SPATIAL AND TEMPORAL PATTERNS IN THE POPULATION AND THE FEEDING OF *PALAEMON PERINGUEYI* (MACPHERSON 1990) (DECAPODA, PALAEMONIDAE) IN THE KARIEGA ESTUARY, SOUTH AFRICA

NONHLANHLA PRECOTIA NYALUNGU

A thesis submitted in fulfilment of the requirements for the degree of

Master of Science

at

RHODES UNIVERSITY

May 2012

Declaration

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

Abstract

The spatial and temporal patterns in the population demographs and feeding ecology of the caridean shrimp, *Palaemon peringueyi*, was investigated over a 12 month period in the permanently open Kariega Estuary situated on the south-east coastline of South Africa. Shrimps were sampled monthly from three stations corresponding to the lower, middle and upper reaches of the Kariega Estuary. The shrimps were collected at the different stations using a pull net. Temperature, salinity, dissolved oxygen and % cover of submerged vegetation were measured at each sampling station. Finally, the feeding ecology of the shrimp was investigated employing stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes analysis.

Temperature, salinity, dissolved oxygen and vegetation cover showed distinct seasonal patterns. The shrimps attained total abundances and biomass of between 0 and 245.6 individuals per m^2 (ind.m^{-2}) and between 0 and 13.6 grams wet weight per m^2 (g wwt.m^{-2}), respectively. Mean abundance ranged between 2.3 (± 3.0) and 88 (± 27.3) ind.m^{-2} in the lower reach, between 0.9 (± 0.4) to 21.5 (± 4.5) ind.m^{-2} in the middle reach and 0 to 1.6 (± 0.5) ind.m^{-2} in the upper reach. Mean biomass ranged between 0.4 (± 0.5) and 4.4 (± 1.4) g wwt.m^{-2} in the lower reach, between 0.1 (± 0) to 4.3 (± 0.9) g wwt.m^{-2} in the middle reach and between 0 to 1.6 (± 0.5) g wwt.m^{-2} in the upper reach. Greatest abundances and biomasses were recorded in winter following heavy rainfall within the catchment area. Freshwater inflow which is due to rainfall is thought to provide a cue for the recruitment of marine breeding organisms. The spatial patterns in the distribution of the shrimps showed that juveniles occupied the lower and middle reaches and adults the entire length of the estuary. There were no significant relationships between the abundance and biomass of the shrimps and the selected physico-chemical variables ($p > 0.05$ in all cases).

Results of the stable isotope study indicated that the mean $\delta^{13}C$ of the shrimps in the lower, middle and upper reaches were -12.4 (± 1.3) ‰, -15.6 (± 0.5) ‰ and -17.5 (± 0.5) ‰, respectively. The $\delta^{15}N$ isotopes of the shrimps in the lower reach was 11.6 (± 0.5) ‰ with middle and upper reaches having similar δ^{15}N values, 13.5 (± 0.4) ‰ and 13.4 (± 0.4) ‰, respectively. There was no significant difference in the δ^{13}C and δ^{15}N isotope ($p > 0.05$) between the sexes of the shrimps. Two-way ANOVA indicated a significant difference in the δ^{13}C isotope of the shrimps between the sites ($p < 0.05$).

The difference in the δ^{13}C and δ^{15}N ratios of the shrimps suggests spatial variability in the diet of *P. peringueyi* within the Kariega Estuary. The diet of the shrimps in the lower reach is primarily composed of *Nanozostera capensis* epibionts. In the middle reach the diet of the shrimps is likely comprised of the detritus of benthic algae. In the upper reach of the estuary, *P. peringueyi* likely derives its carbon from a combination of epibionts, benthic algae and detritus derived from *Codium*.

Acknowledgements

I would like to thank the following people:

- My two supervisors Professor Allan Hodgson and William Froneman for their assistance throughout my thesis.
- Dylan, Matthew, Simone and Ryan for assisting with my field work
- Sherwin Mack for the helping with illustration of maps
- My mother Rally Nyalungu and Emily Antonio for all the encouragement

Lastly, I would like to thank the National Research Foundation (NRF) and Rhodes University for their financial assistance.

Table of Contents

List of Figures

List of Tables

Nomenclature

Although the terms ‘shrimp’ and ‘prawn’ have no taxonomic validity, there has been some confusion in the use of these terms. For example some authors refer to *Palaemon peringueyi* as a prawn (Achituv and Cook 1984; de Villiers *et al.* 1999), while other authors refer to this species as shrimp (Robertson 1984; Bernard and Froneman 2005; Allan *et al.* 2006; Froneman 2006). Mostly the term ‘prawn’ is used in South Africa and Australia and is used to refer to species of the penaeid crustaceans, particularly the commercial species. Generally, species in the division Caridea are referred as shrimps (Kensley 1972).

Chapter 1

Introduction

1. General Introduction

The caridean shrimp *Palaemon peringueyi* belongs to the family Palaemonidae in the subgenus *Palaemon* (genus *Palaemon*). Initially four subgenera were recorded in the genera of *Palaemon*, namely *Palaemon*, *Palaeander*, *Nematopalaemon* and *Exopalaemon* (Holthuis 1950). However, Chance and Bruce (1993) granted the subgenus *Nematopalaemon* its full generic status. To date, 34 species have been recorded in the genus *Palaemon*, with 23 species belonging to the subgenus *Palaemon* (Jayachandran 2001). *Palaemon* is distributed worldwide (cosmopolitan), they form an important component of the hyperbenthos within estuaries (deVilliers *et al.* 1999; Bernard and Froneman 2005) and generally occupy intertidal to shallow waters down to 170 m (Jayachandran 2001). In southern Africa, four species have been recorded within the subgenus *Palaemon* (*capensis*, *debilis*, *peringueyi* and *concinnus*) and are represented by freshwater, marine and estuarine species (Kensley 1972).

Palaemon peringueyi (McPherson 1990) is found along the South African coastline, from Walvis Bay on the west coast (Barnard 1950) to Kosi Bay on the east coast (Broekhuysen and Taylor 1959) (Figure 1.1). In South Africa, *P. peringueyi* was previously known as *Palaemon pacificus*, it is found in rock pools, estuaries and in near-shore waters to a depth of 45 m (Barnard 1950). They are extremely abundant in warm temperate Eastern Cape waters, especially in summer when their numbers can reach over 1000 ind.m^{-2} in both estuaries and tidal pools (Hanekom 1982). However, they are less abundant in the cooler west coast waters, where small number of *P. peringueyi* can be found in tidal pools (Achituv and Cook 1984). In South Africa, studies on *P. peringueyi* include, population dynamics (Emmerson 1983;1985; 1986; 1987; Robertson 1984; Bernard and Froneman 2005; Froneman 2006), effect of temperature and salinity on its biology (Robertson 1984; Achituv and Cook 1984; Emmerson 1985; Allan *et al.* 2006) and aspects of its feeding ecology (Froneman 2001, 2002; Richoux and Froneman 2007; 2008; Froneman and Henninger 2010). Although these shrimps have no commercial value in South Africa (de Villiers *et al.* 1999), research on their feeding dynamics in estuaries indicate that they form an important link in the food chain between the phytoplankton, detritus and associated bacteria on which they feed and, the fish species which prey on them (Day *et al.* 1954; Millard and Harrison 1954; Emmerson and Baird 1982; Froneman and Henninger 2010). Predators of these shrimps include common Eastern Cape fishes such as the kob (*Argyrosomus hololepidotus),* white steenbras *(Lithognathus lithognathus),* shad *(Pomatomus saltatrix),* garrick *(Lichia amia),* yellowbelly rockcod *(Epinephelus guaza)* and spotted grunter *(Pomadasys commersonnii)* (de Villiers *et al.* 1999).

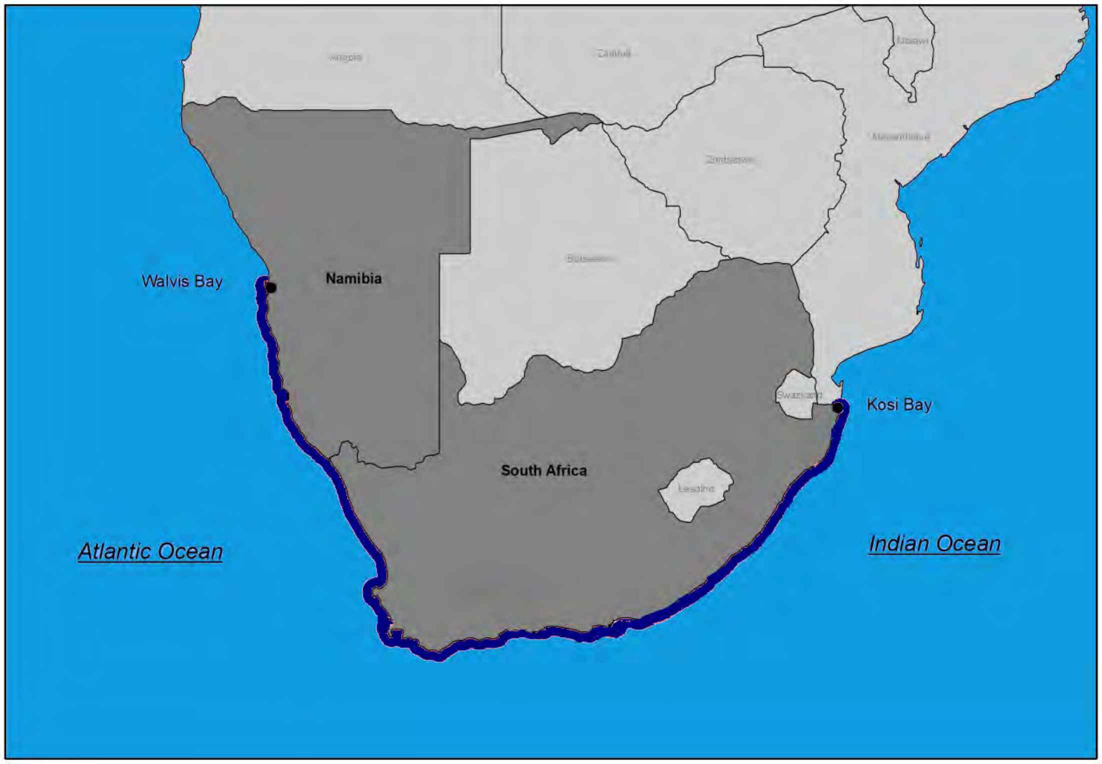


Figure 1.1: The geographic distribution of *Palaemon peringueyi* as mentioned in the text.

1.1. Life cycle and recruitment of *P. peringueyi*

The life cycle of *P. peringueyi* includes both marine and estuarine phases (Emmerson 1983). The shrimp has an adult marine phase and a juvenile phase which can either be completed in estuaries or in rock pools (de Villiers *et al.* 1999; Bernard and Froneman 2005). Adults breed in spring in the nearshore marine waters and where larval development also occurs (Emmerson 1985b; 1986). However, Robertson (1984) recorded stage 6 and post-larval *P. peringueyi* migrating from the breeding grounds into estuaries and rock pools on nocturnal tides throughout the year. The inconsistency in the recruitment of juvenile *P. peringueyi* into estuaries probably indicates that recruitment may vary yearly. The shrimps are usually between the length of 6 and 10 mm (TL) when they recruit into the estuaries (Emmerson 1986; de Villiers *et al.* 1999). A peak recruitment of juveniles into estuaries and tidal pools occurs during summer (November/December) with a smaller peak in winter (August) (Emmerson 1983). The juveniles spend ~9 months in these nursery habitats (Wooldridge 1999). When the shrimps reach a total length of between 30 to 40 mm, they begin emigration from estuaries to the marine environment (Emmerson 1983). The shrimp can reach a total length of *c.* 65 mm and females can produce between 400 and 1600 eggs depending on the size (de Villiers *et al.* 1999).

Palaemon peringueyi is more abundant in permanently open estuary (POEs) than in temporarily open closed estuaries (TOCEs) (Whitfield and Bate 2007). The lower abundance in TOCEs is due to the presence of the sand bar across the mouth which prohibits the recruitment of shrimps into these systems (de Villiers *et al.* 1999; Whitfield and Bate 2007; Bernard and Froneman 2005). A study by Bernard and Froneman (2005) found that the abundance and biomass of *P. peringueyi* in the temporarily open closed West Kleinemonde Estuary is between 0 and 14.3 individuals per m^2 ($ind.m^{-2}$) and between 0 and 5.9 g $wwt.m^{-2}$, respectively. These estimates were lower than those found in the permanently open Swartkops, Kromme and Sundays River estuaries where abundance levels of between 28 and 200 $ind.m^{-2}$ and a biomass of between 1 and 15.3 g $wwt.m^{-2}$ were recorded (Emmerson 1986) (see Table 5.1 for conversions of dry mass to wet mass). The low abundance and biomass in the West Kleinemonde were due to mouth closure and limited habitat availability in the form of submerged macrophytes beds (Bernard and Froneman 2005). In TOCEs, recruitment of *P. peringueyi* takes place during breaching and storm surge over topping events (Froneman 2006; Whitfield *et al*. 2008), although the magnitude of recruitment during over topping is lower than that of breaching (Whitfield and Bate 2007). Breaching events can result in a mass recruitment of juveniles into the estuary (Whitfield and Bate 2007).

Estuaries represent important nursery areas for juveniles of many marine breeding vertebrate and invertebrate species (McHugh 1967; Staples 1980; Wallace *et al.* 1984; Primavera 1998) and therefore estuarine nursery areas are important in the life cycle of many marine organisms including fishes and shrimps (McHugh 1967; Brito and Pena 2007). Estuarine habitats provide advantages over marine environments in terms of abundance of high vegetation cover and food (Clark 1974; Cushing 1975). Many studies indicate that once the shrimps enter the estuarine environment, a particular species tends to prefer a biotope with specific physical characteristics as its final nursery habitat (Williams 1958; Gunther 1961; Hughes 1966; Young 1978). Juveniles of *Penaeus aztecus* and *P. setiferus* prefer *Spartina alterniflora* over non-vegetated substrata, while juveniles of *Metapenaeus stebbingi*, selected the swash zone with bare sandy substratum as its nursery. *Penaeus semisalcatus* was found in intertidal flats in areas covered with submerged seagrass, *Marsupenaeus japonicus* in intertidal flats in bare, sandy mud to muddy sand areas, *Fenneropenaeus indicus* and *P. monodon* preferred mangrove swamps while *M. monoceros* was found from areas of submerged macrophytes to the deeper reaches of mangrove swamps (Giles and Zamora 1973; de Freitas 1986). The caridean shrimp *P. peringueyi* has been found by many authors to be associated with submerged macrophytes (Robertson 1984; Emmerson 1986) while the brown shrimp juveniles *Crangon crangon* use tidal flats as nurseries (Beukema 1992).

1.2. Association of *P. peringueyi* with aquatic macrophytes

Palaemon peringueyi has been cited as the single most important vagile invertebrate associated with *Nanozostera* beds (Emmerson 1983). Seagrass meadows are extremely productive areas (Thyler *et al.* 1975); they support diverse and abundant assemblages of macrofauna and provide nursery areas for fish and crustaceans worldwide (Kikuch 1980; Young 1981; Pollard 1984). Decapod crustaceans have been shown to form a conspicuous component of the assemblage of seagrass macrofauna (Young and Wadley 1979). It has also been suggested that caridean shrimps may play an essential role in determining the structure and dynamics of communities in seagrass as they often occur in great densities (Kikuchi 1974; Hooks *et al.* 1976). Emmerson (1983) showed that the abundance of shrimps in estuaries investigated was strongly associated with the presence and percentage cover of submerged macrophytes and that the loss of *Nanozostera* beds in the Kromme Estuary by siltation during flooding was followed by a period of decreased numbers of *P. peringueyi*. These submerged macrophytes are thought to restrict predator access to adults and juveniles, and are also areas of increased food availability (Emmerson 1986; 1987; Rozas and Odum 1987; Knieb and Wagner 1984; Walsh and Mitchell 1998; Adams *et al.* 1999).

1.3. Effect of temperature and salinity on the distribution of *P. peringueyi*

Water temperature is an important environmental factor for shrimps and other invertebrates (Rahman *et al.* 2007). It has a direct influence on metabolic rate, growth, survival, moulting rate, requirement of dissolved oxygen, tolerances to ammonia-N and the immune response of shrimps (Wyban *et al.* 1995; Vijayan and Diwan 1995; Ponce-Polafox *et al.* 1997; Le Moullac and Haffner 2000; Tian *et al.* 2004; Cheng *et al.* 2005; Zhang *et al.* 2006; Allan *et al.* 2006). *Palaemon peringueyi* is able to remain active and grow between temperatures of 10 and 30 °C and salinities (practical salinity unit) of between 10 and 50 (Robertson 1984; deVilliers *et al.* 1999). Temperatures > 30 °C tend to be lethal (Robertson 1984; de Villiers *et al.* 1999; Allan *et al.* 2006).

Achituv and Cook (1984) found that 25 °C is the optimum temperature for the growth of *P. peringueyi* and suggested that the shrimps may prefer warmer water over the cold waters of the west coast, while Robertson (1984) found that post-larvae and sub-adults of *P. peringueyi* are intolerant of temperature > 32 °C. Robertson (1984) also indicated that temperatures less than 4.3 °C are lethal for the shrimps.

Salinity plays an important role in determining species distribution within estuaries (de Villiers *et al*. 1999). Schmidt-Nielsen (1983) and Spanopoulos-Hernándeza *et al.* (2005) demonstrated that salinity places an osmoregulatory demand on aquatic organisms. In sub-tropical estuaries, *P. peringueyi* is replaced in low salinities by *Macrobrachium equidens* and *Caridina nilotica* both of which extend to freshwater environments (Day 1981a). Allan *et al.* (2006) found that increased salinity was associated with an increase in the respiration rate of *P. peringueyi*, while Kirkpatrick and Jones (1985) showed that *P. peringueyi* suffered mortalities in salinity less than 5. A comparison of *Palaemon affinis* to other *Palaemon* species was conducted by Kirkpatrick and Jones (1985). Results showed that *Palaemon* species that inhibit marine or brackish water are unable to tolerate low salinities. Emmerson (1986) suggested that mortalities at lower salinities may suggest that the upper distribution of *P. peringueyi* may be reduced by physiological tolerances, particularly in permanently open estuaries with sustained freshwater inflow.

In most cases, changes in temperature and salinity occurs together (de Villiers *et al.* 1999). Temperature and salinity are important variables that affect the physiological response of most invertebrates (Schmidt-Nielsen 1983). Most studies on the effect of temperature and salinity on crustaceans including penaeids show that survival peaks at temperature and salinity near those of their natural habitat (e.g. Lester and Pante 1991). Robertson (1984) showed that high temperatures and low salinity combinations resulted in mortalities of *P. peringueyi*. The shrimps suffered mortalities after 144 hours of exposure to low temperature (10 °C) and low salinity (≤ 4) while survival at low salinities was best at 15 °C (Robertson 1984). Allan *et al.* (2006) also demonstrated that at salinities < 5 and four temperatures (15, 20, 25, 30 º C) *P. peringueyi* suffered a 100 % mortalities.

1.4. Objectives and thesis structure

The caridean shrimp *P. peringueyi* can be dominant component of hyperbenthos within southern African estuaries (de Villiers *et al.* 1999; Bernard and Froneman 2005). Hyperbenthos are important in linking the benthic and pelagic foodwebs (Perissonotto and McQuaid 1990). Although the shrimps have no commercial value in South Africa, they represent an important component in the diet of commercially importance estuarine fishes (de Villiers *et al.* 1999). The shrimps also play asn important role in the export of organic matter in estuaries (Froneman and Henninger 2010). It is important to gain a better understanding on the ecology of the shrimp in estuaries and the role they play in foodwebs. In POEs, *P. peringueyi* is more abundant in the lower and middle reaches of these systems (Emmerson 1986). The reduced abundances of the shrimps in the upper reaches of POEs may be due to physiological intolerances (Kibirige and Perissinotto 2003; Bernard and Froneman 2004). Most South African permanently open estuaries have been affected by anthropogenic changes due to abstraction of freshwater input. These anthropogenic changes result in some estuaries experiencing hypersaline conditions, low nutrient concentrations and elevated water temperatures. More studies are needed to determine how reduced freshwater input affects the biota of estuaries. This study aimed to:

1. Assess the spatial and temporal patterns in the abundance and biomass, and size structure of *Palaemon peringueyi* in the permanently open freshwater deprived, Kariega Estuary. This will enable us to determine how the shrimps are distributed in the Kariega Estuary and which physiological and biological factors play an important role in structuring the shrimp community.

2. Investigate the feeding of *P. peringueyi* in the Kariega Estuary using stable carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$), to determine the diet of the shrimp and to gain information on the regions that represent important sources of dietary carbon for the shrimp in the estuary.

A complete description of the study site is presented in Chapter 2. In addition, South African estuaries, climatic and coastal dynamics of the Eastern Cape Province is presented. In Chapter 3, spatial and temporal patterns in the abundance and biomass, and distribution of size structure of *P. peringueyi* is investigated. The feeding aspect of the shrimps in the Kariega Estuary using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes is presented in Chapter 4. Lastly, Chapter 5 presents a general discussion in which possible future studies are suggested.

Chapter 2

Study Site

2.1. South African estuaries

Initially, Pritchard (1967) defined an estuary as 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 from land drainage". However, the problem with this definition is that it focused on the features of northern hemisphere estuaries and did not take into account certain characteristics of many South African (Day 1980) and south Australian estuaries (Hodgkin and Lenanton 1981; Roy *et al.* 2001), such as separation from the sea due to formation of a sand bar across their mouths and that some of these systems become hypersaline during dry periods when evaporation becomes high (Potter *et al.* 2010). This has led to Day (1980) to redefine an estuary as a "semi-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 mixture of seawater with freshwater derived from land drainage". Although Day (1980) definition of an estuary can be accepted, Potter *et al.* (2010) suggests that this definition can be applied in microtidal, mesotidal and macrotidal systems of both the northern and southern hemisphere. Potter *et al.* (2010) further suggested that Day's (1980) definition requires modification to emphasise that some freshwater input into the estuary must be derived from the rivers and that occasionally salinities can exceed that of full-strength sea water. This led to Potter *et al.* (2010) to propose the following definition of an estuary: "An estuary is a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river and thus while its salinity is typically less than that of natural sea water and varies temporally along its length, it can be hypersaline in regions when evaporative water loss is high and freshwater and tidal input are negligible".

In South Africa, different terminologies have been used to describe the same type of estuaries. Begg (1978) and Bird (1984) described temporary closed estuaries as "lagoons", Day (1981) as "blind estuaries" and, Bennett (1989) as "seasonally open" and "normally closed" estuaries. This confusion of terminology in South African estuaries led Whitfield (1992) to classify South African estuaries into five classes based on physiological, hydrographical and salinity characteristics. Whitfield (1992) classified South African estuaries into: river mouths, estuarine bays, estuarine lakes, permanently open estuaries, and temporarily open closed estuaries. According to Reddering and Rust (1990), common features of South African estuaries are:

i. "Most are small with a tidal prism of 10^6 m^3 or less".

ii. "Mostly developed from a drowned river valley, only a few developed from coastal plains".

iii. "Tidal inlets are constricted or blocked by a sand bar".

iv. "They have well developed flood tidal deltas while the ebb deltas are poorly developed".

Between two successive high and low tides, the maximum tidal range of the South African coast is ≈ 2 m, while most estuaries have a range of less than 1.5 m. This has led to the description of South African estuaries as microtidal inlets (Whitfield 1998).

2.2. Permanently Open Estuaries (POEs)

In South Africa, only about 25 % of estuaries are permanently connected to the sea (Whitfield 1998). These systems are characterised by a moderate tidal prism with the horizontal salinity gradient and vertical salinity stratification being dependent on factors such as bathymetry, tidal cycle and river inflow (Mackay and Schumann 1990). Water column mixing of these systems is usually driven by tidal and riverine currents and they have a mean salinity of between 15 and 35 (Whitfield 1998). However, salinities of > 40 have been recorded in the upper reaches of POEs with little freshwater inflow e.g. Kromme, Bushmans and Kariega Estuaries, or during periods of drought (Whitfield 1998). Permanently open estuaries usually have a catchment area larger than 500 km^2 and their rivers naturally have perennial flow (Whitfield 1998). The large tidal prism and river inflow play a significant role in maintaining an open mouth (Whitfield 1998). As a result of the semi-arid climate of the Eastern Cape Province, most rivers have been impounded to meet the water demand of the South African population; this has resulted in reduced freshwater inflow into estuaries (Davies *et al.* 1993). The low freshwater inflow together with high evaporation rates in summer have resulted in hypersaline conditions (> 45) in the upper reaches of some estuaries in the Southern and Eastern Cape Provinces (Whitfield 1998). Anthropogenic alterations in estuaries redirect the natural flow and change the patterns of freshwater discharge (Gillanders and Kingsford 2002). Reduced riverine inputs may change water chemistry and sediments which in turn, affects the biota of these systems (Gillanders and Kingsford 2002). Long term reduction of freshwater input has been shown to change the biota of Eastern Cape POEs (Whitfield 1998), such as a decline in phytoplankton in the water column (Grange and Allanson 1995). Adams *et al.* (1999) found that the Kariega Estuary has lower primary production rates when compared to the freshwater sustained Great Fish River. Chlorophyll-*a* concentrations in the Kariega Estuary ranged between 1 and 8 µgL^{-1} and between 0 and 52 µgL^{-1} in the Great Fish River (Adams *et al.* 1999). During a period of increased freshwater inflow, the Great Fish River showed higher phytoplankton production while seston production showed seasonal and spatial patterns which can be related to freshwater changes (Grange and Allanson 1995). Reduced freshwater inflow in a POEs can also result in an increase in macrophytes such as *Nanozostera capensis* (Adams and Tallbot 1992) and a reduction in zooplankton production which in turn, results in a decrease of fish stocks such as *Gilchristella aestuaria* (Whitfield and Harrison 1996). Low freshwater input results in higher salinity, lower turbidity and an increases light penetration which promotes growth of eelgrass beds (Allanson and Read 1995). Zooplankton densities are associated with an increased in phytoplankton production as a result of increased freshwater inflow (Wooldridge 1999; Grange *et al.* 2000).

2.3. Climate

According to Stephenson and Stephenson (1972) and de Villiers *et al.* (1999), the South African coastline can be divided into three climatic regions. The cool-temperate region from the west coast to Cape point, a warm temperate region from Cape Point to the Mbashe River, and a sub-tropical region on the east coast from the Mbashe to Mozambique. The site of the current study is located within the warm temperate region approximately 30 km west of Port Alfred. Rainfall in this region is predominantly in summer (Heydorn and Tinley 1980; Day 1981a). The coastal town of Port Alfred in close proximity to the Kariega Estuary has weather information (Stone *et al.* 1998). As a consequence, climatic data for the estuary will be similar to that of Port Alfred.

Port Alfred experience minimum air temperatures of 10 °C (July) and maximum of 26 °C (February), and rainfall of about 600 mm per annum (Lubke 1998). Between 1996 and 2005, maximum and minimum air temperatures recorded in Port Alfred were 38.5 °C (March 2003) and 1.9 °C (July 2002) (as measured at 08h00, South African Weather Bureau records, *in litt.*). Rainfall in this region has an autumn spring bimodal pattern, with a spring peak (Kopke 1988). Mean annual rainfall recorded in Port Alfred between 1996 and 2005 was 604 mm with a maximum (731 mm) recorded in 1998 and a minimum (396 mm) recorded in 1999 (South African Weather Bureau records, *in litt.)*.

2.4. Coastal dynamics

Ocean currents have been shown to affect coastal climates, sea temperature and upwelling (Lubke 1998). The Agulhas Current influences the Eastern and Southern Cape coast (Lutjeharms 1998). It is formed by waters from the Mozambique Channel which is joined by those of East Madagascar Current, carrying warm waters southwards to form the Agulhas Current (de Ruiter *et al.* 2004; Lutjeharms 2006). The Agulhas Current is supplied with water from two different sources, the

South Equatorial Current and recirculation in the south western Indian Ocean sub-gyre (Stramma and Lutjeharms 1997). The Agulhas Current flows past the southern tip of Africa and retroflects to carry most of its water eastward as the Agulhas Return Current (Lutjeharms 1998) (Figure 2.2).

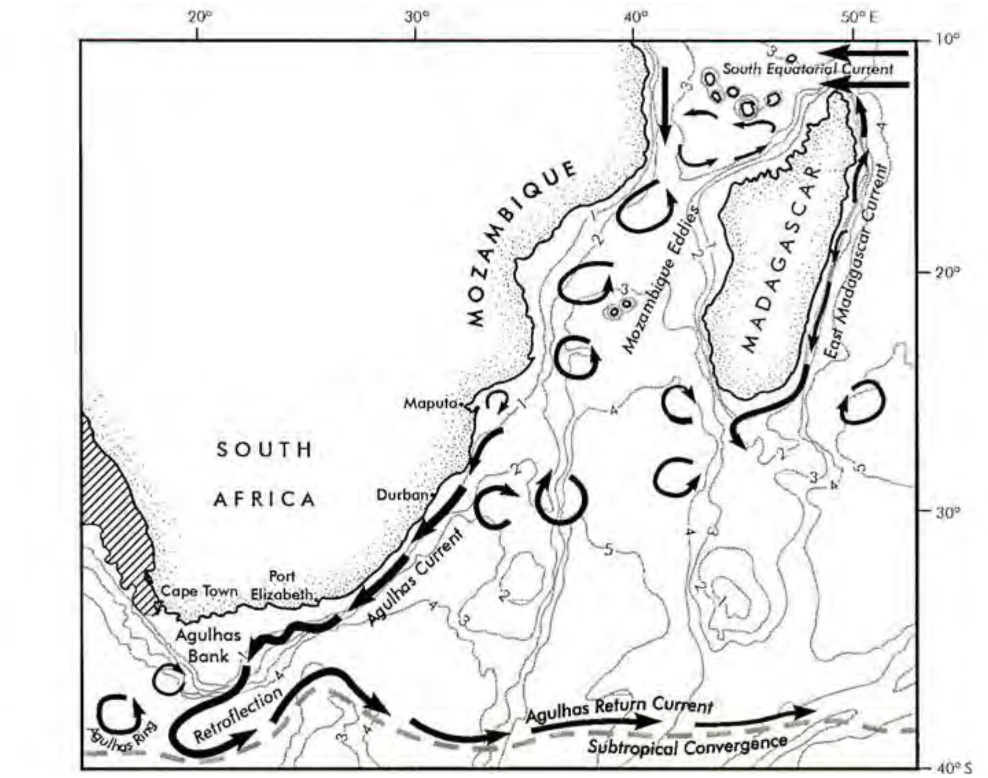


Figure 2.1: The flow direction of the Agulhas Current in the Indian Ocean (After Lutjeharms 2005).

Lutjeharms *et al*. (2000) and Lutjeharms (2007) recognised two upwelling regions within the Agulhas Current, one situated in KwaZulu-Natal and the other near Port Alfred which is in close proximity with the study area. Both of these upwelling regions occur due to the widening of the continental shelf and jet effect on the inshore edge of the current pulling deeper water towards the surface and close to the coast (Vorwerk 2006). The upwelled water characterised by elevated nutrients and oxygen concentrations may periodically penetrate into the permanently open estuaries within the region and contribute to elevated rates of primary and secondary production within these systems (Schumann *et al.* 1999). For example, cold and nutrient rich water has been recorded in the Kariega Estuary after an upwelling event (Taylor 1992). An estimate of the volume flux of the Agulhas Current is about 65 million m^{-3} sec^{-1}, the current may reach a speed of 2 m sec^{-1} on the surface which is considered very high for a deep sea current (Lutjeharms 1998). On the sea surface the current is about 60 to 100 km wide and temperatures range between 28 ˚C in summer and 20 ˚C in winter (Lutjeharms 1998). Seasonal changes in temperature can only penetrate the upper 100 m to 200 m (Lutjeharms 1998). The upwelling cells and eddies are associated with the Agulhas Current and have been demonstrated to influence coastal rainfall and storm patterns along the coastal zone (Perissinotto *et al.* 2000; Froneman 2004).

2.5. Description of the estuary and study site

The Kariega Estuary is a permanently open estuary situated on the southeast coast of South Africa (33˚41' S 26˚ 42' E). The catchment size of the estuary is relatively small with a total area of ~ 686 km^2 (Paterson and Whitfield 1997). The system is 17.4 km long with an average width of 110 m and a depth of < 3 m (Taylor and Allanson 1995). The width of the channel in the upper reach of the estuary is between 40 and 60 m (Jennings 2005).

