THE DYNAMICS OF LARVAL FISH AND ZOOPLANKTON ASSEMBLAGES IN THE SUNDAYS ESTUARY, SOUTH AFRICA

by

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GENERAL ABSTRACT

The larval fish and zooplankton assemblages were studied in the permanently open Sundays Estuary on the south-east coast of South Africa, using standard boat-based plankton towing methods. A total of 8174 larval and early juvenile fishes were caught, representing 12 families and 23 taxa. The Clupeidae, Gobiidae and Blenniidae were the dominant fish families. Common species included *Gilchristella aestuaria*, *Caffrogobius gilchristi*, *Omobranchus woodi*, *Liza dumerilii*, *Glossogobius callidus* and *Myxus capensis*. Estuarine resident species (Category I) predominantly in the preflexion developmental stage, dominated the system. A total of 19 zooplankton taxa were recorded. Copepoda dominated the zooplankton community. Dominant species included *Pseudodiaptomus hessei*, *Acartia longipatella*, *Halicyclops* sp., *Mesopodopsis wooldridgei*, and the larvae of *Paratylodiplax edwardsii* and *Hymenosoma orbiculare*. Mean larval fish density showed similar trends seasonally, spatially and across salinity zones, with mean zooplankton density in the Sundays Estuary. Gut content analysis of five larval fish species: *Gilchristella aestuaria*, *Pomadasys commersonnii*, *Monodactylus falciformis*, *Myxus cap*ensis and *Rhabdosargus holubi*, revealed species specific diet and prey selection. Although larval fish diet contained a variety of prey items, guts were dominated by *P. hessei*, chironomid larvae, *Corophium triaenonyx*, copepod eggs and insect larvae. Physico-chemical drivers and the interactions between these two plankton communities provide information that enables a more holistic view of the dynamics occurring in the Sundays Estuary planktonic ecosystem.

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CHAPTER 1

GENERAL INTRODUCTION

1. AN OVERVIEW OF ESTUARINE LARVAL FISH RESEARCH IN SOUTH AFRICA

Larval fish research in South Africa first began in the early 1900's with the pioneering work of Gilchrist who published annotations on marine fish eggs and fish larvae (Gilchrist 1903, 1904, 1914, 1916, 1921, Gilchrist & Hunter 1919). This was followed by work on estuarine larval fish in the late 1970's (Melville-Smith 1978). Abundance, distribution and species composition in the Swartkops (Melville-Smith & Baird 1980) and Kromme Estuary (Melville-Smith 1981), formed the foundation of these earlier investigations, but also included utilization of tidal currents by an estuarine resident larval fish species, *Gilchristella aestuaria* (Melville-Smith *et al*. 1981). Larval fish exchange was the focus of Beckley's (1985) work in the Swartkops Estuary, while Whitfield (1989a) focused on the Swartvlei estuarine lake. Whitfield (1989b) also investigated the larval fish composition, abundance and seasonality in this lake system. In KwaZulu Natal, Martin *et al*. (1992), reported on the flushing effects of cyclone-induced floods on larval fish in the St Lucia Estuary. This was followed by work done by Harris & Cyrus (1995), who reported on the occurrence of larval fishes in the same estuary. Composition, abundance, distribution and seasonality of larval fishes in the Kosi Estuary (Harris *et al*. 1995), Richards Bay Harbour (Harris & Cyrus 1997) and Durban Bay Harbour (Harris & Cyrus 1999) were also important contributions to our understanding of estuarine larval fish dynamics in South Africa.

