundancy Analysis (RDA) was performed in the software package XLSTAT 2009.6.3 (A software add-in for Microsoft Excel) to determine which environmental variables were most important in structuring the hyperbenthic community during the study (Zuur *et al.* 2007). The analysis was performed on the mean abundance of each net at each station over the period of study.

3.3. RESULTS

3.3.1. PHYSICO-CHEMICAL VARIABLES

Water temperatures and dissolved oxygen (dO_2) concentrations demonstrated a strong seasonal pattern (Figures 3.2A, B). Maximum water temperatures were recorded during the summer (26.4 ± 2.6 °C) and minimum during winter (14.5 ± 0.7 °C) (Figure 3.2A). Conversely, the lowest dO_2 levels were recorded in summer (3.2 ± 0.7 mg.L $^{-1}$) and the highest during winter (6.3 ± 0.7 mg.L^{-1}) (Figure 3.2B). Intermediate values were recorded in spring and autumn (Figure 3.2A, B). No seasonality in salinity and secchi disk depth (SSD) were detected during the study (Figure 3.2C, D). Salinities ranged between 33 and 44 and SDD between 1.04 and 2.48 meters. A weak spatial pattern was detected in most of the physico-chemical variables. Salinity and temperature consistently recorded highest values in the upper reaches while SSD and dO_2 concentrations were highest at those stations situated neat the mouth of the Kariega Estuary (Figure 3.2).

3.3.2. CHLOROPHYLL-*a* AND SESTON

Although variable, the mean total chlorophyll-*a* (chl-*a*) concentration showed a weak seasonal pattern with the highest values measured in late summer (1.8 ± 0.6 mg.chl-*a*.m^{-3}) and minimum during winter (0.4 ± 0.1 mg.chl-*a*.m^{-3}) (Figure 3.3A). During the study, no seasonality was detected in seston concentrations, which ranged between 86.0 and 144.5 mg.L^{-1} (Figure 3.3B). Seston and chl-*a* concentrations demonstrated a spatial pattern, both consistently measuring highest values in the upper reaches of the Kariega Estuary (Figure 3.3).

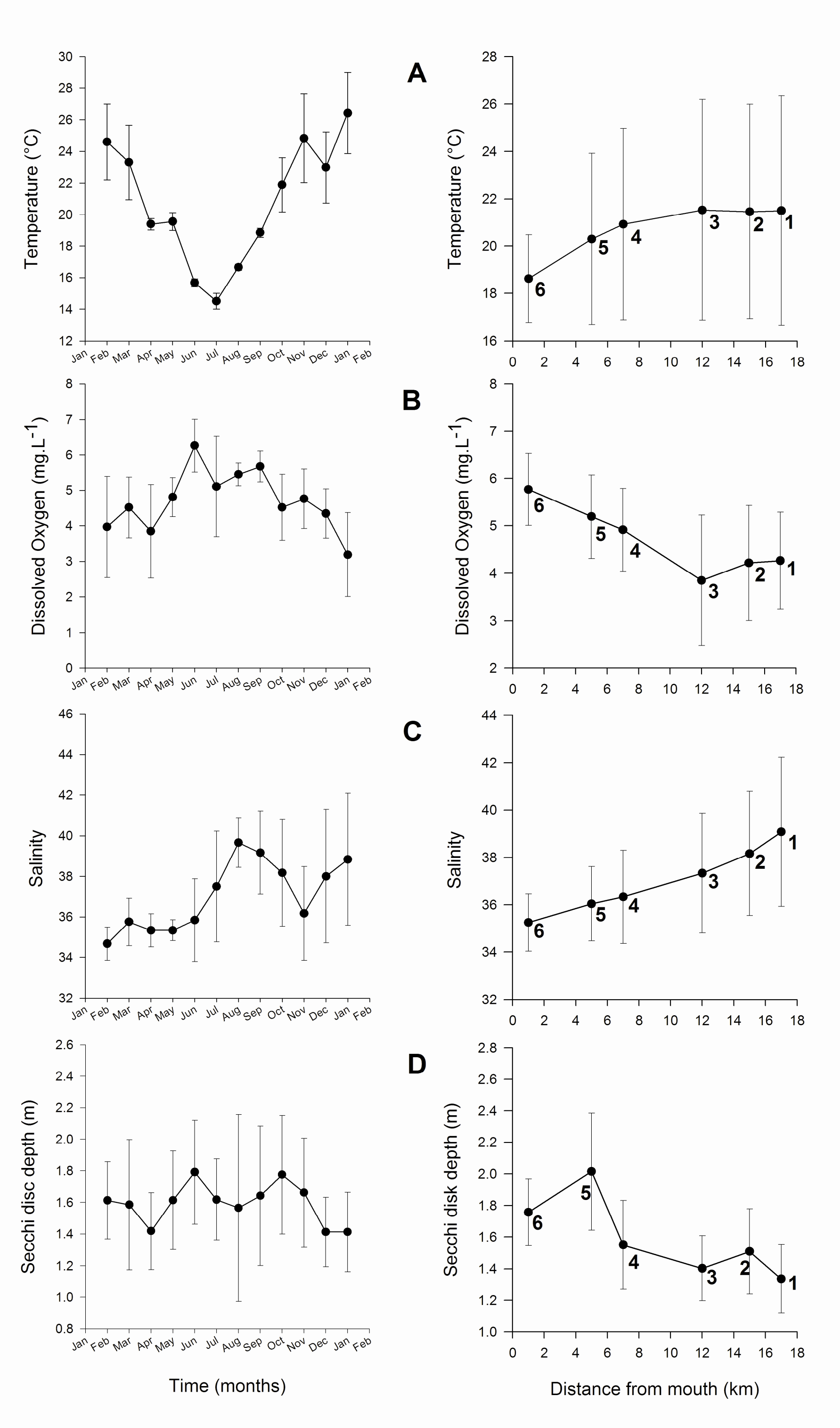


Figure 3.2. Temporal (left) and spatial (right) patterns in temperature (A), dissolved oxygen (B), salinity (C) and secchi disc depth (D). Error bars represent the standard deviations (*n* = 6 seasonally; *n* = 12 spatially). Station numbers are indicated below data points.

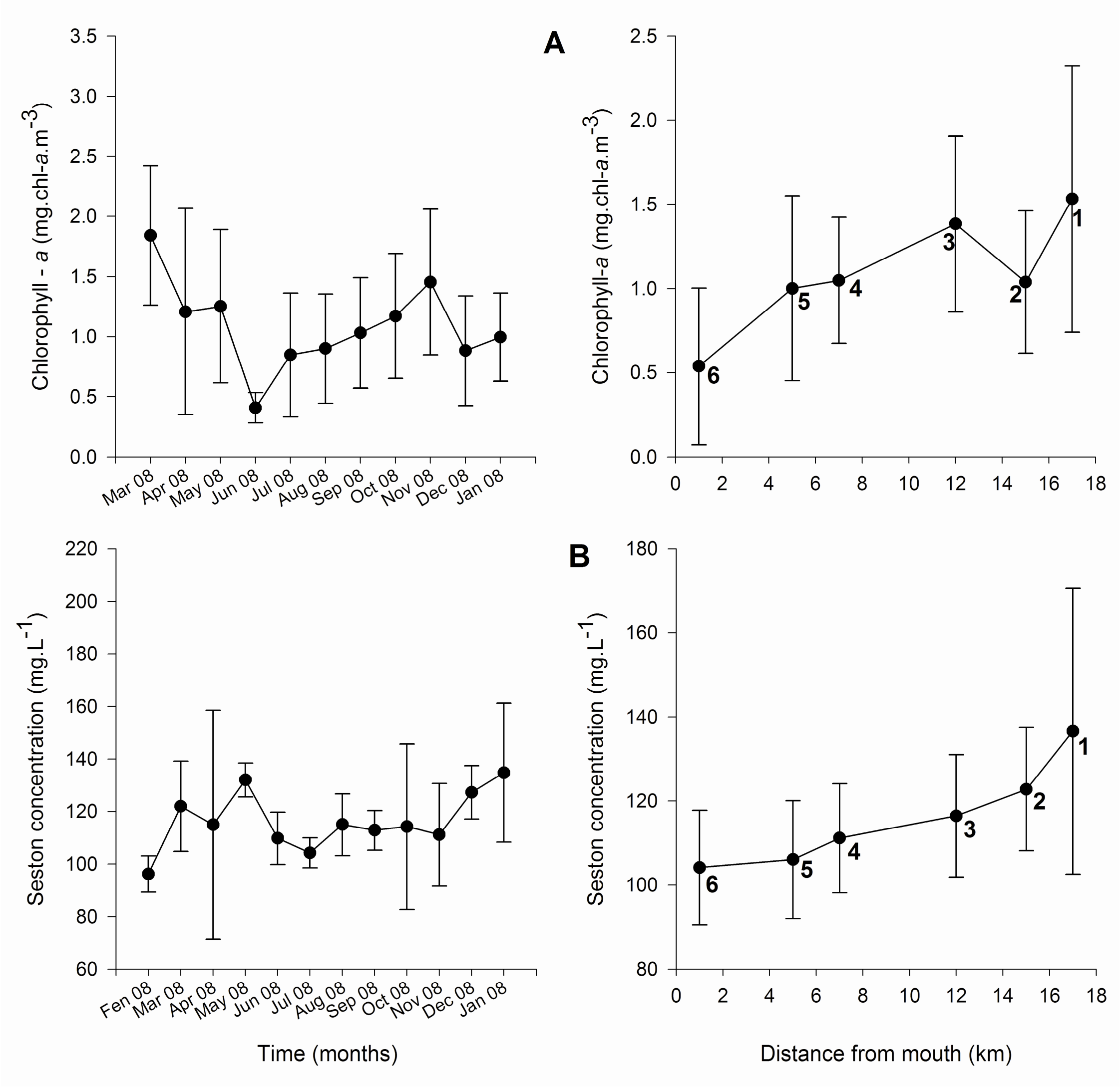


Figure 3.3. Temporal (left) and spatial (right) variations in total chlorophyll-*a* (A) and seston (B) concentrations. Error bars represent the standard deviations (n = 6 seasonally; n = 12 spatially). Station numbers indicated below data points.

3.3.3. ORGANIC CONTENT

The mean percentage organic content of the sediment ranged between 1.7 ± 0.99% (station 6) and 12.5 ± 5.7% (station 5) (Figure 3.4). Sediment organic content concentrations showed a gradual increase moving away from the upper reaches, reaching a maximum concentration at station 5 located near the mouth of the estuary. Thereafter a sharp decrease in organic content of the sediment at station 6 was evident.

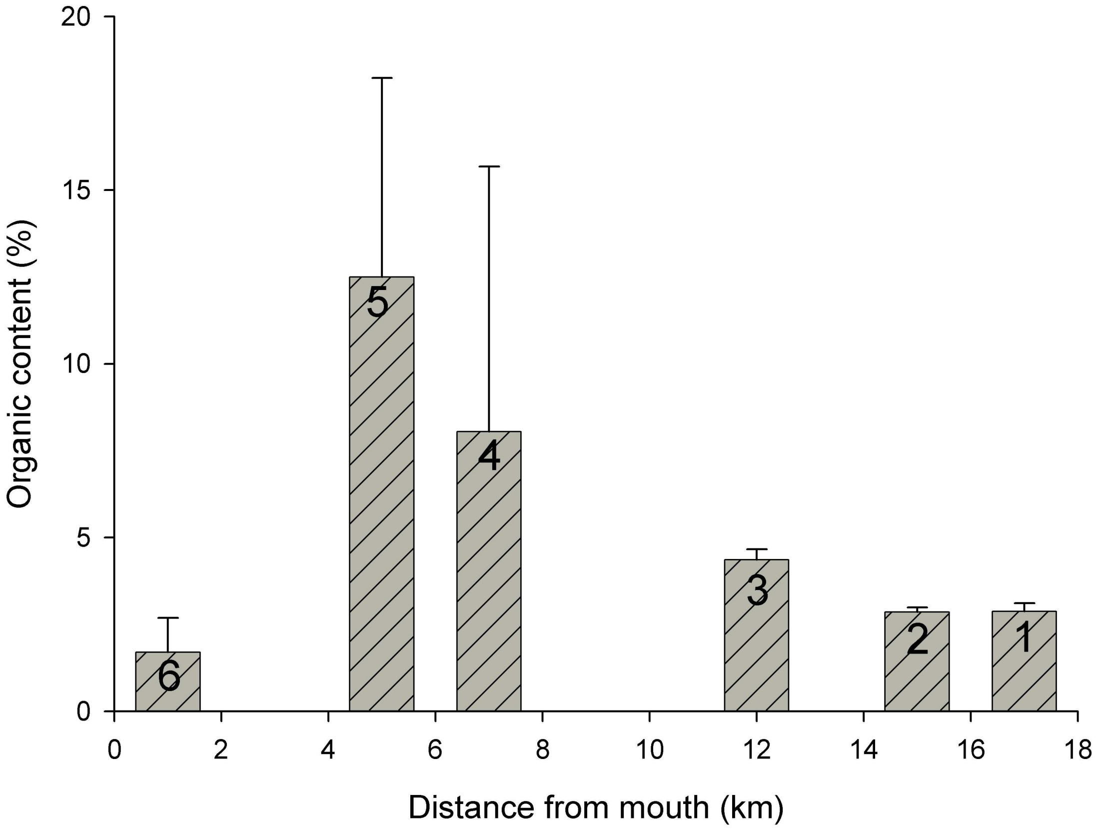


Figure 3.4. Percentage organic content determined from each station along the length of the Kariega Estuary. Error bars represent the standard deviations (*n* = 3). The stations are indicated by the numbers in the respective bars.