The Kariega Estuary is a marine dominated system with a 106:1 ratio of tidal prism volume to river volume (Grange *et al.* 2000). The system has been impounded by three dams, the largest being the Settlers Dam situated 50 km from the mouth (Jennings 2005). The mean annual runoff of the Kariega catchment is estimated to be 15×10^6 m^3 per annum (Grange and Allanson 1995). The semi-arid climate of the Eastern Cape and the construction of dams in the catchment have resulted in little or no freshwater inflow into the estuary over the past three decades (Grange *et al.* 2000). This has led to development of hypersaline (> 40) conditions in the upper reaches of the estuary (Jennings 2005). The absence of freshwater inflow has resulted in limited salinity or thermal stratification in the water column (Grange and Allanson 1995; Grange *et al.* 2000), a uniformly marine system with salinity of ~ 35 throughout the lower and middle reaches and a well-mixed water column with low turbidity (Hodgson 1987; Allanson and Read 1995).

Salinity in the Kariega Estuary during the year 2009 ranged between 33 and 44 and maximum and minimum water temperature recorded was 26.4 ± 2.6 ˚C in summer and 14.5 ± 0.7 ˚C in winter with the highest value recorded in the upper reaches for both variables (Heyns and Froneman 2010). The Kariega Estuary is considered as being oligotrophic as the result of low freshwater input (Grange and Allanson 1995). The concentration of chlorophyll-*a* (chl-*a*) in the water column is < 2 $\mu g.L^{-1}$ which is mostly dominated by nanõ (2 to 20 µm) and picophytoplankon (0.45 to 2 µm) size classes (Froneman 2000). The low nutrient concentrations in the Kariega has resulted in low zooplankton abundance (50 $ind.m^{-2}$) when compared to the freshwater sustained Great Fish River within the same geographical region (256 to 4253 $ind.m^{-2}$) (Grange *et al.* 2000). The Kariega Estuary was assessed as being in good condition in terms of ichthyofaunal communities, and the water quality in a moderate condition (Harrison *et al.* 2000). The low freshwater input in the system contributes to high abundance of macrobenthic organisms particularly crustaceans such as *Cleistostoma edwardsii*, *C. algoense*, *Upogebia africana*, *Sesarma catenata* and *Uca urvillei* and the bivalve *Solen cylindraceus*, compared to other Eastern Cape estuaries (Hodgson 1987). This elevated abundance was due to the growth of the eelgrass beds along the entire length of the system (Hodgson 1987). The marine dominance in the Kariega Estuary has resulted in the eelgrass *N. capensis*, occurring along the entire length of the estuary as a littoral band around the spring low tide level (Ter Morshuizen and Whitfield 1994). The eelgrass beds in the system vary in width from approximately 5.2 m in the lower reaches to 3.3 m in the upper reaches (Ter Morshuizen and Whitfield 1994). Other macrophytes dominating the estuary include the salt marsh plants *Spartina maritima*, *Sarcocornia perennis* and *Chenolea diffusa* which occupy the lower and middle reaches (Paterson and Whitfield 1997). These salt marshes are important in exchanging carbon, nitrogen and phosphorous with the adjacent estuary (Taylor 1987).

Most studies in the Kariega Estuary have focused on community patterns of fish (Whitfield 1994; Paterson and Whitfield 1997a; Bate *et al.* 2002; Whitfield and Paterson 2003; Richardson *et al.* 2006; Vorwerk *et al*. 2007), invertebrates (Hodgson 1987; Froneman and McQuaid 1997; Froneman 2002; Heyns and Froneman 2010), and food web structures (Paterson and Whitfield 1997; Froneman 2000; 2001; Richoux and Froneman 2007; 2008). There have been a few autecological studies conducted in the Kariega Estuary. de Villiers (1989) investigated the feeding dynamics of the bivalve *Solen cylindraceus* using stable carbon isotopes ($\delta^{13}C$). The results of the study found that the bivalve had depleted $\delta^{13}C$ values compared to the dominant macrophytes (*N. capensis* and *Spartina maritima*). The results also suggested that terrestrial vegetation may have contributed to the depleted $\delta^{13}C$ isotopes of the bivalve. Taylor and Allanson (1993) investigated the impact of crabs (*Sesarma catenata* and *Cleistostoma edwardsii*) on carbon exchange in salt marshes of the Kariega Estuary (*S. maritima*, *S. perennis* and *Chenolea diffusa*). The results showed that both crabs enhanced carbon losses relative to uptake by the salt marshes. When crabs were absent, the salt marsh acts as a carbon sink and when crabs were present, the salt marsh functioned as a carbon source. Marshall and McQuaid (1994) investigated the seasonal (summer and winter) and diel variations of in situ heartbeat of the limpet *Siphonaria oculus*. They found that the heart rate in the air was not significantly different from submerged limpets and that heart rate was significantly lower at night than during the day.

Froneman (2001) conducted a study the feeding of the mysid *Mesopodopsis wooldridgei* using *in vitro* incubations and the gut fluorescent technique. The results of the study suggested that the diet of the mysid changes with age and that this may be due to inability of adults to feed on the small phytoplankton cells (< 10 µm) which dominate the total chlorophyll-*a* in the estuary. Finally, Vorwerk *et al.* (2007) investigated the recovery of the pipefish *Syngnathus watermeyeri* within the estuary. The pipefish was recorded for the first time in the estuary after 4 decades. Their presence was attributed to the heavy rainfall which resulted in mesohyline (5 to 18) conditions and increased food availability.

To date, no autecological studies have been conducted on *P. peringueyi* in the Kariega Estuary. These shrimps form an important component of hyperbenthos in temperate estuaries (Bernard and Froneman 2005); they play a role in the nutrient dynamics within estuaries (Froneman and Henninger 2010) and are prey of several estuarine fishes (Whitfield 1998). This current study aims to provide further information on the role that these shrimps play in estuaries.

Chapter 3

Population dynamics of the caridean shrimp *Palaemon peringueyi* (Decapoda; Caridea) in the permanently open Kariega Estuary.

3.1. Introduction

South Africa has only about 25 % of estuaries that are permanently connected to the sea (Whitfield 1998) most of which are threatened by reduction of freshwater input as a result of impoundments (Whitfield 2005). Because of the semi-arid climate and the growing population in South Africa, most rivers have undergone anthropogenic disturbance mostly due to impoundments (Davies *et al.* 1993). These impoundments contribute to reduced freshwater inflow into estuaries which has negative effects on the estuarine food webs within these systems (Whitfield and Bruton 1989).

The Kariega Estuary is regarded as a permanently open freshwater deprived system (Hodgson 1987). The low freshwater inflow into this estuary often contributes to hypersaline conditions (>40) in the upper reach of the system (Heyns and Froneman 2010). It has been demonstrated that a natural river flow is required for estuarine communities to function optimally (Ter Morshuizen *et al.* 1996; Froneman 2002; Garcia *et al.* 2003; Kibirige *et al.* 2006). Vorwerk (2006) further demonstrated strong links of volumes of freshwater inflow into estuaries and the biota in the near-shore environment.

Palaemon peringueyi is a common component of the hyperbenthos within permanently open (POEs) and temporarily open closed estuaries (TOCEs) (de Villiers *et al.* 1999; Bernard and Froneman 2005) along the coastline of southern Africa. Comparative studies of population dynamics in estuaries (de Villiers *et al.* 1999; Bernard and Froneman 2005; Froneman 2006) indicate that the shrimp is most abundant in POEs. The lower abundance in TOCEs is due to the presence of a sandbar across the mouth which reduces recruitment opportunities and the limited habitat availability (beds of submerged macrophytes) (Bernard and Froneman 2005).

In those estuaries studied to date, *P. peringueyi* is more abundant in the lower and middle reaches (Bernard and Froneman 2005; Froneman 2006). The reduced numbers of shrimps in the upper reach may be due to physiological tolerances (Allan *et al.* 2006) and / or the limited percentage cover of aquatic macrophytes (Bernard and Froneman 2005). The marine dominance in the Kariega Estuary has resulted in macrophytes such as *Nanozostera capensis* extending into the upper reach of the estuary (Paterson 1999). Therefore it is expected that *P.peringueyi* will occur further upstream within the Kariega Estuary. Although some work has been undertaken in South Africa on the ecology and biology *P. peringueyi* in POEs (Emmerson 1983; 1985; 1986; Robertson 1984) and TOCEs (Bernard and Froneman 2005; Froneman 2006), there is little information on the community structure and distribution of this species in freshwater deprived systems. More studies are required to gain a better understanding of how the absence or reduced freshwater input into an estuary affects the ecology of the shrimps.

This study aims to:

1. Assess the spatial and temporal patterns in the abundance and biomass of *P. peringueyi* in the freshwater deprived Kariega Estuary.
2. Assess the size structure and distribution of *P. peringueyi* along the length of the estuary.
3. Compare whether the abundance, biomass and size structure of *P. peringueyi* in the Kariega Estuary are in the same range as that reported in the other POEs such as Kromme and Swartkops estuaries which are in the same biogeographic region.

3.2. Materials and Methods

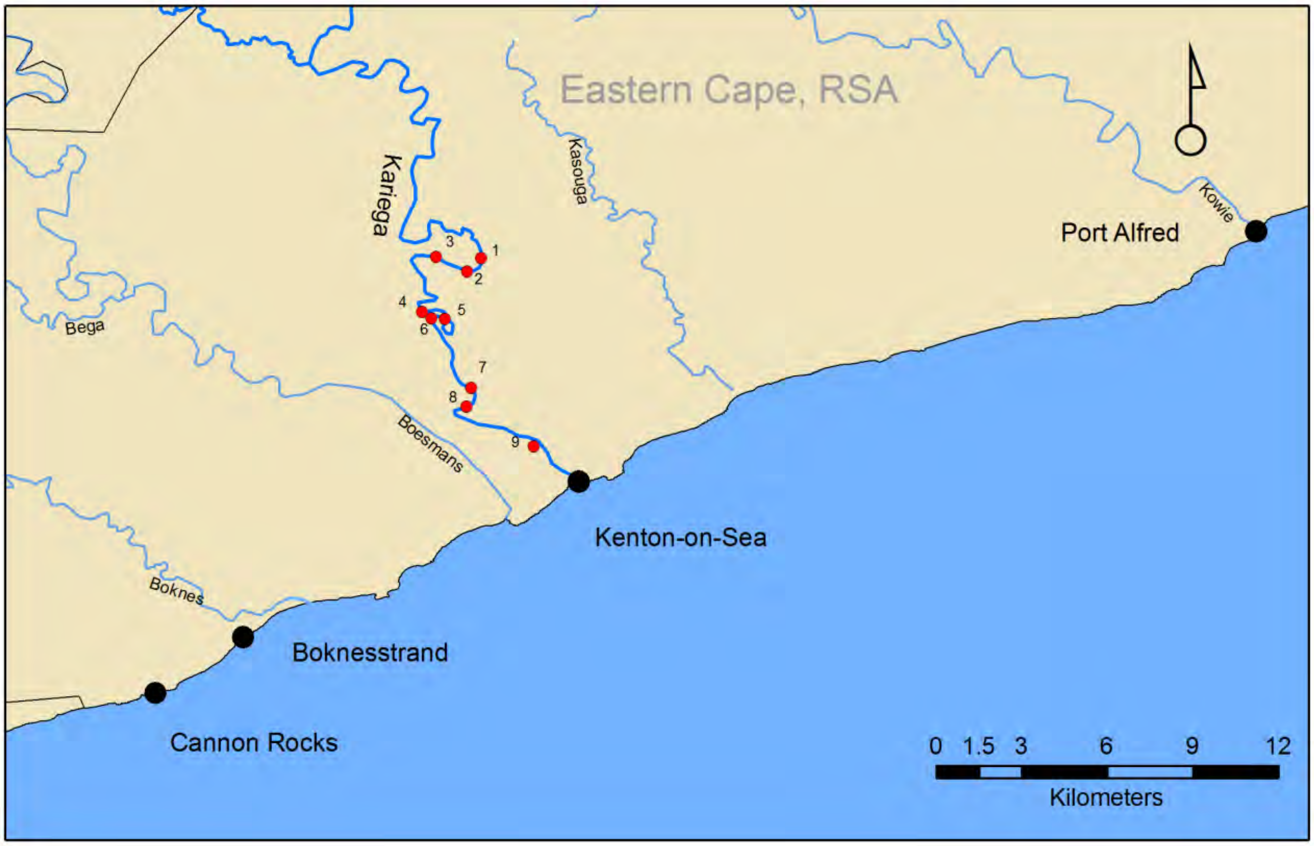


Figure 3.1: Positions of the sampling sites (1 - 9) located in the upper (1 - 3), middle (4 - 6) and lower (7 - 9) reaches of the Kariega Estuary.

3.2.1. Determination of sampling technique for *P. peringueyi*

To determine the most efficient method for sampling shrimps, in August 2010 a survey was undertaken to compare the difference in catch per unit effort (CPUE) between two sampling techniques. The sampling methods used were 1) a net with a triangular opening (area 0.6 m^2, mesh size 1 mm) at the end of a 1.5 m long pole (hereinafter referred to as a pull net) dragged for a distance of 1.5 m, and 2) a benthic sled (mouth area 0.5 m^2, mesh size 1 mm) pulled for a distance of 5 m. Five replicates were collected with each sampling technique with a total area of 3 m^2 sampled for the pull net and 2.5 m^2 for the benthic sled. The sampling was undertaken in the lower reach of the Kariega Estuary (Site 9) (Figure 3.1) in areas covered by seagrass beds, mostly *N. capensis*. Sampling was conducted during low tides in a water depth of approximately 0.4 m. Visual estimates of the submerged vegetation cover (% cover in a 30 cm x 30 cm quadrat) were made. All shrimps collected were preserved in 10 % formalin for later analysis.

In the laboratory, shrimps were counted and abundance (per m^2) was determined by dividing the number of shrimps caught with the total area sampled. To obtain the biomass (per m^2), wet weight was measured to two decimal places of a gram by blotting the shrimps with paper towel and weighing the shrimps on a Sauter AR 100 microbalance, and then by dividing the weights by the area sampled. Mean abundance (individuals per m^2) and biomass (grams wet weight per m^2) for each sampling method were calculated.

The carapace length (CL) of all shrimps (region from the anterior tip of the rostrum to the dorsal midline of the posterior margin of the carapace), was measured in mm using a digital Vernier calliper. The sex of each shrimp, determined by the presence (male) or absence (female) of an appendix masculine (A.M.) on the endopod of the second pleopod was recorded with the aid of a dissecting microscope. The sex of the male *P. peringueyi* could only be identified in individuals with CL > 9 mm. Therefore all shrimps with CL < 9 mm were considered as juveniles (Bernard and Froneman 2005).

3.2.2. Population dynamics

Quantitative samples were collected monthly from all nine sites within the Kariega Estuary, from September 2010 to August 2011(Figure 3.1). Since the pull net resulted in a significantly higher number of animals caught (Section 3.3.1), this method was used to collect the shrimps throughout the sampling period. Three replicate samples (pull net distance was 1.5 m, sample area = 0.9 m^2) were collected from each site. The samples were always collected at low tide. Since it was not possible to sample in the same water depth, water depths during the sampling period ranged between 0. 3 to 0.6 m. The shrimps were collected in an area covered by submerged aquatic macrophytes and processed as described in section 3.2.1.

3.2.3. Physico-chemical parameters

Temperature, salinity and dissolved oxygen (DO) were measured during the morning at each site. Temperature (° C) and DO ($mg.L^{-1}$) were measured using a YSI 550 DO Probe (with a precision of 0.1 $mg.L^{-1}$), while salinity (Practical Salinity Scale) was measured using a hand held refractometer (Atago S10). Only surface water was measured since the system is well mixed (Hodgson 1987; Allanson and Read 1995; Froneman pers. comm.). The mean value (± SE) for each reach (lower, middle, upper) was then calculated from the values of the three sites within a reach.

3.2.4. Chlorophyll-*a*

Surface water was collected in 1L plastic bottles from each site in the estuary. The water samples collected were kept in a cool dark container during transportation to prevent photosynthesis. In the laboratory, total chlorophyll-*a* (chl-*a*) concentration was determined by filtering (vacuum < 5.0 cm Hg) 200 ml of water through a 47 mm Glass Fibre Filter (Macherey-Nagel). After filtration, the chlorophyll was extracted in 8 ml of 90 % acetone in the dark for 24 hours at -20 °C. The samples were then centrifuged for five minutes at 5000 rpm. Total chlorophyll-*a* concentration was then determined using a Turner Designs 10AU Fluorumeter according to the the method of Holm-Hansen and Riemann (1978). The chlorophyll-*a* concentrations were expressed as micrograms chl-*a* per litre (ug chl-*a*.L^{-1}).

3.2.5. Particulate organic matter (POM)

POM concentrations were determined by pre-weighing glass filter papers on a Sauter AR 100 microbalance with a precision of 0.0001 mg. A 500 ml surface water sample was filtered (vacuum < 5.0 cm Hg) through the pre-weighted filters. The filters were oven dried at 60 °C for 48 hours and reweighed. The difference between the weights of the filter papers was calculated and multiplied by 2 in to obtain µg POM.L^{-1}.

3.2.6. Analysis of data

Chi-squared analysis was used to determine whether there was any significant deviation from a 1:1 sex ratio of males and females at all sampling sites.

One-way ANOVA (Analysis of Variance) was used to assess the spatial and temporal patterns in the size, abundance and biomass of *P. peringueyi*. Spatial and temporal patterns in the physico-chemical parameters were also determined using ANOVA. A post-hoc test (Fisher LSD) was used to determine sources of variation. Regression analysis was used to determine the relationship between physico-chemical parameters and the abundance and biomass of the shrimps at the different stations. A t-test (independent by groups) was used to determine differences between the size (CL) of males and females. All data analysis was carried out using Statistica version 10 (StatSoft).

3.3. Results

3.3.1. Determination of sampling technique for *P. peringueyi*

There was a significant difference in shrimp abundance and biomass ($p < 0.05$) (t-tests) between the two sampling methods. A total of 216 shrimps were caught with five sweeps of pull the net whereas only 99 shrimps were caught with five tows of the benthic sled. The mean (± SD) abundances were 14.3 (± 2.5) ind.m^{-2} for the pull net and 8.08 (± 1.4) ind.m^{-2} for the benthic sled. Mean biomass was 3.1 (± 1.5) g wwt.m^{-2} for the pull net, and 2.68 (± 1.4) g wwt.m^{-2} for the benthic sled. There was no significant difference in the CL of males and females caught using the two sampling methods ($p > 0.05$) (t-test). Shrimps with a CL of between 7 to 16 mm were caught using a pull net while shrimps with CL of between 9 to 22 mm were caught using a benthic sled (Figure 3.2). The male to female sex ratio was 0.4: 1 ♀: ♂ for the pull net, and 0.5: 1 ♀: ♂ for benthic sled. There was no significant difference in male and female sex ratios between the two sampling methods ($p < 0.05$) (Chi-squared test). The sex ratios differed significantly from a 1:1 ratio (pull net: $p < 0.0001$, $X^2 = 48.3$) (sled: $p = 0.0006$, $X^2 = 11.7$) with both sampling methods (Chi-squared test).

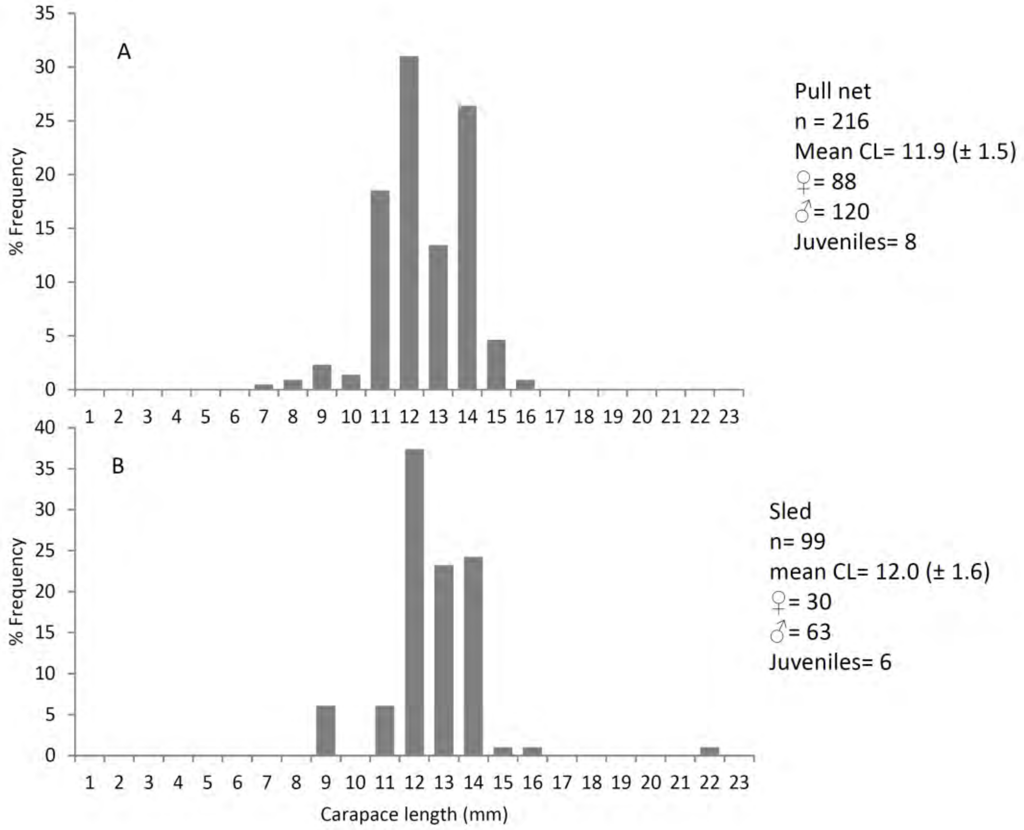


Figure 3.2: Comparison of the size structure of *Palaemon peringueyi* sampling, using (A) pull net (5 pulls) and (B) benthic sled (5 tows).

3.3.2. Population dynamics

3.3.2.1. Seasonal variations

In order to determine any seasonal variation of *P. peringueyi* during this study, sampling intervals were divided as follows: Spring = September to November (2010), Summer = December to February (2010/ 2011), Autumn = March to May (2011) and Winter = June to August (2011).

There was a significant effect of season on abundance at each site ($p < 0.05$) (ANOVA). There was also a significant effect of seasons between the sites ($p < 0.05$). A post-hoc tests (Fisher LSD) showed that in the lower reach in winter (37.1 ± 29.9 ind.m^{-2}), there were significantly more shrimps than in the other seasons (spring = 11.8 ± 7.1 ind.m^{-2}, summer = 2.7 ± 1.8 ind.m^{-2}, autumn = 9.8 ± 5.2 ind.m^{-2}). In the middle reach, there was a significantly greater abundance of shrimps in spring (10.8 ± 6.3 ind.m^{-2}) when compared to other seasons (summer = 3.3 ± 2.5 ind.m^{-2}, autumn = 6 ± 3.2 ind.m^{-2}, winter = 3.5 ± 3.1 ind.m^{-2}), and to the shrimps in the upper reach in summer (0 ind.m^{-2}) and winter (0 ind.m^{-2}). A post- hoc test showed that shrimp abundance in the upper reach (0.6 ± 0.2 ind.m^{-2}) was significantly different from the lower (15.3 ± 3.2 ind.m^{-2}) and middle (5.0 ± 0.8 ind.m^{-2}) reaches (Figures 3.3; 3.5).

There was a significant difference in biomass between the seasons and sites ($p < 0.05$) (ANOVA). A post- hoc tests (Fisher LSD) showed that in the lower reach, summer (0.5 ± 0.4 g wwt.m^{-2}) which had lowest biomass, was significantly different from other seasons (spring = 1.9 ± 1.1 g wwt.m^{-2}, autumn = 2 ± 1.1 g wwt.m^{-2}, winter = 2.1 ± 1.6 g wwt.m^{-2}). In the middle reach, biomass in spring (1.9 ± 1.2 g wwt.m^{-2}) was significantly different from the other seasons (summer = 0.6 ± 0.4 g wwt.m^{-2}, autumn = 1.4 ± 0.8 g wwt.m^{-2}, winter = 0.7 ± 0.7 g wwt.m^{-2}). In the upper reach, biomass in spring (0.7 ± 0.6 g wwt.m^{-2}) and autumn (0.3 ± 0.4 g wwt.m^{-2}) were significantly different from summer and winter. No shrimps were recorded in the upper reach in summer and winter (Figures 3.4; 3.6). A post- hoc test also showed that biomass in the lower (1.6 ± 0.2 g wwt.m^{-2}) and middle (1.1 ± 0.2 g wwt.m^{-2}) reaches differed significantly from the upper reach (0.2 ± 0.1 wwt.m^{-2}) (Figure 3.4).

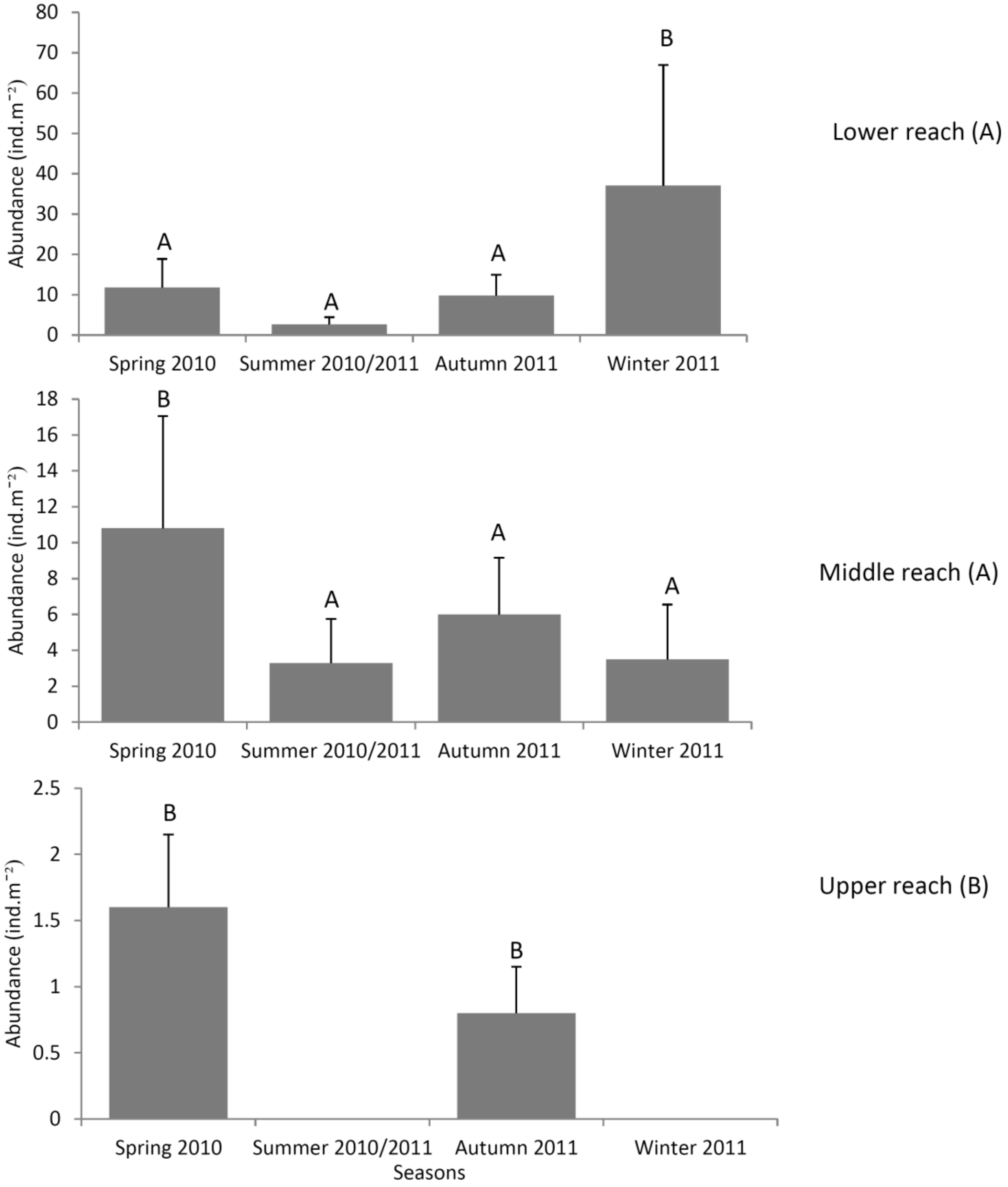


Figure 3.3: Mean (± SE) seasonal abundance (ind.m^{-2}) of *Palaemon peringueyi* in the Kariega Estuary from September 2010 to August 2011. Error bars indicate standard errors; different letters indicate significant difference ($p < 0.05$) (Note different scales on the y-axes).

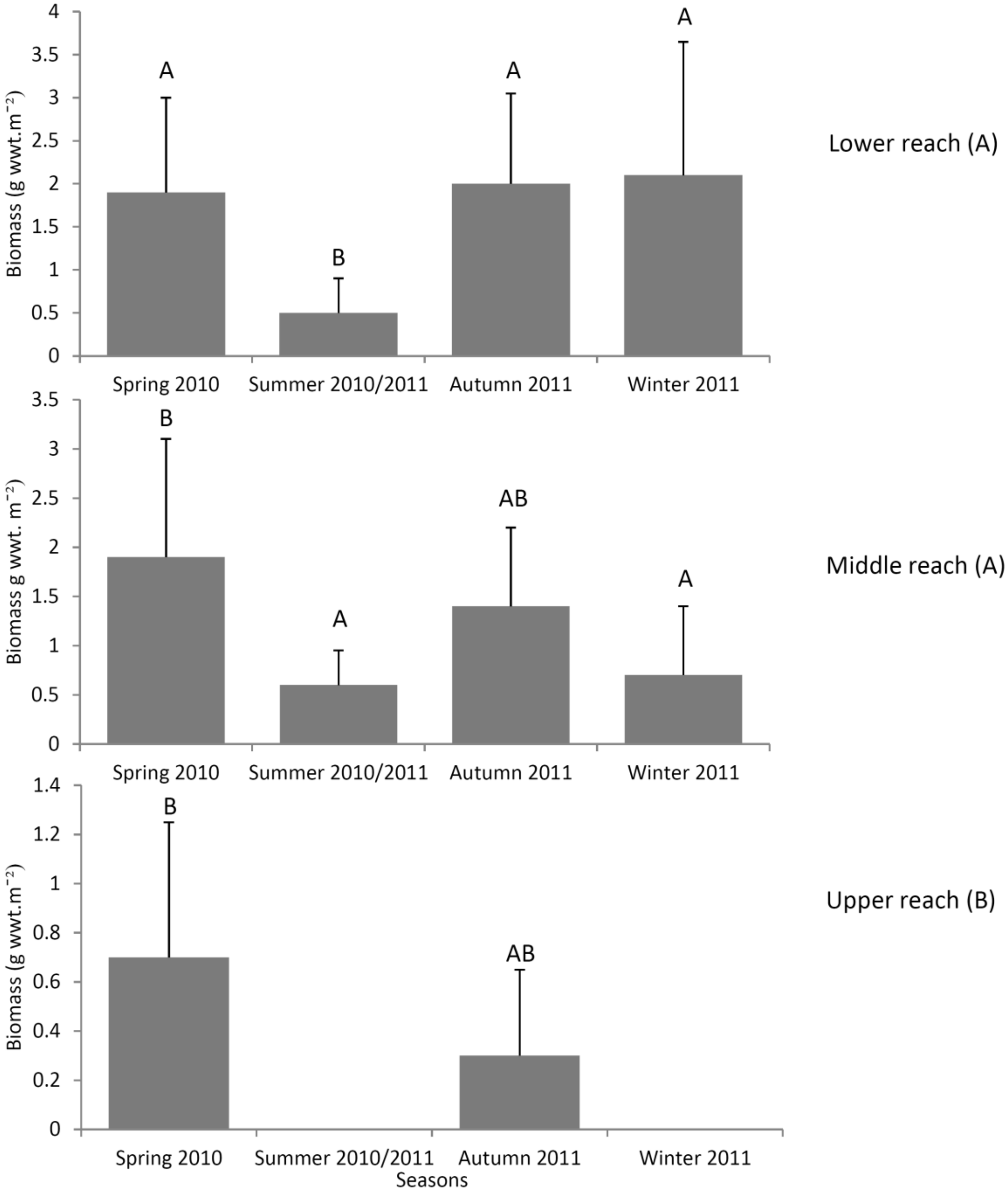


Figure 3.4: Mean (± SE) seasonal biomass (g wwt.m^{-2}) of *Palaemon peringueyi* in the Kariega Estuary from September 2010 to August 2011. Error bars indicate standard errors; different letters indicate significant difference ($p < 0.05$) (Note different scales on the y-axes).