At the turn of the century, Strydom & Whitfield (2000) assessed the effects of freshwater from an artificial dam release on larval fish recruitment in the Kromme Estuary as well as how elevated supplies of freshwater flow affected the abundance of the estuarine roundherring, *G. aestuaria* (Strydom *et al*. 2002). Thereafter, the role of estuarine type in characterizing early stage fish was studied (Strydom *et al*. 2003). On the Transkei coast, Pattrick *et al*. (2007) investigated the composition, abundance, distribution and seasonality of larval fishes in the Mngazi Estuary, followed by work done by Wasserman *et al*. 2010 in the Nxaxo-Ngqusi Estuary complex. Biological response to freshwater release in the Kariega Estuary (Vorwerk *et al*. 2008), a description of larval fish in nine south and west coast estuaries (Montoya-Maya & Strydom 2009a) and the spatial and temporal variability in larval fish and effects of artificial channeling on this assemblage in the Kowie Estuary (Kruger & Strydom submitted) were among the later investigations reported in the literature.

2. AN OVERVIEW OF ESTUARINE ZOOPLANKTON RESEARCH IN SOUTH AFRICA

Zooplankton research in South Africa began in the early 1960's with work done by Grindley. These studies included descriptions of copepods (Grindley 1963, 1969, 1978a), vertical migration behaviour of estuarine plankton (Grindley 1964, 1972) and descriptions of zooplankton assemblages in estuaries (Grindley 1970, 1976a, 1978b, 1979), lagoons and bay areas (Grindley 1976b, 1977, Grindley & Wooldridge 1973, 1974). The zooplankton of the Knysna Estuary was investigated by Day (1967) whilst conducting a study on the biology of the estuary. This was followed by an investigation into the mysids of the Mtentu Estuary (Connell 1974) and a description of two species of *Acartia* (Copepoda, Calanoida) (Connell & Grindley

1974). On the Transkei coast, Wooldridge (1976, 1977a) investigated the zooplankton assemblages of the Msikaba and Mgazana estuaries. A description of a species of *Halicyclops* (Copepoda, Cyclopoida) from estuaries in the Transkei (Wooldridge 1977b) and the ecology of two estuarine species of *Acartia* (Wooldridge 1979) followed. Estuarine plankton research conducted before the 1980's was compiled in a book about estuarine ecology authored by Grindley (1981). In the 1980's estuarine plankton research to date was compiled by Grindley (1981). Thereafter, the effects of environmental conditions on the zooplankton assemblage in the Bot Estuary (Coetzee 1985) and the zooplankton communities of an artificially divided subtropical coastal estuarine-lake system (Jerling & Cyrus 1999) were investigated. Wooldridge (1999) then described the estuarine zooplankton community structure and dynamics of South Africa.

At the turn of the century, feeding studies by selected zooplankton (Froneman 2000) the relationship between zoo- and phytoplankton in a warm-temperate, semi-permanently closed estuary (Perissinotto *et al*. 2000) and the effects of freshwater from an artificial dam release on zooplankton in the Kromme Estuary (Wooldridge & Callahan 2000) were assessed. This was followed by quantitative studies on the zooplankton community structures of the Mhlathuze Estuary (Jerling 2003), Mpenjati Estuary (Kibirige & Perissinotto 2003) and Kasouga Estuary (Froneman 2004). Perissinotto *et al*. (2003) also investigated planktonic food webs in three temporarily-open estuaries, followed by a description of zooplankton and hyperbenthos in the Mngazana Estuary on the Transkei coast (Deyzel 2004). Some of the most recent investigations reported in the literature include the composition, abundance and distribution of zooplankton in selected south and west coast estuaries (Montoya-

Maya & Strydom 2009b) and the effects of temperature and salinity on zooplankton community dynamics in the Great Berg Estuary (Wooldridge & Deyzel 2009).