3.3.4. DENSITY AND BIOMASS

Total average hyperbenthic densities ranged between 0.2 and 377.2 ind.m^{-3} (see appendix Table A1.1). Hyperbenthic densities in the lower net ranged between 0.04 and 166.0 ind.m^{-3} and between 0.12 and 224.9 ind.m^{-3} in the upper net (Figure 3.5; see also appendix Table A1.1). There was no significant difference in the total average densities between the lower and upper nets (U = 2354, p = 0.3). A spatial and temporal pattern in total densities was detected with an increase in densities over the period September to October 2008 particularly in the middle reaches (Stations 3 and 4) (Figure 3.5). Results from the two-way crossed ANOSIM (PRIMER 5) (includes density data of all recorded species) suggests that certain months were more similar to each other than any others;

these being February and March (*R* = 0.23); June and July (*R* = 0.21); September and October (*R* = 0.38) and November and January (*R* = 0.38), suggesting the presence of a seasonal pattern. Furthermore, the summer months of February to April were most different from the winter months (June, July, August; R ≥ 0.8). Spatially, stations 1 and 2 (*R* = 0.39); stations 3 and 4 (*R* = 0.29) and stations 4 and 5 (*R* = 0.32) demonstrated similar density values. The density of stations 2 and 6 (*R* = 0.80) demonstrated greatest dissimilarities.

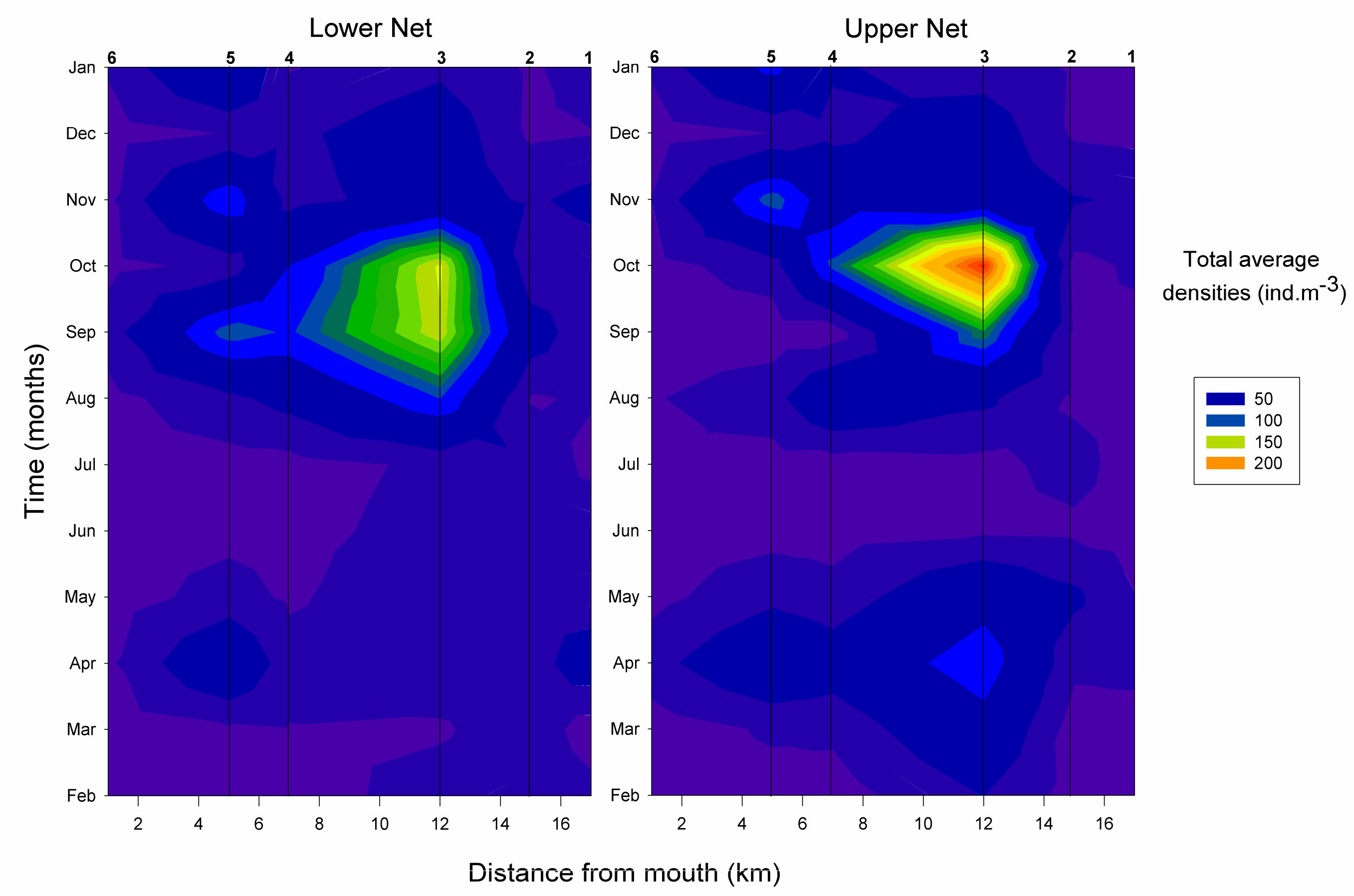


Figure 3.5. Contour plots of the total average hyperbenthic densities (ind.m^{-3}) collected in the lower and upper nets along the length of the Kariega Estuary from February 2008 to January 2009. Values presented are mean value from three tows per station. The positions of the stations are indicated by vertical lines and the corresponding station number above each line.

The total average hyperbenthic biomass during the study ranged between 0.05 and 24.1 mg.dry weight.m^{-3} (see Table A1.1 in appendix). In the lower net, the average hyperbenthic biomass ranged between 0.02 and 11.9 mg.dry weight.m^{-3}, and between 0.02 and 17.4 mg.dry weight.m^{-3} in the upper net (Figure 3.6; see also Table A1.1 in the appendix). Maximum and minimum values were consistently measured at stations two and six, respectively. The total hyperbenthic biomass recorded at station six was significantly different from all other stations, which could be related to reduced biomass values consistently measured at this station ($H_{5,342} = 118.93$, $p<0.0001$). A weak spatial and temporal pattern was observed in the biomass data with increase in biomass from spring (September 2008) to January 2009 in the lower net, and from September to December 2008 in the upper net (Figure 3.6). This was most evident in the upper reaches of the estuary. The biomass recorded in February, March and November 2008 differed most from the other months and was significantly different from September, October, December and January ($H_{11,\ 420} = 87.38$, $p<0.0001$). The total average biomass of the lower and upper nets were significantly different ($U = 18251.5$, $p = 0.002$, Figure 3.6).

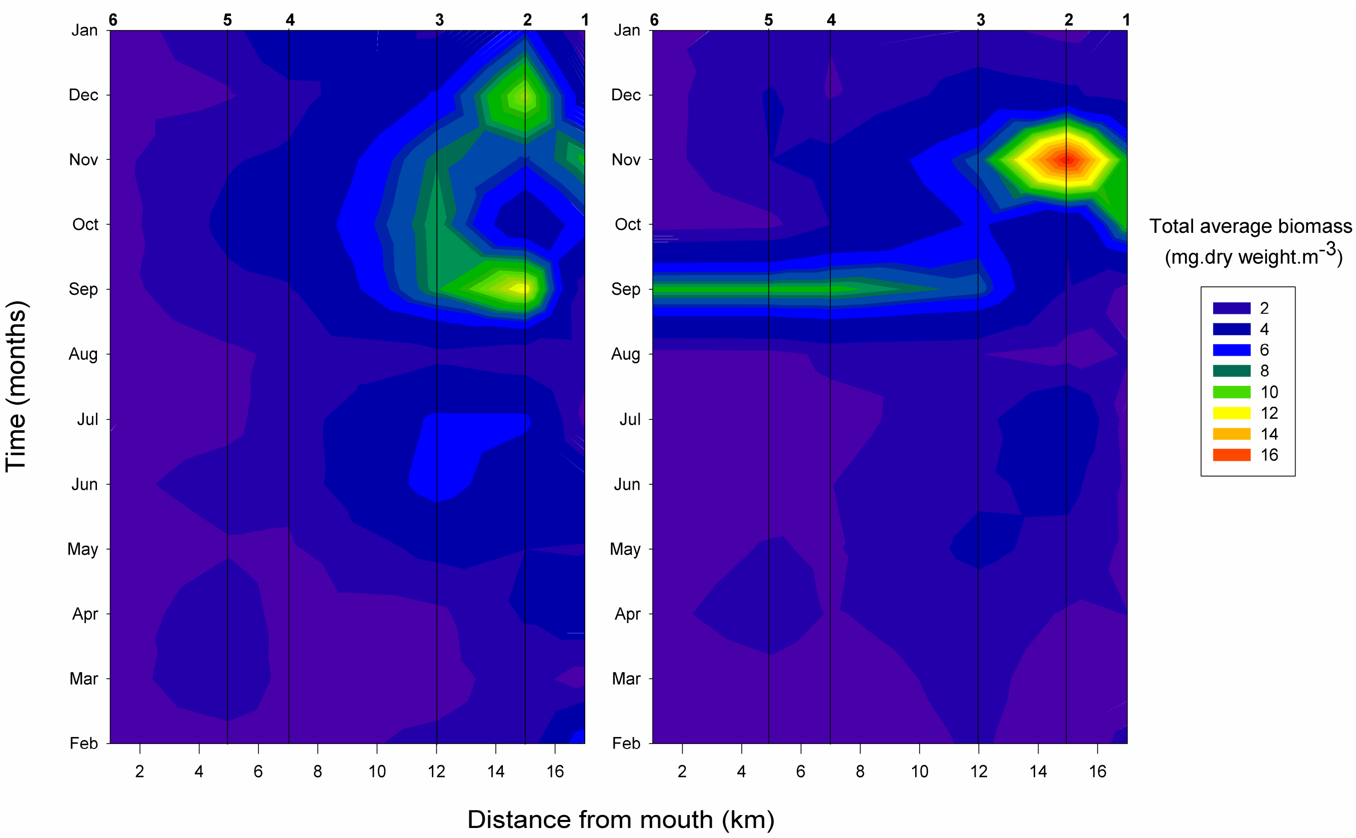


Figure 3.6. Total average biomass (mg.dry weight.m^{-3}) recorded in the lower and upper nets along the length of the Kariega Estuary from February 2008 to January 2009. Values presented as mean value from three tows per station. The positions of the stations are indicated by vertical lines and the corresponding station number above each line.

Spearman's rank order correlation between seston, chl-*a*, biomass and abundance was performed. The correlation indicated that biomass and salinity (R^2 = 0.33); abundance and organic content (R^2 = 0.32) and diversity and organic content of the sediment (R^2 = -0.32) were most related. No other environmental variables demonstrated strong correlations with the density and biomass of the hyperbenthos within the Kariega during the period of study. Spatially, the organic content of the sediment contribute most to the density and diversity of the hyperbenthos within the Kariega Estuary. Salinity however demonstrates both spatial and temporal gradients. Spatially highest salinities were consistently measured in the upper reaches (Figure 3.2C), which coincides with highest biomass. Salinity demonstrated only a weak seasonal pattern (Figure 3.2C) and was therefore not considered important in structuring the hyperbenthic community over time.

3.3.5. IDENTIFICATION & COMMUNITY COMPOSITION

To remain consistent with the published literature, accidentally caught adult crabs, shrimp and demersal and pelagic fish species were excluded from the analysis (Mees *et al*. 1993). Different developmental stages of the same species or taxonomic groups (e.g. crab zoeae and megalopae) were treated as different functional groups as their ecology differs (Mees *et al*. 1993, 1995). Thus from a total of 41 recorded species only 36 were retained after data reduction (Table 3.1).

Table 3.1. List of the species caught within the hyperbenthal of the Kariega Estuary over the period from February 2008 to January 2009. Species denoted with asterisk (*) were excluded from the analysis.