3.3.2.2 Abundance

A total of 2096 shrimps were caught in the Kariega Estuary from September 2010 to August 2011. Of these, 1585 shrimps were recorded from the lower reach, 477 the middle reach and 34 shrimps in the upper reach of the estuary. Minimum abundances recorded in one of the tows was 0 while maximum was 245.6 ind.m^{-2} and was recorded in June in the lower reach. There was a significant difference in abundance between the months for all the regions and sites ($p < 0.05$) (ANOVA). A post-hoc test (Fisher LSD) showed that the significant difference was due to high abundance of shrimps in June in the lower reach, which was when its peak was recorded (Figure 3.5). In the middle and upper reaches, variation occurred throughout the year with some months being similar (Figure 3.4). The lower and upper reaches were significantly different from each other (Post-hoc, Fisher LSD) (Figure 3.5). In general, the lower reach had the highest mean abundances followed by the middle and upper reaches, respectively (Figure 3.5). Regression analysis did not show any significant relationships between abundance and the physico-chemical parameters (temperature, salinity and DO). There was, however, a weak positive correlation between abundance and percentage vegetation cover ($r^2 = 0.109$; $p < 0.05$) (Table 3.2; Appendix I; II).

In the lower reach, abundance decreased from September (23.3 ± 6.6 ind.m^{-2}) to February (2.6 ± 1.3 ind.m^{-2}). However, abundance increased in April to 15.6 (± 4.2) ind.m^{-2} followed by a decrease in May (9.9 ± 3.2 ind.m^{-2}). The highest mean abundance was recorded in June (88 ± 27.3 ind.m^{-2}) after which abundance declined to about 11.5 (± 6.2) ind.m^{-2} (Figure 3.5).

In the middle reach, the highest abundance was recorded in September (21.5 ± 4.5 ind.m^{-2}). This was followed by a decline up to November (0.6 ± 0.3 ind.m^{-2}), after which numbers fluctuated peaking in April (8.8 ± 2.3 ind.m^{-2}). In July abundances decreased to 1.4 ± 0.5 ind.m^{-2} (Figure 3.5).

In the upper reach, shrimps were absent on seven sampling occasions, November to February; June to August. The highest abundance was recorded in September (3.8 ± 1.1 ind.m^{-2}) after which abundances decreased until October to 1 (± 0.4) ind.m^{-2}. After a four month absence, the shrimps returned to the upper reach until May, which was when the second highest abundance was recorded (1.1 ± 0.8 ind.m^{-2}) (Figure 3.5).

Table 3.1: Results for One-way ANOVA (Statistica version 10) to examine any significant difference in abundance, biomass and carapace length (CL) between seasons, months and sites (lower, middle and upper reaches) of the Kariega Estuary.

Variation	Sum of Squares	Degree of Freedom	Mean Squares	F- ratios	P
Abundance					
Months	23013.6	11	2092.1	5.6	$p < 0.001$
Sites	1384.5	2	692.3	3.6	0.04
Abundance					
Seasons	5620.0	3	1873.3	4.5	0.004
Sites	12013.6	2	6006.8	15.2	$p < 0.001$
Biomass					
Months	247.8	11	22.5	9.2	$p < 0.001$
Sites	17.2	2	8.6	6.3	0.004
Biomass					
Seasons	57.1	3	19.0	6.4	0.0003
Sites	104.2	2	52.1	18.4	$p < 0.001$
Carapace length					
Months	73.1	11	6.7	1.2	0.3
Sites	37.0	2	18.5	3.4	0.05

Table 3.2: Results of Regression Analysis, to examine the relationship between the abundance and biomass of *Palaemon peringueyi* and the selected physical and biological parameters.

Regression Statistics	**Vegetation Cover**	**Salinity**	**Temperature**	**Dissolved oxygen (DO)**
Abundance				
Multiple R	0.331	0.096	0.268	0.010
R Square	0.109	0.009	0.072	0.000
Adjusted R Square	0.083	-0.020	0.045	-0.029
Standard Error	14.316	15.100	14.614	15.169
Biomass				
Multiple R	0.430	0.039	0.256	0.065
R Square	0.185	0.002	0.065	0.004
Adjusted R Square	0.161	-0.028	0.038	-0.025
Standard Error	1.221	1.351	1.307	1.349

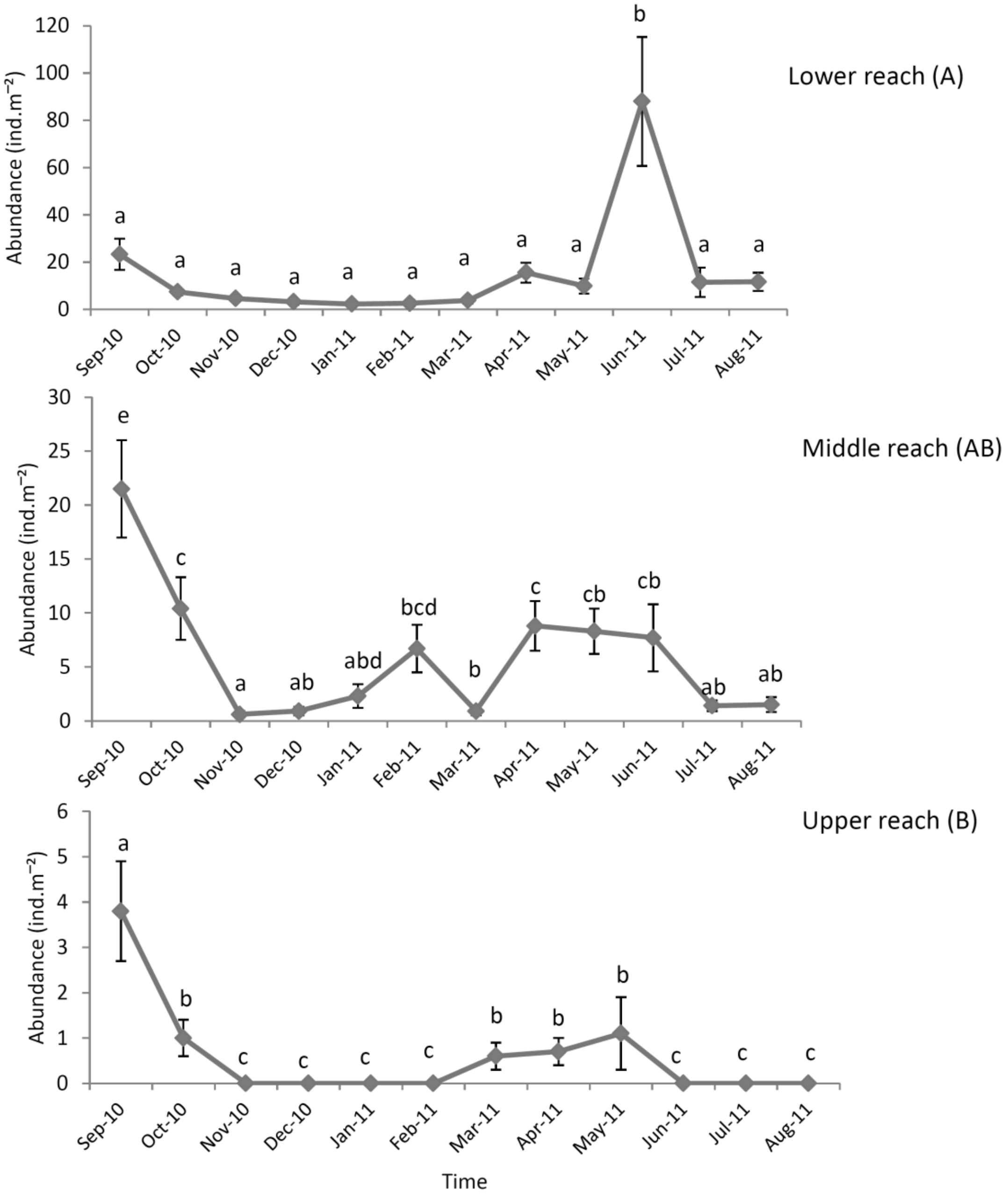


Figure 3.5: Mean (± SE) abundance (ind.m^{-2}) of *Palaemon peringueyi* in the Kariega Estuary from September 2010 to August 2011. Error bars indicate standard error; different letters indicate significant difference ($p < 0.05$) (Note different scales on the y-axes).

3.3.2.3. Biomass

During this study, minimum biomass recorded in one of the tows was 0 and maximum was 13.6 g $wwt.m^{-2}$ and was recorded in June in the lower reach. There was a significant difference in the shrimp biomass between the months and sites ($p < 0.05$) (ANOVA). Post-hoc tests (Fisher LSD) showed that in the lower reach, September, April and June differed from the other months. In the middle reach, most of the months were significantly different (Figure 3.6) while only September and April differed in the upper reach. All the reaches were significantly different from each other (Figure 3.6). Regression analysis did not show any significant relationships between shrimp biomass and physico-chemical parameters but showed a weak correlation between vegetation cover and biomass ($r^2 = 0.1848$, $p < 0.05$) (Table 3.2; Appendix I; III).

There was a decrease in biomass in the lower reach from September (3.8 ± 0.9 g $wwt.m^{-2}$) to January (0.4 ± 0.2 g $wwt.m^{-2}$) after which biomass fluctuated between February and June which was when the highest biomass was recorded (4.4 ± 1.4 g $wwt.m^{-2}$). However, in July biomass decreased to 0.6 ± 0.3 g $wwt.m^{-2}$) but increased again in August (1.2 ± 0.5 g $wwt.m^{-2}$) (Figure 3.6).

In the middle reach, highest biomass was recorded in September (4.3 ± 0.9 g $wwt.m^{-2}$). Biomass decreased from September (4.3 ± 0.9 g $wwt.m^{-2}$) to November (0.2 ± 0.1 g $wwt.m^{-2}$) after which it fluctuated between January and May when the second highest biomass was recorded (2.5 ± 0.6 g $wwt.m^{-2}$). Biomass decreased from 0.6 (± 0.3) g $wwt.m^{-2}$ in June to 0.1 (± 0) g $wwt.m^{-2}$ in July and increased again in August (1.5 ± 0.7 g $wwt.m^{-2}$) (Figure 3.6).

In the upper reach, biomass decreased from September (1.6 ± 0.5 g $wwt.m^{-2}$) to October (0.4 ± 0.2 g $wwt.m^{-2}$). This was followed by an absence of shrimps from November to February. Shrimps returned to the upper reach from March to May with the second highest biomass being recorded in April (0.7 ± 0.3 g $wwt.m^{-2}$) (Figure 3.6).

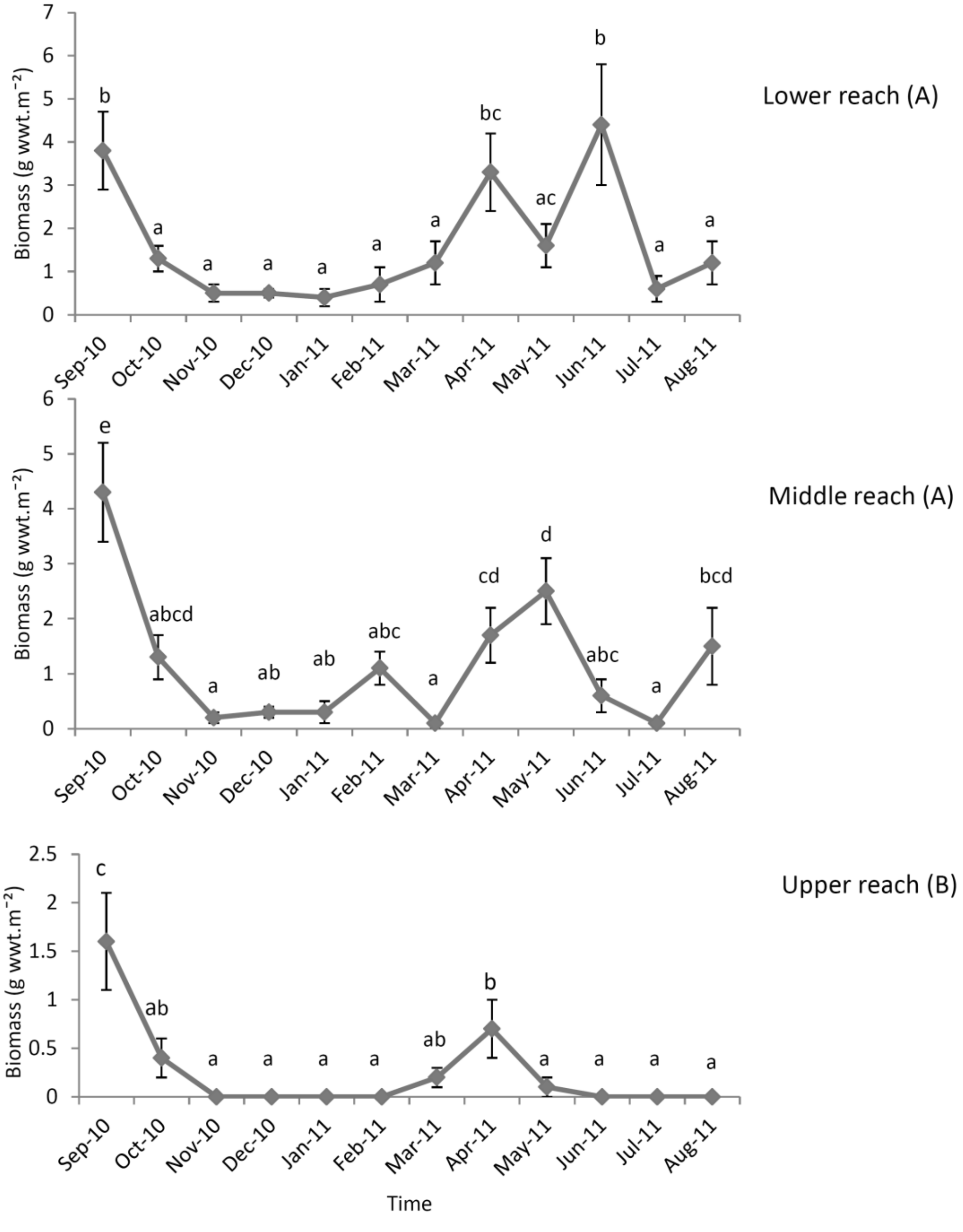


Figure 3.6: Mean (± SE) biomass of *Palaemon peringueyi* in the Kariega Estuary from September 2010 to August 2011. Error bars indicate standard error; different letters indicate a significant difference ($p < 0.05$) (Note different scales on the y-axes).

3.3.2.4. Population structure and size frequency analysis

There was no significant difference in carapace length (CL) of the shrimps between the months and sites ($p < 0.05$) (ANOVA). The CL of *P. peringueyi* caught during this study ranged between 5 to 25 mm (Figures 3.8.0 - 3.8.5). Juveniles (CL < 9 mm) were almost always present in the estuary and occupied the lower and middle reaches while adults occupied all three reaches of the estuary (Figures 3.7; 3.8.0 - 3.8.5).

In the lower reach, greatest numbers of juveniles were recorded in June, July, May, September and November, respectively. The least number of juveniles were recorded in February, January, December, October and April, respectively. The greatest number of adults occurred in March, February, January, December, October and April. No juveniles were recorded in this reach in March (Figure 3.7).

In the middle reach, greatest numbers of juveniles were recorded in January, June, October, July, and May, respectively. No juveniles were recorded in November and March. The least number of juveniles occurred in February, September and December, respectively. Only females were caught in this reach in November. Adults dominated in November, March, February, September, December and August, respectively (Figure 3.7).

In the upper reach, shrimps were absent on seven occasions of the sampling period (November to February and, June to August). Adults were dominant in this reach. Juveniles were recorded in September and May only (Figure 3.7). Only juveniles and females were caught in this reach in May (Figure 3.7; Table 3.3).

Overall, the greatest numbers of shrimps were always recorded in the lower reach, and then the middle and upper reaches, respectively (Figure 3.8.0 - 3.8.5). There was always a decrease in the number of adults in the estuary whenever juveniles dominated. From May to August shrimps with larger CL disappeared and the estuary was dominated with shrimps with CL of between 5 and 15 mm (Figure 3.8.4; 3.8.5). Although adult shrimps were still present in the estuary in May, their numbers decreased (Figure 3.8.4). Whilst most adults found in most months had a carapace length of between 10 and 18 mm, larger adults (CL between 19 and 24 mm) were found in the middle and upper reaches in September. In October, December and February larger shrimps were found in the upper reach, April in the middle and upper reaches and May in the middle reach. The greatest mean CL of the shrimps was recorded in the upper reach, in April (19.4 ± 4.7 mm) and October (16.1 ± 3.4 mm), respectively.

3.3.2.5. Sex ratios

A t-test did not show any significant difference in the size of males and females ($p = 0.399$, $t = 0.847$). Females were always more abundant than males, except in March in the upper reach (Table 3.3). There were equal number of males and females in the lower reach in April (Figure 3.7; Table 3.3). No males were recorded in the lower and middle reaches in July and November in the middle reach and, also in May in the upper reach (Table 3.3). The greatest variation in male: female sex ratios occurred in December in the lower and middle reaches (Table 3.3). Overall the sex ratios for the lower, middle and upper reaches were 2:1, 1.9:1 and 1.4:1 ♀/♂, respectively (Table 3.3). Overall male: female sex ratios in the lower and middle reaches differed significantly from an expected 1:1 ratio ($p < 0.05$) (Chi-test). However, there was no significant difference between the male: female sex ratio in the upper reach ($p > 0.05$) (Chi-test) (Table 3.4).

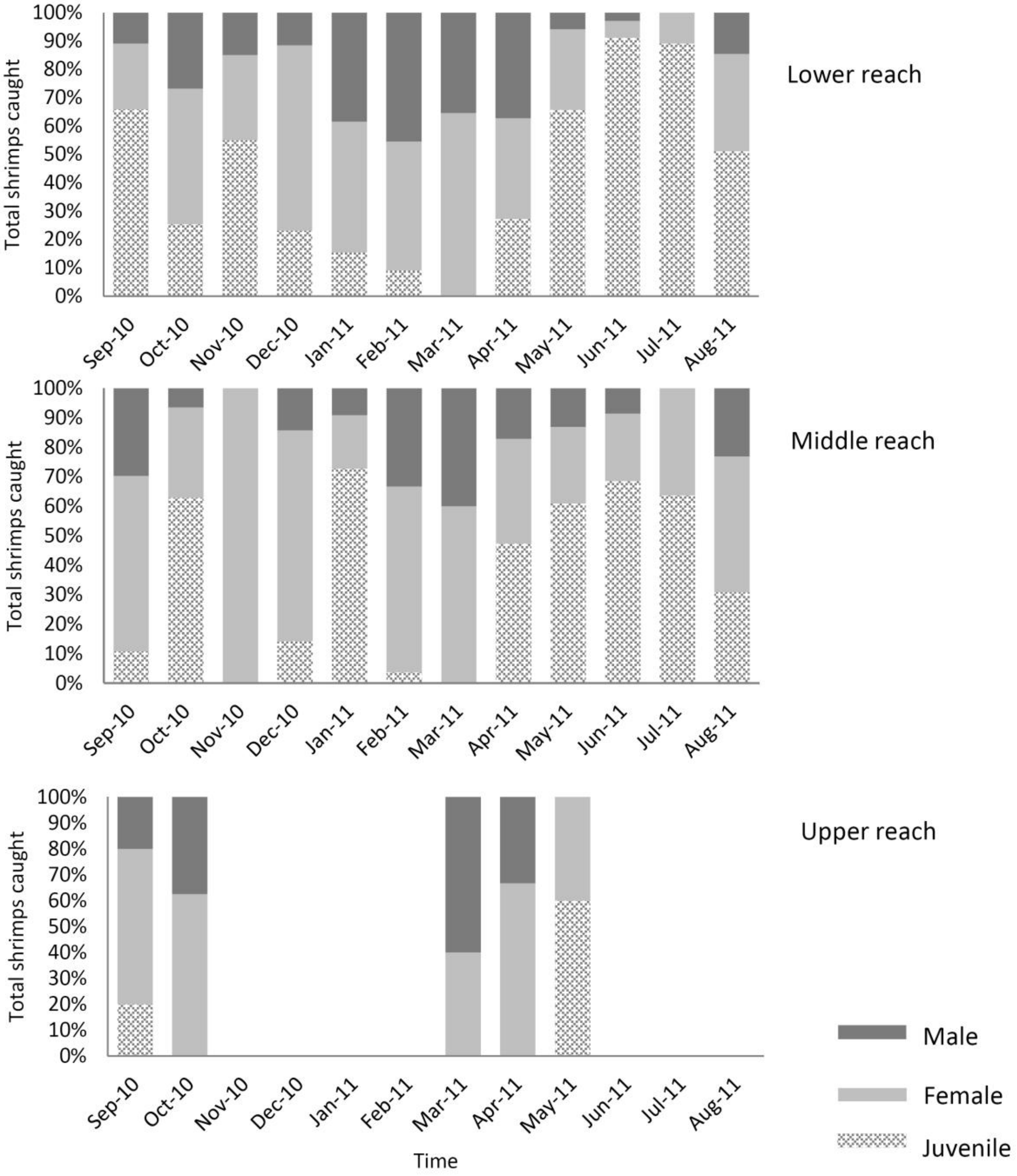


Figure 3.7: Temporal and spatial patterns in the percentage of male, female and juvenile *Palaemon peringueyi* in the Kariega Estuary from September 2010 to August 2011.

Table 3.3: Female to male sex ratios of *Palaemon peringueyi* in the lower, middle and upper reaches of the Kariega Estuary.

Time	**Sex ratios (♀/♂)**		
	Lower reach	**Middle reach**	**Upper reach**
Sep-10	2.1: 1	2.1: 1	3.1: 1
Oct-10	1.7: 1	4.8: 1	1.7: 1
Nov-10	2:1	All females	shrimps absent
Dec-10	5.6:1	5:1	shrimps absent
Jan-11	1.2: 1	2:1	shrimps absent
Feb-11	1.2: 1	1.9: 1	shrimps absent
Mar-11	1.8: 1	1.5: 1	0.6: 1
Apr-11	1: 1	2.1: 1	2:1
May-11	4.9: 1	2.1: 1	All females
Jun-11	2.1: 1	2.7: 1	shrimps absent
Jul-11	All females	All females	shrimps absent
Aug-11	2.4: 1	2.1: 1	shrimps absent
Overall sex ratios	2:1	1.9:1	1.4:1

Table 3.4: Results of chi-square test for sex ratio of *Palaemon peringueyi* in the lower, middle and upper reaches of the Kariega Estuary.

Time	**Lower reach**		**Middle reach**		**Upper reach**	
	X^2	P	X^2	P	X^2	P
Sept-10	7.480	0.010	8.330	0.004	1.000	0.317
Oct-10	3.920	0.047	9.783	0.002	0.500	0.470
Nov-10	2.000	0.157	5.000	0.030	shrimps absent	
Dec-10	9.800	0.002	2.700	0.102	shrimps absent	
Jan-11	0.182	0.667	0.333	0.564	shrimps absent	
Feb-11	0.200	0.657	4.923	0.023	shrimps absent	
Mar-11	2.612	0.106	1.285	0.257	0.200	0.655
Apr-11	0.000	1.000	4.900	0.027	0.333	0.563
May-11	20.447	$p < 0.001$	5.000	0.025	4.000	0.045
Jun-11	7.333	0.006	2.272	0.132	shrimps absent	
Jul-11	10.000	0.002	4.000	0.045	shrimps absent	
Aug-11	7.681	0.006	1.000	0.317	shrimps absent	
Overall sex ratios	46.488	$p < 0.001$	38.623	$p < 0.001$	0.667	0.414

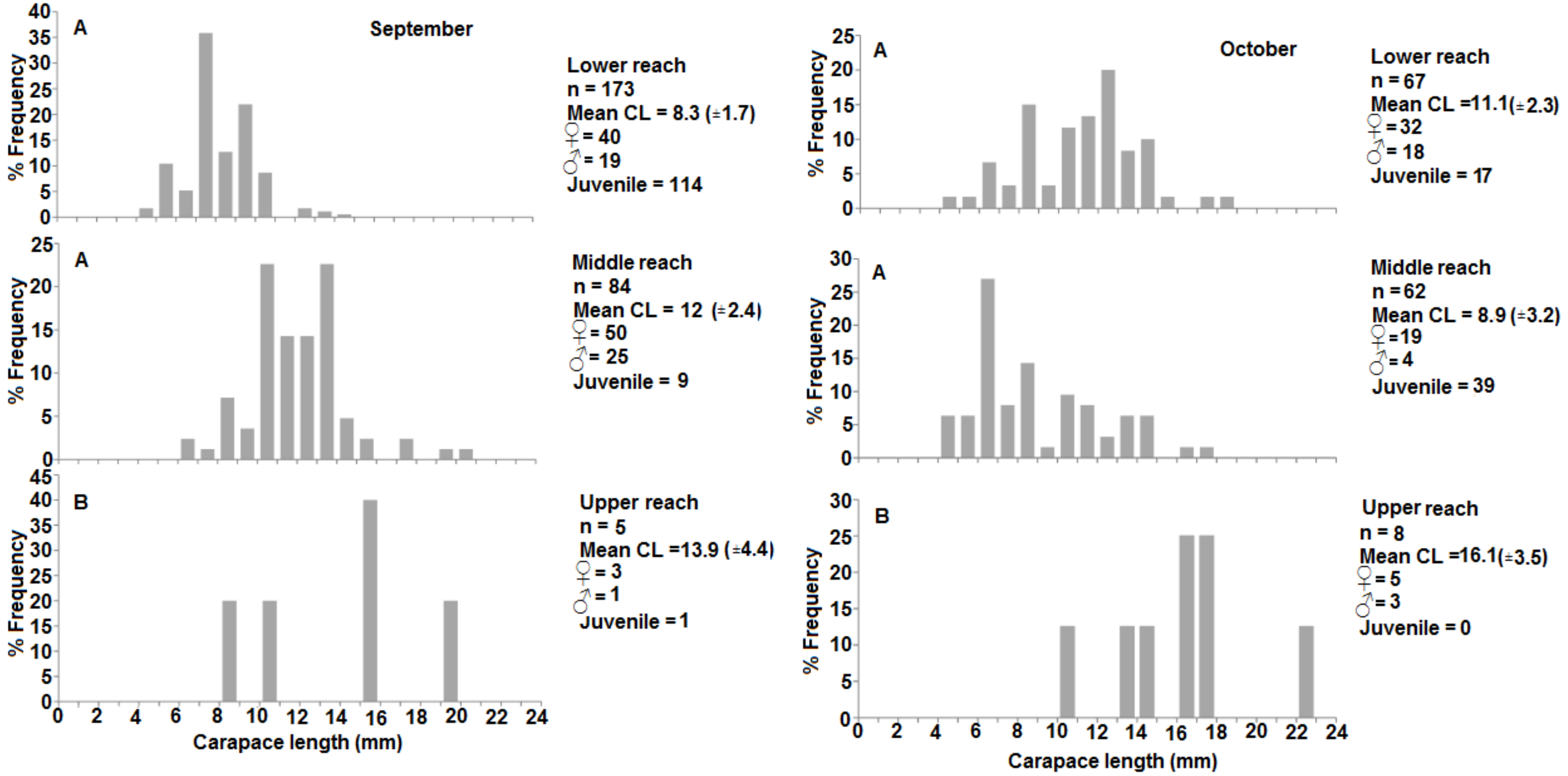


Figure 3.8.0: Carapace length (mm) of *Palaemon peringueyi* in the lower, middle and upper reaches of the Kariega Estuary from September 2010 to November 2010.

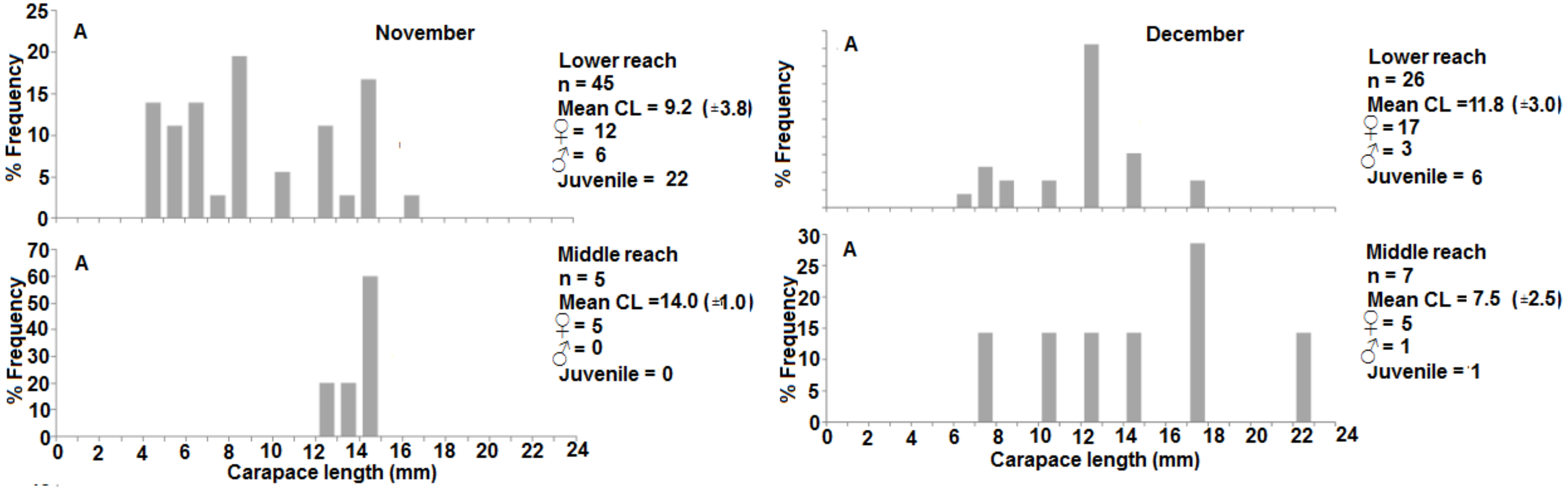


Figure 3.8.1: Carapace length (mm) of *Palaemon peringueyi* in the lower and middle reaches of the Kariega Estuary from November to December 2010.

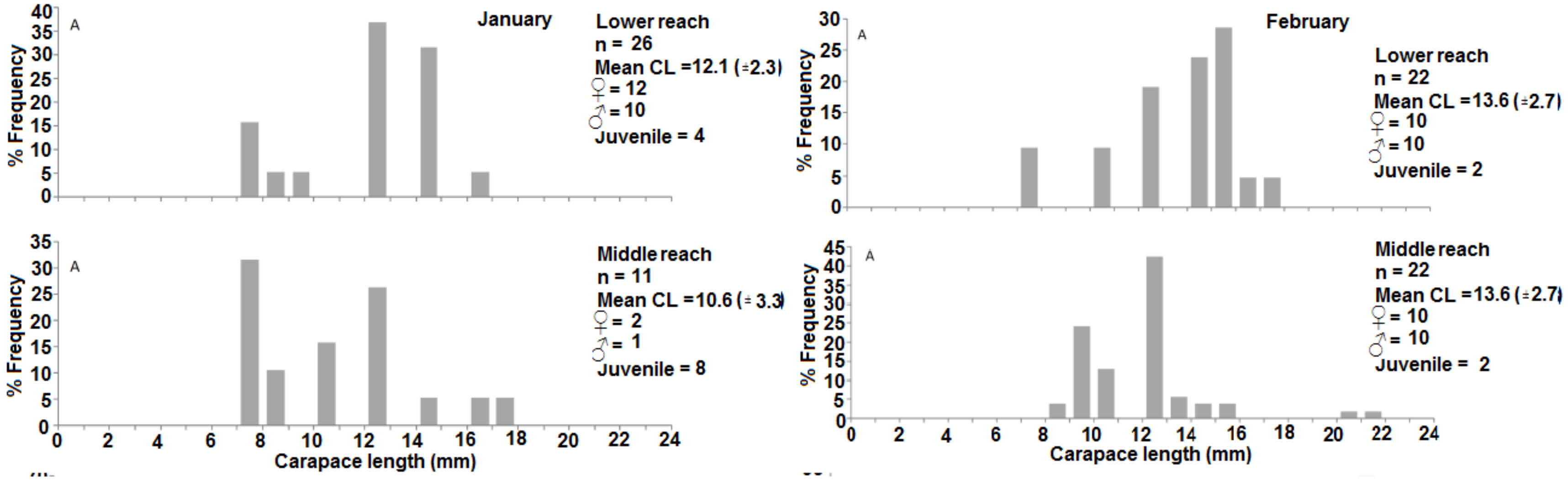


Figure 3.8.2: Carapace length (mm) of *Palaemon peringueyi* in the lower and middle reaches of the Kariega Estuary from January to February 2011.