3. PLANKTONIC RESEARCH IN THE SUNDAYS ESTUARY: A PERSPECTIVE

Planktonic studies in the Sundays Estuary began in the 1970’s, with a description of the seasonal succession of copepods by Wooldridge & Melville-Smith (1979). It was then noted that strong tidal currents prevailed in the Sundays Estuary, prompting an investigation by Wooldridge & Erasmus (1980) on zooplankton utilization of these tidal currents as a means of avoiding being flushed from the estuary. It was found that copepods *Pseudodiaptomus hessei* and *Acartia longipatella* avoided strong currents whilst *A. natalensis* was present in greater numbers in faster flowing currents which facilitated movement into the higher reaches of the estuary (Wooldridge & Erasmus 1980). A study by Wooldridge & Bailey (1982) reported on the composition, abundance and distribution of the euryhaline zooplankton, as well as predator-prey relationships between the dominant mysid *Rhopalopthalmus terranatalis* and the juveniles and adults of the most common fish species *Gilchristella aestuaria*. Wooldridge & Bailey (1982) indicated that temperature and salinity regulated the temporal and spatial distribution of euryhaline zooplankton. The significance of zooplankton as a planktonic prey of larval fish for a variety of estuary associated species was also noted. The predatory behaviour of the mysid *R. terranatalis* was then assessed (Wooldridge & Webb 1988) in terms of its impact on the spatial distribution of the mysid *Mesopodopsis wooldridgei*. Adult *R. terranatalis* were found to prey on juveniles *of M. wooldridgei* and this led to low recruitment into the *M. wooldridgei* population where *R. terranatalis* is abundant.

Larval fish studies were initiated by an investigation into the composition, distribution and abundance of the ichthyoplankton (Harrison & Whitfield 1990) followed by an assessment of the effects of freshwater inputs on larval and juvenile fish that included the Great Fish and Kariega estuaries (Whitfield 1994). Together clupeid and gobies were found to contribute the highest percentage to the larval fish community with highest densities occurring in the middle and upper estuary (Harrison & Whitfield 1990). The importance of salinity, temperature and turbidity as factors influencing larval fish abundance in the Sundays Estuary was noted by Whitfield (1994). Jerling & Wooldridge (1995a, 1995b) continued with investigations that included the feeding dynamics of the mysids *M. wooldridgei* and *R. terranatalis*. Whitfield and Harrison (1996) continued with trophic studies where *G. aestuaria* biomass and consumption of zooplankton was described enabling a better understanding of trophic linkages between larval fish and zooplankton.

4. RATIONALE FOR THIS STUDY

The importance of estuaries as nursery areas for larval and juvenile stages of estuary associated fishes is well known (Whitfield 1998, Strydom & Whitfield 2000, Strydom *et al*. 2003). The productive, sheltered and varied habitats generally provided by South African estuaries in contrast to strong currents, heavy wave action and a variety of predators in the nearshore marine environment (Wallace & van der Elst 1975) enhance the nursery function of estuaries, particularly for larvae of estuary associated marine fishes (Beckley 1984). The recruitment of postflexion larval fish into estuaries includes larvae of marine species as well as those of certain estuary-resident species whose preflexion larvae undergo a marine phase (Strydom & Whitfield 2000). The study of larval fishes forms the basis for understanding the fish population occurring in an estuary.

Zooplankton are important in the transfer of energy from primary producers to secondary consumers, and therefore form an important food resource for larval fish occurring in estuaries (Whitfield & Harrison 1996). Both micro- and macrozooplankton are utilized by larvae (Whitfield 1998). Whitfield (1985), stated that calanoid copepods formed the primary diet of newly recruited ichthyoplankton after which diet rapidly changed to one dominated by the zoobenthos, detritus or aquatic plants between 10mm - 30mm standard length. However, few studies have focused on the relationship between these two components of the planktonic community. Such information is necessary when investigating the overall resource utilization, trophic structure and habitat choice of individual fish species (Whitfield 1985).

In South Africa, a high demand for freshwater has lead to the building of dams and introduction of inter-basin water-transfer schemes. The downstream supply of riverine flow and nutrients to estuaries are influenced by such practices (Strydom *et al*. 2002). The sustainability of primary and secondary production within estuaries is dependent on the essential nutrients provided by freshwater and good water quality (Wooldridge & Bailey 1982, Hilmer & Bate 1991). Freshwater input into estuaries have been identified as a cue in facilitating recruitment of larval fish into estuarine nursery areas (Boehlert & Mundy 1988, Whitfield 1994, Strydom & Whitfield 2000).