Taxonomic group

- Crustacea
  - Isopoda
    - *Exosphaeroma estuarium*
    - *Excirolana natalensis*
    - *Apanthura sandalensis*
    - *Exosphaeroma hylocoetes*
  - Amphipoda
    - *Munna sheltoni*
    - *Podoceropsis* spp.
    - *Melita zeylanica*
    - *Grandiedirella lignorum* (male)
    - *Grandiedirella* spp. (female)
    - *Gitanopsis pusilla*
    - *Corophuim triaenonyx*
  - Mysidacea
    - *Mesopodopsis wooldridgei*
    - *Rhopalophthalamus terranatalis*
    - *Gastrosaccus brevifissura*
  - Tanaidacea
    - Tanaids
  - Copepoda
    - Gammarid
    - *Labidocera nerii*
    - *Labidocera detruncata*
    - *Centropages calaninus*
    - *Pseudodiaptomus hessei*
    - *Calanus aghulensis*
    - *Acartia* spp.
    - *Harpacticoidea* spp.
    - *Sappirina* spp.
  - Cumacea
    - Cumaceans
  - Decapoda
    - Caridea
      - *Palaemon peringueyi*
      - Caridean shrimp
    - Brachyura
      - Crab zoea
      - Decapod larvae
      - Crab megalopae
      - *Hymenosoma orbiculare* (Crown crab)*
  - Phyllocarida
    - Leptostraca
      - *Nebulia capensis*
- Teleostei
  - Fish larvae
  - Juvenile fish spp.*
- Cnidaria
  - Hydrozoa
    - Hydromedusae
  - Anthozoa
    - Sea anemones*
- Chelicerata
  - Pycnogonida

In both the lower and upper nets, decapod larvae (mostly represented by brachyuran crab zoeae) numerically dominated the counts, accounting on average 64 ± 71.3% of the total densities recorded in the lower net and 74.5 ± 66.5% in the upper net (see Table A1.2 in the appendix). Exception to this was seen during June and July 2008 when mysids numerically dominated the hyperbenthic counts (Figure 3.7). In the lower net mysids, especially *Mesopodopsis wooldridgei* (previously *M. slabberi*, see Wittmann 1992), were the second most abundant (15.4 ± 10.4%) followed by copepods (10 ± 11.25%) and amphipods (6 ± 2.7%). In the upper net, however, copepods (11.9 ± 15.7%) were the second most well represented taxon within the hyperbenthal, and mysids (8.8 ± 11.48%) the third (Table A1.2 – appendix).

When considering the total average densities of the major taxonomic groups recorded in the hyperbenthos, significant differences between the upper and lower nets in isopods, amphipods and mysids numbers were detected (U = 1883.50, p = 0.007; U = 14574.00, p = 0.001; U = 17978.50, p = 0.001, respectively; Figure 3.7). No significant difference was found in the copepods, decapod larvae and the group “other” (Figure 3.7).

With the exception of the crab zoeae, the planktonic hyperbenthic species were uniformly distributed along the length of the estuary (Figure 3.8A). Maximum density values of the crab zoeae were recorded in the middle and lower reaches (stations 3 to 5) of the estuary (Figure 3.8A). Hyperbenthic species that burrow, including isopods, amphipods, cumaceans, tanaids and some mysid species, showed a distinct spatial pattern, with maximum values recorded in the upper reaches (stations 1 to 3) and minimum values at the mouth of the Kariega Estuary (Figure 3.8B). Seasonally decapod larvae (mostly represented by brachyuran crab zoeae) demonstrated a bimodal peak in abundances with maximum values recorded in March and September 2008 (Figure 3.7).

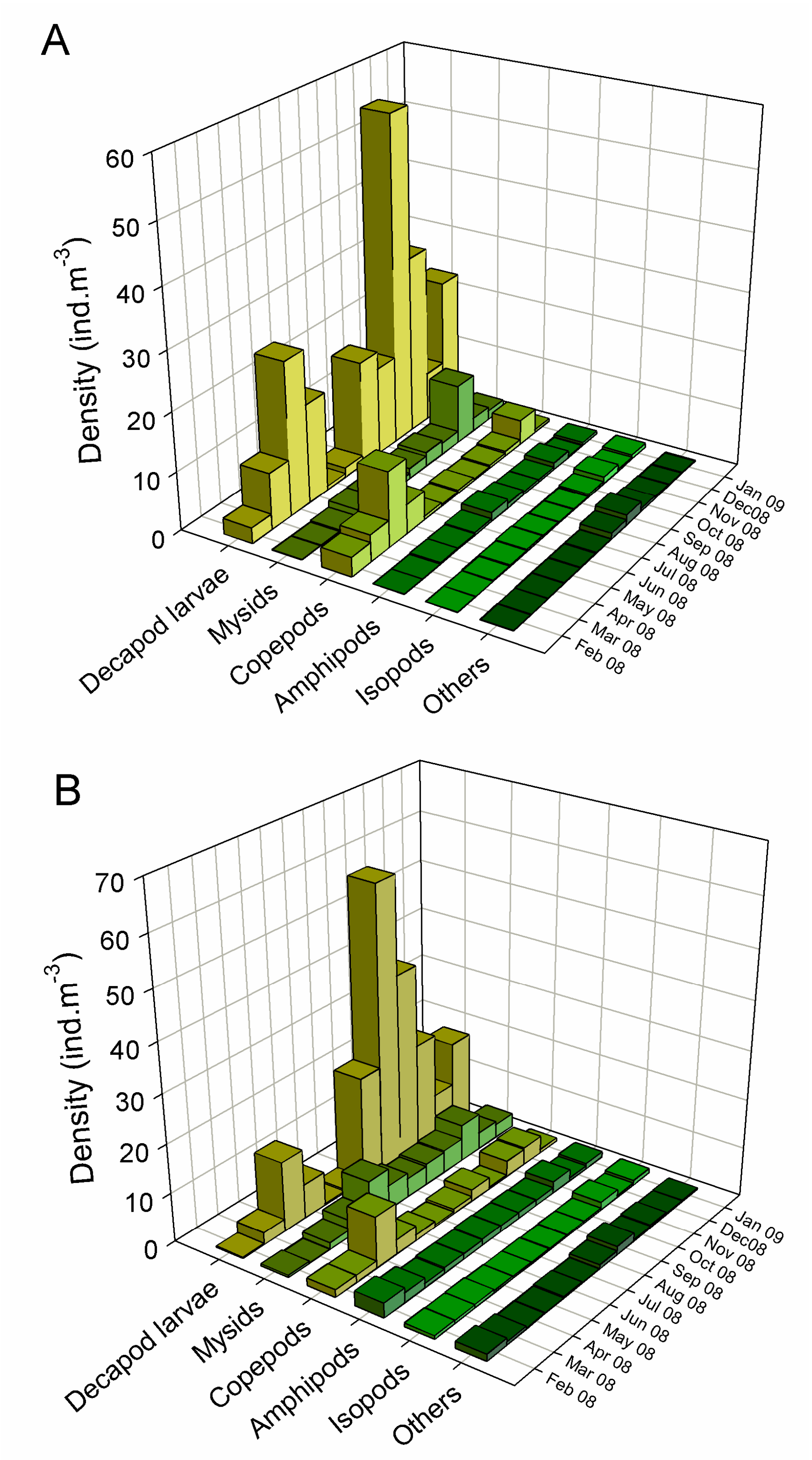


Figure 3.7. Average contribution of the major taxonomic groups to the total hyperbenthic densities within the Kariega Estuary, collected in the upper (A) and the lower (B) net from February 2008 to January 2009. Values represented are means from six stations occupied along the length of the estuary.

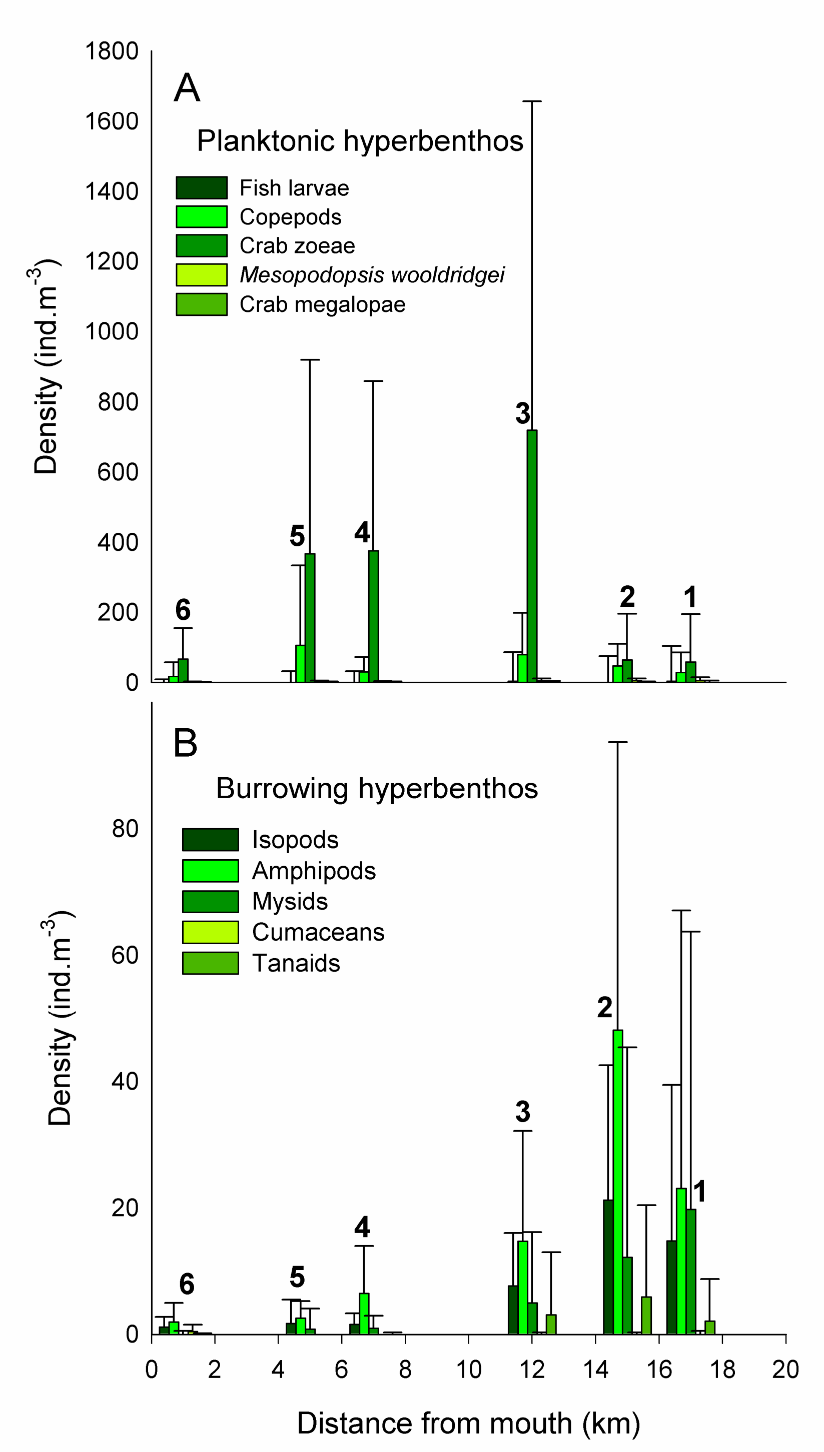


Figure 3.8. The spatial distribution of hyperbenthic animals with different affinities to the estuarine substratum. Planktonic species (A) and burrowing species (B). Error bars represent the standard deviation (*n* = 12). Station numbers are indicated above each set of bars.

3.3.6. DIVERSITY

Over the duration of the study, all diversity indices measured (Hill's N_1, N_2 and N_{inf}) indicated that the highest species diversity occurred during the summer months of February 2008 and November 2008 and lowest during the months of April and August 2008 (Figure 3.9A). No significant temporal pattern was detected in the diversity indices measured during the period of study ($p > 0.05$). In terms of vertical zonation, the lower nets showed higher diversity compared to the upper net (all Hill's diversity numbers). However none of the diversity indices were significantly different between the lower and upper nets ($p > 0.05$; Figure 3.9B). Spatially, the highest species diversity was consistently recorded in the upper reaches (stations 1 and 2) of the estuary, with maximum diversity at station 2 (Figure 3.9C). Species diversity gradually decreased from the upper reaches to the mouth of the estuary (Figure 3.9C). Station 2 was significantly different from all stations in terms of all Hill's diversity indices (N_1: $H_5 = 59.83$, $p<0.05$; N_2: $H_5 = 50.96$, $p<0.05$; N_{inf}: $H_5 = 46{,}54$ $p<0.05$). Furthermore, station 1 demonstrated significantly different values from stations 3 to 6 in all diversity indices ($p < 0.05$ in all instances).