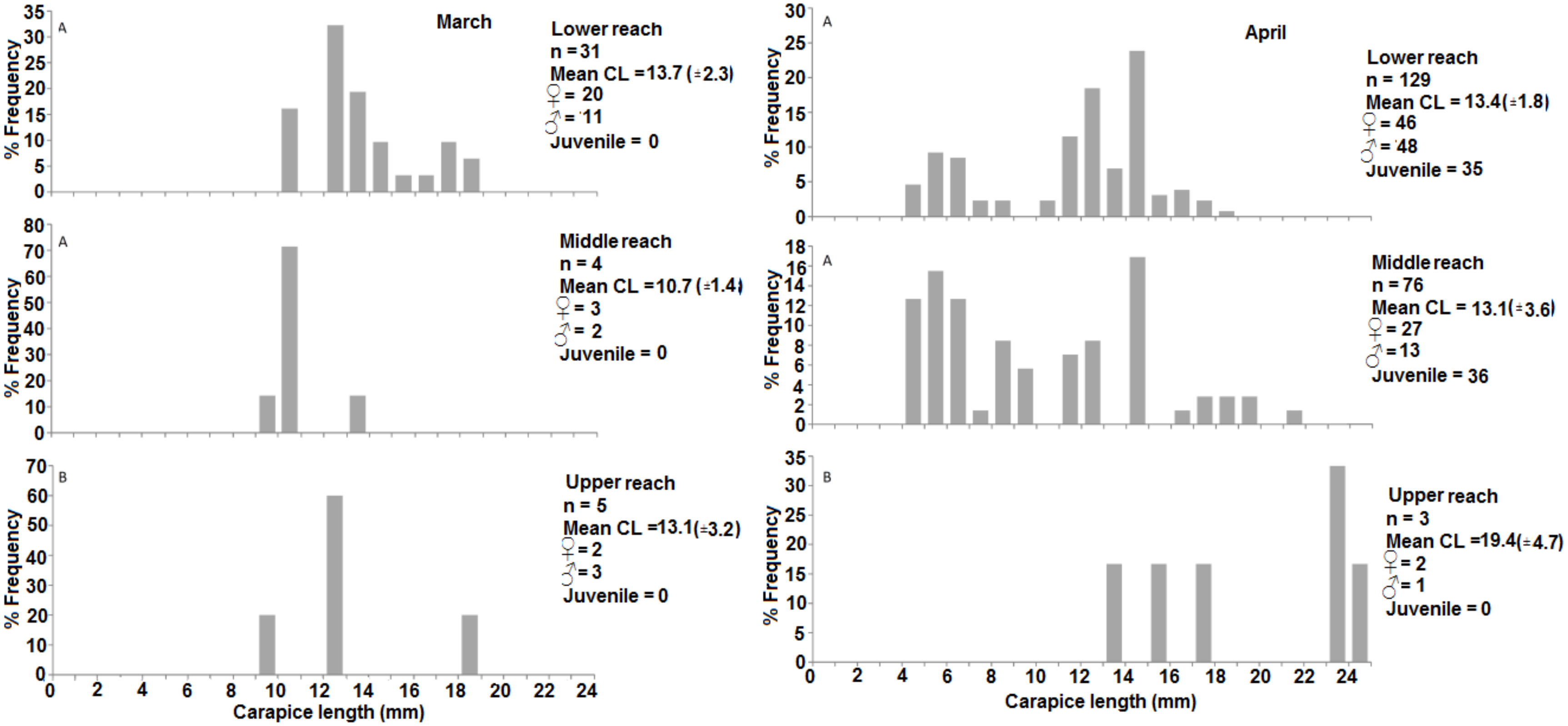


Figure 3.8.3: Carapace length (mm) of *Palaemon peringueyi* in the lower, middle and upper reaches of the Kariega Estuary from March to April 2011.

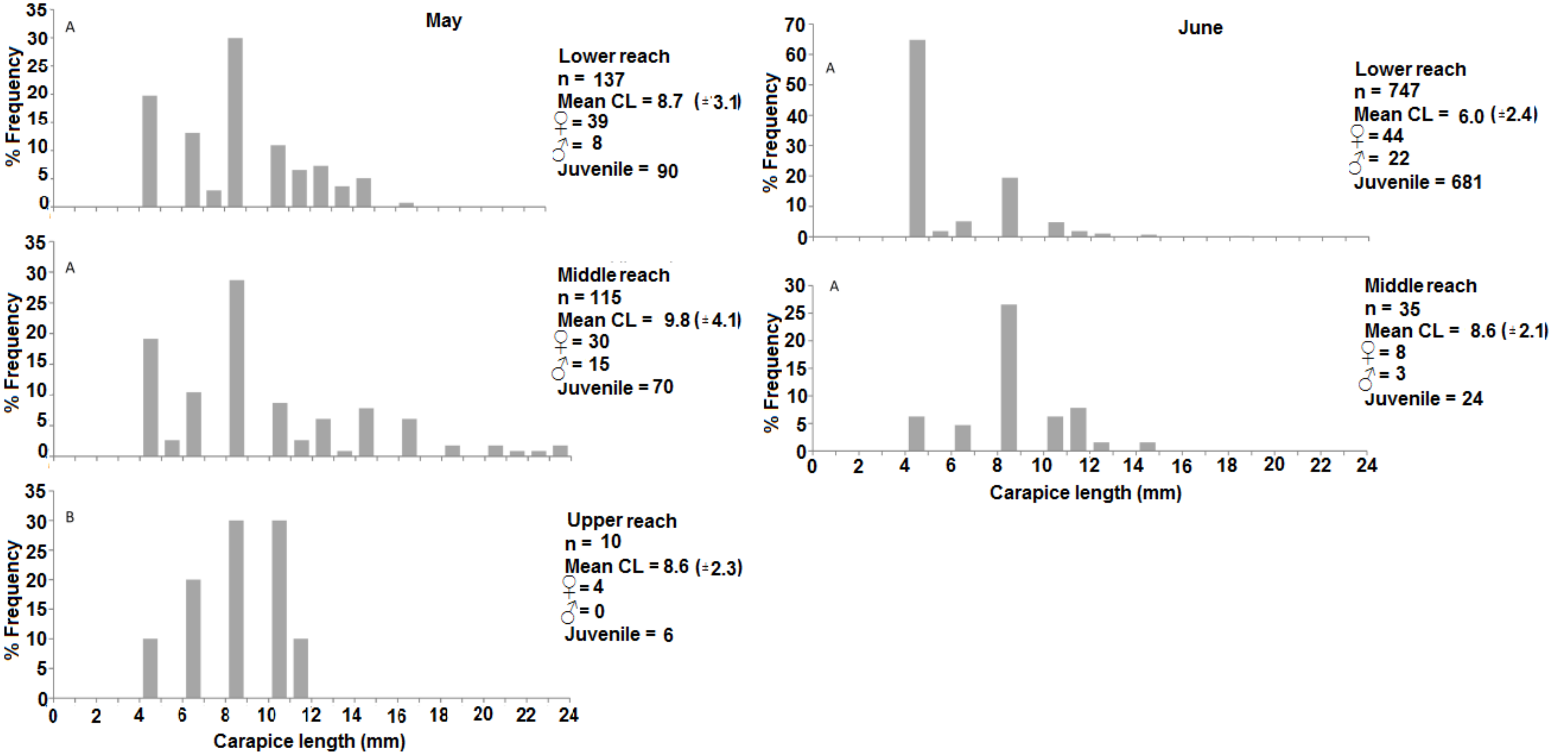


Figure 3.8.4: Carapace length (mm) of *Palaemon peringueyi* in the lower, middle and upper reaches of the Kariega Estuary from May to June 2011.

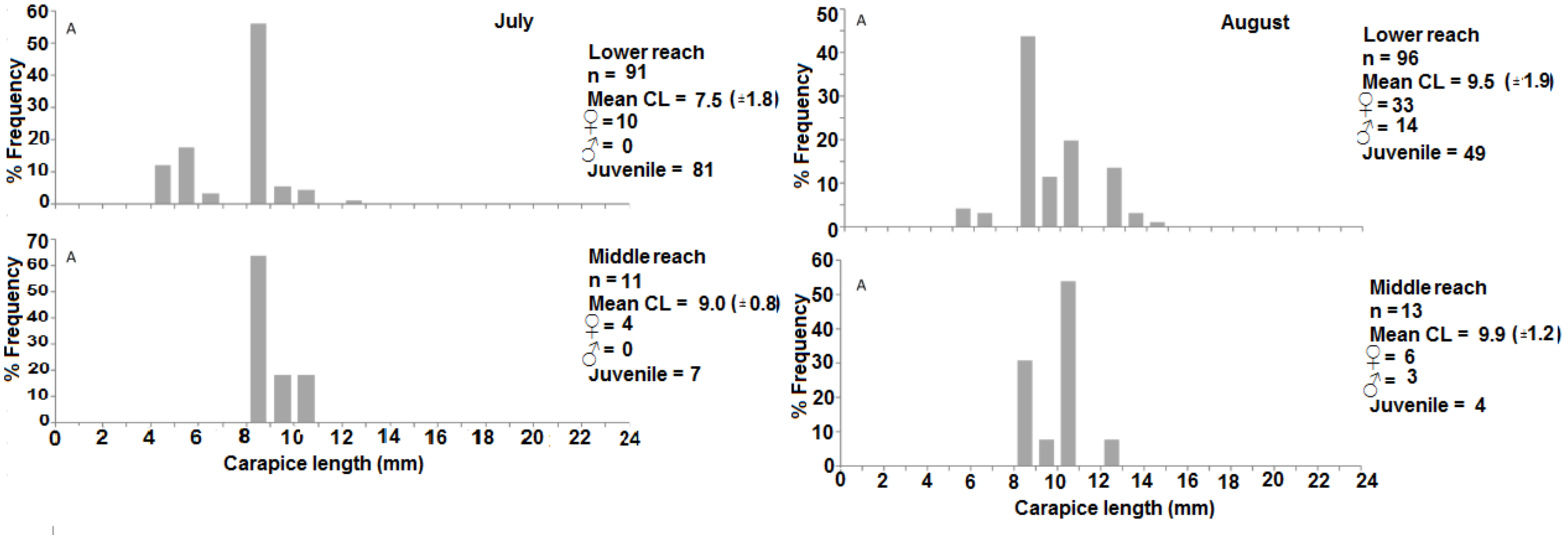


Figure 3.8.5: Carapace length (mm) of *Palaemon peringueyi* in the lower and middle reaches of the Kariega Estuary from July to August 2011.

3.3.2.6. Biological data

There was a significant effect of time (month) and site on the percentage vegetation cover ($p < 0.05$) (ANOVA). Mean vegetation cover during the study ranged between 0 and 100 (± 0) %. A Post-hoc test (Fisher LSD) showed that in the lower reach, July and August were different from other months (Figure 3.9). In the middle reach, variation occurred between all the months with the exception of June and August (Figure 3.9) while in the upper reach variation occurred throughout the year with some months being similar (Figure 3.9). The highest vegetation cover was recorded in the lower reach, followed by the middle and the upper reaches, respectively (Figure 3.9) with highest vegetation cover being recorded in spring (September) and lowest in winter (July). The overall pattern in all reaches showed a decline of vegetation cover from late spring to winter.

In the lower reach, vegetation cover decreased from 100 % in September to 86.7 (± 1.9) % in January. Vegetation cover remained high until July where there was a decrease (36.7 ± 17). There was a slight increase of vegetation cover in August (45 ± 14.2 %) (Figure 3.9).

In the middle reach, vegetation cover decreased from September (96 ± 1.9 %) to April (55 ± 4.4 %). However, in May, vegetation increased to 76.7 (± 5.1) % but decreased again from June to July where the lowest percentage vegetation cover was observed (1.7 ± 0.9 %) and vegetation cover increase to 26 (± 1.9) % in August (Figure 3.9).

In the upper reach, the percentage vegetation cover decreased from September (86.7 ± 3.9 %) to December (20 ± 5 %). In January, vegetation increased to 68.3 (± 8.6) % after which it fluctuated until July where the no vegetation cover was observed (Figure 3.9).

Due to laboratory logistical constraints, no chlorophyll-*a* and POM data were collected over the period of November to January. Data indicate that the mean particulate organic matter ranged from 0.04 (±0.02) µg POM.L^{-1} to 1.6 (± 0.05) µg POM.L^{-1} in the lower reach, from 0.06 (± 0.04) µg POM.L^{-1} to 1.55 (± 0.06) µg POM.L^{-1} in the middle reach and from 0.03 (± 0.01) to 1.59 (± 0.08) µg POM.L^{-1} in the upper reach. The highest mean POM concentrations were recorded in May and lowest in August for all the reaches (Figure 3.10).

Mean chlorophyll-*a* concentration ranged from 0.01 (± 0.003) to 4.04 (± 2.53) µg chl-*a*.L^{-1} in the lower reach, 0.02 (± 0.01) to 4.4 (± 2.24) µg chl-*a*.L^{-1}in the middle reach and 0.02 (± 0.01) to 4 .94 µg chl-*a*.L^{-1} in the upper reach. The highest chlorophyll-*a* concentrations were recorded in March (4 ± 2.525 µg chl-*a*. L^{-1}) in the lower reach, May (4 ± 2.239 µg chl-*a*.L^{-1}) middle reach and April (5 ± 3.235 µg chl-*a*.L^{-1}) upper reach (Figure 3.11).

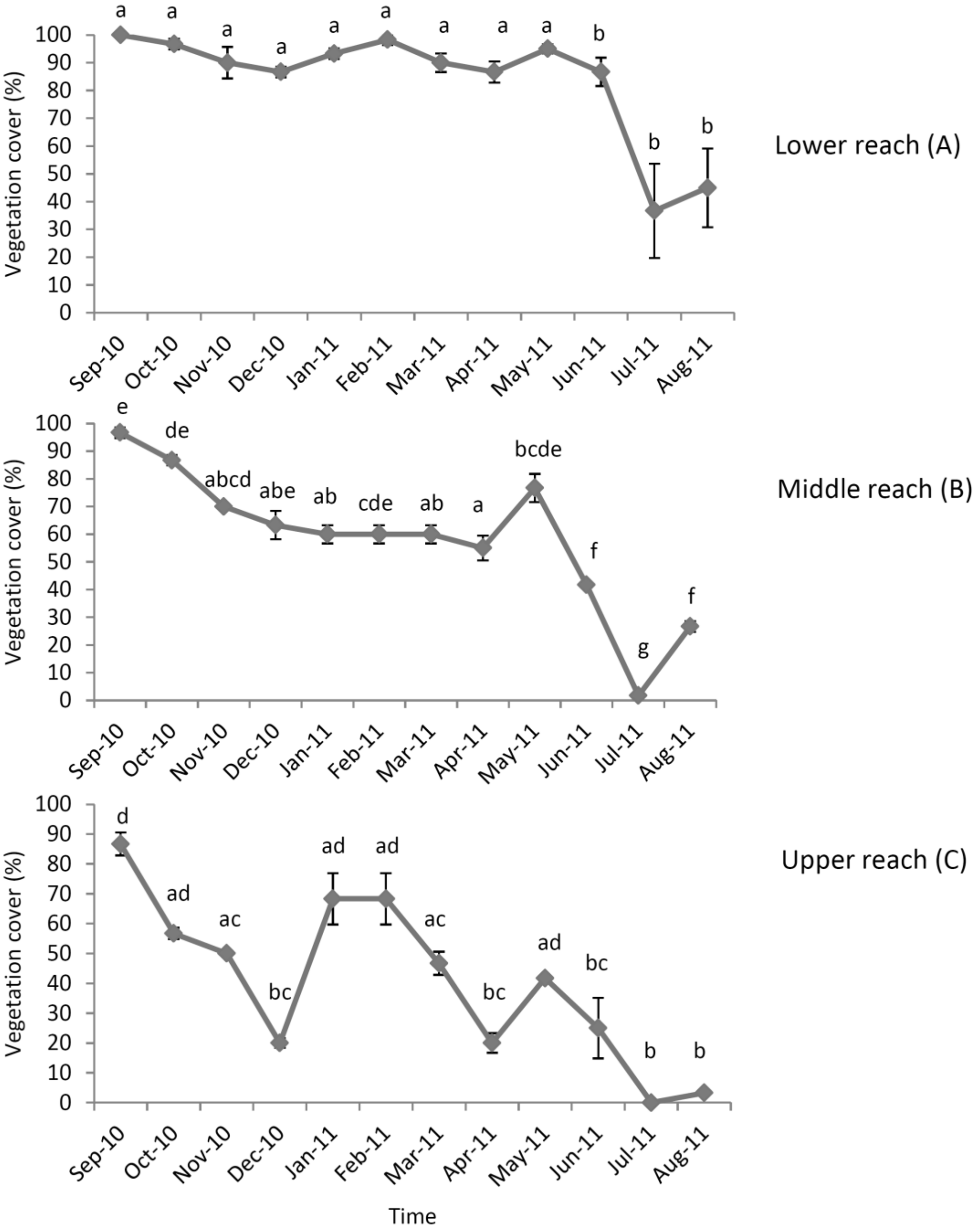


Figure 3.9: Mean (± SE) vegetation cover (%) in the lower, middle and upper reaches of the Kariega Estuary from September 2010 to August 2011. Error bars are standard error; different letters indicate significant difference ($p < 0.05$).

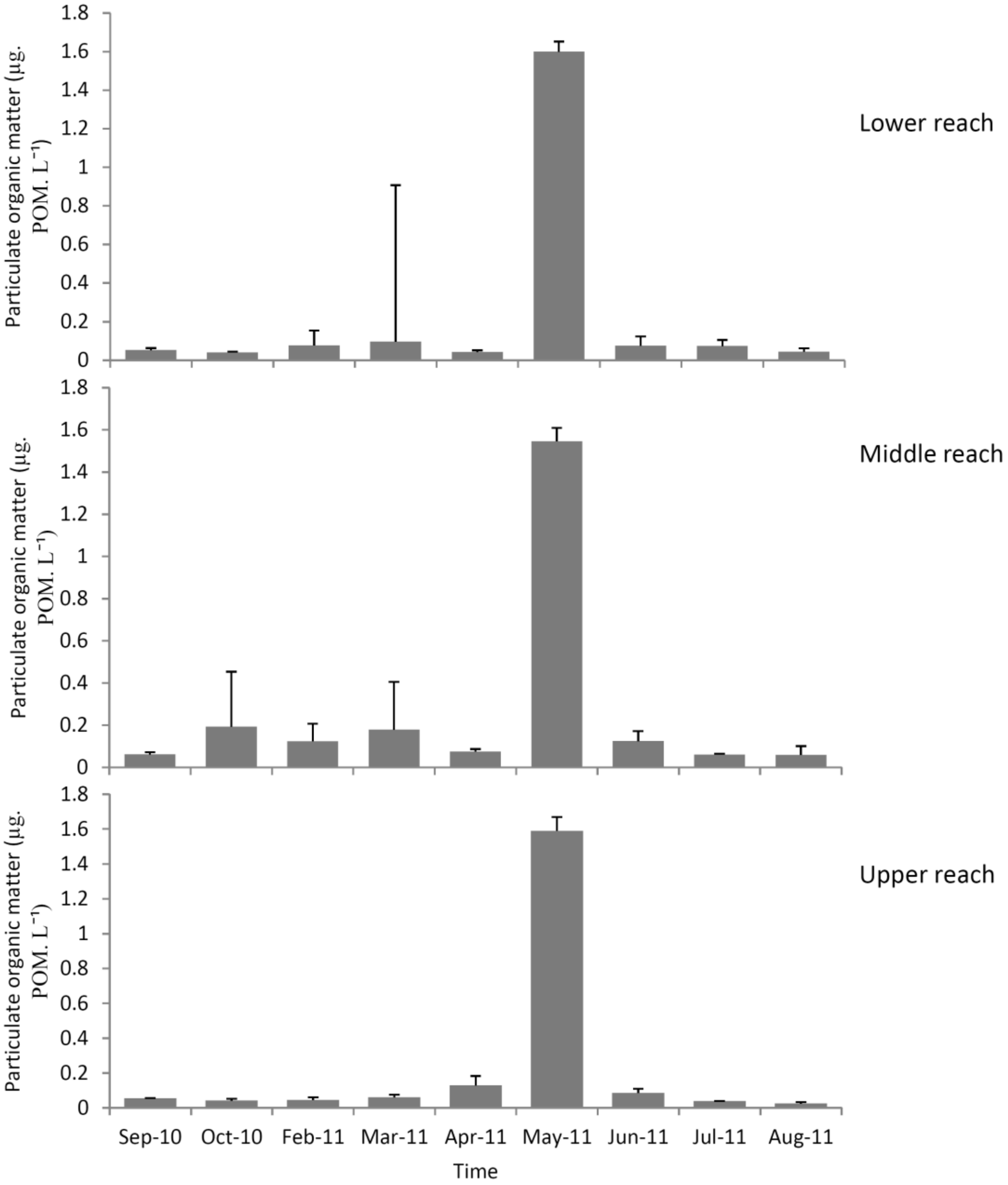


Figure 3.10: Mean (± SE) particulate organic matter (µg POM.L^{-1}) concentrations from the surface water of the lower, middle and upper reaches of the Kariega Estuary from September 2010 to August 2011 (error bars are standard error).

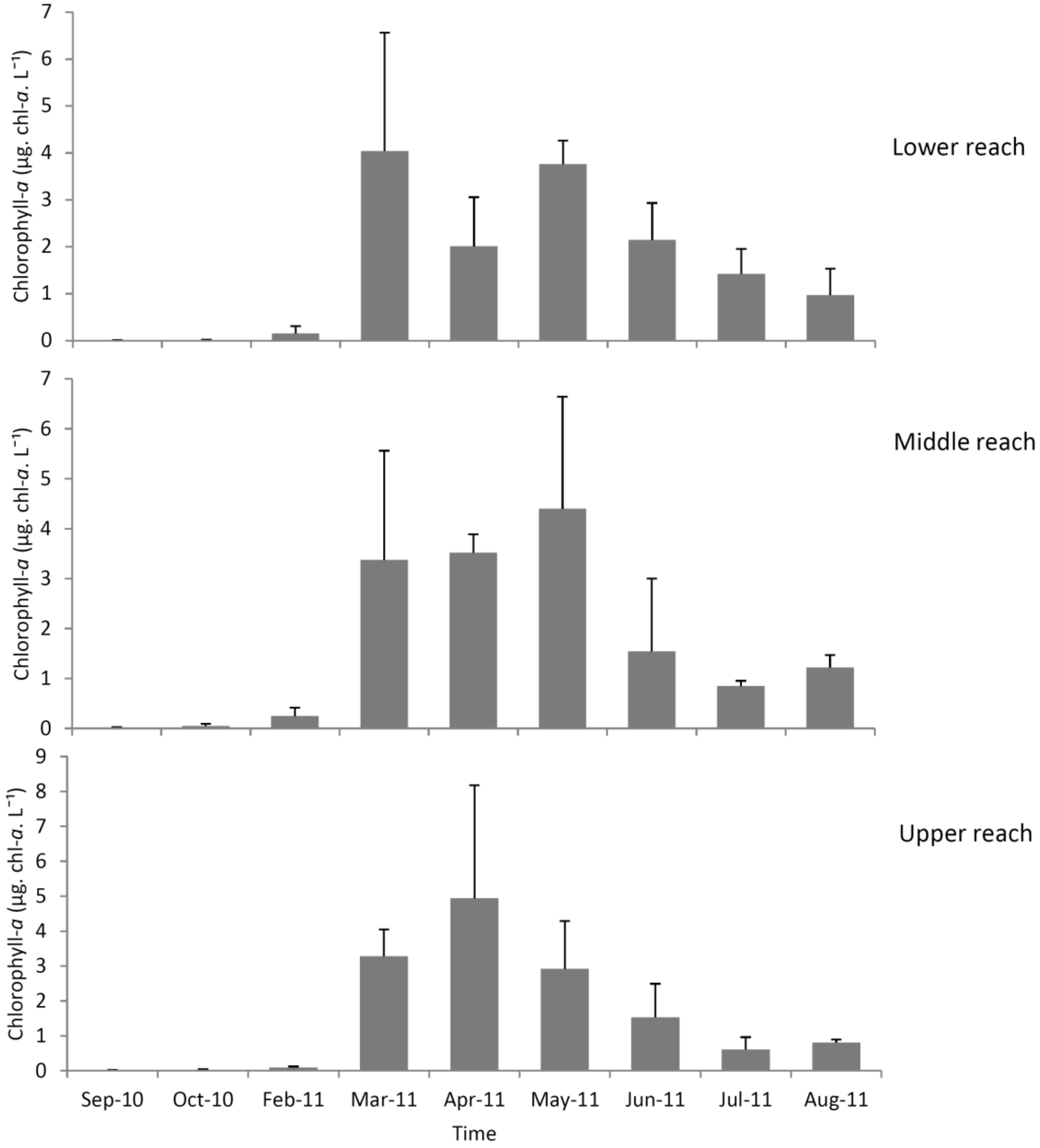


Figure 3.11: Mean (± SE) chlorophyll-*a* (µg chl-*a*.L^{-1}) concentrations from the surface water of the lower, middle and upper reaches of the Kariega Estuary from September 2010 to August 2011 (error bars are standard error).

3.3.2.7. Physico-chemical parameters

There was a significant difference in temperature between months ($p < 0.05$) (ANOVA) but not between the sites ($p > 0.05$) (ANOVA). Variation in temperature occurred between the months in all reaches with some months being similar (Post-hoc test, Fisher LSD) (Figure 3.12).

Mean water temperature recorded in the estuary during the study ranged between 12.3 (± 0.3) ˚C to 27.5 (± 0.1) ˚C. The highest temperature was recorded in February (27.5 ° C) and lowest in July (12.3 ° C) both of which were recorded in the upper reach. Temperature demonstrated similar patterns in all the regions although the lower reach had lower temperatures compared to the middle and upper reaches.

Initially, temperature increased from September to February in the middle and upper reaches of the estuary. While in the lower reach, temperature increased from September to December. From March to July, temperature decreased with the lowest temperatures being recorded in July for all the reaches. In August, there was a slight increase in temperatures in all the reaches (Figure 3.12).

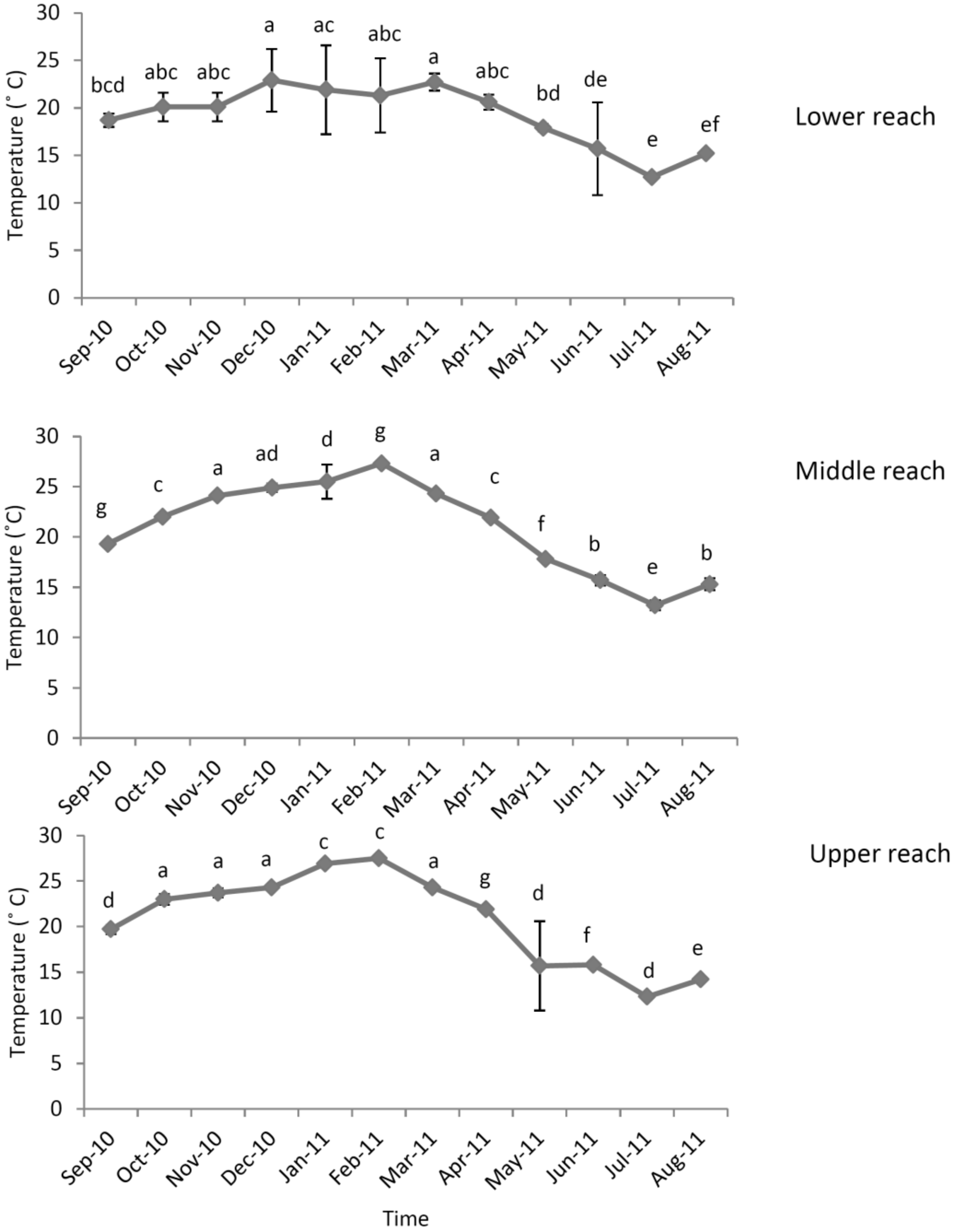


Figure 3.12: Mean (± SE) temperature (˚C) from the surface water of the lower, middle and upper reaches of the Kariega Estuary from September 2010 to August 2011. Error bars are standard error; different letters indicate significant difference ($p < 0.05$).

Mean salinity recorded during the study ranged from 0 to 44.3 (± 1.2) (Figure 3.13). Changes in salinity followed a similar pattern in all regions of the estuary. Salinity decreased from September to October in all the reaches. In July, the lower reach became freshwater, however, in August salinity in the lower reach increased to 14.1 (± 2.3) (Figure 3.13).

Salinity patterns in the middle reach were similar to the lower reach except in June and July, the water of this reach became fresh. Salinity rose again in the middle reach in August to 2.3 (± 0.8). The upper reach demonstrated similar patterns but became freshwater dominated from June to August. There was a significant difference in salinity between the months ($p < 0.05$) (ANOVA). Salinity varied amongst the months in all three reaches with some months being similar (Post-hoc test, Fisher LSD) (Figure 3.13).

Dissolved oxygen concentrations varied significantly between months ($p < 0.05$) (ANOVA) but not between the sites ($p > 0.05$) (ANOVA). Post-hoc test (Fisher LSD) also showed that variation occurred throughout the months with some months being similar (Figure 3.14). Dissolved oxygen concentrations increased in all the regions from September to October. However, there was a decrease in DO in the lower reach from October (9.1 ± 1.2 $mg.L^{-1}$) to December (5.6 ± 0.8 $mg.L^{-1}$). Dissolved oxygen fluctuated from January to August with highest DO being recorded in October (9.1 ± 1.2 $mg.L^{-1}$) and April (9.3 ± 0.8 $mg.L^{-1}$) (Figure 3.14). In the middle reach, DO concentrations decreased from October (8.6 ± 0.3 $mg.L^{-1}$) to December (4.8 ± 0.5 $mg.L^{-1}$) and fluctuated until August (Figure 3.14). In the upper reach, DO concentrations also decreased from October (10 ± 0.5 $mg.L^{-1}$) to December (4.2 ± 0.1 $mg.L^{-1}$) after which the DO records fluctuated. However DO increased again from February (3.8 ± 0.5 $mg.L^{-1}$) to August (10.4 ± 0.3 $mg.L^{-1}$). Highest (10.4 $mg.L^{-1}$) and lowest (3.8 $mg.L^{-1}$) DO concentrations were recorded in the upper reach (Figure 3.14).