The initiation of the inter-basin water-transfer scheme to the Sundays Estuary due to the high freshwater demand for agricultural practices in the area warrants a need for a larger ecological study. As stated by Strydom *et al*. (2002) the full ecological consequence of such transfers occurring in South Africa, due to the scarcity of freshwater, warrants a need for the monitoring of such schemes. Although freshwater input into estuaries is naturally variable, the main causes for changes in freshwater quality in river catchment areas are human activities (Wooldridge 1999). High chlorophyll-*a* levels in the middle and upper reaches of the Sundays Estuary were recorded by Hilmer (1990). This may be explained by the intense cultivation upstream contributing to the generally high nutrient levels. The question is no longer only regarding the quantity of freshwater being supplied to the Sundays Estuary but also the quality of this freshwater.

Although detailed studies are available for some estuaries, most South African estuaries still lack basic information on estuarine zooplankton and larval fish communities. There are existent gaps in a wide variety of topics that need to be studied (Whitfield & Marais 1999). In terms of the interactions between the various components of the planktonic ecosystem, studies are even more data deficient and this underlines the value of the larval fish diet and prey selection analysis undertaken in the present study.

5. OBJECTIVES AND AIMS

The objectives of this research was to conduct a two-year study on the plankton assemblage in the Sundays Estuary in order firstly to provide more information on the temporal and spatial dynamics of the larval fish and zooplankton assemblages occurring in the estuary and secondly, to further understand the interactions between the larval fish and zooplankton assemblages.

The specific aims of the present study were to determine the:

- Composition, abundance, distribution and seasonality of the larval fish (Chapter 2) and zooplankton communities (Chapter 3) of the Sundays Estuary.
- Larval fish diet, feeding guilds and selection of zooplankton prey species in the Sundays Estuary (Chapter 4).

6. THESIS STRUCTURE

Three focal chapters are presented in this thesis, preceded by a general introduction and ending with a synthesis and conclusion. This thesis was written in a format that will facilitate publication and therefore there is some degree of repetition in the methods and study area of each focal chapter.

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CHAPTER 2

COMPOSITION, ABUNDANCE, DISTRIBUTION AND SEASONALITY OF LARVAL FISHES IN THE SUNDAYS ESTUARY, SOUTH AFRICA

1. SYNOPSIS

The larval fish assemblage was studied in the permanently open Sundays Estuary on the south-east coast of South Africa. Seasonal samples were collected between winter 2007 and autumn 2009 at eight sites along the estuary by means of boat-based plankton tows using two modified WP2 nets. Salinity ranged from 1.5 - 36.5 and temperature from 11.6 - 26.8ºC during the study period. A total of 8174 larval and early juvenile fishes were caught, representing 12 families and 23 taxa. The Clupeidae, Gobiidae and Blenniidae were the numerically dominant fish families. Common species included *Gilchristella aestuaria* (Clupeidae), *Omobranchus woodi* (Blenniidae), *Caffrogobius gilchristi*, *Glossogobius callidus* (Gobiidae), *Liza dumerilii*, and *Myxus capensis* (Mugilidae). Catches varied significantly between seasons, but not between sites and salinity zones within the estuary. Highest catches were recorded in summer (mean of 464 and 928 larvae per 100m^3 in 2008 and 2009 respectively). Species diversity also varied seasonally, with highest diversity occurring during summer. Highest larval fish density occurred in the euhaline zone while the oligohaline zone supported the highest diversity. Estuarine resident species (Category I) dominated the system (91%). The preflexion stage of development dominated the catches suggesting a high degree of local production in the Sundays Estuary. Larval sizes of the estuarine resident *G. aestuaria* and catadromous species *M. capensis* tended to increase towards the middle and upper reaches of the estuary. Important variables regulating larval fish dynamics in the Sundays Estuary included salinity, temperature and turbidity.