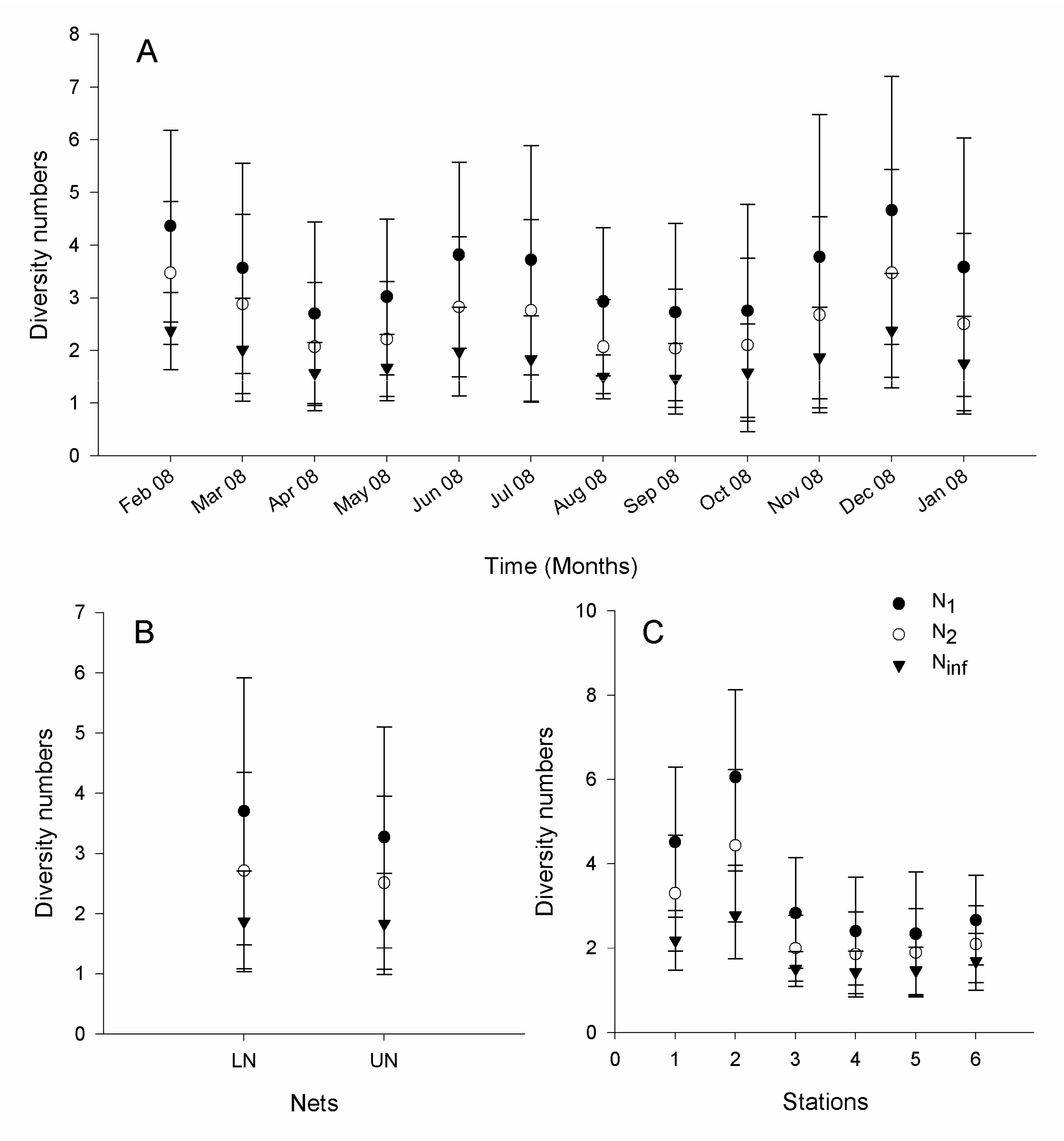
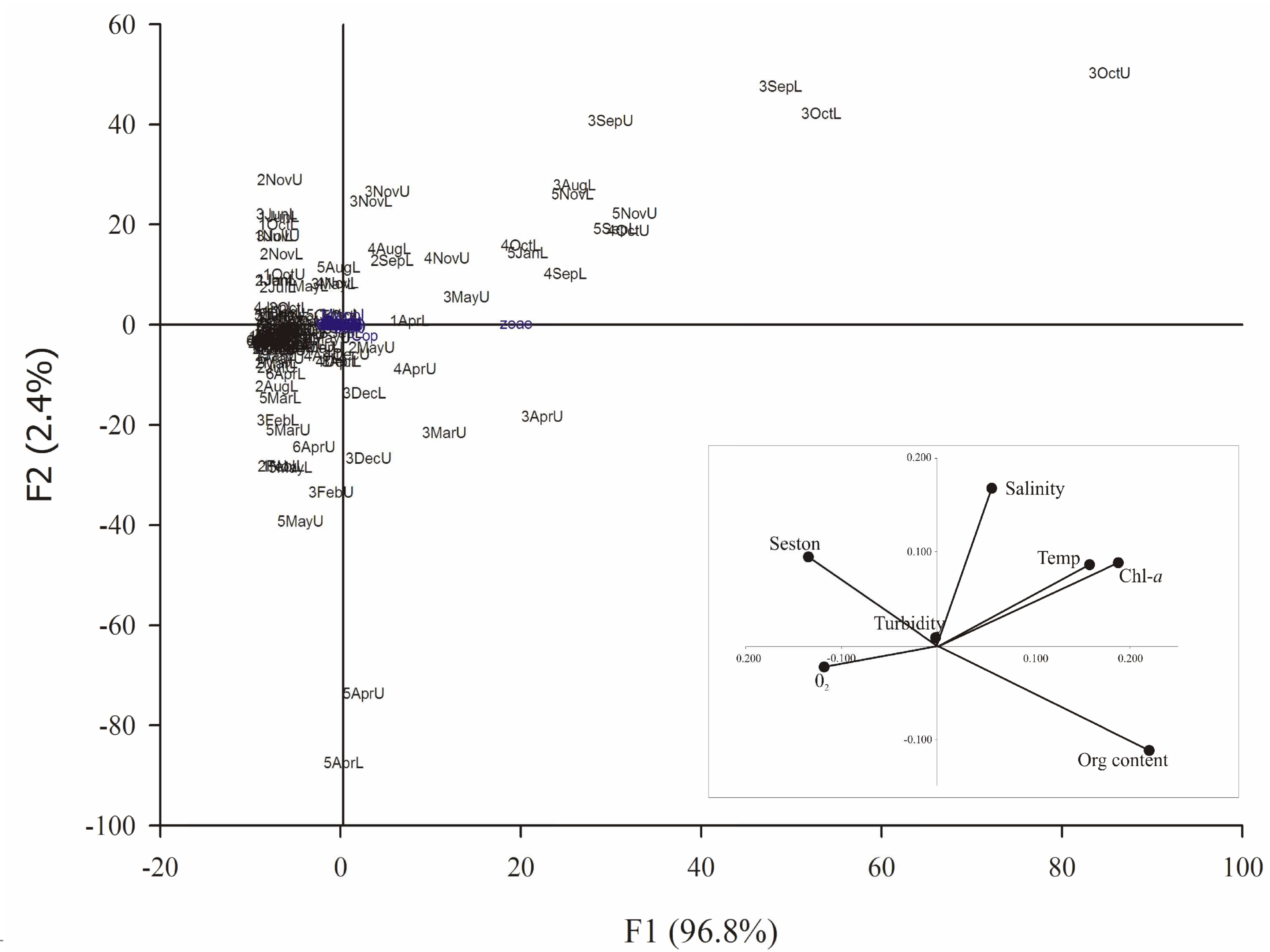


Figure 3.9. Hill's diversity numbers (N_1, N_2 and N_{inf}) calculated over time (A), vertical zonation (B) and space (C). LN= lower net; UN = Upper net. Error bars represent the standard deviations (*n* = 6 seasonally; *n* = 12 spatially).

3.3.7. COMMUNITY ANALYSES

Results from the redundancy analysis (RDA) on the data for both the upper and lower nets over the duration of the study, indicate that the first two axes accounted for 99.2% of the total variation detected [eigenvalues: 9057 (96.8%) and 221.7 (2.4%) for axis one and two, respectively] (Figure 3.10). The biplot (see insert Figure 3.10) of the environmental variables reveals a main gradient connecting organic content of the sediment and chl-*a* with seston and oxygen concentration on the left (See Appendix Table A1.3 for scores of the environmental variables). The vectors for the organic content of the sediment and chl-*a* are quite long suggesting that these variables are highly correlated to the ordination plane. Thus sedimentary organic content and chl-*a*, together with seston and dO_2 concentrations, are key in determining the first canonical axis and seems to define the main gradient structuring the hyperbenthic community within the Kariega Estuary. There is a gradient from the right of the biplot diagram marked with organic rich sediments and high chl-*a* content, which were mostly found in austral spring and the middle reaches of the Kariega Estuary. This gradient moves to the left of the ordination plot to conditions found in the upper reaches which is marked with low dO_2 and high seston concentrations. The correlations with the second axis are slightly less obvious, although salinity lies close to the second axis (Figure 3.10). Both axes indicate spatial and temporal variation. The cluster of stations which are positioned on the negative side of axes one and two were mostly collected during the summer and winter months, and exclude most data collected during austral spring.



Redundancy Analysis (RDA) on the abundances of both the upper and lower nets of the hyperbenthos sampled in the Kariega Estuary between February and January 2009. The codes can be interpreted as follows (from left to right); the numbers represent the station number, the month samples were collected and the position of the net (lower or upper net). The bipolt (insert: bottom right corner) represent environmental variables.

3.4. DISCUSSION

The estimates of the total hyperbenthic density and biomass during the present study are in the range reported for previous studies conducted in both shallow systems (e.g., the Mondego Estuary in Portugal; Azeiteiro and Marques 1999; Morgado *et al*. 2003) and deep water systems such as the English Channel and the Guadalquivir Estuary in Spain (Drake *et al*. 2002; Vallet and Dauvin 2004). The presence of a seasonal pattern observed in the hyperbenthic densities and biomass during the present study, especially the peracarids (amphipods, isopods, and mysids) is also in agreement with findings in the published literature which have demonstrated that the hyperbenthic abundance and biomass peak in spring and early summer (Mees *et al*. 1993; Cartes *et al*. 2007). According to Richoux *et al.* (2004a,b) the sudden decrease in peracarid density observed after spring, can be related to post-reproductive mortality of females. The decline in densities values in peracarids demonstrated potential knock-on effects on hyperbenthic diversity values, as the lowest diversity values were recorded in October 2008 (austral spring). Only the copepods did not show an increase in densities in spring and early summer, and highest densities were recorded in autumn.

Most studies conducted on the hyperbenthic community elsewhere in the world indicate that mysids numerically dominate the hyperbenthos (Mees and Hamerlynck 1992; Mees *et al*. 1993, 1995; Morgado *et al*. 2003; San Vicente and Sorbe 1999, 2001). During the present study merohyperbenthic decapod larvae, especially brachyuran crab zoeae, were consistently the most dominant group, except during the months June and July, when mysids were most numerous (Figure 3.7). The high densities of the crab zoeae can likely be attributed to reproductive activities of the large populations of crabs associated with the extensive salt marshes of the Kariega Estuary (De Villiers *et al*. 1999). Indeed, it is worth noting that the maximum densities of crab zoeae were recorded in the middle and lower reaches of the estuary where the most extensive salt marshes occur (Figure 3.8). This said, the hyperbenthic community structure during the present study broadly consisted of the same taxonomic groups recorded elsewhere in the world. These include species of mysids, copepods, decapods (especially larvae), amphipods and isopods (Sibert 1981; Mees and Hamerlynck 1992; San Vicente and Sorbe 1999, 2001; Morgado *et al*. 2003).

Several authors have demonstrated small scale vertical zonation in hyperbenthic abundance and biomass values both in estuaries and deeper ocean environments (Sibert 1981; Cunha *et al*. 1997; Vallet and Dauvin 2004). Overall, higher densities are recorded in the bottom layers of the hyperbenthal (Sibert 1981; Dauvin *et al*. 1994; Cunha *et al*. 1997). In the present study, significantly higher densities of isopods, amphipods and mysids were recorded in the lower net ($p<0.05$). Furthermore, the hyperbenthic community also showed higher species diversity closer to the estuarine substrate. The elevated hyperbenthic densities and species diversity recorded in the lower nets can likely be ascribed to increased food availability, macrophytal and amorphous detritus that accumulates on the sediments of the estuary (Fockedey and Mees 1999). In contrast there were no significant differences in the total densities of decapod larvae and copepods between the upper and lower nets. Decapod larvae have been demonstrated to have high swimming speeds and are, as a consequence, able to change their position within the water column both to feed and to avoid unfavourable environmental parameters (Chu *et al*. 1996). Also, copepods exhibit a more homogenous distribution from the water surface to sea bottom (Vallet and Dauvin 2004).

Results of the current study indicate that the hyperbenthic densities, biomass and diversity indices were highest at those stations occupied in the upper reaches of the Kariega Estuary (Figure 3.5, 3.6 and 3.9B). This finding is in contrast to studies conducted in the Northern Hemisphere systems where species diversity is highest at the mouth of the estuary (Mees and Hamerlynck 1992; Mees *et al*. 1993, 1995; Azeiteiro and Marques 1999). The reduced diversity values recorded in the upper reaches of Northern Hemisphere systems are thought to reflect the absence of marine species due to high freshwater inflow into these systems (Mees *et al*. 1993). The marine dominance in the Kariega Estuary allows euryhaline species (e.g., the mysid *Mesopodopsis wooldridgei*, the isopod *Excirolana natalensis* and the amphipod *Gitanopsis pusilla*) to penetrate the upper reaches of the system. Concomitantly, the elevated abundance and biomass values in the upper reaches coincided with the highest total chlorophyll-*a* (chl-*a*) and seston concentrations (Figure 3.3, 3.5 and 3.6). The observed pattern in the hyperbenthic density and biomass data thus reflects the intricate interaction between the physical environment and increased food availability.