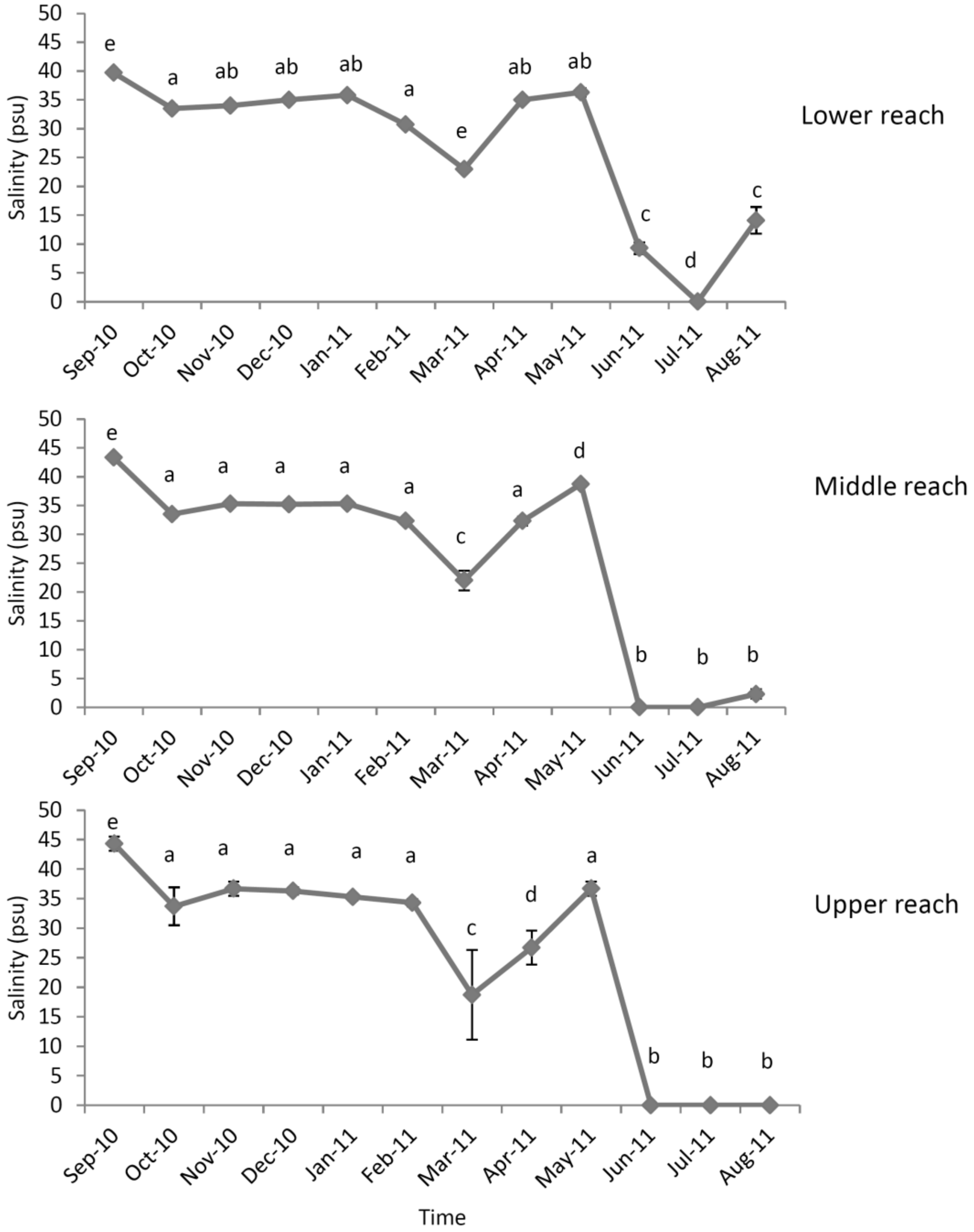


Figure 3.13: Mean (± SE) salinity (PSU) from the surface water of the lower, middle and upper reaches of the Kariega Estuary from September 2010 to August 2011. Error bars are standard error; different letters indicate significant difference ($p < 0.05$).

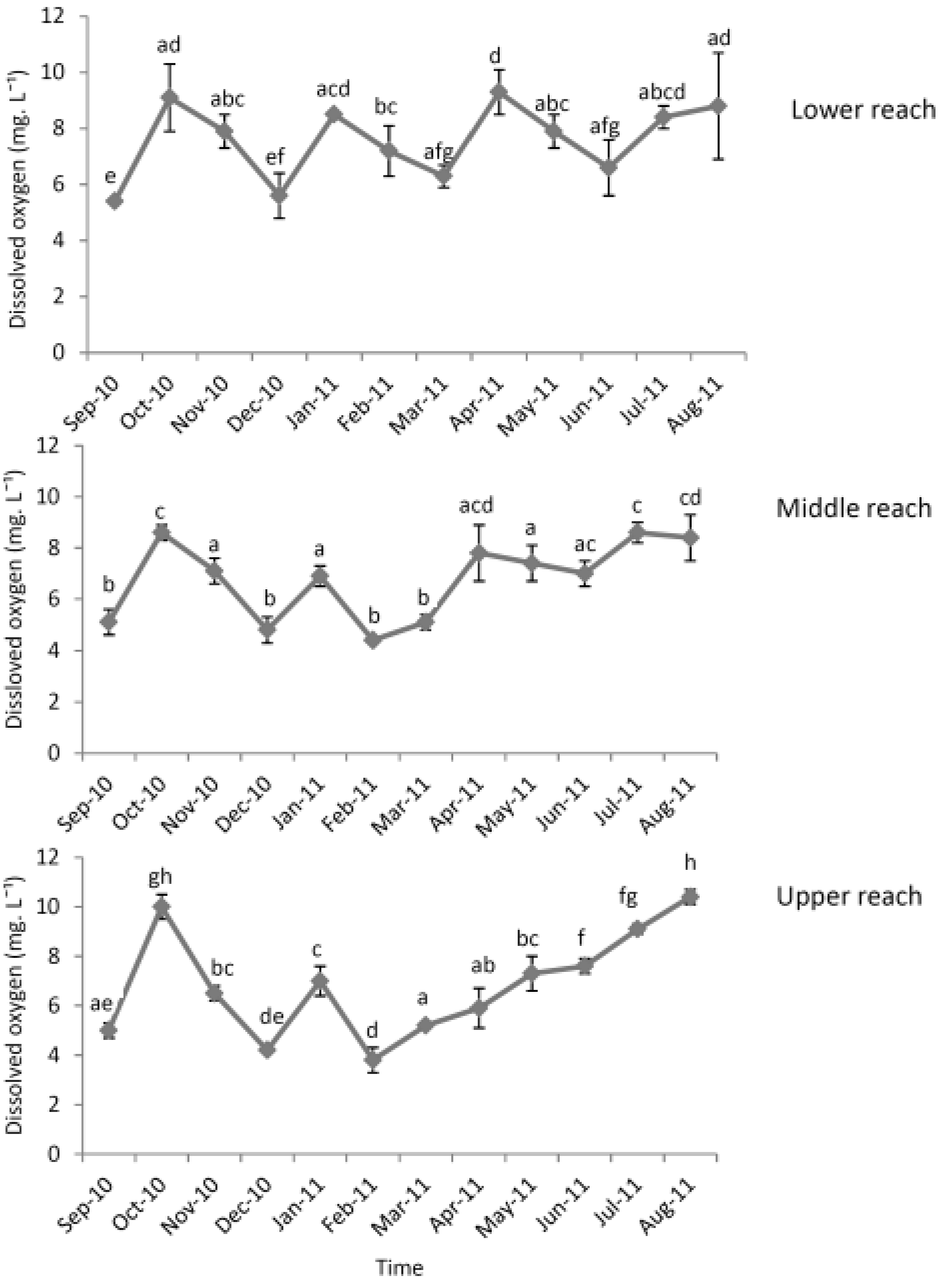


Figure 3.14: Mean (± SE) dissolved oxygen concentrations (mg.L^{-1}) from the surface water of the lower, middle and upper reaches of the Kariega Estuary from September 2010 to August 2011. Error bars are standard error; different letters indicate significant difference ($p < 0.05$).

Table 3.5: Results for One-way ANOVA (Statistica version 10) to determine the significant difference in temperature, salinity, dissolved oxygen and vegetation cover between months and sites (lower, middle and upper reaches) of the Kariega Estuary.

Variation	Sum of squares	Degree of freedom	Mean Squares	F- ratios	P
Temperature					
Months	1716.290	11	156.030	47.550	$p < 0.001$
Sites	131.080	8	16.390	0.854	0.558
Salinity					
Months	21903.930	11	1991.270	148.858	$p < 0.001$
Sites	157.390	8	19.670	0.085	0.999
Dissolved oxygen					
Months	246.004	11	22.364	14.043	$p < 0.001$
Sites	5.757	2	2.879	0.941	0.400
Vegetation cover					
Months	53297.000	11	4845.200	7.401	$p < 0.001$
Sites	12164.300	2	6082.100	9.912	0.0004

3.4. Discussion

The results of the physico-chemical study indicate that temperature demonstrated a strong seasonal pattern with the highest water temperature recorded in summer and the lowest in winter. Intermediate temperatures were recorded in spring and autumn (Figure 3.12). This pattern is consistent with the published literature and can be correlated to the climate regime within which the estuary is found. Additional changes in water temperature are probably associated with the inflow of freshwater into the estuary following heavy winter (June to August) rainfall within the catchment area, and the inflow of cooler marine waters into the lower reach of the estuary. The changes in vegetation cover particularly in the upper reach, is probably linked to hypersaline conditions present in the begging of the study and freshwater inflow as the result of the winter rainfall. Optimal salinity ranges for *Nanozostera capensis* has been shown to be in the ranges of between 15 and 35 (Iyer and Barnabas 1993; Adams and Bate 1994; 1996). The absence of rainfall within the catchment area of the Kariega Estuary at the beginning of the study contributed to hypersaline conditions predominating within the upper reach of the system (Figure 3.13). This result is consistent with previous studies conducted within the estuary (Heyns and Froneman 2010).

Statistical analysis for chl-*a* and POM could not be performed due to laboratory logistical constraints. Existing data for POM shows that there was a significant increase in May; this was probably due to high rain fall during the sampling. There was a significant decline in chlorophyll-*a* in spring and late summer, this was probably due to low rainfall in the region. Rainfall has been associated with the input of nutrients in estuaries (Allanson and Read 1987; Grange and Allanson 1995).

3.4.1. Recruitment and size distribution

The absence of berried females in the Kariega Estuary during this study is consistent with the published literature that *P. peringueyi* is an obligate marine breeder. This offshore breeding phase is a common feature for most species of penaeid (Kutkuhn 1966; Allen 1966) and caridean prawns including *Crangon franciscorum* and *C. nigricauda* (Israel 1936) and *Palaemon serratus* (Foster 1951). Recruitment of *P. peringueyi* into estuaries occurs at stage 6 zoea and post-larvae (Robertson 1984). With the exception of March, *P. peringueyi* juveniles were always present in the estuary during the survey (Figure 3.7). Greatest number of juvenile *P. peringueyi* in the Kariega Estuary was recorded in winter (Figure 3.7). The presence of high density of juveniles in May to July suggests that peak recruitment of juvenile *P. peringueyi* in the Kariega Estuary takes place mostly in late autumn and early winter. In the present study, juveniles in September accounted more than 60 % of the total population caught (Figure 3.7); this may further suggest that, a second smaller peak in recruitment also occurs in spring. Emmerson (1985) also reported a continuous recruitment of juvenile *P. peringueyi* in Port Elizabeth tidal pools with peak recruitment in November and a second smaller peak in winter. Robertson (1984) found that peak recruitment of *P. peringueyi* in the adjacent Bushmans Estuary occurred in February and April and further suggested that *P. peringueyi* is a perennial breeder with spawning activity occurring at various times of the year along the warm temperate south and east coasts of South Africa. The difference in the recruitment of juveniles between the Kariega Estuary and the Bushmans Estuary could be an indication that recruitment of juvenile *P. peringueyi* may vary yearly or it was probably due to the difference in estuarine temperatures, tidal currents and salinities which are often cited as having influence on the recruitment of juveniles into estuaries (Hughes 1969; Young and Carpenter 1977; Robertson 1984). Long term studies are probably required to establish the annual patterns of juvenile recruitment into POEs. Year round breeding of shrimps has been recorded elsewhere in the world (Heck 1977; Dugan 1983; Bauer 1989). The decrease in the number of adults caught in the estuary in May was probably due to migration to the sea for breeding purpose (Figure 3.7).

In the present study, CL of the shrimps was measured as the region from the anterior tip of the carapace to the dorsal midline of the posterior margin of the carapace (Section 3.2.1). Emmerson (1986) measured the total length (TL) of *P. peringueyi* (distance from the tip of the rostrum to tip of the telson). Robertson (1984) compared the relationship between CL and TL of *P. peringueyi*. The relationship between CL and SL were found to be linear ($r^2 = 0.989$) (Figure 3.15). To enable the comparison of Emmerson (1986), the regression equation of Robertson (1984), was used to convert the minimum and maximum SL reported by Emmerson (1986) to CL. Emmerson (1986) recorded minimum CL of 1.3 mm (SL = 6 mm) and maximum of 12.1 mm (SL = 50 mm) in the permanently open Swartkops Estuary. In TOCEs, Bernard and Froneman (2005) recorded CL of between 5 and 16 mm while Froneman (2006) recorded CL of between 6.9 to 16.2 mm. The shrimps caught in the present study were larger compared to those found by the previous authors. Carapace length of *P. peringueyi* caught during this study ranged between 5 to 25 mm (Figures 3.8.0 to 3.8.5). The large CL of *P. peringueyi* in the Kariega Estuary may probably be attributed to reduced number of predators which probably result in longer life span for the shrimps; this has been established for *Palaemonetes pugio* in two South Carolina estuaries (Alon and Stancyk 1982).

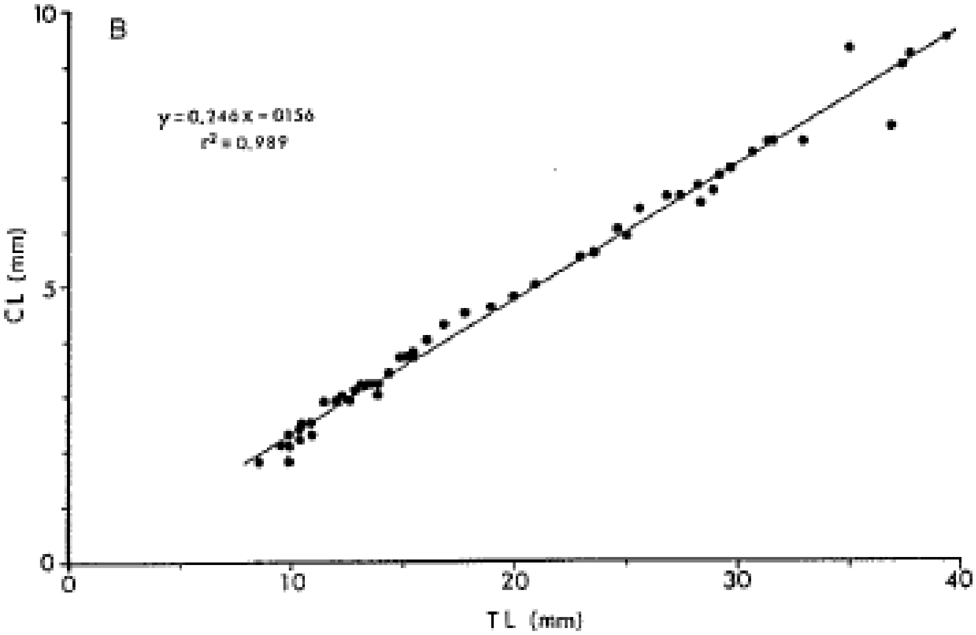


Figure 3.15: Relationship between carapace length (CL) and total length (TL) of *Palaemon peringueyi* (Adapted from Robertson 1984).

There was a distinct spatial pattern in the size distribution of *P. peringueyi* in the Kariega Estuary (Figure 3.7). Juveniles were more abundant in the lower and middle reaches while adults generally occurred in all the reaches. However, juveniles were more abundant in the lower reach compared to the middle reach (Figure 3.7). The high abundance of juveniles in the lower reach was probably due to high percentage cover of vegetation and the recruitment of smaller individuals from the marine environment. Adult *P. peringueyi* were only recorded in 5 occasions (September to October and March to May) in the upper reach of the Kariega Estuary. Juveniles were noticeably absent from the upper reach except in two occasions (September and May) of the sampling periods (Figure 3.7). Robertson (1984) showed that adult *P. peringueyi* can tolerate salinities of between 1 to 79 and juveniles between 2 to 60. Therefore, the absence of juveniles from the upper reach could be attributed mostly to the reduced vegetation cover rather than physiological constraints. Similar size distribution pattern have been observed in TOCEs within the same biogeographic region (Bernard and Froneman 2005; Froneman 2006). The size distribution pattern of *P. peringueyi* may be linked to the distribution of submerged macrophytes (Froneman 2006) or may reflect their recruitment and subsequent migration of shrimps up the estuary with development (Bernard and Froneman 2005).

3.4.2. Abundance and biomass

Minimum and maximum total abundance and biomass recorded in one tow ranged between 0 and 245.6 ind.m^{-2} and between 0 and 13.6 g wwt.m^{-2}, respectively. Mean abundances of the shrimp ranged between 0 and 88 (± 27.3) ind.m^{-2} (Figure 3.5) and mean biomass ranged between 0 and 4.4 (± 1.4) g wwt.m^{-2} (Figure 3.6). These values are low when compared to other permanently open estuaries within the same biogeographic region with sustained freshwater inflow. For example, Emmerson (1986) found that the abundance of *P. peringueyi* in the seagrass beds of the permanently open Swartkops and Sundays River Estuaries ranged between 100 and 200 ind.m^{-2} in summer and between 20 to 100 ind.m^{-2} in winter. The low abundances of *P. peringueyi* in the Kariega Estuary might be attributed to the reduced freshwater inflow. Mair (1980) demonstrated experimentally that postlarvae of four penaeid species in the western Mexico preferred low salinity inland waters over seawater when recruiting into estuaries and suggested that this could be significant in locating estuarine nursery grounds.

When compared to TOCEs within the same biogeographic region, the abundance and biomass values obtained in the current study were high. Bernard and Froneman (2005) found the abundance of *P. peringueyi* in the West Kleinemonde Estuary in the ranges of between 0 and 14.3 ind.m^{-2} and the biomass between 0 and 5.9 g wwt.m^{-2}. Similarly, Froneman (2006) found the abundance and biomass in the Grants River Estuary in the range of between 0 and 23 ind.m^{-2} and between 0 to 2.3 g wwt.m^{-2}, respectively. The reduced abundance and biomass values in TOCEs can be attributed to the presence of a sand bar across the mouth of the estuary which reduces recruitment opportunities into the system (Bernard and Froneman 2005; Froneman 2006; Whitfield *et al.* 2008). Statistical results (regression analysis) showed a lack of any significant relationships between the selected physico-chemical parameters (temperature, salinity, DO and vegetation) and abundance and biomass of *P. peringueyi* (Table 3.2). A weak but significant correlation was observed between abundance (r^2 = 0.109), biomass (r^2 = 0.185) and percentage vegetation cover (Table 3.2). Despite the weak correlation between submerged vegetation and abundance and biomass found in this study, several studies have demonstrated a significant correlation between submerged macrophytes and abundance of *P. peringueyi* (Robertson 1984; Emmerson 1986; Bernard and Froneman 2005; Froneman 2006). Submerged macrophytes are thought to provide the shrimps with food and refuge against predation (Emmerson 1986; Rozas and Odum 1987; Knieb and Wegner 1984; Walsh and Mitchell 1998; Adam *et al.* 1999). In the present study, the highest abundances and biomasses of *P. peringueyi* were recorded in the lower reach followed by the middle reach. Both these reaches were characterized by high percentage vegetation cover (Figures 3.5; 3.6 and 3.9). Similarly, lowest abundances and biomasses of the shrimps were recorded in the upper reach which had the least vegetation cover (Figures 3.5; 3.6 and 3.9). The reduced abundances of *P. peringueyi* in the upper reach of the estuary were probably due to the low density of vegetation or low salinity. Allan *et al.* (2006) found that temperatures of < 20 °C and salinity > 35 contributed to increases in the metabolic rate of *P. peringueyi* and further suggested that the shrimps may experience osmotic stress in estuaries that experience hypersaline (> 40) conditions. The observed pattern in distribution of *P. peringueyi* within the Kariega Estuary can therefore be attributed to both habitat availability and physiological constraints.

3.4.3. Factors affecting recruitment

Several factors have been shown to influence migration of shrimps into estuaries. Forbes and Cyrus (1991) associated the arrival of prawn post-larvae at the mouth of estuaries with the presence of suitable currents. The Agulhas Current is believed to have a significant influence on the distribution and migration of marine organisms occurring in the east coast waters of southern Africa (Macnae 1962; Heydorn *et al.* 1978). It has been established that more post-larvae enters the estuary on the flood tide than on the ebb tide (Copeland and Truitt 1966). Robertson (1984) also found that the larvae of *P. peringueyi* entered the Bushmans Estuary during the night tide flood. Crocos and Kerr (1983) and Rothlisberg *et al.* (1983) have demonstrated the influence of currents in the post-larval recruitment of *Panaeus merguensis* in the Gulf of Carpentaria. It is also believed that larvae are attracted to the nursery areas by the quality of a salinity gradient related to the ocean thus implying that the mysis and post-larvae are sensitive to changes of salinity (Williams and Deubler 1968; Hughes 1969; Young and Carpenter 1977). This was further supported by the findings of the current study where juveniles were concentrated in the lower reach. Considerable work has been carried out on the importance of salinity and substrata as factors influencing nursery habitats (Williams 1958; Gunther 1961; Hughes 1966; Young and Carpenter 1977; Young 1978; Mair 1980; Branford 1981; Rulifson 1981). These studies indicate that once juveniles enter an estuary, a particular species tend to prefer a biotope with a specific physical characteristics as its final nursery area. For example, Mair (1980) demonstrated experimentally that postlarvae of prawn species of Western Mexico showed a preference for low salinity inland water over seawater and suggested that this could be significant in locating estuarine nursery area, while Penn (1975) confirmed the entry of *Penaeus latisulacatus* in estuaries when there is a reverse salinity gradient. Mair (1980) and Dall (1981) further suggested that estuarine water characteristics other than salinity play a role in governing larval stages to theirs nursery areas.

Offshore migration is typical penaeid (Kutkuhn 1966; Allen 1966) and caridean shrimp (Israel 1936; Forster 1951) life cycles. Several authors (Idlly *et al.* 1964; Yokel *et al.* 1969; Garcia 1977) established that penaeid prawns emigrate from nursery areas during the nocturnal ebb tide. Rainfall and tidal phase are some of the factors found to stimulate emigration of shrimps (Staples and Vance 1986). Garcia and LeReste (1981) found that in areas where seasonal range of temperature is small with seasonal rainfall, migration is stimulated by rainfall and Staples (1980) reported that areas where temperature fluctuations are seasonal, temperature is a driving force for migration.

3.4.4. Sex ratios

The sex ratios of *P. peringueyi* recorded in this investigation showed a female biased ratio (Table 3.3). Wildish (1977) suggested that a female biased sex ratio increases the reproductive potential of the species, as it is assumed that one male can fertilize several females, resulting in a reduced need for males (Wong and Moore 1996). The female biased sex ratio in *P. peringueyi*, might be a result of misidentifying the sex of smaller individuals, this is because the appendix masculine may only develop in larger males (Robertson 1984). Although there was no significance difference between the CL of males and females, the largest shrimps caught during the study were females. Size variation in males and females is common in most prawn and caridean species (Walker 1979; Howard 1981; Alon and Stacyk 1982;Gray 1991). However, in some *Macrobrachium* species males attain larger size than female (Ling 1969; Koshy 1971; Guest 1979). Differences in growth between male and female *P. peringueyi* has been recorded by Emmerson (1986). The author found that male *P. peringueyi* matures and migrate earlier than females with the smallest mature male being 11 mm in CL. The high female numbers in the estuary could probably be related to the early migration of males to the sea. An estimate of *P. peringueyi* longevity is 2 to 3 years (Emmerson 1986). Some caridean shrimps have been found to breed two or three times in one season (Walker 1979; Gray unpublished data), however this has not been established for *P. peringueyi*.

3.5. Conclusions

The estimates of the abundance and biomass of *P. peringueyi* in the Kariega Estuary were lower than the abundances found in other POEs with sustained freshwater inflow within the same geographic region. Temperature and salinity did not appear to have an effect on the abundance and biomass of the shrimp in the estuary. The shrimps showed a spatial variation in their distribution patterns with highest abundances found in the lower and middle reaches of the estuary. The observed pattern can likely be attributed to the recruitment of the shrimp from the marine environment into the estuary and the availability of habitat in the form of *N. capensis*. Both the lower and middle reaches had high vegetation cover and the lowest vegetation cover was recorded in the upper reach. The upper reach of the estuary had the lowest abundance which was probably due to sparse vegetation cover and physiological constraints. Abundance and biomass of *P. peringueyi* showed a seasonal variation. Juveniles were mostly found in the lower reach while adults were found in all three reaches which probably indicate that juveniles are less tolerant to salinity changes and that adults can tolerate wide salinity ranges. The results also suggest that submerged vegetation (mostly *N. capensis*) plays an important role in determining the distribution of *P. peringueyi* in the estuary (predator avoidance and increased food availabity).

Chapter 4

Feeding of *Palaemon peringueyi* in the Kariega Estuary determined by using carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios

4.1. Introduction

Estuarine organisms can derive their carbon from both imported sources (allochthonous) and sources that are produced within the estuary (autochthonous) (Richoux and Froneman 2007). Comparing the stable carbon isotope ratio of primary consumers with the isotope ratio of the primary producers can indicate the food source of the animal (Haines and Montague 1979; Fry and Sherr 1984; Gearing *et al.* 1984; Peterson *et al.* 1985; Jerling and Wooldridge 1995; France *et al.* 1998). Analysis of carbon isotopes can provide information on the origins and pathways of organic matter since the stable isotope composition of consumers is closely related to that of their diet (Peterson *et al.* 1985; France and Peters 1997). Previous studies have shown that during feeding, the nitrogen isotopes of an animal becomes extremely fractionated compared to carbon and hydrogen (Minagawa and Wada 1984), and that $\delta^{15}N$ isotope of an organism is enriched by ~ 3.4 ‰ compared to its diet (Peterson and Fry 1987; Post 2002). Therefore, $\delta^{15}N$ signatures can indicate the trophic level of an organism within food webs (DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002).

The reduced freshwater input in the Kariega Estuary has resulted in an oligotrophic (Grange and Allanson 1995; Grange *et al.* 2000) marine dominated system (Hodgson 1987). As a result of the marine dominance in the Kariega Estuary, submerged macrophytes such as the *Nanozostera capensis* occur along the entire length of the system (Paterson 1999). The marine dominance in the Kariega has also resulted in *N. capensis* and salt marsh plants to occupy ~ 24% of the system (Froneman 2001). These macrophytes are thought to contribute significantly to the detrital pool of the estuary (Paterson 1999).

The shrimp, *Palaemon peringueyi*, is a common component of the macrofauna in temperate estuaries along the Eastern Cape coastline of South Africa where maximum densities are typically recorded in the submerged macrophyte beds (Emmerson 1983; 1987). Studies on feeding ecology of *P. peringueyi* using stable carbon isotope and fatty acids by Richoux and Froneman (2007; 2008) indicate that the shrimp feeds mainly on detritus and plant materials derived from submerged macrophytes which with they are associated. Although feeding of *P. peringueyi* using $\delta\ ^{13}$C and δ^{15}N isotopes have been investigated in the Kariega Estuary, most of these studies have been restricted to the middle reach of the estuary (Paterson and Whitfield 1997; Froneman 2001; Richoux and Froneman 2007). During the sampling survey of the population dynamics of *P. peringueyi* in the Kariega Estuary (Chapter 3), it was establish that the shrimps are distributed along the entire length of the estuary, and that they are most abundant in the lower reach of the estuary. In some aquatic systems, it has been demonstrated that carbon sources may be distributed homogeneously which may result in animals from separate sites having similar diets (Connolly *et al*. 2005). However, it has been shown that even in stable systems, sources of carbon may differ due to the variable nature of detritus (Kreeger and Newell 2000) and differences in the presence of salt marshes in different areas of the estuary (Richoux and Froneman 2007). Therefore, I hypothesize that feeding of *P. peringueyi* will be different in the different regions of the estuary due to possible variation of carbon sources, but is similar between the sexes of the shrimp since both males and females utilize the same habitat (submerged aquatic macrophytes). This study therefore aims to use carbon and nitrogen stable isotope analysis to determine the spatial changes in the feeding ecology of *P. peringueyi* in three regions in the Kariega Estuary.

4.2. Materials and Methods

4.2.1. Sample collection

The shrimps were collected by using a pull net from three sites in the Kariega Estuary in April 2011. Site 1 was situated in the lower reach at 33˚40’300 S; 26˚40’310 E, site 2 in the middle reach at 33˚37’873 S; 26˚38’629 E and Site 3 was situated in the upper reach at 33˚36’709 S; 26˚38’457 E (Figure 3.1). The shrimps were collected in areas covered by vegetation (mostly *N. capensis*). The percentage vegetation cover ranged from 30 to 80 % at the different stations.

4.2.2. Stable isotope analysis

A total of 26 shrimps were processed for δ^{13} C and δ^{15} N isotope analysis (lower reach n = 10, middle reach n = 12 and upper reach n = 4). In the laboratory, the shrimps were sexed with the aid of a dissecting microscope and the carapace length (CL) of each individual shrimp was measured to the nearest mm (see Chapter 3). The shrimps were separated into sexes (lower reach = 5 males and 5 females, middle reach = 6 males and 6 females, and upper reach = 2 males and 2 females) and dissected. In order to avoid contamination, the gut and exoskeleton of the shrimps were removed; only the muscle tissues from the abdomen were used for stable isotope analysis. Sufficient amount of tissue sample was obtained from each animal for an isotope result. The samples were oven dried at 60 ˚C for 24 hours and homogenized using a mortar and pestle. The samples were treated with 1 M HCL to eliminate carbonates, rinsed with distilled water, oven dried again for 24 hours and homogenized. Lipids were not extracted as only muscle tissues were analysed. Muscle tissues are characterized by low lipid content (Bodin *et al.* 2007). The tissue samples were analysed for stable carbon and nitrogen isotope at the IsoEnvironmental cc, Department of Botany, Rhodes University using a Europa Scientific Elemental Analyser coupled to a 20-20 Isotope Ratio mass Spectrometer (IRMS). In-house standards (Casein and a mixture of beet sugar and ammonium), calibrated against International Atomic Energy Agency (IAEA) standards, were used as internal calibrants. Isotope results were expressed in the δ notation:

δ (‰) = (R_{sample}/ $R_{standard}$ - 1) × 1000, where δ (‰) is δ^{13} or δN^{15} and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively.

4.3. Data analysis

A One-way ANOVA was used to test the differences of stable carbon and nitrogen isotope ratios of *P. peringueyi* at the different sites and sex. A Post-hoc test (Fisher LSD) was used to determine the sources of variations between the $\delta^{13}C$ and $\delta^{15}N$ ratios of males and females from the three study sites (lower, middle and upper reaches). Statistica version 10 was used to perform all analyses.

4.4. Results

4.4.1. Statistical analysis

There was no significant difference in the $\delta^{13}C$ and $\delta^{15}N$ isotopes of males and females ($p > 0.05$) (ANOVA). However, there was a significant difference in the $\delta^{13}C$ and $\delta^{15}N$ isotopes between the sites ($p < 0.05$) (ANOVA). A post- hoc test (Fisher LSD) showed that shrimps from the lower reach are significantly different from those in the middle and upper reaches in both $\delta^{13}C$ and $\delta^{15}N$ isotopes (Figures 4.1; 4.2; Table 4.1).

Table 4.1: Results for One-way ANOVA (Statistica version 10) to examine any significant difference in the δ^{13} C and δ^{15}N isotope between males and females and the regions (lower, middle and upper reaches) of the Kariega Estuary.