2. INTRODUCTION

Fish species worldwide make extensive use of estuarine systems as settlement, spawning, feeding and nursery areas (Whitfield 1985, Harris & Cyrus 1995, Whitfield 1998, Strydom *et al*. 2003, Berasategui *et al*. 2004, Able *et al*. 2006, Aceves-Medina *et al*. 2008). Estuarine nursery areas are therefore crucial habitats for the survival of many endemic fish species. The study of larval fishes is the basis for understanding fish populations occurring in estuaries. For those species entering estuaries to use them as nurseries, many do not only enter estuaries during their juvenile stages, but also during their larval stages (Strydom *et al*. 2003). Postflexion larvae of estuarine-dependent marine species recruit from marine breeding grounds into estuarine nurseries. Passive tidal entrance of preflexion larvae of certain fish species into estuaries is also known to occur (Beckley 1985, Whitfield 1989a, Strydom 1998, Strydom & Wooldridge 2005). The recruitment of postflexion larvae also includes certain estuary-resident species after an obligatory marine phase during flexion (Beckley 1985, Whitfield 1989a). Worldwide, factors driving the recruitment process and the dynamics of the use of estuaries by these early developmental stages have been the focus of much research attention (Neira & Potter 1994, Barletta-Bergan *et al*. 2002, Hagan & Able 2003, Faria *et al*. 2006, Ramos *et al*. 2006, Aceves-Medina *et al*. 2008).

South African larval fish studies have included both single (Melville-Smith & Baird 1980, Strydom & Whitfield 2000, Pattrick *et al*. 2007, Wasserman *et al*. 2010) and multiple estuary studies (Harris & Cyrus 2000, Strydom *et al*. 2003, Montoya-Maya & Strydom 2009). In these studies aspects such as the influence of estuary type (Strydom *et al*. 2003), tidal exchange (Beckley 1985, Whitfield 1989a, Strydom & Wooldridge 2005) and the effects of altered freshwater input (Strydom & Whitfield

2000, Strydom *et al*. 2002, Vorwerk *et al*. 2008) on species distribution and success in estuaries was assessed.

In the Sundays Estuary, previous studies include those on the juvenile (Beckley 1984) and adult (Marais 1981) components of the fish community. Harrison & Whitfield (1990) complemented these studies with an analysis of the larval fish composition, distribution and abundance of the Sundays Estuary fish community. The effects of freshwater inputs on larval and juvenile marine fishes and the biomass and consumption of zooplankton by the Clupeidae, *Gilchristella aestuaria* were studied by Whitfield (1994a) and Whitfield & Harrison (1996) respectively.

The location of estuaries and the active behavioural mediated recruitment into them is critical for at least 22 South African teleost species (James *et al*. 2008). Several mechanisms have been suggested as cues for the recruitment response including turbidity, salinity, temperature, current speed, food, habitat availability and olfactory cues. Freshwater input into estuaries is recognized as a possible driver in facilitating recruitment of larval fish into estuarine systems (Boehlert & Mundy 1988, Whitfield 1994a, Strydom & Whitfield 2000). Larval fish possess high chemo-sensitivity due to the presence of an olfactory bulb, similar in organization to that of higher vertebrates (Hara 1992, James *et al*. 2008). This together with freshwater as a driver, assists fish species to locate these estuaries (Strydom & Whitfield 2000, James *et al*. 2008). Therefore, the high demand for freshwater and the subsequent altered river flow regimes through the initiation of inter-basin water-transfer schemes will affect the recruitment of larval fishes into estuaries.