Shifts in the hyperbenthic community structure in northern hemisphere estuaries have largely been attributed to salinity gradients, secchi disc depth (SDD), temperature and to a lesser extent oxygen concentrations and sediment characteristics (Mees and Hamerlynck, 1992; Mees et al., 1993, 1995; Beyst et al., 1999; Drake et al., 2002; Morgado et al., 2003). The results from the RDA indicate that the organic content of the sediments largely accounted for the shifts in the hyperbenthic community structure in the Kariega Estuary. This result is consistent with a study by Richardson et al. (2006) who demonstrated that the demersal ichthyofaunal composition and distribution in the Kariega Estuary was largely determined by the organic content of the sediment. Teske and Wooldridge (2001) indicated that mud content was the most important environmental variable that structured the distribution of the macrobenthos found in thirteen Eastern Cape estuaries. These findings are also in agreement with studies conducted on demersal fishes and hyperbenthic fauna from other parts of the world (Meuter and Norcross, 1999; Cartes et al., 2008). In addition to organic content, the RDA analyses also indicate that the observed patterns in the hyperbenthic community structure could also be attributed to the chl-*a* concentration (Figure 3.10). Crab zoeae seem to be strongly influenced by chl-*a* concentrations (Figure 3.10), suggesting that the distribution of the planktonic hyperbenthos are influenced not only by the source of recruits but also by availability of food (chl-*a*) within the water column (Figure 3.8). This is agreement with Froneman (2001a) who indicated that zooplankton densities and biomass within the Kariega Estuary demonstrated a seasonal pattern which was strongly correlated with chl-*a* concentrations. In contrast, hyperbenthic species with a higher affinity for the sediment, such as isopods, amphipods and some mysids (*Gastrosaccus brevifissura* and *Rhopalophthalamus terranatalis*) seem to be strongly influenced by sediment characteristics and the organic content of the sediment.

3.5. CONCLUSIONS

Results of the current study indicate that community structure and small scale vertical zonation observed in the hyperbenthic community structure in the permanently open Kariega Estuary are broadly similar to that recorded in estuaries elsewhere in the world (Sibert 1981; Mees and Hamerlynck 1992; San Vicente and Sorbe 1999, 2001; Morgado et al. 2003). No studies have been conducted on the hyperbenthic community structure in Southern Hemisphere estuaries, although limited investigations have been conducted on selected components of the hyperbenthos including mysids (i.e. *Mesopodopsis wooldridgei*; see Wooldridge and Erasmus 1980; Wooldridge and Webb 1988) and shrimp (e.g. *Palaemon peringueyi*; see Allan et al. 2006). However, studies concerning the hyperbenthos as a community have not been conducted in a South African estuary and thus comparison is difficult. In the present study, the organic content of the sediment and chl-*a* concentrations appear to be the most important variables that structuring the hyperbenthic community within the Kariega Estuary. This finding is broadly in agreement with similar studies conducted in larger permanently open Northern Hemisphere estuaries (Drake *et al*. 2002; Morgado *et al*. 2003).

CHAPTER 4

DIEL PATTERNS IN THE HYPERBENTHIC COMMUNITY STRUCTURE IN A PERMANENTLY OPEN, EASTERN CAPE ESTUARY

4.1. INTRODUCTION

Diel vertical migrating patterns demonstrated by invertebrates in aquatic environments have been suggested as one of the largest animal migrations in the world in terms of biomass (Hays 2003). It is therefore not surprising that obvious ecosystem consequences would result from such a large phenomenon (Hays 2003). The vertical carbon flux and marine trophodynamics are just some of the physical and biological processes that are affected by this large migration (Vallet and Dauvin 2001; Shimode and Shirayama 2004). Indeed, many predators modify their behaviour to take advantage of the daily vertical movements of planktonic forms (Hays 2003).

The general pattern in terms of diel vertical migration involves animals being recorded at depth during the day and in surface waters at night (Hays 2003). Environmental stimuli that induce vertical migration include food availability, light intensity and tidal cycles (Shimode and Shirayama 2004). Several hypotheses have been proposed to explain diel vertical migration demonstrated by marine invertebrates. These include increased food availability, the advantage of lower metabolism in the deeper water layers, avoidance of visual predation (Enright 1977; Enright and Honegger 1977), horizontal dispersal and breeding migrations (Creutzberg 1975; Alldredge and King 1985; Mees and Jones 1997).

Many hyperbenthic species, including amphipods, isopods, copepods, mysids, cumaceans, decapods and crab larvae, demonstrate some degree of diel vertical migration (Sulkin 1984; Kaartvedt 1985, 1986; Mees and Jones 1997). Amphipods and cumaceans are known to burrow in the upper layers of the sediment for extended periods and emerge for different lengths of time to swim in the water column at night (Kaartvedt 1986). However, contrasting behaviour has been documented: species would either remain within the water column throughout the nocturnal period, or a prolonged interchange between the water column and sediment may occur (Alldredge and King 1980; Kaartvedt 1986).

In estuaries, diel vertical migrations are often tidally orientated (Mees and Jones 1997). This can be related to the fact that tidal change in estuaries is often accompanied by environmental changes in the water column, especially close to the benthos. These changes include flow induced turbulence, changes in salinity, dissolved organic substances, inorganic nutrients and temperature (Cronin and Forward 1979). Cronin and Forward (1979) showed that, compared to laboratory reared crab larvae, which showed no tidal migration, field caught specimens exhibit a marked tidal migration. They suggested that for short lived planktonic larvae, vertically migrating in time with the tidal cycle would offer more control of horizontal movements than diel vertical migration, ultimately enabling larvae to maintain position near their parent population (Cronin and Forward 1979).

The main aim for this chapter was to assess the diel variability in the hyperbenthic community structure in the permanently open, fresh water deprived Kariega Estuary.

4.2. MATERIALS AND METHODS

Sampling was conducted at Station 3 in the middle reaches of the Kariega Estuary during the month of March 2009 (Figure 2.1). Samples were collected during day and night, using a modified hyperbenthic sledge (mesh size of 500 µm) (Bossanyi 1951; Colman and Segrove 1955; Macer 1967). At each station the net was deployed and towed behind a boat at approximately 1.5 knots for 2 minutes (which constitutes to 8.4 m^3 per tow). Three parallel replicate tows were conducted on each occasion. However, due to logistical constraints, only two day-time and two night-time samples were collected from the hyperbenthos. Environmental variables (temperature, salinity and dissolved oxygen) were recorded during each sampling trip. Water samples (250 ml at depth of 0.5 meters) were collected to determine total chlorophyll-*a* (chl-*a*) and seston concentrations during each sampling trip. Seston and chl-*a* concentrations were determined as described previously (see section 3.2.2).

After sample collection, samples were fixed in 10% formalin and stored for 24 hours, before rinsing and subsequent identification using a Wild M5A dissecting microscope operated at 60× magnification. Identified specimens were separated into the following broad taxonomic groups: isopods, amphipods, mysids, copepods, decapod larvae, fish larvae, tanaids and cumaceans. Results were expressed as individuals per meter cube ($ind.m^{-3}$). For more details on the materials and methods employed during this study see section 3.2 in the previous chapter.

4.2.1. STATISTICAL ANALYSIS

To test for significance between day and night samples collected within the hyperbenthos, a non-parametric Mann–Whitney *U* test in the statistical package STATISTICA 8.1 was performed on all data sets that were not normally distributed. On normally distributed data sets, a student's t-test was performed. To determine if the species composition differed between day and night samples, a hierarchical agglomerative cluster analysis (using group-average linking) in the statistical package PRIMER 5 (Plymouth Routines in Multivariate Ecological Research) was performed on the three replicate samples from each net and time period, based on the Bray–Curtis similarity matrix (Clarke and Warwick 1994). To test for differences between the groups formed in the cluster analyses, a one-way analysis of similarity (ANOSIM) in the statistical program PRIMER 5 was performed. Prior to analyses, samples were square root transformed and the analysis was performed on a Bray–Curtis similarity matrix. Finally to identify which species were responsible for the observed groupings, a similarity percentage analysis (SIMPER) was performed in the statistical package PRIMER 5 (Clarke and Warwick 1994). A SIMPER examines the contribution of each species to the average Bray–Curtis dissimilarity between both groups and samples, and expresses results as a percentage.

4.3. RESULTS

4.3.1. PHYSICO-CHEMICAL VARIABLES

Physico-chemical variables measured during the present study are presented in Table 4.1. Most of the variables showed no clear change or pattern over time, and conditions at the study site remained stable. Notably different were the dissolved oxygen (dO_2) concentrations which appeared to demonstrate a strong diel pattern with the highest values recorded during the night-time (Table 4.1). Salinity values ranged from 38 to 40, temperature between 22.9 and 23 °C and dO_2 concentrations between 1.31 and 4.47 $mg.L^{-1}$ (Table 4.1).

4.3.2. CHLOROPHYLL-*a* AND SESTON

Total seston and chlorophyll-*a* (chl-*a*) concentrations during the study ranged from 95.5 to 102.0 $mg.L^{-1}$ and from 0.6 to 1.7 $mg.chl\text{-}a.m^{-3}$, respectively (Table 4.1). Maximum seston concentrations were recorded during night-time while the highest chl-*a* concentrations were recorded during the day-time sampling.

Table 4.1. The physico-chemical and biological variables measured at Station 3 over the 12 hour sampling period.

Time	Seston ($mg.L^{-1}$)	Chl-*a* ($mg.chl\text{-}a\ .m^{-3}$)	Temperature (°C)	Oxygen ($mg.L^{-1}$)	Salinity
12h00	95.5	1.7	23.6	4.47	40
16h00	98.5	1.6	23.7	4.68	38
20h00	105.5	1.8	23.4	1.07	38
00h00	102.0	0.6	22.9	1.31	38

4.3.3. DIEL PATTERNS IN THE HYPERBENTHOS

Total average hyperbenthic density during the day-time was 497.9 ± 254.1 $ind.m^{-3}$ and the biomass 3.8 ± 3.1 mg.dry $weight.m^{-3}$ (Figure 4.1; see also Table A2.1 in the appendix). During the night-time mean densities and biomass were 129.9 ± 38.5 $ind.m^{-3}$ and 5.1 ± 2.4 mg.dry $weight.m^{-3}$, respectively (Figure 4.1; Table A2.1, appendix). Mann–Whitney *U* test indicated that day-time densities were significantly higher than night-time densities ($U = 0.00$, $p = 0.004$). Total hyperbenthic biomass values were highest at night, but did not differ significantly from the day samples ($p = 0.43$; see Table A2.1 in the appendix).

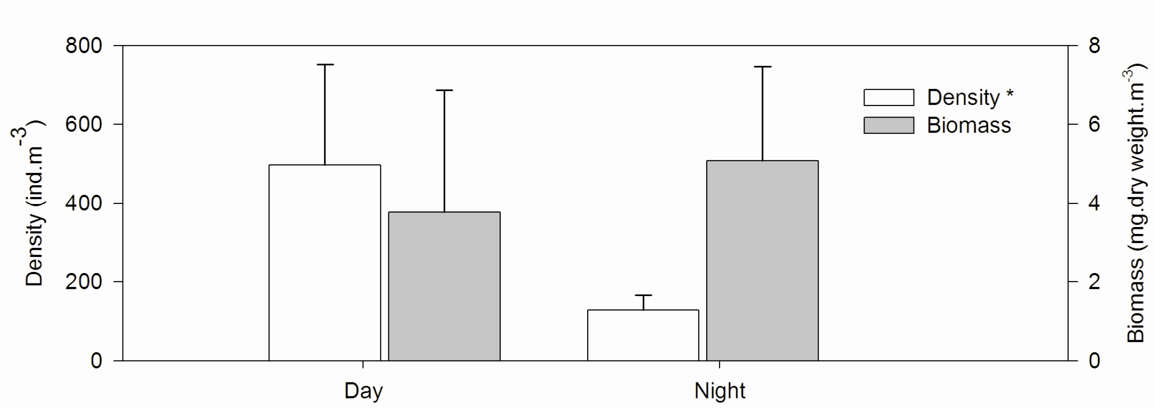


Figure 4.1. Total average day and night-time densities and biomass values ($n = 6$). Density values were significantly higher during the day-time and indicated with asterisk.

Total densities of the isopods, amphipods, tanaids and cumaceans recorded during the night-time were significantly higher than those recorded during the day-time sampling ($p<0.05$ in all cases). In terms of biomass, however, only isopods and cumaceans demonstrated significantly higher biomass values during the night-time (Figures 4.2A and 4.3A, see also appendix Table A2.1). There were no significant differences in the estimates of the total mysids and copepods densities and biomass between the day and night ($p>0.05$ in all cases; Figure 4.2C, D). Finally, the total densities and biomass of decapod larvae (composed mainly of brachyuran crab zoeae) during the day-time were significantly higher than those recorded during the night-time ($U = 0$, $p = 0.004$; $U = 1$, $p = 0.007$, respectively) (Figure 4.3A; Table A2.1 in the appendix).