Variation	Sum of squares	Degree of freedom	Mean Squares	F-ratios	P
δ^{13} C isotopes (Sex)					
Lower reach	0.523	1	0.523	0.267	0.619
Middle reach	0.152	1	0.152	0.159	0.701
Upper reach	0.348	1	0.348	1.759	0.316
δ^{15}N isotopes (Sex)					
Lower reach	0.787	1	0.787	5.235	0.051
Middle reach	0.015	1	0.015	0.056	0.819
Upper reach	0.3603	1	0.360	18.550	0.049
δ^{13} C isotopes (Site)	93.728	2	46.864	38.289	$p < 0.001$
δ^{15}N isotopes (Site)	20.842	2	10.421	52.420	$p < 0.001$

4.4.2. Primary producers

Data for the primary producers and sediments were obtained from Richoux and Froneman (2007). Stable carbon isotopes for primary producers ranged between 5 to 27 ‰. Sediments had the most enriched δ^{13}C signatures (-5.3 ±0.1, ‰), followed by the eelgrass *Nanozostera capensis* epibionts (algae that grown on *N. capensis*) (-11.7 ± 0.3, ‰), *N. capensis* fresh (-8 ± 0.2, ‰) and *N. capensis* dry (-8.3 ± 0.1, ‰). Benthic algae (comprising mainly of macrophytobenthic algae) and *Codium* which grows in the estuary had intermediate signatures while the salt marsh (*Sarcocornia perennis* and *Chenolea diffusa*) and riparian plants had depleted δ^{13}C signatures (Table 4.1). Stable nitrogen isotopes ratios ranged from 3 – 11 ‰. Riparian plants and seston had the most enriched δ^{15}N signatures (3.7 ± 0.3 and 3.6 ± 0.9, ‰, respectively) with the salt marsh *C. diffusa* having the most depleted δ^{15}N signatures (11.1 ± 0.9, ‰).

Table 4.2: δ^{13}C and δ^{15} N signatures for producers collected from the Kariega Estuary in February 2006, obtained from Richoux and Froneman (2007).

Primary producers	**δ^{13} C**	**δ^{15} N**
Nanozostera capensis epibionts	-11.7 ± 0.3	9.5 ± 0.1
N. capensis fresh	-8.0 ± 0.2	5.7 ± 0.8
N. capensis dry	-8.3 ± 0.1	7.1 ± 0.4
Benthic algae	-15.5 ± 1.0	10.3 ± 2.7
Codium sp.	-17.2 ± 0.9	9.3 ± 0.1
Seston	-23.0 ± 0.5	3.6 ± 0.9
Sarcocornia perennis	-27.6 ± 0.2	9.5 ± 0.2
Chenolea diffusa	-26.9 ± 0.2	11.1 ± 0.9
Riparian plants	-27.8 ± 0.4	3.7 ± 0.3
Sediments	-5.3 ± 0.1	5.7 ± 0.8

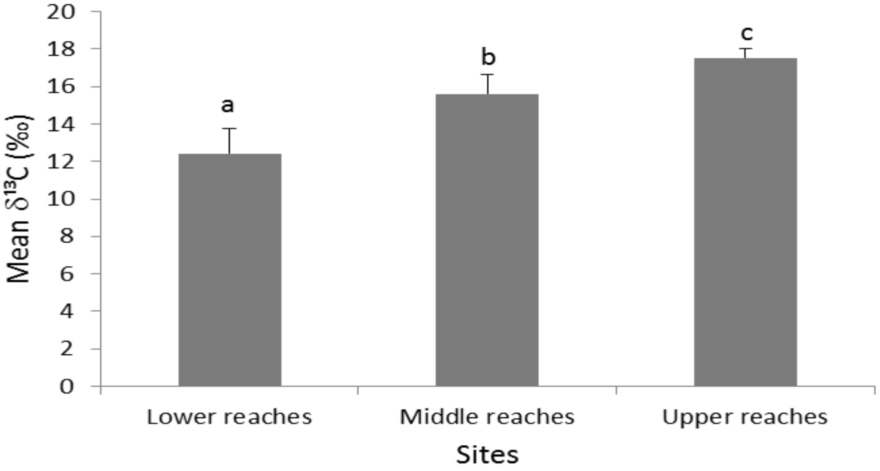


Figure 4.1: Mean (± SD) δ^{13} C (‰) values for *Palaemon peringueyi* collected from the Kariega Estuary in April 2011. Different letters indicate a significant difference ($p < 0.05$), males and females were pooled.

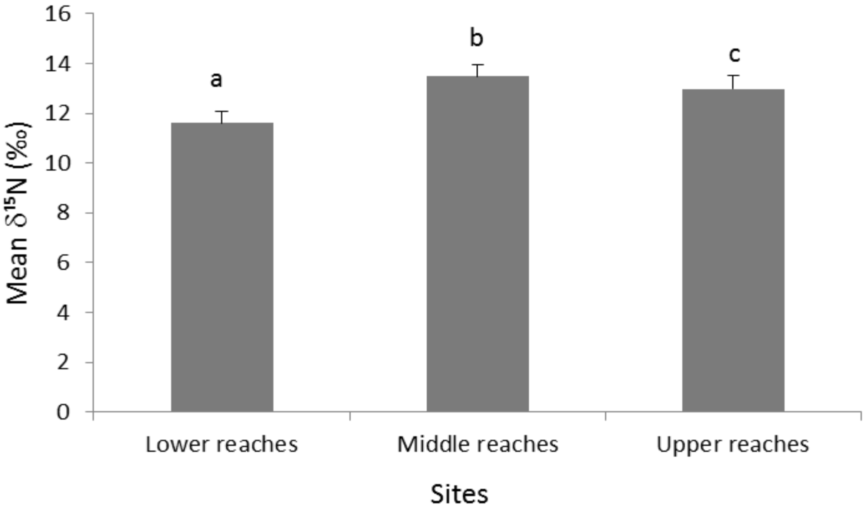


Figure 4.2: Mean (± SD) δ^{15}N (‰) values for *Palaemon peringueyi* collected from the Kariega Estuary in April 2011. Different letters indicate a significant difference ($p < 0.05$), males and females were pooled.

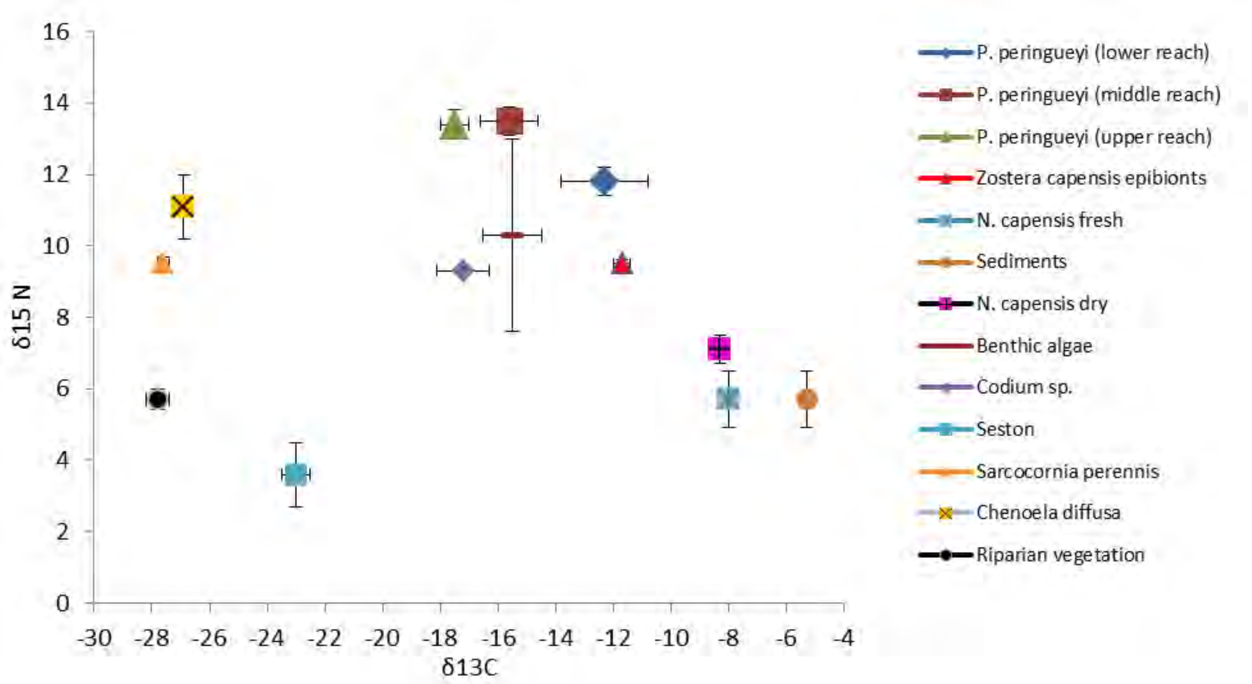


Figure 4.3: δ^{13}C and δ^{15}N (‰) values (± SD) for primary producers and sediments (obtained from Richoux and Froneman 2007) and *Palaemon peringueyi* (this study) collected from three sites (lower, middle and upper reaches) in the Kariega Estuary. (Horizontal bars are standard deviation).

4.4.3. *Palaemon peringueyi*

There were no significant differences in the stable carbon and nitrogen isotope ratios between the male and female *P. peringueyi* ($p > 0.05$) (Figures 4.4; 4.5). Mean stable carbon values for *P. peringueyi* ranged from -12.4 (± 1.3) to -17.5 (± 0.5) ‰ and mean δ^{15}N ranged from 11.6 (± 0.5) to 13.5 (± 0.4) ‰. There was an enrichment of δ^{13}C values of *P. peringueyi* from downstream to upstream of the Kariega Estuary (Figure 4.1). The shrimps with the most enriched δ^{13}C signatures occupied the lower reach (-12.4 ± 1.3, ‰), the shrimps with moderately enriched δ^{13}C signatures occupied the middle reach (-15.6 ± 0.5, ‰) with the upper reach being occupied by shrimps with the most depleted δ^{13}C signatures (-17.5 ± 0.5, ‰) (Figures 4.1; 4.3). Stable nitrogen isotope was enriched in the lower reach (11.6 ± 0.5, ‰) with the middle and upper reaches having similar isotope values of 13.5 (± 0.4) ‰ and 13.4 (± 0.4) ‰, respectively (Figure 4.2).

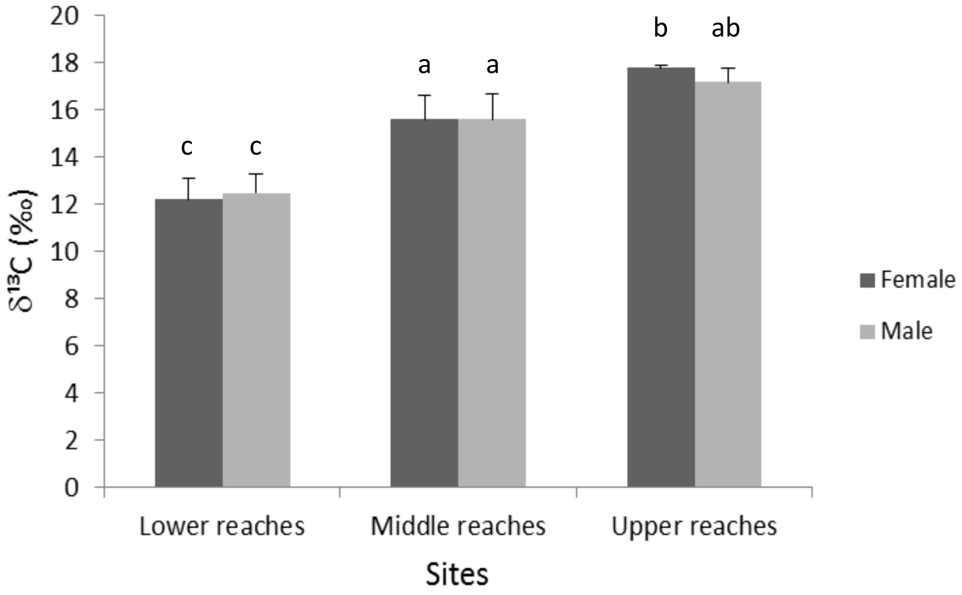


Figure 4.4: Mean (± SD) $\delta^{13}C$ values of male and female *Palaemon peringueyi* in the Kariega Estuary in April 2011. Different letters indicate a significant difference ($p < 0.05$).

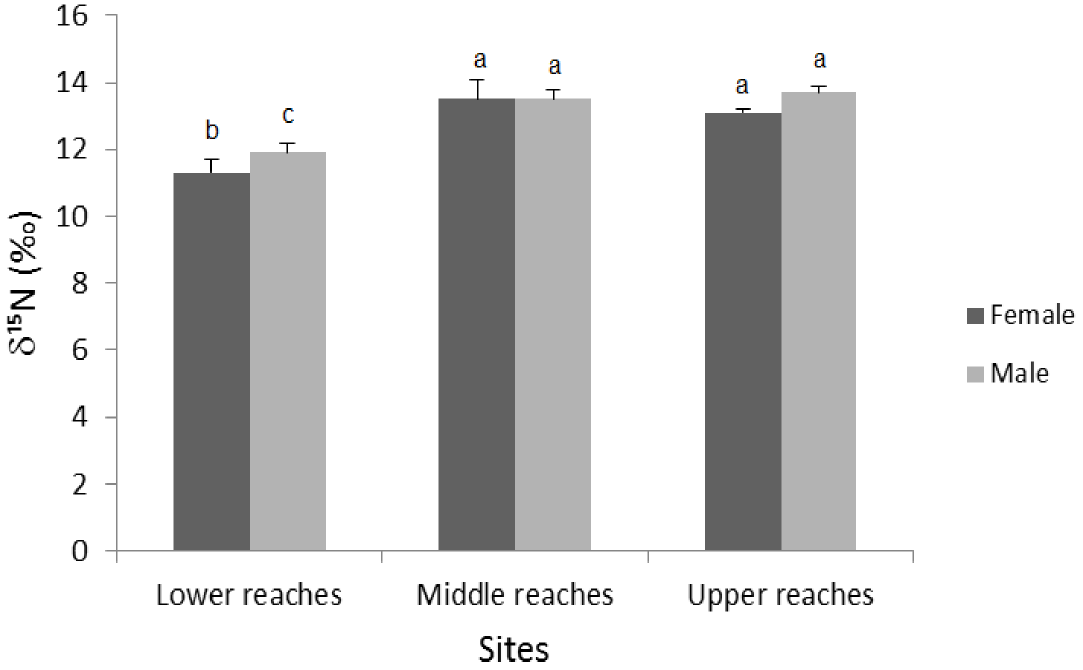


Figure 4.5: Mean (± SD) $\delta^{15}N$ values of male and female *Palaemon peringueyi* in the Kariega Estuary in April 2011. Different letters indicate a significant difference ($p < 0.05$).

4.5. Discussion

Stable carbon isotopes ($\delta^{13}C$) can be used to indicate feeding and carbon flow pathways because of the limited fractionation from prey to predator (Hecky and Hesslein 1995), while the $\delta^{15}N$ isotope can be used to determine the trophic position of an animal in the ecosystem (Gu *et al.* 1996; Vizzini *et al.* 2002) since the $\delta^{15}N$ of an organism is enriched by ~3 ‰ compared to its diet (Peterson and Fry 1987; Post 2002). Based on the stable isotope values of primary producers obtained from Richoux and Froneman (2007), the $\delta^{13}C$ and $\delta^{15}N$ isotope of primary producers in the Kariega Estuary demonstrated distinct values, those that were depleted, those that were moderately depleted and those that were enriched (Table 4.2). *Nanozostera capensis* epibionts, benthic algae and *Codium* possessed less enriched $\delta^{13}C$ and $\delta^{15}N$ isotopes compared to *N. capensis* (fresh and dry) and sediments which had the most enriched δ^{13}C and δ^{15}N isotopes (Table 4.2). The values of δ^{13}C for *N. capensis* (-8.3 ‰) fell within expected ranges of seagrasses (-3 to -13 ‰) (Calder 1969; Parker and Calder 1970; Smith *et al.* 1976; Fry 1977). The primary producers that were depleted were seston (-23 ‰), the salt marsh plants *C. diffusa* (-26.9 ± 0.2, ‰) and *S. perennis* (-27 ± 0.2, ‰) and the riparian vegetation (-27.9 ± 0.4, ‰) (Table 4.2). The value of the salt marsh plants are similar to those that are reported in Paterson and Whitfield (1997) where δ^{13}C values of *S. perennis* was -24.9 ‰ and -25.8 ‰ for *C. diffusa*. The depleted δ^{13}C values for seston (-23 ‰) were similar to those reported in Paterson and Whitfield (1997) and Froneman (2001). However, Froneman (2001) associated the depleted values of seston to the close proximity of the salt marshes. This may be the explanation for the depleted seston since the investigation by Richoux and Froneman (2007) was taken within proximity to the salt marshes in the lower middle reach of the Kariega Estuary.

Like the primary producers, *P. peringueyi* also demonstrated a pattern of δ^{13}C and δ^{15}N signatures. There was an enrichment of δ^{13}C signatures for the shrimps from downstream to upstream in the Kariega Estuary (Figures 4.1; 4.3). The differences in the δ^{13}C signatures of shrimps from the different sites indicate that the shrimps are likely feeding on different carbon sources. The shrimps in the lower reach appear to be feeding mainly on *N. capensis* epibionts (Figure 4.3). This was confirmed by the similarities of the δ^{13}C values between the shrimps and *N. capensis* epibionts. However, it is more likely that *N. capensis* epibionts could be the major food source of the shrimps in the lower reach since previous studies (Emmerson1987; Froneman 2002a; Richoux and Froneman 2007) found that *P. peringueyi* feeds mainly on plant material associated with *N. capensis*. The δ^{13}C and δ^{15}N isotope values of *P. peringueyi* suggest that the major diet for shrimps in the middle reach is benthic algae; *Codium* is probably ingested but not frequently (Figure 4.3). In the upper reach, possible diet for the shrimps is *Codium*; benthic algae is probably also ingested (Figure 4.3). However due to the thick filamentous structure of the both *Codium* and benthic algae, it is less likely that the shrimps may be able to masticate and digest these macrophytes. The shrimps are therefore probably feeding on detritus. However, there is also a possibility that *P. peringueyi* may be feeding on carbon and nitrogen sources that have not been recorded during sampling. Although *N. capensis* fresh, *N. capensis* dry and sediments possessed the most enriched $\delta^{13}C$ values (Table 4.2; Figure 4.3), these food sources are too enriched and are probably not utilized by the shrimps. These findings are in agreement with the study by Richoux and Froneman (2008) where the higher plants fatty acid (s) (HPFA) observed in *P. peringueyi* confirmed that epibionts and microalgae associated with seagrass and benthic algae are the key dietary items for the shrimps.

DeNiro and Epstein (1978) and Fry *et al.* (1977) found that small ranges of stable isotope ratios (1.8–2 ‰) or less among conspecific animals indicate that individual animals have similar diets, while ranges greater than 2‰ indicate isotopically different diet. Therefore, the variations in the $\delta^{13}C$ and $\delta^{15}N$ at the sites does not imply a change in trophic position but may indicate that the shrimps may be feeding on different food sources. The enrichment of $\delta^{13}C$ and $\delta^{15}N$ isotopes of the shrimps towards the mouth of the Kariega Estuary can be attributed to the enrichment of $\delta^{13}C$ isotopes of the dissolved inorganic carbon fraction of oceanic water relative to estuarine water (Simenstad and Wissmar 1985) and the increase in phytoplankton production and biomass in the lower reach (Richoux and Froneman 2007). Similar patterns were observed in Richoux and Froneman (2007) where there was an enrichment of $\delta^{13}C$ at a downstream site compared to an upstream site. It also appears that the enriched $\delta^{13}C$ of primary producers (*N. capensis*) in the lower reach probably resulted in the enrichment of $\delta^{13}C$ and $\delta^{15}N$ isotopes the shrimps at that site.

Results from ANOVA showed that the $\delta^{15}N$ isotopes in the lower reach were significantly different from the middle and upper reaches (Figure 4.2). The mean $\delta^{15}N$ isotopes was 11.6 (± 0.5) ‰ in the lower reach, 13.5 (± 0.4) ‰ in the middle reach and 13.4 (± 0.4) ‰ in the upper reach. Since the difference in $\delta^{15}N$ ratios between the three regions is less than 3 ‰, the difference in the $\delta^{15}N$ isotopes between the sites does not indicate different trophic levels. The enriched $\delta^{15}N$ ratios in the lower reach probably resulted from the enriched *N. capensis* epibionts (Table 4.1) or other sources of primary producers that have not been recorded.

Maynou and Carters (1998) suggested that investigating food consumption by organisms is essential in understanding their ecological role in the ecosystem. A number of studies have demonstrated that *P. peringueyi* is the dominant component of the hyperbenthos in southern African estuaries (Bernard and Froneman 2005; Froneman 2006; Whitfield *et al.* 2008). The hyperbenthos plays an important role in linking benthic and pelagic food webs (Perissinotto and MaQuaid 1990). Whitfield (1998) found that *P. peringueyi* is an essential component in the diet of several estuarine fishes, these shrimps have also been found to play an important role in the nutrient and energy dynamics of temporarily open closed estuaries (Froneman and Henninger 2010). Froneman and Henninger (2010) also established that the shrimps may consume < 0.01 to 0.07 g dwt detritus m^2 per day and as a byproduct of feeding. As a consequence, the shrimps may contribute to the export of particulate and dissolved organic matter from the littoral zone to the channel of the estuary. The shrimps therefore represent an important link between littoral zone and nekton within the Kariega Estuary.

4.6. Conclusion

The results of the $\delta^{13}C$ values suggest that in the lower reach of Kariega Estuary, *P. peringueyi* probably feeds on *N. capensis* epibionts. In the middle reach, possible diet for the shrimps is the detritus derived from benthic algae and the detritus of *Codium* in the upper reach (Figure 4.3). The result of this study also indicated an enrichment of $\delta^{13}C$ and $\delta^{15}N$ of *P. peringueyi* towards the mouth of the Kariega Estuary. The variation of $\delta^{13}C$ and $\delta^{15}N$ isotopes of *P. peringueyi* among sites suggests that the shrimps are feeding on diets that are isotopically different. Kling *et al.* (1992) suggests the $\delta^{15}N$ enrichment is larger if the consumer is a strict predator, intermediate if the consumer feeds at different trophic level and small if the consumer is a strict herbivore. This may imply that shrimps in the lower reach are strict herbivores and that shrimps in the upper reach may be feeding at different trophic levels, indicating omnivory. Indeed, Emmerson (1987) found that *P. peringueyi* feed on epiphytic diatoms, detritus and a small contribution of nematodes.

Chapter 5

General Discussion

The majority of South Africa's POEs are ecologically threatened by decrease of freshwater inflow (Whitfield 2005). Freshwater input has been regarded as a critical component to the functioning of South African estuaries and indeed, in estuaries worldwide (Day *et al.* 1954). A comparative study between the freshwater dominated Great Fish Estuary and the freshwater deprived Kariega Estuary indicates that freshwater inflow can influence the structure and functioning of selected biota in POEs (Whitfield 2005). For example, Grange *et al.* (2000) found that the maximum chlorophyll-*a* value in the Kariega Estuary was 1 µg. chla-*a*.L^{-1} while a maximum value of 22 µg. chla-*a*.L^{-1} was recorded in the Great Fish Estuary. In the Kariega Estuary particulate organic material concentrations ranged between 11 and 23 µg. POM. L^{-1} compared to 29 and 76 µg. POM. L^{-1} in the Great Fish Estuary (Grange *et al.* 2000). Mean zooplankton biomass in the Kariega Estuary was < 50 $mg.m^{-3}$ while in the Great Fish Estuary values ranged between 256 and 4253 $mg.m^{-3}$. Finally, the mean larval and early juvenile fish abundance in the Kariega Estuary was 49 $ind.m^{-2}$ and 279 $ind.m^{-2}$ in the Great Fish Estuary.

Mean (± SE) abundances of *Palaemon peringueyi* recorded in the Kariega Estuary during the present study ranged between 2.3 (± 3.0) and 88 (± 27.3) $ind.m^{-2}$ in the lower reach, from 0.9 (± 0.4) to 21.5 (± 4.5) $ind.m^{-2}$ in the middle reach, and from 0 to 1.6 (± 0.5) $ind.m^{-2}$ in the upper reach (Figure 3.5). Mean biomass ranged between 0.4 (± 0.5) and 4.4 (± 1.4) g $wwt.m^{-2}$ in the lower reach, from 0.1 (± 0) to 4.3 (± 0.9) g $wwt.m^{-2}$ in the middle reach and from 0 to 1.6 (± 0.5) g $wwt.m^{-2}$ in the upper reach (Figure 3.6). These values are low when compared to the abundance and biomass of the shrimp in other permanently open estuaries within the same region. A comparative study of abundance and biomass for *P. peringueyi* in selected POEs and TOCEs within the Eastern Cape region is presented in Table 5.1. The mean biomasses of Emmerson (1986) and

Bernard and Froneman (2005) were converted to wet weight by using a linear regression equation obtained from Bernard and Froneman (2005). Emmerson (1986) estimated the mean abundance and biomass of 163 ind.m^{-2} and 13.3 g wwt.m^{-2}, respectively, in the lower reach of Sundays River Estuary. In the lower reach of Swartkops Estuary, mean abundance was between 117 and 135 ind.m^{-2} and mean biomass between 10.4 and 10.9 g wwt.m^{-2} (Emmerson 1986). Mean abundance of 186 ind.m^{-2} and biomass of 14.3 g wwt.m^{-2} were recorded in the lower reach of the Kromme Estuary while mean abundance and biomass of between 28 to 211 ind.m^{-2} and 1.0 to 15.3 g wwt.m^{-2}, respectively were recorded towards the upper reach of the Kromme Estuary (Table 5.1) (Emmerson 1986). The reason for the low abundance and biomass of *P. peringueyi* in the Kariega Estuary when compared to other POEs is unknown and requires further investigations.

The abundance and biomass of *P. peringueyi* attained during this investigation were greater than those recorded in selected TOCEs within the same biogeographic region. Bernard and Froneman (2005) obtained mean abundance and biomass of between 0 and 14.3 ind.m^{-2} and 0 and 5.9 g wwt.m^{-2}, respectively in the West Kleinemonde Estuary while Froneman (2006) obtained mean abundance of between 0 and 23.2 ind.m^{-2} and biomass of between 0 and 2.3 g wwt.m^{-2} in the Grants River Estuary (Table 5.1). The low abundance and biomass of *P. peringueyi* in TOCEs can be attributed to the presence of the sandbar across the mouth which restricts recruitment of the shrimps into these estuaries. Some authors (Beck and Cowell 1976; Berglund 1980; Alon and Stancyk 1982; Bauer 1985; Gray 1991) found that in some *Palaemonid* shrimps, intraspecific variation can occur in different habitats and in different geographic regions or latitudes. Therefore, differences in habitats and environmental conditions may have also resulted in the reduced abundance of *P. peringueyi* in TOCEs. Increased number of predators such as fish may also have resulted in the reduced abundance and biomass *P. peringueyi* in TOCEs.

The mean abundances of *P. peringueyi* in the Eastern Cape POEs are high when compared to abundances other species of *Palaemon* elsewhere in the world. For example, in a two year sampling conducted in Alfacs Bay, western Mediterranean (Ebro delta), *Palaemon serratus*, *P. adspersus* and

P. xiphias attained mean abundances of 0 to 59, 3 to 55 and 2 to 59 ind.m^{-2}, respectively in the seagrass, *Cymodecea nodosa* (Guerao and Ribera 2000). In Namhae, South Korea, *P. gravieri* attained total abundance of between 2 and 59 ind.m^{-2} and mean abundance of 15 ind.m^{-2} over a period of two years (Kim 2005). The differences habitats or conditions within geographic regions may have resulted in the reduced abundances of these shrimps (Sastry and Vargo 1977; Sikora 1977).

There was a distinct spatial pattern in the abundance and biomass of *P. peringueyi* in the Kariega Estuary. The lower reach had significantly higher abundance and biomass of *P. peringueyi* than the middle and upper reaches, respectively (Figures 3.5; 3.6). Similar distributional patterns have been observed in other POEs (Emmerson 1986) and TOCEs (Bernard and Froneman 2005; Froneman 2006) within the same biogeographic region (Table 5.1). Similarly, the spatial pattern in the distribution of size structure of *P. peringueyi* indicated that juvenile shrimps occupied the lower and middle reaches, although they were more abundant in the lower reach while adults occupied all three reaches of the Kariega Estuary (Figure 3.7). The observed distribution pattern is thought to reflect a re-colonization pattern where established shrimps in the lower reach migrate up the estuary (Bernard and Froneman 2005). The low abundance and biomass of *P. peringueyi* in the upper reach during the study was probably due to reduced vegetation cover and / or physiological tolerance.

Table 5.1: Comparisons of the mean abundance and biomass of *Palaemon peringueyi* in POEs and TOCEs within the Eastern Cape region, South Africa.

Study	**Estuary**	**Type**	**Abundance (ind.m^{-2})**	**Biomass (g wwt.m^{-2})**
This study	Kariega	POE	0.0 - 88.0	0 - 4.4
Emmerson (1986)	Sundays	POE	163.0	13.3
Emmerson (1986)	Swartkops, lower reach	POE	117.0	10.4
Emmerson (1986)	Swartkops, lower reach	POE	135.0	10.9
Emmerson (1986)	Kromme, upper reach	POE	28.0 - 211.0	1.0 - 15.3
Emmerson (1986)	Kromme, lower reach	POE	186.0	14.3
Froneman (2006)	Grants River Estuary	TOCE	0.0 - 23.2	0.0 - 2.3
Benard and Froneman (2005)	West Kleinemonde	TOCE	0.0 - 14.3	0.0 - 5.9

The weak relationship observed between percentage vegetation cover and abundance and biomass of the shrimps during this investigation, however suggest that the abundance and distribution of the shrimp in estuaries could also in part, be related to availability of submerged macrophytes rather than physiological constraints. It appears that vegetation, mainly *N. capensis*, is important to the success of *P. peringueyi* in estuaries. Hanekom (1982) conducted a study in the Kromme Estuary comparing the abundances of various nekton species occurring in *Nanozostera* beds with the same species occurring in bare substratum. The results indicated that ~ 97 % of *P. peringueyi* population collected were found in the *Nanozostera* beds. This is not surprising since *N. capensis* provide food sources for the shrimps as established in Chapter 4, and are thought to provide the shrimps with refuge against predators (Emmerson 1986; Walsh and Mitchell 1988).

Studies that have been undertaken on *Palaemon* species both locally (Emmerson 1985; 1986; 1987) and elsewhere in the world (Lewis and Stoner 1983; Zimmerman *et al.* 1984; Bilgin *et al.* 2008) show that the shrimps are more abundant in vegetated areas compared to bare substratum. It is believed that seagrass beds provide food and increased protection from predators compared to non-vegetated areas (Zimmerman *et al.* 1984; Canion and Heck 2009). Canion and Heck (2009), demonstrated experimentally that the turtlegrass *Thalassaia testudium* provided the shrimp *Palaemonetes pugio* with greater protection from the predatory pinfish *Lagadon rhomboids* in the Gulf of Mexico. Some studies indicate that dense vegetation provides the shrimps with even more protection from predators compared to sparse vegetation (Nelson 1979; Heck and Thoman 1981; Crowder and Cooper 1982). This suggests that *P. peringueyi* will probably not succeed in non-vegetated areas.

In the current study, *P. peringueyi* showed a regular recruitment of juveniles with the largest number of juveniles occurring in winter. *Palaemon peringueyi* has been reported to emigrate from POEs when they attain a TL of between 30 to 40 mm which corresponds to residence time of ~9 months (Emmerson 1986). A linear regression equation ($r^2 = 0.99$, $TL = 0.668 + 2.46 \times CL$) obtained from Bernard and Froneman (2005) was used to convert CL of the shrimps to TL. The shrimps would probably start migrating from the estuary to their spawning ground when they attain CL of about 13 mm. In the current study, very few adult *P. peringueyi* (CL > 13 mm) were caught in the estuary from May to August. The loss of adults was probably due to migration of adults into the sea for breeding. However, the large numbers of adults with CL > 13 mm in September may indicate that the shrimps probably attain maturation size after about 4 months of recruitment of juveniles (Figures 3.7; 3.8.0 - 3.8.5).

There may have been an underestimation of the abundance and biomass of *P. peringueyi* in the current study due to factors such as net avoidance and the time of sampling. The sampling for this study took place during daytime low tides. Emmerson (1986) found that in the permanently open Swartkops and Kromme Estuary, the seagrass *N. capensis* is largely exposed during low tide and that the shrimps migrate out of the *Nanozostera* beds to other places before low tides. Seagrass beds in the Kariega Estuary are also partly exposed during low tide and it is possible that most of the shrimps may have migrated out of the *Nanozostera* before sampling took place. In the north coast of

Puerto Rico, Bauer (1985) recorded higher abundances for nine species of caridean shrimps at night than in day samples; the high abundance of shrimps at night was associated with nocturnal activity, net avoidance during the day and migration into seagrass beds from other areas. Shrimps like *Alpheus normanni* burrows during daytime, other shrimps like *Latreutes fucorum* and *Hippolyte curacaoensis* cling to seagrass leaves during daytime and swim actively at night (Bauer 1985); it is possible that *P. peringueyi* may demonstrate similar behaviour which may result in reduced catches during the day and more at night.