To understand the fish population occurring in an estuary the study of larval fishes is imperative. Longer term studies on larval fish communities of estuaries are lacking and although short term investigations are available for some estuaries, most South African estuaries lack basic information. The objective of this study was to describe the spatio-temporal dynamics of the larval fish assemblage in the Sundays Estuary over a two year period. The specific aims were to identify the species composition, abundance, distribution and seasonality of the larval fish community in the estuary and relate this to the physico-chemical variability within the system.

3. MATERIALS AND METHODS

3.1. Study area

The Sundays Estuary is a permanently open system located on the south-east coast of South Africa. It rises in the Karoo (south central South Africa), draining a catchment area of 20 729 km^2 before flowing into Algoa Bay (33 04 3'S, 25 05 1'E) (Beckley 1984). The Sundays Estuary is part of the Addo Elephant National Park (AENP). The estuary is channel-like along the majority of its 21 km length with a depth variation from 5 m in the lower and middle reaches to less than 2 m in the upper reaches (Wooldridge & Erasmus 1980, Whitfield & Harrison 1996). The estuary is approximately 800 m at its widest point near the mouth, becoming increasingly narrower to approximately 20 m wide at the head of the estuary (Marais 1981, Whitfield & Harrison 1996). The Sundays Estuary is characterised by steep banks (about 3-4 m high) with limited marginal vegetation. There is an absence of salt marshes or large mud flats (Beckley 1984). Submerged macrophytes such as *Potamogeton crispus* occur at the head of the estuary while *Phragmites australis* occurs in the upper reaches. Benthic algae dominate the middle reaches and a small bed of *Zostera capensis* sometimes establishes itself near the mouth (Harrison &

Whitfield 1990). Hilmer (1990) recorded high chlorophyll-*a* levels in the middle and upper reaches extending into the lower reaches of the estuary during summer. This is due to intense agricultural practices along the river contributing to generally high nutrient levels (Emmerson 1989).

The estuary has continuous freshwater inflow (Jerling & Wooldridge 1995) supplemented by an inter-basin water-transfer scheme (Pech *et al*. 1995). The mean annual rainfall in the region is 323 mm with a mean annual runoff of approximately 200 X 10^6 m^3 (Whitfield & Harrison 1996). Spring tidal range is about 1.2 - 1.5 m and at neap tide 0.1 - 0.3 m (Harrison & Whitfield 1990). Water temperatures range from 13ºC in winter to 26ºC in summer (Jerling & Wooldridge 1991). The estuary displays a full salinity gradient linked to the inter-basin water-transfer scheme and return flows from the citrus farming practices above the estuary (Wooldridge & Bailey 1982, MacKay & Schumann 1990). Salinity levels are highest near the mouth of the estuary due to the permanent connection with the ocean.