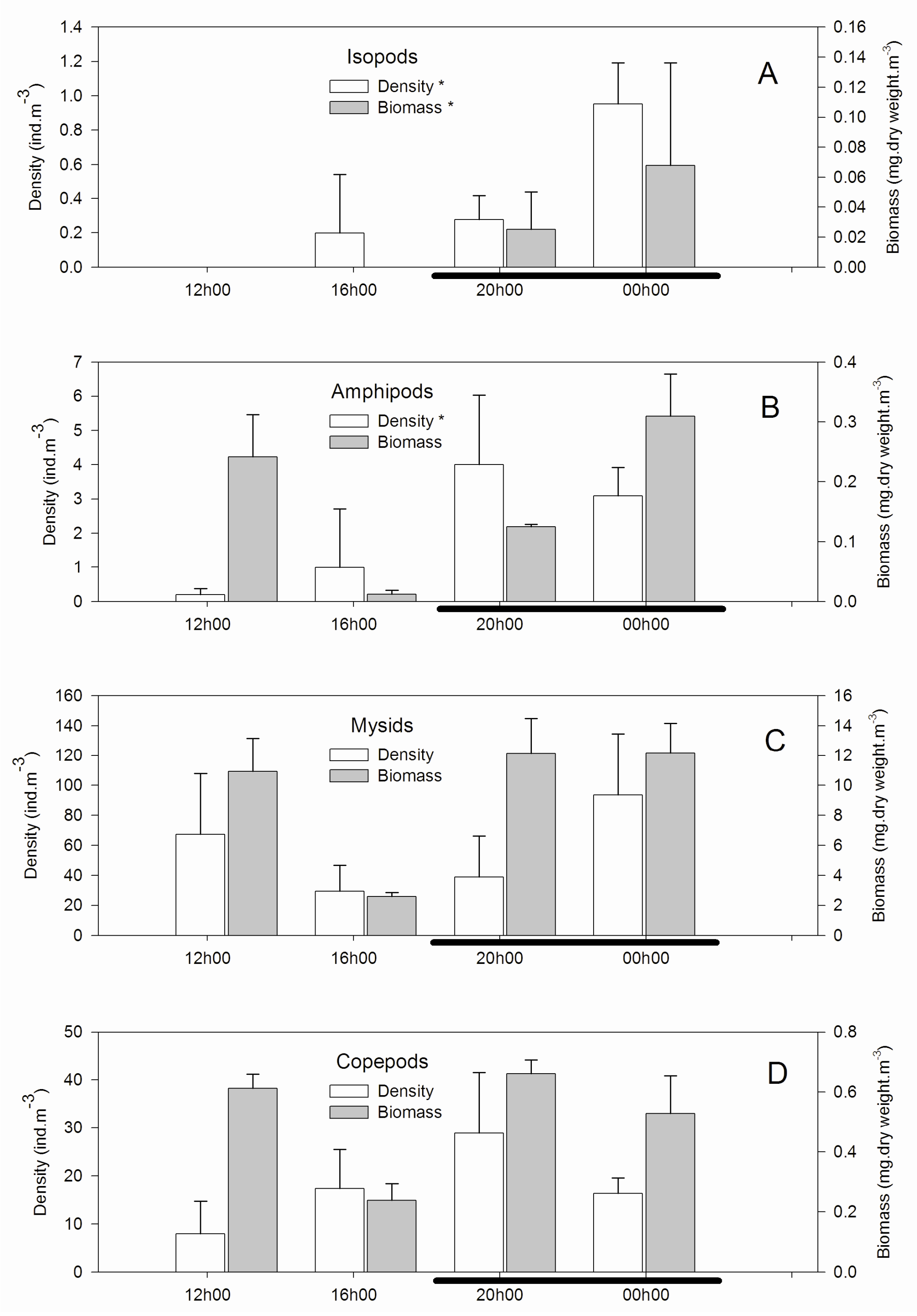


Figure 4.2. Hyperbenthic density and biomass values recorded over a 12 hour period. Isopods (A), amphipods (B), mysids (C) and copepods (D). Samples that differ significantly between day and night are indicated with an asterisk (*). To test for significance, Mann-Whitney *U* and Students T-test (normally distributed data) were employed. The black lines indicate samples collected at night. Error bars represent the standard deviations (*n* = 6). Note that y-axes have different scales.

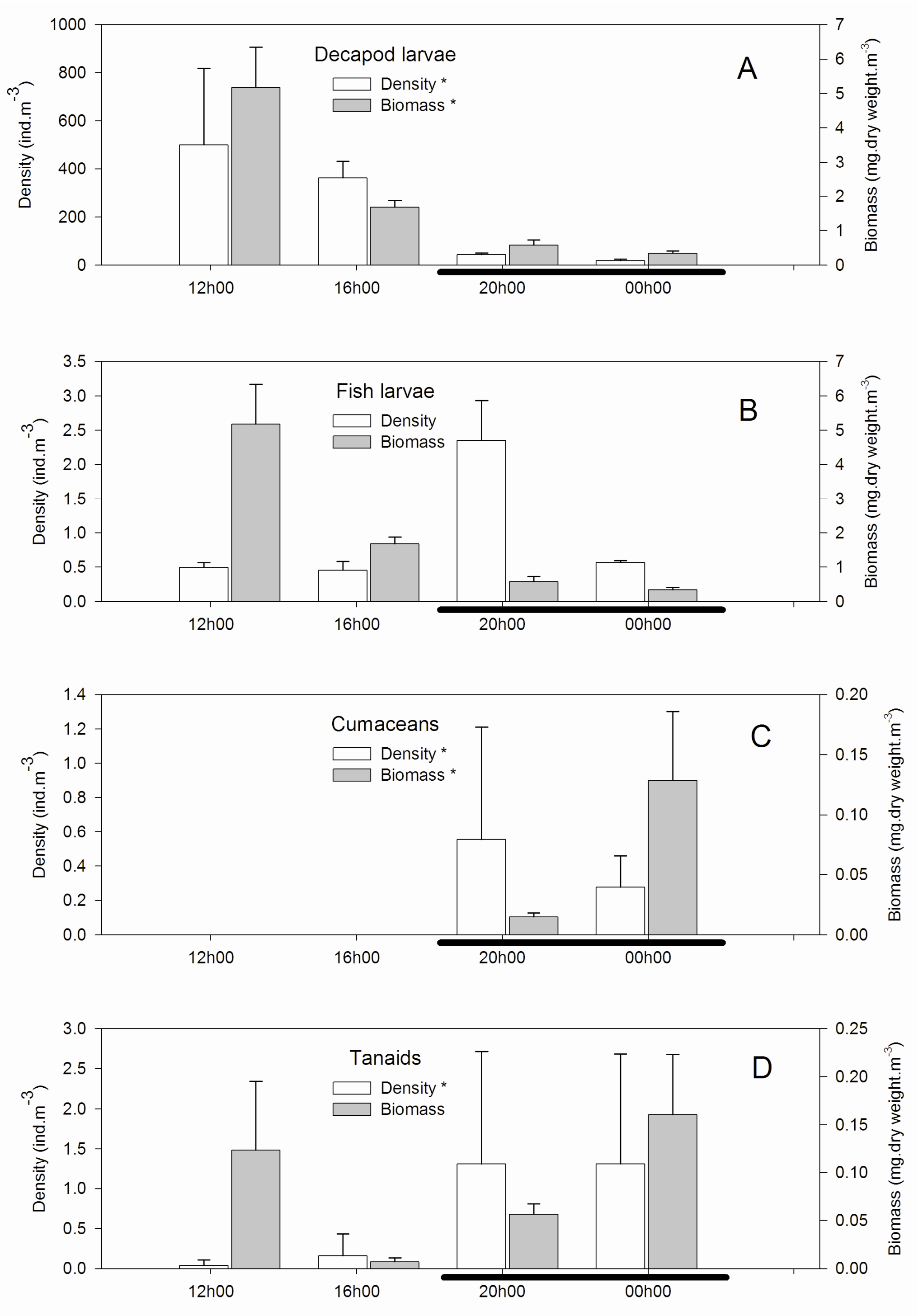


Figure 4.3. Hyperbenthic density and biomass values recorded over a 12 hour period. Decapod larvae (mostly Brachyuran crab zoeae (A), fish larvae (B), tanaids (C) and cumaceans (D). Samples that differed significantly between day and night are indicated with an asterisk (*). To test for significance, Mann-Whitney *U* and Students T-test (normally distributed data) were employed. The black lines indicate samples collected at night. Error bars represent the standard deviations (*n* = 6). Note different scales on y-axes.

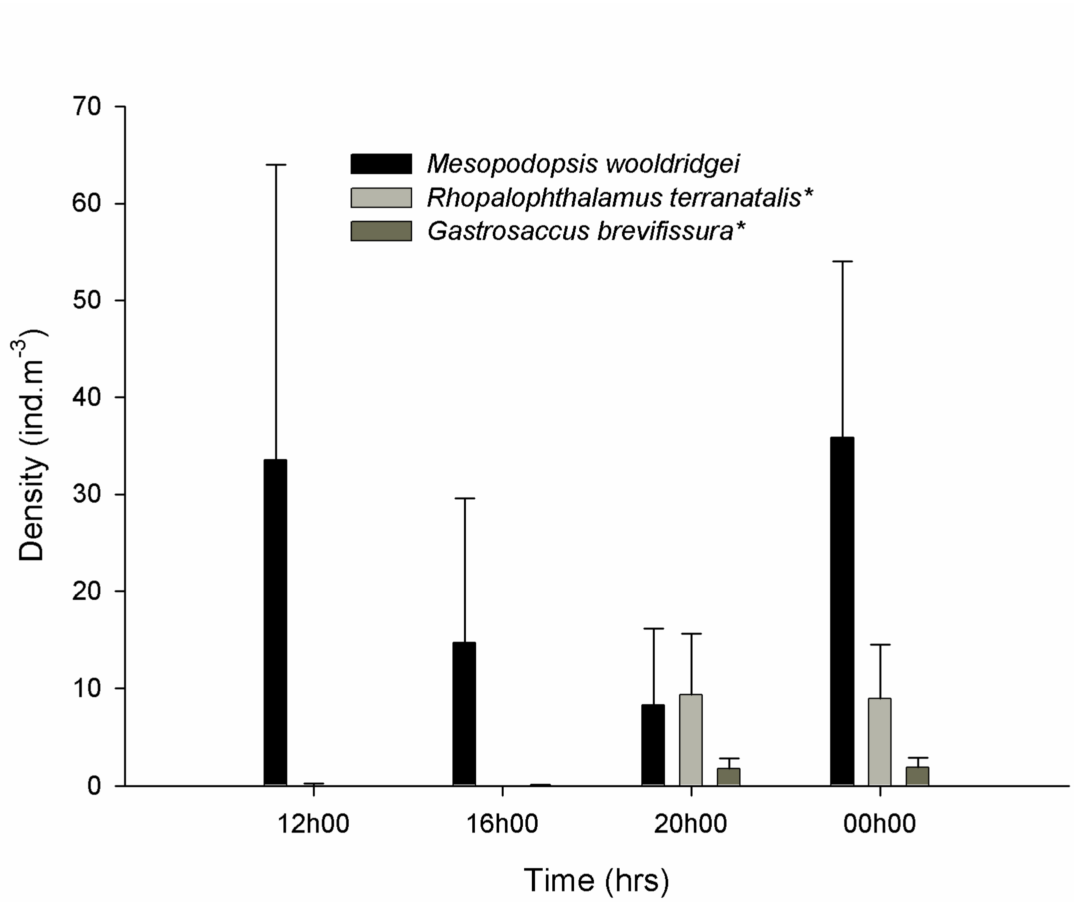


Figure 4.4. The density of mysid species represented within the hyperbenthal over the 12 hour sampling period. The black line signifies night-time. Samples that were significantly different between day-time and night samples are indicated with an asterisk (*). Error bars correspond to standard deviations (*n* = 6).

The densities of the different mysid species collected within the hyperbenthal over the 12 hour sampling period were highly variable over time (Figure 4.4). *Mesopodopsis wooldridgei* densities were not significantly different between day- and night-time samples, suggesting a more uniform distribution for this species, both in space and time. *Rhopalophthalamus terranatalis* and *Gastrosaccus brevifissura* were absent from the hyperbenthal during the day-time (Figure 4.4). Not surprisingly, *R. terranatalis* and *G. brevifissura* densities differed significantly between day and night samples ($U = 0$, $p = 0.003$; $U = 0$, $p = 0.004$, respectively). The biomass was not measured for each individual species, and thus species specific changes in biomass over time cannot be included in this result.

4.3.4. NUMERICAL ANALYSES

At the 60% similarity level, the hierarchical cluster analysis identified two distinct groupings, designated the day and night samples (Figure 4.5). These two groups were significantly different from one another (ANOSIM; $p<0.05$; Figure 4.5). Results from the SIMPER procedure indicate that the abundance of crab zoeae accounted for the majority of the dissimilarity between the two groupings (44.7%). Crab zoeae, *M. wooldridgei* and copepods collectively contributed ≈ 91% of the similarity within samples forming the day-time grouping, whereas *M. wooldridgei*, copepods, *R. terranatalis*, crab zoeae, *G. brevifissura*, *Grandidierella* spp. and fish larvae contributed up to ≈ 80% of the similarity between samples collected during night-time (Figure 4.5).