Stable isotope ratios are used to gain information on the origins and pathways of an organism's food source as their isotopic composition are closely related to that of their diet (Peterson *et al.* 1985; France and Peters 1997). In Chapter 4, the feeding ecology of *P. peringueyi* employing $\delta^{13}C$ and $\delta^{15}N$ isotope was investigated. The hypothesis of the study proposed that the diet of the shrimps would be different in the different sites of the Kariega Estuary but similar in both males and females. The results showed a significant difference in $\delta^{13}C$ and $\delta^{15}N$ isotope for *P. peringueyi* ($p < 0.05$) (Table 4.1) between the sites of the Kariega Estuary. Stable isotope ratios of the shrimps were enriched in the lower reach (-12.4 ± 1.3, ‰) followed by the middle reach (-15.6 ± 0.5, ‰) and upper reach (-17.5 ±0.5, ‰), respectively (Figure 4.1). The $\delta^{15}N$ isotope was enriched in the lower reach (11.6 ± 0.4 ‰), the middle and the upper reaches possessed depleted $\delta^{15}N$ isotope values of 13.5 (± 0.4) ‰ and 13.4 (± 0.4) ‰, respectively (Figure 4.2). However, no significant difference was observed between the male and female $\delta^{13}C$ and $\delta^{15}N$ isotope ratios ($p > 0.05$) (Table 4.1). The differences in $\delta^{13}C$ isotopes values between the sites suggest a variation of carbon source utilisation within the sites of Kariega Estuary which supported the proposed hypothesis. Results of the stable isotope analysis for the primary producers suggest that the diet of *P. peringueyi* in the lower reach is likely comprised of *N. capensis* epibionts. In the middle reach, possible diet of the shrimps is probably the detritus benthic algae and, *Codium* detritus in the upper reach (Figure 4.3). The enriched $\delta^{13}C$ and $\delta^{15}N$ isotope in the lower reach was probably the result of the enriched *N. capensis* epibionts or other sources of primary producers that have not been recorded. Emmerson

(1987) found that *P. peringueyi* is an omnivore and can feed on detritus and animal such as nematodes. Similar diets in other species within the genus *Palaemon* have been observed (Guearo 1995; Janas and Baranska 2008). Janas and Baranska (2008) found that, in the Gulf of Gdansk (Baltic Sea), the main diet of *P. elegans* is detritus, although various benthic animals also contribute to their diet. Guerao (1995) found that *P. xiphias* in Alfacs Bay (northwest Mediterranean) is carnivorous and feeds mainly of crustaceans and that plant materials are also ingested but not often. However, TOCEs such as Kasouga and West Kleinemonde Estuary are dominated by submerged macrophytes such as *Ruppia maritima* and *Phragmites australis* (Henninger 2008). Therefore, the diet of *P. peringueyi* in TOCEs may differ from the diet of those found in POEs. In TOCEs such as Kasouga and West Kleinemonde, *P. peringueyi* would probably feed on the detritus or other organisms associated with *R. maritima* and *P. australis*. These data would suggest that *P. peringueyi* is a generalist feeder / scavenger.

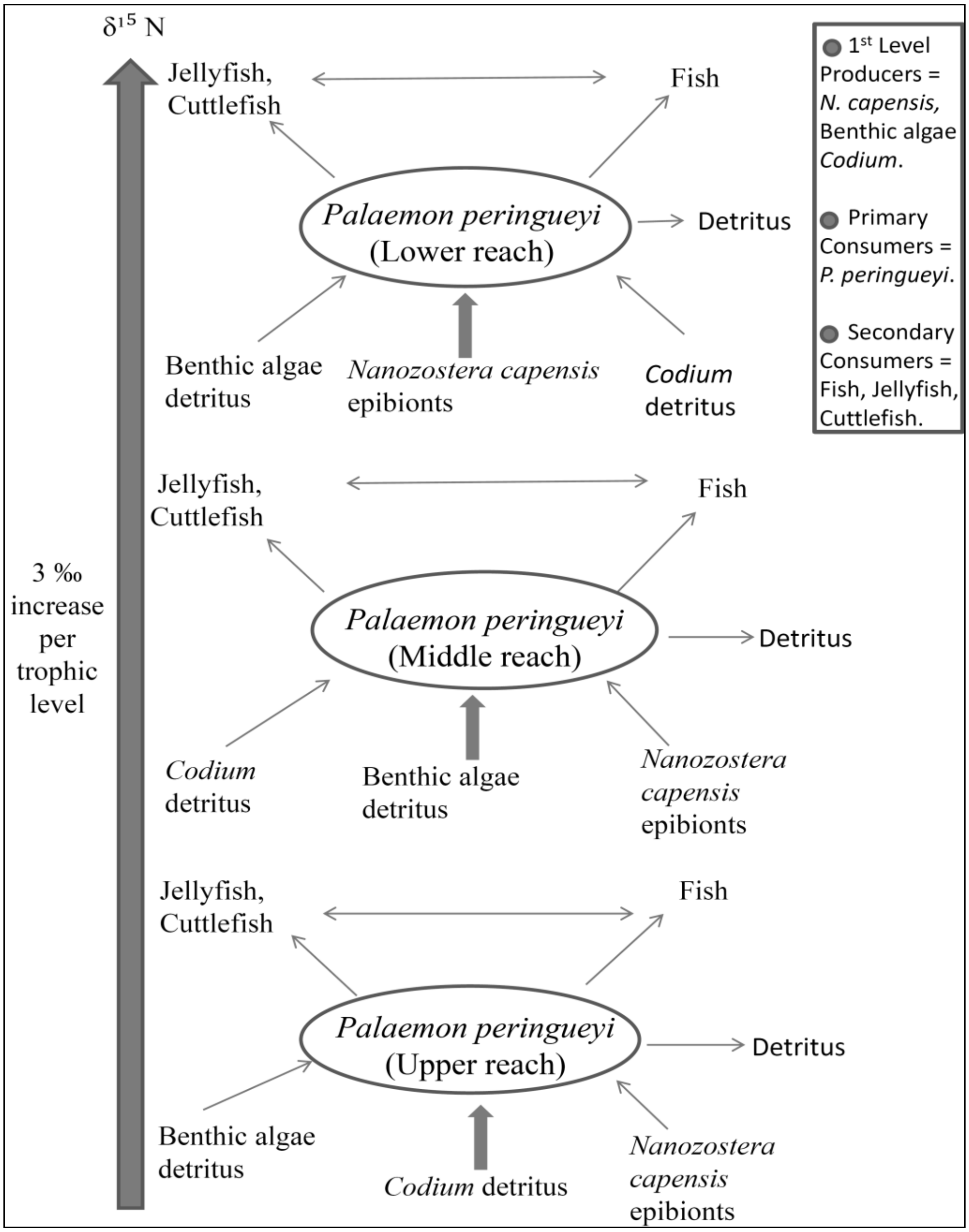


Figure 5.1: Hypothetical food web of *Palaemon peringueyi* from the lower, middle and upper reaches in the Kariega Estuary. Thick arrows represent the main diet of the shrimps in that reach.

Figure 5.1 shows the role that *P. peringueyi* may play in the foodweb structure in the Kariega Estuary. The major diet for *P. peringueyi* in the lower reach of Kariega Estuary would probably be the seagrass *N. capensis* epibionts, the detritus of *Codium* and benthic algae are probably consumed but not frequently. It is also not surprising that *P. peringueyi* in the lower reach feed on *N. capensis* epibionts, since it was established in Chapter 3 that *N. capensis* is more abundant in the lower reach of the Kariega Estuary. In fact, *N. capensis* epibionts are probably consumed in all three reaches of Kariega Estuary since the seagrass extends the entire length of the estuary. In the middle reach, *P. peringueyi* feeds mainly on the detritus of benthic algae. *N. capensis* epibionts and *Codium* detritus may be consumed, but not as frequently as benthic algae. In the upper reach, major diet for *P. peringueyi* is probably the detritus of *Codium*, although *N. capensis* epibionts and benthic algae may contribute to its diet. Predators for *P. peringueyi* in the Kariega Estuary are species of some estuarine fishes and probably other invertebrates such as cuttlefish and some species of jellyfish. The shrimp may contribute to the export of detritus through defecation.

Palaemon peringueyi is a common component of the hyperbenthos in Southern African estuaries (Emmerson 1986; Bernard and Froneman 2005) and plays an important role in the nutrient and energy dynamics of estuaries (Froneman and Henninger 2010). Froneman and Henninger (2010) demonstrated that the feeding activity of *P. peringueyi* may contribute to the export of particulate and dissolved organic matter within estuaries. Assuming that the daily food intake of male and female *P. peringueyi* in the Kariega Estuary is the same as that attained by Froneman and Henninger (2010) for this species in the Kasouga Estuary, the daily food of the shrimp during this investigation can be estimated. The daily food intake of *P. peringueyi* in the Kariega Estuary in winter can be estimated to be between 3.3 to 3.8 g dwt detritus m^{-2} and 0.62 to 1.7 g dwt detritus m^{-2} for females and males, respectively in the lower reaches. In the middle reaches between 0.7 to 2.6 g dwt detritus m^{-2} for females and 0.2 to 1.2 g dwt detritus m^{-2} for males, and between 0 to 0.34 g dwt detritus m^{-2} for females and 0 and for males in the upper reaches. In summer an estimate of daily food consumed *P. peringueyi* in the lower reaches is between 1.7 to 2.4 g dwt detritus m^{-2} for females and 2.1 to 1.2 g dwt detritus m^{-2} for males, between 0.71 to 0.3 g dwt detritus m^{-2} for females and 0.2 to 0.2 g dwt detritus m^{-2} for males in the middle reaches and 0 in the upper reach since the shrimps were absent. Hyperbenthos play an important role in the remineralisation of nutrients in estuaries (Mees and Jones 1997; Carleton and Hamner 2007). It is thought that as a byproduct of feeding, or defecation, *P. peringueyi* may contribute to the export of particulate and dissolved organic matter from the littoral zone into the channel of the estuary (Froneman and Henninger 2010). Therefore, *P. peringueyi* probably also play a role in nutrient cycle in the Kariega Estuaries.

5.1. Future Research

Palaemon peringueyi has often been cited as being a dominant component of the hyperbenthos within POEs and TOCEs in South Africa (de Villiers *et al.* 1999; Kibirige and Perissinotto 2003; Bernard and Froneman 2004; Kemp and Froneman 2004). Results from this study suggest that *P. peringueyi* plays an important role in the community and food web structures within estuaries. However, it is not fully understood how the shrimp responds to various abiotic factors within estuaries. Further research on *P. peringueyi* could include the following:

1. Investigate the abundance and biomass of *Palaemon peringueyi* by nocturnal sampling, as many studies (see Bauer 1985 and the references within) show that some decapod crustaceans are more active at night. This will probably provide a more accurate estimation of the abundances and biomass of the shrimp.

2. Assess how temperature and salinity affects larval and adult growth of *P. peringueyi*. This will give a better understanding of how survival and growth rate changes between the two age groups.

3. Investigate the effect of temperature and salinity on the feeding of *P. peringueyi*. Although the studies show that the shrimp can tolerate a wide range of temperature and salinity (Robertson 1984), it has been suggested that mortality should not be the only manner to assess how

physico-chemical variables affect an organism (Kinne 1963; 1971; Read and Cumming 1967; Ansell and McLachlan 1980; McLachlan and Young 1982). It is important to determine the point at which these variables begin to affect the physiology of an organism.

4. Investigate feeding of *P. peringueyi* by using a combination of gut content analysis and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) or fatty acid analysis. A combination of stable isotope and gut content analysis has been shown provide a more detailed and accurate evaluation of diet of organisms (Drazen *et al.* 2008).

References

ADAMS, J.B. and TALBOT, M.M .1992. The influence of river impoundment on the estuarine seagrass *Zostera capensis* Setchell. *Botanica Marina.* **35**: 69- 75.

ADAMS, J.B. and BATE, G.C. 1994. The ecological implications of tolerance to salinity by *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. *Botanica Marina* **37**: 449-456.

ADAMS, J.B. and BATE, G.C. 1996. Understanding the freshwater requirements of estuarine plants. In: Salaman, A.H.P.M., Langeveld, M.J. and Bonazountas, M. (eds.) Coastal Management and Habitat Conservation, The Netherlands, 181- 192.

ADAMS J., BATE, G. and O'CALLAGHAM, M. 1999. Primary producers. In: Allanson B.R., Baird D. (eds), Estuaries of South Africa. Cambridge University Press, Cambridge, United Kingdom, 91- 98.

ALLAN, E.L., FRONEMAN, P.W. and HODGSON, A.N. 2006. Effects of temperature and salinity on the standard metabolic rate (SMR) of the caridean shrimp *Palaemon peringueyi. J.ournal of Experimental Marine Bioliogy and Ecology* **337**: 103-108.

ALLANSON, B. R. and READ, G. H. L. 1987. The response of estuaries along the south eastern coast of southern Africa to marked variation in freshwater. Institute for Freshwater Studies, Rhodes University, Grahamstown,Special *Report No. 2/87*. 40 pp.

ALLANSON, B.R. and READ, G.H.L. 1995. Further comment on the response of Eastern Cape province estuaries to variable freshwater inflows. *South African Journal of Aquatic Science* **21**: 56-70.

ALLEN, J.A. 1966. The rhythms and population dynamics of decapod crustacea. *Oceanography and Marine Biology Annual Review* **4**: 247- 265.

ALON, N.C. and STANCYK, S.E. 1982. Variation in life-history patterns of the grass shrimps *Palaemontes pugio* in two South Carolina estuarine system. *Marine Biology* **68**: 265- 276.

ANSELL, A.D. and MCLACHLAN, A. 1980. Upper temperature tolerances of three mollusc from South African sandy beaches. *Journal of experimental Marine Biology and Ecology* **48**: 243- 251.

ARCHITUV, Y. and COOK, P.A. 1984. The influence of temperature variations and thermal pollution on various aspects of the biology of the prawn *Palaemon pacificus* (Stimpson), *Journal Experimental Marine Biology and Ecology* **74**: 291- 302.

BARAJAS F.J.M., VILLEGAS R.S., CLARK G.P. and MORENO B.L. 2006. *Litopenaeus vannamei* (Boone) post-larval survival related to age, temperature, pH and ammonium concentration. *Aquaulture Research* **37**: 492- 499.

BARNARD, K.H. 1950. Descriptive catalogue of South African decapods Crustacea. *Annls of the South African Museum* **38**: 1- 837.

BATE, G.C., WHITFIELD, A.K., ADAMS, J.B., HUIZINGA, P. and WOOLDRIDGE, T.H. 2002. The importance of the river estuary interface zone in estuaries. *Water SA* 28, **3**: 271-279.

BAUER, R.T. 1985. Diel and seasonal variation in species composition and abundance of Caridean shrimps (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico. *Bulletin of Marine Science*, **36**: 150-162.

BAUER, R.T. 1989. Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a strong seagrass meadow. *Journal of experimental Marine Biology and Ecology* **127**: 175- 187.

BECK, J.T. and COWELL, B.C. 1976. Life history and ecology of freshwater caridean shrimp, *Palaemonentes paludosus* (Gibbes). *American Midland Naturalist* **96**: 52- 65.

BEGG, G.W. 1978. The estuaries of Natal. *Natal Town and Regional Planning Report* **41**: 1- 657.

BENNETT, B.A. 1989. A Comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the south-western Cape, South Africa. *South African Journal of Marine Science* **8**: 43- 55.

BERGLUND, A. 1980. Niche differentiation between two littoral prawns in Gullmar Fjord, Sweden *Palaemon adspersus* and *P. squilla*. *Holartic Ecology* **3**: 1- 15.

BERNARD, A.T.F. and FRONEMAN, P.W. 2005. Population dynamics of the caridean shrimp, *Palaemon peringueyi*, in temporary open/closed Southern African estuary. *Estuarine Coastal and Shelf Science* **63:** 73-81.

BEUKEMA, J.J. 1992. Dynamics of the juvenile shrimp Crangon crangon in tidal-flat nursey of the Wadden sea after mild and cold winters. *Marine Ecology Progress Series* **83**: 157-165.

BILGIN, S., OZEN, O., and ATES, A.S. 2008. Spatial and temporal variation of *Palaemon adspersus, Palaemon elegans* and *Crangon crangon* (Decapoda: Caridea) in the south Black Sea. *Estuarine, Coastal and Shelf Science*, **79**: 671- 678.

BIRD, E.C.F. 1984. *Coasts: An introduction to coastal morphology*. Australian National University, Canberra: 320 pp.

BODIEN, N., LE LOCH, F. and HILY, C. 2007. Effect of lipid removal on carbon and nitrogen stable isotope ratios in crustacean tissues. *Journal of Experimental Marine Biology and Ecology* **341**: 168- 175.

BRANFORD, J.R. 1981. Sediments preferences and morphometric equations for *Penaeus monodon* and *P. indicus* from creek of the Red Sea. *Estuarine, Coastal and Shelf Science* **13**: 473- 476.

BRITO, A. and PENA, A. 2007. Population structure and recruitment of penaeid shrimps from the Pungue river estuary to the Sofala Bank fishery, Mozambique. Western Indian Ocean, *Journal of Marine Science* **6**: 2, 147-158.

BROEKHUYSEN, G.J. and TAYLOR, H. 1959. The ecology of Southern African estuaries Part 8. Kosi Bay estuary system. *Annals of South African Museum* **44**: 279-296.

CALDER, J.A. 1969. Carbon isotope effects in biochemical and geochemicall systems. Unpublishes Ph.D. Dissertation, Univeristy of Texas, Austin, 132 pp.

CANION, C.R. and HECK, K.L. 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Marine Ecology Progress Series* **393:** 37-46.

CARLETON, J.H. and HAMNER, W.M. 1989. Resident mysids: community structure, abundance and small-scale distributions in a coral reef lagoon. *Marine Biology* **102**: 461-472.

CHANCE, F.A. and BRUCE, A.J. 1993. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition 1907- 1910, Part 6: Superfamily Palaemonoidae. *Smithsonian Contribution to Zoology* **543**: 1- 152.

CHENG, W., WANG, L.U. and CHEN, J.C. 2005. Effect of water temperature on the immune response of white shrimp *Litopenaeus vannamei* to *Vibrio alginolyticus*. *Aquaculture* **250**: 592- 601.

CLARK, J. 1974. *Coastal Ecosystems*. Ecological considerations for the management of the Coastal Zone, Washington D.C Conservation Foundation.

CONNOLLY, R.M., GORMAND, and GUEST, M.A. 2005. Movement of carbon among estuarine habitats and its assimilation by invertebrates. *Oecologia* **144**:684–69.

COPELAND, B.J. and TRUITT, M.V. 1966. Fauna of the Aransas Pass Inlet, Texas. 11. Penaeid shrimp postlarvae. *Texas Journal of Science* **18**: 65- 74.

CROCOS, P.J. and KERR, K.D. 1983. Maturation and spawning of the banana prawn *Penaeus merguiensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpentria, Australia. *Journal of Experimental Marine Biology and Ecology* **69**: 37- 59.

CROWDER, L.B. and COOPER, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**: 1802- 1813.

CUSHING, D.H. 1975. Marine ecology and Fisheries, Cambridge: Cambridge University Press, page 278.

DALL, W. 1981. Osmoregulatory ability and juvenile habitat preferences in some penaeid prawn. *Journal of Experimental Marine Biology and Ecology* **54**: 55- 64.

DAVIES, B.R., O'KEEFFE, J.H., and SNADDON, C.D. 1993. A synthesis of the ecological functioning, conservation and management of South African River ecosystems. *WRC Report TT 62/93*. Pretoria: Water Research Commission.

DAY, J.H. 1980. What is an estuary? *South African Journal of Science* **76**: 198- 133.

DAY, J.H. 1981. Estuarine ecology with particular reference to Southern African. Cape Town: A.A. Balkema.

DAY, J.H. 1981a. Nature, origin and classification of estuaries. In: *Estuarine Ecology with Particular Reference to Southern Africa,* (eds) Day J.H., Cape Town A.A. Balkema, 1- 6.

DAY, J.H., MILLARD, N.A.H. and BROEKHUYSEN G.J. 1954. The ecology of South African estuaries. Part 4: The St Lucia system. *Transaction of the Royal Society of South Africa* **34**: 129- 156.

DE FREITAS, A. J. 1986. Selection of nursery areas by six southeast African penaeidae. *Estuarine Coastal and Shelf Science* **23**: 901-908.

DE NIRO, M. J. and ESPSTEIN S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta **4**: 495-506.

DE RUIJTER, W.P.M., VAN AKEN, H.M., BEIER, E., LUTJEHARMS, J. R. E. MATANO, R. P. and SCHOUTEN, M.W. 2004. Eddies and dipoles around South Madagascar: formation, pathways and large-scale impact. *Deep-Sea Research I*, **51**: 383-400.

DE VILLIERS, C. J. 1989. Aspects of the biology of the infaunal bivalve mollusc *Solen cylindraceus* (Hanley) in the Kariega Estuary. PhD thesis, Rhodes University, Grahamstown.

DE VILLIERS, C.J., HODGOSON, A.N., and FORBES, A. 1999. Studies of estuarine macroinvertebrates. In: Allanson, B.R. and Baird, D., (eds), estuaries of South Africa, Cambridge University Press, Cambridge, UK, 167- 208.

DEPARTMENT OF WATER AFFAIRS AND FORESTRY 1986. Management of the Water Resources of the Republic of South Africa. Government printer, Pretoria.

DRAZEN, J.C., POPP, B.N., CHOY, C.A., CLEMENTE, T., DE FOREST, L. and SMITH, K.L. 2008. Bypassing the abyssal benthic food web: macrourid diet in the eastern North Pacific inferred from stomach content and stable isotope analysis. *Limnology and Oceanography* **53**: 2644- 2654.

DUGAN, P.J. 1983. Seasonal and geograhphic distribution of seven decapods crustaceans in Apalachee Bay, Florida. *Contribution to the Marine* **26**: 65- 79.

EMMERSON, W.D. 1983. Tidal exchange of two decapods larvae *Palaemon pacificus* (Caridea) and *Upogebia africana* (Thalassinidae) between the Swartkop River estuary and adjacent coastal waters. *South African Journal of Zoology* **18**: 326- 330.

EMMERSON, W.D. 1985. Oxygen consumption in *Palaemon pacificus* (Stimpson) (Decapoda:Palaemonidae) in relation to temperature, size and season. *Comparative Biochemistry and Physiology, Part A: Physiology* **81**: 71- 78.

EMMERSON, W.D. 1985b. Fecundity, larval rearing and laboratory growth of *Palaemon pacificus* (Stimpson) (Decapoda, Palaemonidae). *Crustaceana* **49**: 277- 89.

EMMERSON, W.D. 1986. The ecology of *Palaemon pacificus* (Stimpson) associated with *Zostera capensis* Setchell. *Transactions of the Royal Society of South Africa* **46**: 79- 97.

EMMERSON, W.D. 1987. Tidal migration and feeding of the shrimp, *Palaemon pacificus* (Stimpson). *South African Journal of Science* **83:** 413- 416.

EMMERSON, W.D. and BAIRD, D. 1982. The ecology and energetic of the free swimming crustacean Palaemon pacificus (Stimpson). Unpublished S.A.N.C.O.R. report.

FORBES, A.T. and CYRUS, D.P. 1991. Recruitment and origin of Panaeid prawn post larvae in two South-east African estuaries. *Estuarine, Coastal and Shelf Science* **33**: 281- 289.

FOSTER, G.R. 1951. The biology of the common prawn, *Leander serratus* Pennant. *Journal of the Marine Biological Association of the United Kingdom* **30**: 333- 360.

FRANCE, R. and PETERS, R. 1997. Ecosystems differences in the trophic enrichment of 13-C in aquatic food webs. *Canadian Journal of Fisheries and Aquatic Science* **54**: 1255- 1258.

FRANCE, R., CHANDLER, M. and PETERS, R. 1998. Mapping trophic continua of benthic food webs: body size and δ^{15}N relashionships. *Marine Ecology progress Series* **174**: 301-306.

FRONEMAN, P.W. 2000. Feeding studies on selected zooplankton in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51**: 543- 552.

FRONEMAN, P.W. 2001. Seasonal changes in zooplankton biomass and grazing in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science* **52**: 543- 553.

FRONEMAN, P.W. 2002. Response of the plankton to three different hydrological phases of the temporarily open/closed Kasouga Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **55**: 535- 546.

FRONEMAN, P.W. 2002a. Food web structure in three contrasting estuaries determined using stable isotope (δ^{13} C) analysis. *African Journal of Aquatic Science* **27**: 107- 115.

FRONEMAN P.W. 2004. Seasonal patterns in the zooplankton community structure and biomass in an eastern Cape temporarily open/ closed estuary. *Estuarine Coastal and Shelf Science* **60**: 125- 132.

FRONEMAN, P.W. 2006. The population dynamics of the caridean shrimp, *Palaemon peringueyi,* in a small intermittently open Eastern Cape estuary. *African Journal of Aquatic Science* **31**: 197- 203.

FRONEMAN, P.W. and MCQUAID, C.D. 1997. Preliminary investigation of the ecological role of microzooplankton in the Kariega estuary, South Africa. *Estuarine, Coastal and Shelf Science* **45**: 689- 695.

FRONEMAN, P.W. and HENNINGER, T.O. 2010. Feeding dynamics of *Palaemon peringueyi* (decapoda, Caridea) in temporarily open closed Kasouga Eastuary, South Africa. *Journal of Aquatic Science* **35**: 2, 193- 198.

FRY, B. 1977. Stable carbon isotope ratios-a tool for tracing food chains. Unpublished M.A. thesis, University of Texas, Austin. 126 pp.

FRY, B. and SHERR, E.B. 1984. Delta 13C measurement as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* **27**: 13- 47.

FRY, B. SCALAN, R.S. and PARKER, P.L. 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. *Geochimica et Coswwchimica Acta* **41**: 1875- 1877.

GARCIA, S. 1977. Les migrations des crevettes penaeids tropicales. *Oceanis* **1977**: 365- 380.

GARCIA, S. and LERESTE L. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. *FAO Fish Technical Papers* **203**: 1- 215.

GARCIA, A.M., VIEIRA, J.P. and WINEMILLER, K.O. 2003. Effects of the 1997-1998 El Niño on the dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). *Estuarine Coastal and Shelf Science* **57**: 489-500.

GEARING, J.N., GEARING, P.I., RUDNICKD, T., REQUEJO, A.G and HUTCHINS, M.J. 1984 Isotope variability of organic carbon in a phytoplankton based, temperate estuary. *Geochemica et Cosmochimica Acta* **48**: 1089- 1098.

GILES, J. J. and ZAMORA, G. 1973. Cover as a factor in habitat selection by juvenile brown (*Penaeus aztecus*) and white (*P. setiferus)* shrimp. *Transactions of the American Fisheries Society* **102**: 144- 145.

GILLANDERS, B.M. and KINGSFORD, M.J. 2002. Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology: an Annual Review* **40**: 233- 309.

GRANGE, N. and ALLANSON, B.R. 1995. The influence of freshwater inflow on the nature, amount and distribution of seston in estuaries of the Eastern Cape, South Africa. *Estuarine, Coastal and Shelf Science* **40**: 403- 420.

GRANGE, N., WHITFIELD, A.K., De VILLIERS, C.J. and ALLANSON, B.R. 2000. The response of two South African east coast estuaries to altered river flow regimes. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**: 155- 177.

GRAY, C.A. 1991. Temporal variability in the demography of the Palaemonid prawn *Macrobrachium intermidium* in two seagrasses. *Marine Ecology Progress Series* **75**: 227-237.

GU, B., SCHELSKE, C.L. and HOYER, M.V. 1996. Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hypereutrophic lake. *Journal of Fish Biology* **49**: 1233- 1243.

GUERAO, G. 1995. Locomotor activity patterns and feeding habits in the prawn *Palaemon xiphias* (Crustacea: Decapoda: Palaemonidae) in Alfacs Bay, Ebro Delta (northwest Mediterranean). *Marine Biology* **122**: 115- 119.

GUERAO, G. and RIBERA, C. 2000. Characteristics of the prawn *Palaemon serratus* (Decapoda: Palaemonidae) in a shallow Mediterranean Bay. *Crustacceana* **73**: 459- 468.

GUEST, W.W. 1979. Laboratory life history of the palaemonid shrimp *Machrobrachium amazonicum* (Haller) (Decapoda, Palaemonidae). *Crustacea* **30**: 141- 152

GUNTHER, G. 1961. Habitat of juvenile shrimp (family *Penaeidae*). *Ecology* **43**: 598- 600.

HAGERMAN, L. and WEBER, R.E. 1981. Respiratory rate, haemolymph oxygen tension and haemocyanin level in the shrimp *Palaemon adspersus* Rathke. *Journal of Experiment Marine Boilogy and Eco*logy **54**: 13- 20.

HAINES, E.B. and MONTAGUE, C.L. 1979. Food sources of estuarine invertebrates using 13C/12C ratios. *Ecology* **60**: 48- 56.

HANEKOM, N. 1982. An ecological study of the *Zostera* beds in the Kromme estuaty. *University of Port Elizabeth Zoology Department Report Series* **18***:* 206.

HARRISON, T.D., COOPER, J.A.G. and RAMM, A.E.L. 2000. *State of the Environment Series, Report No: 2, State of South African estuaries*. Department of Environmental Affairs and Tourism, 1-14.

HECK, K.L. 1977. Comparative species richness, composition and abundance of invertebrates in Caribbean seagrass (*Thalassia testudium*) meadows (Panama). *Marine Biology* **41**: 335- 348.

HECK, K.L. and THOMAN, T.A. 1981. Experiments on predator prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* **53**: 125- 134.

HECKY, R.E. and HESSLEIN, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* **14**: 631–653

HENNINGER, T.O. 2008. Aspects of the ecology and biology of the isopod, *Exosphaeroma hylocoetes*, (Barnard, 1940) in three temporarily open/closed southern African estuaries. PhD thesis, Rhodes University, Grahamstown.

HENNINGER, T.O., FRONEMAN, P.W. and HODGON, A.N. 2008. Population dynamics of the estuarine isopod Exosphaeroma hylocoetes (Barnard 1940). *Estuarine, Coastal and Shelf Science* **82**: 285- 293.

HEYDORN, A.E.F., and TINLEY, K. 1980. Estuaries of the Cape. Part 1. *Synopsis of the Cape Coast*. Stellenbosch: CSIR

HEYDORN, A.E.F., BANG, N.D., PEARCE, A.F., FLEMMING, B.W., CARTER, R.A., SCHLEYER, M.N. BERRY, P.F., HUGHES, G.R., BASS, A.J., WALLACE, J.H., VAN DER ELST, R.P., CRAWFORD, R.J.M and SHELTON, P.A. 1978. Ecology of the Agulhas current region: an assessment of biological responses to environmental parameters in the south west Indian Ocean. *Transactions of the Royal Society of South Africa* **43**: 151-190.

HEYNS, E. and FRONEMAN, P.W. 2010. Spatial and temporal patterns in the hyperbenthic community structure in a warm temperate southern African permanently open estuary. *Estuarine, Coastal and Shelf Science* **88**: 105- 115.

HILL, B.J. 1975. Abundance, breeding and growth of the crab, *Scylla serrata* in two south African estuaries. *Marine Biology* **32:** 119-126.

HODGKIN, E.P. and LENANTON, R.C. 1981. Estuaries and coastal lagoons of south western Australia. In: Nielson, I and Cronin, L.E. (eds), Estuaries and Nutrients. Humana Press, New Jersey, 307- 321.

HODGSON, A.N. 1987. Disribution and abundance of the macrobenthic fauna of the Kariega Estuary. *South African Journal of Zoology* **22**: 153- 162.

HOLM-HANSEN, O. and RIEMANN, B. 1978. Chlorophyll-*a* determination: improvements in methodology. *Oikos* **30**: 438- 447.

HOLTHIUS, L.B. 1950. The decapod of the Siboga Expedition, X: The Palaemonidae Collected by the Siboga and Snellius expeditions with remarks on other species, I: subfamily Palamoninae. *Siboga Expedition* **39**: 268.

HOOKS, T. A., K. L HECK, K.L. and LIVINGSTON, R.J. 1976. An inshore marine invertebrate community: structure and habitat associations in the northeastern Gulf of Mexico. *Bulletin of Marine Sciences* **26**: 99- 109.