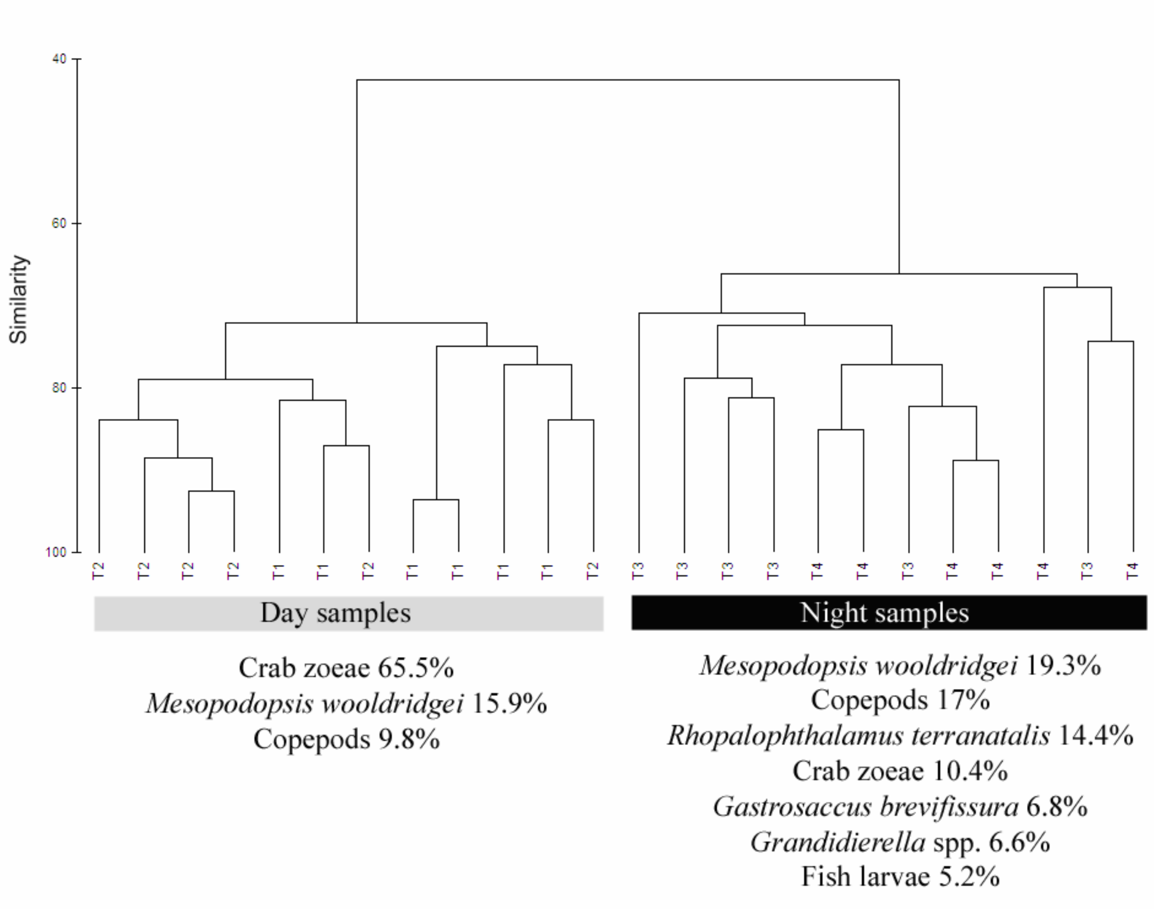


Figure 4.5. A hierarchical cluster analysis (using group-average linking) on the three replicate samples from each net and time period (*n* = 6), based on the Bray–Curtis similarity matrix. T_1 and T_2 represent samples collected during day-time and T_3 and T_4 represent night-time samples. Species and percentages (% similarity) indicated below the clusters represent the contribution that each group/species had in forming the grouping (SIMPER).

4.4. DISCUSSION

Results of numerous studies conducted in permanently open estuaries elsewhere in the world indicate that changes in the horizontal and vertical distribution of the community structure of the hyperbenthos can be ascribed to gradients in physico-chemical variables including salinity, temperature, dissolved oxygen, sediment characteristics (Wooldridge and Erasmus 1980; Dauvin *et al*. 1994; Cunha *et al*. 1997; Vallet and Dauvin 2004), and biological variables including food availability and predation pressure (Enright 1977; Enright and Honegger 1977; Alldredge and King 1985). Results from the present study indicate that the station where the study was conducted was characterised by the virtual absence of temporal changes in the physico-chemical and biological variables between day and night (Table 4.1). The observed changes in the community structure of the hyperbenthos during the present study can therefore mainly be related to behavioural activities of the various components of the hyperbenthic community.

Diel vertical migration (DMV) has been documented for many hyperbenthic species although the extent of migration is often species specific (Alldredge and King 1980; Kaartvedt 1985, 1986; Carleton and Hamner 1989; Mees and Jones 1997). The hyperbenthal can be considered a meeting place of organisms from two neighbouring marine habitats: the plankton or holoplankton, which reach the bottom with diurnal migration, and the bottom dwelling forms that live in or on the benthos during the day and emerge into the water column, usually at night (Alldredge and King 1980; Mees and Jones 1997). The holoplanktonic forms include copepods, mysids, crustacean larvae and fish larvae, and the bottom dwelling species include amphipods, isopods, cumaceans, mysids, tanaids and harpacticoid copepods (Alldredge and King 1980; Mees and Jones 1997).

During the present study, total hyperbenthic densities during the day-time were significantly higher than night-time values ($p<0.05$). The elevated densities recorded in the day samples could largely be attributed to the presence of high numbers of crab zoeae recorded in the samples (Figure 4.3A). Indeed, the crab zoeae appeared to be the only taxonomic group which demonstrated true diel vertical migrating behaviour during the present study. The larvae of brachyuran crabs, particularly within estuaries and near shore environments, have well documented vertical and lateral migration abilities (Wooldridge and Erasmus 1980; Garland *et al*. 2002; Kingsford *et al*. 2002). This behaviour is mostly linked to the hypothesis that they migrate to surface waters at dusk, where favourable light conditions facilitate optimal photosynthesis resulting in greater food availability, and sink to the bottom at dawn, avoiding visual predators during the light hours (Garland *et al*. 2002). On the other hand, the copepods demonstrated no significant difference between day and night densities and biomass (Figure 4.2D), which confirms results from the previous chapter in that copepods demonstrated a more uniform vertical distribution within the Kariega Estuary (see section 3.3.4 in previous chapter). There is however, considerable variation in the behavioural responses of different crustacean zooplankton to cues that direct their vertical movements (Forward 1985). The absence of any significant difference in the biomass values between day and night samples can in all likelihood be attributed to the presence of large mysids in the samples collected during the night-time.

Isopods, amphipods, cumaceans, tanaids and the majority of mysids were largely absent in the hyperbenthal during the day and emerged into the water column only at night (Figures 4.2A, B and 4.3C, D). The observed pattern is in agreement with other studies conducted in other areas throughout the world, and can be related to feeding activities, reproduction and dispersal over short distances (Alldredge and King 1980, 1985; Kaartvedt 1986; Kimmerer *et al.* 2002). Kaartvedt (1985) showed that the mysid, *Boreomysis megalops*, always undertook DMV, whereas the rest of the mysid species found in Fanafjorden (western Norway) either showed increased swimming activity or a more stratified distribution but remained close to the benthos during the night-time. When considering the three mysid species recorded during the present study, different vertical distributions were demonstrated by each species. *Mesopodopsis wooldridgei* were always present within the hyperbenthal, and densities did not differ significantly over time ($p>0.05$; Figure 4.4). Wooldridge and Erasmus (1980) showed that *M.*

wooldridgei demonstrated a more uniform distribution throughout the water column as they utilised the tidal currents, migrating both laterally and vertically, in order to maintain their position in the estuary. In the present study the mysids *Rhopalophthalamus terranatalis* and *Gastrosaccus brevifissura* were recorded in the hyperbenthal only at night and were otherwise completely absent from the hyperbenthal during the day. Species of the genus *Gastrosaccus* are known to burrow in the benthos during the day and emerge into the water column at night (Wooldridge 1983; Beckley 1988). *R. terranatalis* is the largest mysid species found in South African waters and rarely demonstrates vertical or tidal migrating behaviour (Wooldridge and Erasmus 1980; Wooldridge and Webb 1988; Jerling and Wooldridge 1995). *R. terranatalis* which often prey on the mysid *M. slabberi* (now *M. wooldridgei*, see Wittmann 1992) are generally more active at night (Wooldridge and Erasmus 1980; Wooldridge and Webb 1988; Jerling and Wooldridge 1995). This increased activity of *R. terranatalis* at night, may explain the increased abundance and higher biomass values recorded within the hyperbenthal during night-time samples (Figure 4.3, also see appendix Table A2.1).

The observed behavioural responses demonstrated by the various components of the hyperbenthos during the present study contributed to the cluster analyses separating the samples into day and night groupings. Results from the SIMPER procedure of PRIMER 5 indicate that the different groupings were mostly attributed to the elevated crab zoeae densities during the day-time (average densities of crab zoeae varied from 431.2 ± 219.8 ind.m^{-3} during the day to 30.5 ± 15.4 ind.m^{-3} at night; see Table A2.1 in the appendix) and the presence of the mysids *G. brevifissura* and *R. terranatalis* in the samples during the night-time (Figure 4.5).

In conclusion, the diel vertical migrating patterns demonstrated by the different species of the hyperbenthos within the Kariega Estuary during the present study are broadly similar to those recorded in studies conducted elsewhere in the world, particularly the Northern Hemisphere (Forward *et al*. 1984; Forward 1985; Kaartvedt 1985, 1986; Vallet and Dauvin 2001; Morgado *et al*. 2006). Species that tend to be more closely associated with the benthos, including isopods, amphipods, cumaceans, tanaids and certain mysid species, burrow in the benthos during the day, and only emerge into the water column at night. The more planktonic species, such as mysids (mainly *M. wooldridgei*), fish larvae and copepods, seemed to have a more uniform distribution over time. Bollens and Frost (1989a, b) suggested that adult copepods altered their diel vertical migrating behaviour in the presence of predators, suggesting that DMV is not purely a chemically induced behavioural response.

CHAPTER 5

GENERAL DISCUSSION

The physico-chemical variables during the period of study indicated the presence of a constant reverse salinity gradient, with highest salinities measured in the upper reaches and lowest at the mouth of the estuary. The reverse salinity gradient observed within the Kariega Estuary largely reflects evaporation and the reduced freshwater inflow. Strong seasonal patterns in temperature and dissolved oxygen concentration were observed and can be linked to the climate regime of the region. Total chlorophyll-*a* (chl-*a*) concentrations demonstrated a weak seasonal pattern (Figure 3.3A). No seasonality in secchi disk depth (SSD) and seston concentration was detected during the period of study; however a weak spatial pattern in salinity, temperature, seston and chl-*a* concentrations was detected, with highest values of these variables recorded in the upper reaches of the system. The estimates presented here are in general agreement with previous studies conducted within the Kariega Estuary (Whitfield 1994; Froneman 2000a; 2001 a, b).

The estimates of the hyperbenthic densities and biomass recorded in the present study (see appendix Table A1.1) are broadly similar to that recorded in estuaries in the Northern Hemisphere (Table 1.1). For example, in the shallow Mondego Estuary situated on the north-western coast of Portugal, densities and biomass of the hyperbenthos ranged between 4 and 385 ind.m^{-3} and between 1 and 28 mg.AFDW.m^{-3}, respectively (Azeiteiro and Marques 1999; Morgado *et al*. 2003). Similarly in the Gironde Estuary (France) hyperbenthic densities and biomass ranged between 0 and 114 mg.AFDW.m^{-2} and 0 and 50 ind.m^{-2}, respectively (Mees *et al*. 1999). In deeper systems, values tend to be more variable and densities in the English Channel ranged from 1 to 10 000 ind.100m^{-3} (Vallet and Dauvin 2004). However, the estimates of the hyperbenthic abundance and biomass should be viewed with caution as there are several possible sources of underestimation. This include amongst others, mesh size employed (500µm) which would have under-sampled the smaller components of the hyperbenthos, net avoidance and the possible influence of tidal cycle on the spatial distribution of the hyperbenthos. The hyperbenthic community composition recorded in the present study was also broadly similar to that found in European systems. Mysids appear to be the dominant component of the hyperbenthos in Northern Hemisphere systems (Mees and Hamerlynck 1992; Mees *et al*. 1993; Mees *et al*. 1995; San Vicente and Sorbe 1999; Drake *et al*. 2002). During the present study brachyuran crab zoeae numerically dominated the hyperbenthic counts on ten of the twelve sampling trips. The high contribution of the crab zoeae to the total hyperbenthic densities can likely be related to the extensive salt marshes of the Kariega Estuary which are characterised by high densities of the crab *Cleistostoma edwardsii* and *Sesarma catenata* (De Villiers *et al*. 1999). This said, the hyperbenthic community composition during the present study consist mostly of taxonomic groups similar to those recorded elsewhere in the world. These include species of isopods, amphipods, copepods, mysids and decapods (Sibert 1981; Mees and Hamerlynck 1992, San Vicente and Sorbe 1999, 2001; Morgado *et al*. 2003).

The composition of hyperbenthic communities found in estuaries situated in the Northern Hemisphere is generally influenced by the salinity gradients (Mees and Hamerlynck 1992; Mees *et al*. 1993, 1995; Azeiteiro and Marques 1999; Drake *et al*. 2002; Morgado *et al*. 2003). The lack of freshwater flow into the Kariega Estuary during the present study resulted in the presence of a constant reverse salinity gradient and as a consequence the estuary functioned more as an extension of the marine environment. The hyperbenthic community structure therefore was more influenced by changes in the organic content of the sediment than the salinity gradient. However, the salinity gradient still influenced the hyperbenthic community as polyhaline species (e.g. *Rhopalophthalamus terranatalis)* were likely excluded from the upper reaches of the Kariega Estuary where hypersaline (>40) conditions prevailed.

Studies conducted both locally and internationally have demonstrated the importance of freshwater inflow in promoting both primary and secondary production in estuaries (Adams *et al*. 1999; Wooldridge 1999; Grange *et al*. 2000; Gillanders and Kingsford 2002). Not surprisingly the freshwater-deprived Kariega Estuary is characterised by low chl-*a* concentrations (<1 mg.chl-*a*.m^{-3}) and reduced zooplankton densities and biomass (Grange *et al*. 2000). The observed patterns are thought to reflect reduced primary production rates resulting from low macronutrient concentrations and the consequent reduced food availability for zooplankton (Grange and Allanson 1995; Grange *et al*. 2000). This said, the estimates of the total hyperbenthic densities and biomass in the Kariega Estuary are in the range reported for large Northern Hemisphere estuaries with sustained freshwater inflow (Azeiteiro and Marques 1999; Morgado *et al*. 2003). This result suggests that water column processes appear less important in determining the densities and biomass of hyperbenthos within estuaries. The hyperbenthos within the Kariega Estuary is likely sustained by the accumulation of detritus and organic material within the sediment. This is in agreement with Cartes *et al.* (2007) who indicated that hyperbenthic densities in the Ebro Delta dramatically decreased with the appearance of mucilaginous aggregates which resulted in a decrease in the available organic content found within the sediment.

Elevated density and biomass values evident during spring and early summer, and can likely be related to the increased reproductive output of peracarid species (mysids, amphipods and isopods) as well as increased food availability (chl-*a*) during this time (Figure 3.3, 3.5 and 3.6).

Data from the present study indicate that most components of the hyperbenthos demonstrated some degree of diel migrating behaviour (Figures 4.2 and 4.3) and are in agreement with other studies conducted elsewhere in the world (Alldredge and King 1980; Kaartvedt 1985, 1986; Kimmerer *et al*. 2002). Two diel patterns seem to exist. The first group includes species that burrow in the sediment during the day and emerge into the water column at night: the cumaceans, amphipods, isopods and tanaids. This behaviour appears to be related to reproduction, dispersal over short distances and feeding activities of the mentioned taxonomic groups (Alldredge and King 1980, 1985; Kaartvedt 1986; Kimmerer *et al*. 2002). The second group, mainly represented by the larvae of brachyuran crabs, were found in significantly higher densities within the hyperbenthal during the day (431.19 ± 219.83 ind.m^{-3}) and migrated into the surface waters at night (30.46 ± 15.42 ind.m^{-3}) ($p<0.005$). Brachyuran crab zoeae are known to demonstrate vertical and lateral migration associated with both tides and diurnal rhythms (Wooldridge and Erasmus 1980; Garland *et al*. 2002; Kingsford *et al*. 2002). This result thus implies that in order to effectively sample the hyperbenthos, both day- and night-time samples should be collected.

5.1. FINAL CONCLUSIONS

The reverse salinity gradient demonstrated in the present study is in contrast to studies conducted in estuaries elsewhere in the world, where the presence of a strong salinity gradient determined the distribution of most hyperbenthic species. Implications of the reverse salinity gradient detected in the Kariega during the present study are seen when highest densities, biomass and diversity were recorded in the upper reaches of the estuary. This is in contrast to studies conducted in other estuaries, where highest biomass but lowest diversity was detected in the brackish upper reaches of the systems. Furthermore, due to the reverse salinity gradient, the organic content of the sediment was the most important variable that structured the hyperbenthic community within the Kariega Estuary. This is in agreement with Richardson *et al*. (2006), who demonstrated that the distribution of demersal fishes in the Kariega Estuary was strongly correlated to sediment type. Furthermore studies conducted in open marine systems such as the continental margin off the coast of Portugal, where no salinity gradient was present, also indicated that the organic content of the sediment was the most important variable that structured the hyperbenthic community (Cunha *et al*. 1997).

5.2. FUTURE RESEARCH

Results from the current study indicate that although very little research has been conducted on the South African hyperbenthos, the hyperbenthic community structure within the Kariega Estuary is broadly similar to that of estuarine systems elsewhere in the world, particularly in the Northern Hemisphere. The importance of this community within South African estuaries and the marine ecosystem as a whole has not yet been recognised and thus the research needs to be expanded to further include studies with the following components:

1. Expand the study to include studies on the hyperbenthic communities in different types of South African systems, such as estuaries that demonstrate a marked salinity gradient, as well as temporary open/closed systems. This would further clarify the various physico-chemical and biological variables that structure the hyperbenthic community within southern African estuaries.
2. Assess the energy dynamics (i.e., employing stable isotope or fatty acid analyses) of the hyperbenthos in order to determine sources and direction of carbon flow. A better understanding of the processes that govern the trophodynamics of the hyperbenthos would ultimately shed light on the importance of this community within estuarine ecosystems.
3. Knowledge on the recruitment strategies of hyperbenthic species in South African estuaries would give insight into the population dynamics of the various components of the hyperbenthos. This can be linked to spatial and temporal patterns in the biological variables (food availability and predation) that structure the hyperbenthic community.
4. The fact that the hyperbenthos can almost be seen as a transition zone/community between benthic and planktonic communities, establishing how exactly this group of organisms interact and interlink is essential in better understanding the ecological role of the hyperbenthos.
5. The effect of the tidal cycle on the distribution of estuarine organisms has been established in numerous studies. By determining how the hyperbenthos reacts to

the tidal cycle within estuaries will further aid the understanding of both horizontal and vertical distribution and consequent ecological implications.

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APPENDICES

A.1. APPENDIX 1

Table A1.1. Total average hyperbenthic densities and biomass recorded in both the upper and lower nets. N/D indicates nets where no data was collected due to logistical constraints.

		Density (ind.m^{-3})			Biomass (mg.dry weight.m^{-3})		
Date	Station	Lower Net	Upper Net	Total	Lower Net	Upper Net	Total
Feb '08	1	16.03	0.83	16.87	6.71	1.10	7.81
	2	21.79	1.79	23.57	1.26	0.04	1.31
	3	18.10	30.52	48.61	1.06	0.94	2.01
	4	1.39	1.07	2.46	0.33	0.05	0.38
	5	0.79	4.05	4.84	0.08	0.17	0.24
	6	0.04	0.12	0.16	0.03	0.02	0.05
March '08	1	0.48	0.12	0.60	0.09	0.03	0.12
	2	22.30	0.60	22.90	1.44	0.05	1.49
	3	7.54	54.56	62.10	0.30	1.22	1.52
	4	9.25	14.33	23.57	0.21	0.19	0.39
	5	7.34	12.38	19.72	2.23	0.42	2.65
	6	0.16	0.60	0.75	0.02	0.06	0.08
April '08	1	45.36	17.18	62.54	3.96	0.81	4.77
	2	18.37	14.52	32.90	2.60	0.68	3.28
	3	22.58	85.52	108.10	0.46	1.44	1.89
	4	19.48	43.65	63.13	0.28	0.71	1.00
	5	59.09	56.51	115.60	1.55	1.46	3.00
	6	6.47	21.47	27.94	0.18	0.47	0.65
May '08	1	16.35	10.52	26.87	2.28	0.54	2.83
	2	28.61	34.68	63.29	2.40	1.74	4.14
	3	27.26	58.65	85.91	2.90	2.84	5.75
	4	7.42	16.67	24.09	0.58	0.61	1.19
	5	16.98	24.60	41.59	0.69	0.92	1.61
	6	1.43	3.85	5.28	0.11	0.16	0.27
June '08	1	25.99	3.02	29.01	3.77	0.50	4.27
	2	18.06	6.15	24.21	3.65	2.99	6.64
	3	17.06	6.87	23.93	6.14	2.09	8.23
	4	4.56	2.38	6.94	1.21	0.77	1.98
	5	5.24	2.50	7.74	1.20	0.21	1.41
	6	2.90	2.34	5.24	0.56	0.10	0.66
July '08	1	4.68	1.11	5.79	0.43	0.18	0.61
	2	25.28	16.98	42.26	5.60	4.90	10.50
	3	13.61	4.17	17.78	5.59	1.76	7.35
	4	3.13	0.95	4.09	1.39	0.30	1.69
	5	2.38	2.42	4.80	0.54	0.27	0.81
	6	4.92	8.06	12.98	0.37	0.20	0.57
Aug '08	1	11.79	6.55	18.33	1.23	0.91	2.13
	2	8.57	6.75	15.32	0.91	0.18	1.10
	3	90.36	35.08	125.44	1.85	0.83	2.67
	4	37.98	58.89	96.87	1.08	1.11	2.19
	5	24.84	21.59	46.43	0.56	0.33	0.88
	6	3.61	8.57	12.18	0.06	0.25	0.31
Sep '08	1	13.06	5.04	18.10	1.17	0.40	1.58
	2	44.05	7.66	51.71	11.91	2.25	14.16
	3	148.17	108.81	256.98	8.31	7.24	15.55
	4	87.34	N/D	87.34	2.25	N/D	2.25
	5	99.40	N/D	99.40	1.98	N/D	1.98
	6	166.00	N/D	166.00	0.31	N/D	0.31
Oct '08	1	17.38	12.94	30.32	6.08	9.00	15.08
	2	11.75	5.83	17.58	3.42	2.55	5.97
	3	152.18	225.04	377.22	8.40	5.51	13.91
	4	70.24	94.80	165.04	3.67	2.41	6.08
	5	15.67	19.60	35.28	2.87	0.41	3.28
	6	37.33	3.37	40.71	0.07	0.09	0.16
Nov '08	1	37.74	28.02	65.75	8.62	8.52	17.13
	2	26.43	31.63	58.06	6.67	17.40	24.07
	3	42.18	45.63	87.82	7.94	7.20	15.14
	4	22.30	51.23	73.53	2.77	2.95	5.71
	5	88.25	100.08	188.33	2.26	2.42	4.67
	6	50.67	10.44	61.10	0.39	0.15	0.54
Dec '08	1	9.44	4.60	14.05	4.17	1.40	5.56
	2	6.73	7.10	13.83	10.72	2.80	13.52
	3	47.38	45.44	92.82	5.40	3.30	8.70
	4	25.24	25.08	50.32	1.56	0.65	2.21
	5	10.95	10.32	21.27	0.68	2.59	3.27
	6	20.33	1.23	21.56	0.40	0.05	0.44
Jan '08	1	19.21	8.21	27.42	0.05	1.54	1.58
	2	7.46	7.98	15.44	6.23	0.35	6.58
	3	25.44	19.76	45.20	1.98	1.24	3.23
	4	8.73	32.10	40.83	5.06	0.88	5.94
	5	68.81	78.61	147.42	1.55	1.19	2.74
	6	100.00	12.94	112.94	0.27	0.44	0.71

Table A1.2. Total average densities over space and time of the major taxonomic hyperbenthal groups from both the lower and upper nets.

	Lower net		Upper net	
	Ind.m^{-1}	%	Ind.m^{-1}	%
Isopoda	44.8	3%	25.2	1%
Amphipoda	103.6	6%	37.1	2%
Mysidacea	274.1	15%	147.6	9%
Copepoda	178.2	10%	200.1	12%
Decapod lifestages	1141.8	64%	1249.2	74%
Other	39.0	2%	26.6	2%

Table A1.3. The scores of the environmental variables generated by the Redundancy Analysis (RDA). Note that the first two canonical axes (F1 and F2) account for 99.2% of the variation detected.

	F1	F2	F3	F4	F5	F6	F7
Temperature	0.106	0.008	0.151	-0.065	-0.076	-0.012	0.016
O_2	-0.082	0.020	-0.039	0.082	0.057	0.113	-0.041
Salinity	0.097	0.233	-0.049	-0.043	0.043	-0.005	0.039
Turbidity	-0.005	-0.023	0.019	0.113	-0.165	0.017	0.044
Seston	-0.083	0.153	0.000	-0.074	-0.153	-0.031	-0.057
Chl-*a*	0.163	0.036	0.070	-0.019	0.000	-0.084	-0.096
Organic content	0.208	-0.106	-0.041	0.022	-0.203	0.059	-0.003

A.2. APPENDIX 2

Table A2.1. Average density and biomass values for the major taxonomic groups recorded within the hyperbenthal over a 12 hour period. Values indicated in bold differed significantly between day and night samples. (–) absent from samples

	Density (ind.m^{-3})				Biomass (mg.dry weight.m^{-3})			
	Day		Night		Day		Night	
	Average	Stdev	Average	Stdev	Average	Stdev	Average	Stdev
Isopods	**0.10**	**0.24**	**0.62**	**0.41**	**–**	**–**	**0.067**	**0.064**
Amphipods	**0.60**	**1.18**	**3.55**	**1.46**	0.04	0.06	0.07	0.06
Mysids	48.33	34.83	66.13	43.31	2.26	2.08	4.04	1.97
Copepods	12.64	8.45	22.60	10.75	0.14	0.08	0.20	0.09
Decapod larvae	**431.19**	**219.83**	**30.46**	**15.42**	**1.14**	**0.98**	**0.15**	**0.12**
Fish larvae	4.94	4.60	3.21	2.30	0.16	0.09	0.49	0.49
Cumaceans	**–**	**–**	**0.42**	**0.46**	**–**	**–**	**0.024**	**0.042**
Tanaids	**0.10**	**0.19**	**1.31**	**1.24**	0.022	0.050	0.036	0.044
Total	**497.90**	**254.10**	**128.29**	**38.30**	3.77	3.10	5.08	2.4