HOPKINS, T.L., LANCRAFT, T.M., TORRES, J.J. and DONELLY, J. 1993. Community structure and trophic ecology of Zooplankton in the Sea Marginal Ice Zone in winter (1988). *Deep Sea Research* I **40**: 81 – 105.

HOWARD, R.K. 1981. The ecology and trophic role of caridean shrimps in the eelgrass community of Western Port, Victoria. PhD thesis, University of Melbourne.

HUGHES, D.A. 1966. Investigation of the nursery areas and habitat preferences of juvenile penaeid prawns in Mozambique. *Journal of Applied Biology* **3**: 349-354.

HUGHES, D.A. 1969. Responses of salinity changes as a tidal transport mechanism of pink shrimp Penaeus duorarum. *Biological Bulletin of the Marine Biological Laboratory*, *Woods Hole* **136**: 43- 53.

IDYLL, C.P., IVERSEN, E.S. and YOKEL, B. 1964. Movements of juvenile pink shrimps in the Everglades National Park, Florida. *Proceedings of Gulf and Caribbean Fisheries Institute* **1963**: 51- 2.

ISRAE, L.H.R. 1936. A contribution toward the life histories of two California shrimps, *Crangon franciscorum* (Stimpson) and Crago nigricauda (Stimpson). *Division of Fish and Game of California, Fish Bulletin* **46**: 1- 28.

IYER, V. and BARNABAS, A.D. 1996. Effects of varying salinity on leaves of *Zostera capensis* Setchell. I. Ultrastructural changes. *Aquatic Botany* **46**: 141- 153.

JANAS, U. and BARANKSKA, A. 2008. What is the diet of *Plaemon elegans* Rathke, 1837 (Crustacea, Decapoda), a non-indigenous species in the Gulf of Gdansk (southern Baltic Sea)? *Oceanologia* **50**: 221- 237.

JAYACHANDRAN, K.V. 2001. Palaemonid prawns: biodiversity, taxonomy, biology and management. Science Inc Publishers, 198- 214.

JENNINGS M.E. 2005. Nutrient dynamics in and offshore of two permanently open South African estuaries with contrasting freshwater inflow. MSc thesis, Rhodes University, Grahamstown.

JERLING H.L. and WOOLDRIDGE T.H. 1995. Relatively negative $\delta^{13}C$ ratios of mesozooplankton in the Sundays River estuary, comments on potential carbon sources. *Southern African Journal of Aquatic Science* **21**: 71- 77.

KEMP, J.O.G. and FRONEMAN P.W. 2004. Recruitment of ichthyoplankton and macrozooplankton during overtopping events into a temporarily open/closed southern African estuary. *Estuarine, Coastal and Shelf Science* **61**: 529- 537.

KENSLEY, B. 1972. Shrimps and Prawns of Southern Africa. South African Museum, Cape Town, 4- 5.

KIBIRIGE, I. and PERISSINOTTO, R. 2003. The zooplankton community of the Mpenjati Estuary, a South African temporarily open/closed system. *Estuarine, Coastal and Shelf Science*, **58**: 727- 741.

KIBIRIGE, I., PERISSINOTTO, R. and TWALA, X. 2006. A comparative study of zooplankton dynamics in two subtropical temporarily open/closed estuaries, South Africa. *Marine Biology* **148**: 1307- 1324.

KIKUCHI, T. 1974. Japanese contributions on consumer ecology in eelgrass *(Zostera marina* L.) beds with special reference to trophic relationships and resources in inshore fisheries. *Aquaculture* **4**:145- 160.

KIKUCHI, T. 1980. Faunal relationships in temperate seagrass beds. In: Phlllips. R.C. and McRoy, C.P. (eds.) Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York, 153-172.

KIM, S. 2005. Population structure, growth, mortality and size at sexual maturity of *Palaemon gravieri* (Decapoda: Caridea: Palaemodidae). *Journal of Crustacean Biology* **25**: 226- 232.

KINNE, O. 1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanography and Marine Biology Annual Review* **1**: 301- 330.

KINNE, O. 1971. Salinity and animals- invertebrates. In Kinne, O. (eds) Marine Ecology. I. Temperature. *Oceanography and Marine Biology Annual Review* **1**: 301- 330.

KIRKPATRICK, K. and JONES, M.B. 1985. Salinity tolerance and osmoregulation of a prawn, *Palaemon affinis* Milne Edwards (Caridea: Palaemonidae). *Journal of Experimental Marine Biology and Ecology* **93**: 61- 70.

KLING, G., FRY, B. and O'BRIEN, W. 1992. Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology* **73**: 561- 566.

KNEIB, R.T. and WAGNER, S.L. 1984. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* **106**: 227- 238.

KOPKE, D. 1988. The climate of the Eastern Cape. In: Bruton G and Gess, G. (eds.) Towards and Environmental Plan for the Eastern Cape, Rhodes University, Grahamstown, 44-52.

KOSHY, M. 1971. Studies on the sexual dimorphism in the freshwater prawn *Machrobrachium dayanum* (Henderson, 1893) (Decapoda, Caridea). Part I, *Crustaceana* **21**: 72- 78.

KREEGER, D.A. and NEWELL, R.I.E. 2000. Trophic complexity between producers and invertebrate consumers in salt marshes. In: Weinstein M.P. and Kreeger D.A. (eds) Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht, 187- 220.

KUTKUHN J.H. 1966. The role of estuaries in the development and perpetuation of commercial shrimp resources. *American Fishery Society Special Publications* **3**: 16- 36.

LE MOULLAC, G. and HAFFNER, P. 2000. Environmental factors affecting immune responses in crustacea. *Aquaculture* **191**: 121- 131.

LESTER, L.J. and PANTE J.R. 1991. Penaeid temperature and salinity responses. In: Fast, A.W., Lester, L.J. (eds) Marine Shrimp Culture: Principles and Practices **23**: 515-534.

LEWIS, F.G. and STONER, A.W. 1983. Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. *Bulletin of Marine Science* **33**: 296- 304.

LING S.W. 1969. The general biology and development of *Macrobrachium rosenbergii* (De Man). *F.A.O. Fisheries Report* **57**: 589- 606.

LITTLE, C. 2000. The Biology of Soft Shore and Estuaries. *Oxford University Press Inc*., New York pp. 176- 252.

LUBKE, R.A. 1998. The coastal environment. In: Lubke, R.A. and De Moor, I. (eds.) Field Guide to the Eastern and Southern Cape Coasts, University of Cape Town Press, 3- 9.

LUBKE, R.A., GESS, F.W. and BRUTON, M.N. 1988. A field guide to the Eastern Cape Coast. Grahamstown Centre of the Wildlife Society of Southern Africa, Grahamstown, South Africa, 559 pp.

LUTJEHARMS, J.R.E. 1998. Coastal hydrography. In: Lubke, R.A. and De Moor, I. (eds.) Field Guide to the Eastern and Southern Cape Coasts, University of Cape Town Press, 50- 61.

LUTJEHARMS, J.R.E., COOPER, J. and ROBERTS, M. 2000. Upwelling at the inshore edge of the Algulhas Current. *Continental Shelf Research* **20**: 737- 761.

LUTJEHARMS, J.R.E. 2006. The Agulhas current. Springer, Cape Town.

LUTJEHARMS, J.R.E. 2007. Three decades of research on the greater Agulhas Current. *Ocean Science* **3**: 129- 147.

MAC PHERSON, E. 1990. The validation of *Palaemon peringueyi* (Stebbing 1915) from South African waters and its relation with *Palaemon pacificus* (Stimpson 1860) (Decapoda, Palaemonidae) in the Bushmans River estuary. M.Sc. thesis, Rhodes University, South Africa.

MACKAY, H.M. and SCHUMANN, E.H. 1990. Mixing and circulation in the Sundays River estuary, South Africa. *Estuarine, Coastal and Shelf Science* **31**: 203- 216.

MACNAE W. 1962. The faunal and flora of the eastern coasts of southern Africa in relation to ocean currents. *South African Journal of Science* **58**: 208- 212.

MAIR, J. 1980. Salinity and water-type preferences of four species of postlarval shrimp (Penaeus) from west Mexico. *Journal of Experimental Marine Biology and Ecology* **45**: 69-82.

MARSHAL, D.J. and MCQUAID, C.D. 1994. Seasonal and diel variations of in situ heart rateof the intertidal limpet *Siphonaria oculus* Kr (Pulmonata). *Journal of Experimental Marine biology and Ecology* **171**: 1- 9.

MAYNOU, F. and CARTES, J.E. 1998. Daily ration estimates and comparative study of food consumption in nine species of deep-water decapod crustaceans of the NW Mediterranean. *Marine Ecology Progress Series* **171**: 221- 231.

MC HUGH, J. L. 1967. Estuarine nekton. *American Association for the Advancement of Science Publication* **83**: 581- 620.

MC LACHLAN, A. and YOUNG, N. 1982. Effects of low temperature on the burrowing rates of four sandy beach molluscs. *Journal of Experimental Marine Biology and Ecology* **65**: 275-284.

MEES, J. and JONES, M.B. 1997. The hyperbenthos. *Oceanography and Marine Biology: an Annual Review* **35**: 221- 255.

MILLARD, N.A.H. and HARRISON, A.D. 1954. The ecology of South African estuaries. Part 5: Richards Bay. *Transaction of the Royal Society of South Africa* **34**: 157- 179.

MINAGAWA, M. and WADA, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{14}N and animal age. *Geochimica et Cosmochimica Acta* **48**: 1135- 1140.

NELSON, W.G. 1979. An analysis of structural pattern in an eelgrass (*Zostera marima*) amphipod community. *Journal of Experimental marine Biology and Ecology* **39**: 231- 264.

PAKHOMOV, E.A., FRONEMAN P.W., KUNN P.J. and BALARIN M. 1999. Feeding dynamics and respiration of the bottom-dwelling caridean shrimp *Nauticaris marionis* Bate, 1888 (Crustacea: Decapoda) in the vicinity of Marion Island (Southern Ocean). *Polar Biology* **21**: 112- 121.

PAKHOMOV, E.A., MC CLELLAND, J.W., BERNARD, K.S., KAEHLER, S. and MONTOYA, J.P. 2004. Spatial and temporal shifts in stable isotope values of the bottom dwelling shrimp *Nauticaris marionis* at the sub- Antartic archipelago. *Marine Biology* **144**: 31- 325.

PARKER, P.L. and CALDER, J.A. 1970. Stable carbon isotope ratio variations in biological systems, In: Hood, D.W. (ed.) Organic Matter in Natural Waters Institute of Marine Science (Alaska). Occasional Publication (1), 107- 127.

PATERSON, A.W. 1999. Aspects on the ecology of fish associated with salt marshes and adjacent habitats. PhD thesis, Rhodes University, South Africa, 189 pp.

PATERSON, A.W. and WHITFIELD, A.K. 1997. A stable isotope study of the food web in a freshwater-deprived South African Estuary, with particular emphasis on the ichthyofauna. Estuarine Coastal and Shelf Science **45**: 705- 715.

PATERSON, A.W. and WHITFIELD, A.K. 1997a. The fishes associated with an intertidal saltmarsh creek in the Kariega Estuary, South Africa. *Transactions of the Royal Society of South Africa* **51**: 195- 218.

PENN, J.W. 1975. The influence of tidal cycles on the distributional pathway of *Penaeus latisulacatus* Kishinouye in Sharks Bay, Wstern Australia. *Australian Journal of Marine and Freshwater Research* **26**: 93- 102.

PERISSINOTTO, R., WALKER, D.R., WEBB, P., WOOLDRIDGE, T.H., and BALLY, R. 2000. Relationships between the zoo- and phytoplankton in a warm-temperate, semipermanently closed estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51**: 1- 11.

PERSSINOTTO, R. and MAQUAID, C.D. 1990. Role of the sub- Antartic shrimp *Nauticaris marionis* in coupling benthic and pelagic food webs. *Marine Ecology Progress Series* **64**: 81- 87.

PETERSON, B. and FRY, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics **18**: 293- 320.

PETERSON, B.J., HOWARTH, R.W. and GARRITT, R.H. 1985. Multiple stable isotopes used to trace the flow of organic matter through estuarine food webs. *Science* **227**: 1361-1363.

POLLARD, D. A. 1984. A review of ecological studies on seagrass fish communities, with particular reference to recent studies in Australia. *Aquatic Botany* **18**: 3 4 2

PONCE-PALAFOX, J., MARTINEZ-PALACIOS, C.A., and ROSS L.G. 1997. The effects of salinity and temperature on the growth and survival rates of juvenile white shrimp, *Penaeus vannamei*, Boone 1931, *Aquaculture* **157**: 107-115.

POST, D.M. 2002. The long and short of food-chain length. *Trends in Ecology and Evolution* **17**: 269-277.

POTTER, I.C., CHUWEN, B.M., HOEKSEMA, S.D. and ELLIOT, M. 2010. The concept of an estuary: a definition that incorporates systems which can become closed to the ocean and hypersaline. *Estuarine, Coastal and Shelf Sceince* **87**: 497- 500.

PRIMAVERA, J. H. 1998. Mangrove as nurseries: shrimp populations in mangrove and non-mangrove habitats. *Estuarine Coastal and Shelf Science* **46**: 457- 464.

PRITCHARD, D.W. 1967. What is an estuary: Physical viewpoint. In: Lauf, G.H. (eds.) Estuaries. American Association for the dvancement of Science, Washington D.C., public. *No. SS-83*, 3- 5.

RAHMAN, M.M., CORTEE, L.M., DANTAS-LIMA, J.J., WILLE, M., LDAY-SANZ, V., PENSAERT, M.B., SARGELOOS, P. and NAUWYNCK, H.J. 2007. Impact of daily flactuations optimum (27°C) and high water temperature (33°C) on *Penaeus vannamei* juveniles infected with spot syndrome virus (WSSV). *Aquaculture* **269**: 107- 113.

READ, K.R.H. and CUMMUNG, K.B. 1967. Thermal tolerances of the bivalve molluscs *Modiolus modiolus* (L.), *Mytilus edulis* (L.) and *Brachidontes demissus* Dillwyn. *Comparitive biochemistry and Physiology* **22**(A): 149- 155.

REDDERING, J.S.V. and RUST, I.C. 1990. Historical changes and sedimentary characteristics of Southern African estuaries. *South African Journal of Science* **86**: 425- 428.

RICHARDSON, N., WHITFIELD, A.K. and PATERSON, A.W. 2006. The influence of selected environmental parameters on the distribution of dominant demersal fishes in the Kariega Estuary channel, South Africa. *African Zoology* **41**: 89- 102.

RICHOUX, N.B. and FRONEMAN, P.W. 2007. Assessment of spatial variation in carbon utilization by benthic and pelagic invertebrates in a temperate South African estuary using stable isotope signatures. *Estuarine, Coastal and Shelf Science* **71**: 545- 558.

RICHOUX, N.B. and FRONEMAN, P.W. 2008. Trophic ecology of dominant zooplankton and macrofauna in a temperate and oligotrophic South African estuary: a fatty acid approach. *Marine Ecology Progress Series* **357**: 121- 137.

ROBERTSON, W.D. 1984. Aspects of the ecology of the shrimp *Palaemon pacificus* (Stimpson) (Decapoda, Palaemonidae) in the Bushmen River estuary. MSc thesis, Rhodes University, Grahamstown.

ROTHLISBERG, P.C., CHURCH, J. and FORBES, A. 1983. Modelling the advection of vertically migrating shrimp larvae. *Journal of Marine Research* **41**: 511- 538.

ROY, P.S., WILLIAMs, R.J., JONES, A.R., YASSINI. I., GIBBS, P.J., COATES, B., WEST, R.J., SCANES, P.R., HUDSON, J.P. and NICHOL, S. 2001. Structure and function of south-east Australian estuaries. *Estuarine, Coastal and Shelf Science* **53**: 351- 384.

ROZAS, L.P. and ODUM, W.E. 1987. The role of submerged aquatic vegetation in influencing the abundance of nekton on contiguous tidal fresh-water marshes. *Journal of Experimental Marine Biology and Ecology* **114**: 289- 300.

RULIFSIN, R.A. 1981. Substrate preferances of juvenile penaeid shrimps in estuarine habitats. *Contributions in Marine Science* **24**: 35- 52.

SASTRY, A.N. and VARGO, S.L. 1977. Possible significance of variation in the physiological responses of crustacean larvae to temperature. In: Venberg, F.J., Calabrese, A., Thurberg, P. and Vernberg, W.B. (eds) Physiological responses of marine biota to pollutants, New York: Academic press., 401- 423.

SCHMIDT-NIELSIEN, K. 1983. Animal Physiology: Adaptation and Environment (5th ed.), University Press, Cambridge.

SCHUMANN, E.H., LARGIER, J.L. and SLINGER, J.H. 1999. Estuarine hydrodynamics. In: Allanson B.R. and Baird D. (eds) Estuaries of Spouth Africa. Cambridge University Press, Cambridge, 27- 52.

SIKORA, W.B. 1977. The ecology of *Palaemon pugio* in a south eastern saltmarsh ecosystem with particular emphasis on production and trophic relationships. PhD thesis. Columbia, SC. University of South Carolina. 122 pp.

SIMESTAD, C.A. and WISSMAR, R.C. 1985. . δC^{13} evidence of the origins and fates of organic carbon in estuarine and nearshore marine food webs. *Marine Ecology Progress Series* **22**: 141- 152.

SMITH, B.N., OLIVER, J. and MACMILLAN, C. 1976. Influence of carbon source, oxygen concentration, light intensity, and temperature on 13C/’2C ratios in plant tissues. *Botanical Gazette* **137**: 99- 104.

SPANOPOULOS-HERNANDEZA, M., MARTINEZ-PALACIOSB, C.A., VANEGAS-PEREZC, R.C., ROSASD C. And ROSSE, L.G. 2005. The combined effect of salinity and temperature on the oxygen consumption of juvenile shrimps *Litopenaeus stylirostris* (Stimpson 1874), *Aquaculture* **244**: 341- 348.

STAPLES, D.J. 1980. Ecology of juvenile and adolescent banana prawn, *Penaeus merguiensis*, in a mangrove estuary and adjacent offshore area of the Gulf of Carpentaria. I. Immigration and settlement of postlarvae. *Australian Journal of Marine and Freshwater Research* **31**: 635- 652.

STAPLES, D.J. and VANCE, D.J. 1986. Emigration of juveniles banana prawn *Penaeus merguiensis* from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. *Marine Ecology Progrss Series* **27**: 239- 252.

STATSOFT, Inc. 2011. STATISTICA (data analysis software system) version 10. www.statsoft.com

STEPHENSON, T.A. and STEPHENSON, A. 1972. LIFE Bbetween tidemarks on RockyShores. W.H. Freeman: San Francisco.

STONE, A.W., WEAVER, A.B. and WEST, W.O. 1998. Climate and Weather. In: Lubke, R.A. and De Moor, I. (eds.) Field Guide to the Eastern and Southern Cape Coasts, *University of Cape Town Press, South Africa*, 41- 49.

STRAMMA, L. and LUTJEHARMS, J.R.E. 1997. The flow field of the subtropical gyre of the South Indian Ocean. *Journal of Geography Research* **102**: 5513- 5531.

TAYLOR, D.I. 1987. Tidal exchanges of carbon, nitrogen and phosphorus between a *Sarcocornia* salt marsh and the Kariega Estuary, and the role of saltmarsh brachyura in this transfer. Ph.D. thesis, Rhodes University, Grahamstown.

TAYLOR, D.I. and ALLANSON, B.R. 1995. Organic carbon fluxes between a high marsh and estuary, and the implacability of the outwelling hypothesis. *Marine Ecology Progress Series* **120**: 263- 270.

TER MORSHUIZEN, L.D. and WHITFIELD, A.K. 1994. The distribution of littoral fishes associated with eelgrass *Zostera capensis* beds in the Kariega Estuary, a Southern African system with a reversed salinity gradient. *South African Journal of Marine science* **14**: 95- 105.

TER MORSHUIZEN, L.D, WHITFIELD, A.K and PATERSON, A.W. 1996. Influence of freshwater flow regime on fish assemblages in the Great Fish River and Estuary. *South African Journal of Aquatic Science* **22**: 52- 61.

THAYER, G. W., ADAMS, S.M. and LA CROIX, M.W. 1975. Structural and functional aspects of a recently established *Zostera marina* community, 518-540. In: Cronin, L.E. (ed.), Estuarine research, Academic Press, N.Y.

TIAN X., DONG S., WANG, F. and WU, L. 2004. The effects of temperature changes on the oxygen consumption of juvenile Chinese shrimp *Fenneropenaeus chinensis* Osbeck. *Journal Experimental Marine Biology and Ecology* **310**: 59- 72.

VIJAYAN, K.K. and DIWAN, A.D. 1995. Influence of temperature, salinity, pH and light on molting and growth in the Indian white prawn *Penaeus indicus* (Crustacea: Decapoda: Penaeidae) under laboratory conditions. *Asian Fisheries Science* **8**: 63- 72.

VIZZINI, S., SARA, G., MICHENER, R.H. and MAZZOLA, A. 2002. The role and contribution of the seagrass *Posidonia oceanic* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen satable isotope analysis. *Acta Oecologica* **23**: 277- 285.

VORWERK, P.D. 2006. A preliminary examination of selected biological links between four Eastern Cape estuaries and the inshore marine environment. PhD thesis. Rhodes University, Grahamstown.

VORWERK, P.D., FRONEMAN, P.W. and PATERSON, A.W. 2007. Revival of the critically endangered river pipefish, Syngnathus watermeyeri, in Eastern Cape estuaries. *South African Journal of Science* **103**: 199- 201.

WALKER, T.M. 1979. A study of sympatry in two species of Palaemonidae. PhD thesis, University of Tasmania, Australia.

WALLACE, J.H., KOK, H.M., BECKLEY, L.E., BENNETT, B.A., BLABER, S.J.M. and WHITFIELD, A.K. 1984. South African estuaries and their importance to fishes. *South African Journal of Science* **80**: 203- 207.

WALSH, C.J. and MITCHELL, B.D. 1998. Factors associated with variation in abundance of epifaunal caridean shrimps between and within seagrass meadows. *Marine and Freshwater Research* **49**: 769- 777.

WHITFIELD, A.K. 1992. A characterization of southern African estuarine systems. *South African Journal of Aquatic Science* **18**: 89- 103.

WHITFIELD, A.K. 1994. Abundance of larval and 0+ Juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Marine Ecology Progress Series* **105**: 257- 267.

WHITFIELD, A.K. 1998. Biology and ecology of fishes in southern African estuaries. *Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology*, No. 2, 223 pp.

WHITFIELD, A.K. 2005. Fishes and freshwater in Southern African estuaries- A review. *Aquatic Living Resources* **18**: 275- 289.

WHITFIELD, A.K. and BATE, G. 2007. A review of information on temporary open closed estuaries in the warm and cool temperate Biogeographic regions of South Africa, with particular emphasis of the river flow on these systems. *WRC Report No. 1581/1/07.*

WHITFIELD, A.K. and BRUTON, M.N. 1989. Some biological implications of reduced fresh water inflow into Eastern Cape estuaries: a preliminary assessment. *South African Journal of Science* **85**: 691- 695.

WHITFIELD, A.K. and HARRISON, T.D. 1996. *Gilchristella aestuaria* (Pisces: Clupeidae) biomass and consumption of zooplankton in the Sundays Estuary. *South African Journal of Marine Science* **17**: 49- 53.

WHITFIELD, A.K. and PETERSON, A.W. 2003. Distribution of fishes in a freshwater deprived Eastern Cape estuary, with particular emphasis on the geographical headwater region. *Water SA* **29**: 61- 67.

WHITFIELD, A.K., ADAMS, J.B., BAT, G.C, BEZUIDENHOUT, K., BORNMAN, T.G., COWLEY, P.D., FRONEMAN, P.W., GAMA, P.T., JAMES N.C., MACKENZIE, B., RIDDIN, T., SNOW, G.C., STRYDOM, N.A., TALJAARD S., TERORDE, A.L., THERON, A.K., TURPIE, J.K, VAN NIEKERK, L., VORWERK, P.D. and WOOLDRIDGE, T.H. 2008. A multidisciplinary study of a small, temporary open/closed

South African estuary, with particular emphasis on the influence of mouth state on the ecology system. *African Journal of Marine Science* **30**: 453- 473.

WILDISH, D.J. 1977. Factors controlling marine and estuarine sublittoral macrofauna. *Helgolander wiss. Meereunters* **30**: 445- 454.

WILLIAMS, A. B. 1958. Substrates as a factor in shrimp distribution. *Limnology and Oceanography* **3**: 283- 290.

WILLIAMS, A.B. and DEBLER, E.E. 1968. A ten-year study of meroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimp. *Chesapeake Science* **9**: 27- 41.

WONG, Y.M. and MOORE, P.G. 1996. Observations on the activity and life history of the scavenging isopod *Natatolana borealis* Lilljeborg (Isopoda: Cirolanidae) from Loch Fyne, Scotland. *Estuarine, Coastal and Shelf Science* **42**: 247- 262.

WOOLDRIDGE, T.H. 1999. Estuarine zooplankton community structure and dynamics. In: Allanson, B.R. and Baird, D. (eds) Estuaries of South Africa, Cambridge University Press, Cambridge, UK, 141- 166.

WYBAN, J., WALSH, W.A. and GODIN, D.M. 1995. Temperature effects on growth, feeding rate and feed conversion of the Pacific white shrimp *(Penaeus vannamei). Aquaculture* **138**: 267- 279.

YOKEL, B.I., IVERSEN, E.S., IDYLL, C.P. 1969. Prediction of the success of commercial shrimp fishing on the Tortugas grounds, based on enumeration of emigrants from the Everglades National Park estuary. *FAO Fish Report* 5**7**: 1027- 1040.

YOUNG, P.C. 1978. A nursery area for juvenile penaeid prawns. *Australian Journal of Marine and Freshwater Research* **29**: 55- 75.

YOUNG, P. C. 1981. Temporal changes in the vagile epibenthic fauna of two seagrass meadows (*Zostera capricorni* and *Posidonia austraralia*). *Marine Ecology Progress Series* **5**: 91- 102.

YOUNG, P.C. and CARPENTER, S.M. 1977. Recruitment of postlarval penaeid prawn to nursery areas in Moreton Bay, Queensland. *Australian Journal of Marine and Freshwater Research* **28**: 745- 773.

YOUNG, P. C. and WADLEY, V. A. 1979. Distribution of shallow water epibenthic macrofauna in Moreton Bay. Queensland, Australia. *Marine Biology* **53**: 83- 97.

ZHANG, P., ZHANG, X., LI J. and HUANG, G. 2006. The effects of body weight, temperature, salinity, pH, light intensity and feeding condition on lethal DO levels of white leg shrimp, *Litopeaneus vannamei* (Boone, 1931). *Aquaculture* **256**: 579- 587.

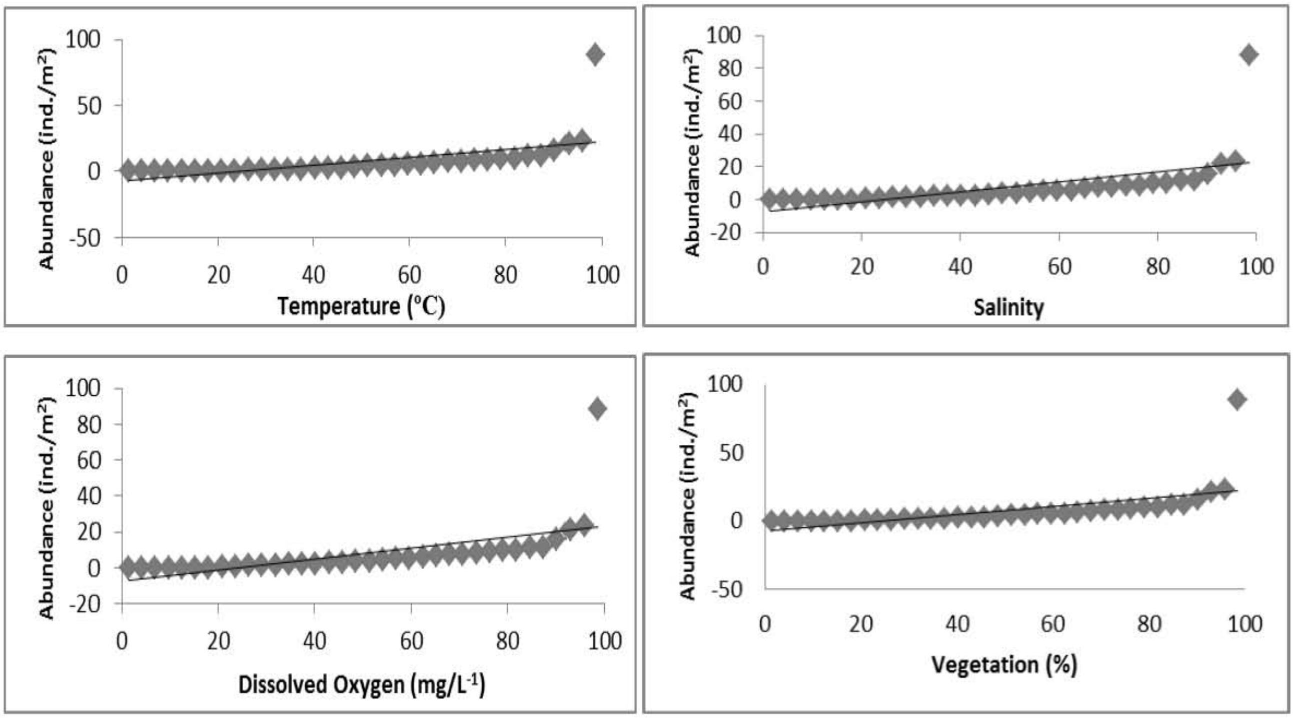
ZIMMERMAN, R.J., MINELLO, T.J. ZAMORA, G. 1984. Selection of vegetation habitat by brown shrimp *penaeus aztecus*, in a Galveston Bay salt marsh. *Fishery Bulletin* **82**: No. 2.

Appendices

Appendix I: Mean (± SE) abundance (ind.m^{-2}) and biomass (g wwt.m^{-2}) of *Palaemon peringueyi* in the lower, middle and upper reaches of the Kariega Estuary.

Time	Abundance			Biomass		
	Lower reaches	Middle reaches	Upper reaches	Lower reaches	Middle reaches	Upper reaches
Sep-10	23.3 (± 6.6)	21.5 (± 4.5)	3.8 (± 1.1)	3.8 (± 0.9)	4.3 (± 0.9)	1.6 (± 0.5)
Oct-10	7.4 (± 1.4)	10.4 (± 2.9)	1.0 (± 0.4)	1.3 (± 0.3)	1.3 (± 0.4)	0.4 (±0.2)
Nov-10	4.6 (± 1.0)	0.6 (± 0.3)	No data	0.5 (± 0.2)	0.2 (± 0.1)	No data
Dec-10	3.2 (± 1.2)	0.9 (± 0.4)	No data	0.5 (± 0.1)	0.3 (± 0.1)	No data
Jan-11	2.3 (± 1.0)	2.3 (± 1.1)	No data	0.4 (± 0.5)	0.3 (± 0.2)	No data
Feb-11	2.6 (± 1.3)	6.7 (± 2.2)	No data	0.7 (± 0.9)	1.1 (± 0.3)	No data
Mar-11	3.8 (± 1.3)	0.9 (± 0.4)	0.6 (± 0.3)	1.2 (± 0.5)	0.1 (± 0.1)	0.2 (± 0.1)
Apr-11	15.6 (± 4.2)	8.8 (± 2.1)	0.7 (± 0.3)	3.3 (± 0.9)	1.7 (± 0.5)	0.7 (± 0.3)
May-11	9.9 (± 3.2)	8.8 (± 3.1)	1.1 (± 0.8)	1.6 (± 0.5)	2.5 (± 0.6)	0.1 (± 0.1)
Jun-11	88 (± 27.3)	7.7 (± 0.5)	No data	4.4 (± 1.4)	0.6 (± 0.3)	No data
Jul-11	11.5 (± 6.2)	1.4 (± 0.7)	No data	0.6 (± 0.3)	0.1 (± 0)	No data
Aug-11	11.7 (± 3.9)	1.5 (± 1.1)	No data	4.4 (± 0.5)	1.2 (± 0.7)	No data

Appendix II: Results of the regression analysis between abundance of *Palaemon peringueyi* and the physico-chemical parameters



Appendix III: Results of the regression analysis between biomass of *Palaemon peringueyi* and the physico-chemical parameters.