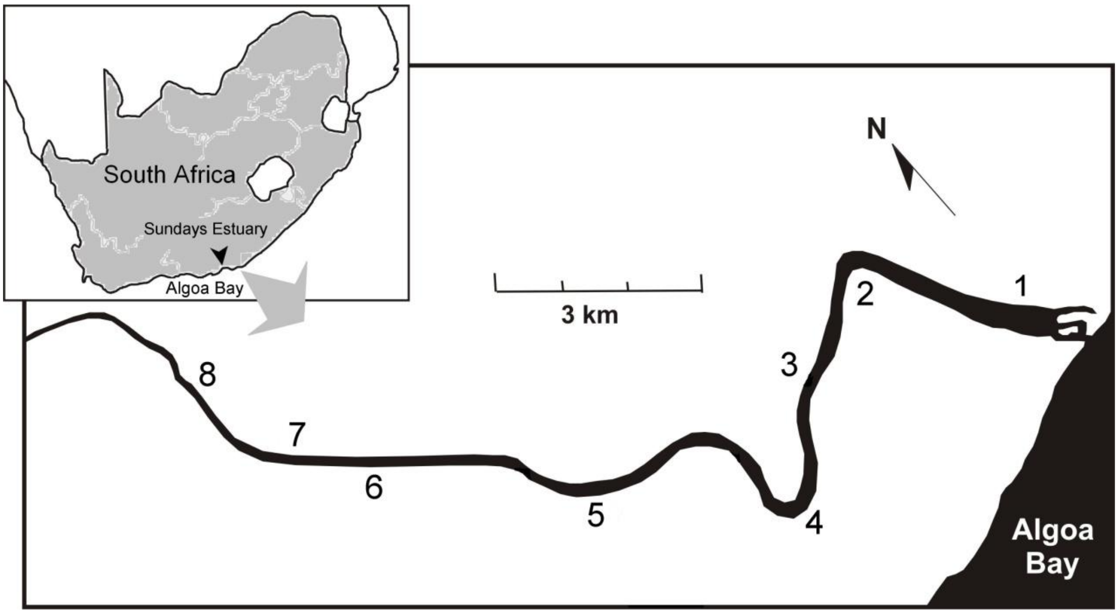

Figure 2.1: Geographical position of the Sundays Estuary showing location of larval fish sampling stations used in the study.

3.2. Field sampling

Plankton tows took place at 8 GPS-fixed sites along the length of the Sundays Estuary at seasonal intervals during July 2007 and 2008, October 2007 and 2008, January 2008 and 2009 and April 2008 and 2009. Two slightly modified WP2 plankton nets (570 mm mouth diameter and 0.2 µm mesh aperture size) fitted with Kahlsico 005 WA 130 flowmeters were used (Strydom *et al*. 2003). Sampling commenced ca 30 min after nightfall on the new moon. Nets were simultaneously lowered and towed alongside the boat for 3 min at a speed of 1-2 knots sampling the subsurface layer (Strydom *et al*. 2003). After each tow, flowmeter readings were taken to determine the water volume filtered. Samples were preserved on site in 10% buffered formalin.

Vertical temperature (ºC) and salinity (expressed as practical salinity units) profiles were obtained at each site using a YSI 6600 multi-parameter instrument. Recordings were conducted at intervals of 0.5 m between the surface and bottom of the water column (Strydom & Whitfield 2000). Integrated values were used for analyses. Water transparency measurements were taken at all sites using a Secchi disc. All Secchi disc depth measurements were converted into an extinction coefficient (k) using methods described by Dawes (1981) where $k = 1.7/D$ (Secchi depth in cm) (Strydom *et al*. 2003).

3.3. Larval identification

In the laboratory, larval fishes were first sorted from plankton samples then identified and counted. Identification was completed to the lowest possible taxon using Smith & Heemstra (1986), Neira *et al*. (1998) and Leis & Carson-Ewart (2000) amongst others. Larvae were measured to the nearest 0.1 mm body length (BL) using an eyepiece micrometer for larvae <10 mm and Vernier callipers for larger specimens. This represents notochord length in preflexion and flexion larvae, and standard length in postflexion larvae (Neira *et al*. 1998). Larvae that were positively identified were grouped into estuary-dependence categories (Table 2.1), as defined by Whitfield (1998). Larval fish density (number of larvae/100 m^3) was calculated using a simple formula based on a predetermined calibration value for each flowmeter used: Total number of fish larvae/100 m^3 = [total number of larvae caught per haul / (revolutions on flowmeter / predetermined calibration value in m^3) X 100].

Table 2.1: Categories of fish that utilize southern African estuaries (Whitfield 1998).

Categories	Description of categories
Ia	Estuarine species, breeding only in estuaries
Ib	Estuarine species that breed in estuaries and in the marine environment
IIa	Euryhaline marine species that usually breed at sea, juveniles are dependent on estuaries for nursery grounds
IIb	Euryhaline marine species that usually breed at sea, juveniles occurring in estuaries but also in the sea
IIc	Euryhaline marine species that usually breed at sea, juveniles occurring in estuaries but more abundant in the sea
III	Marine stragglers not dependent on estuaries
IV	Freshwater species
V	Catadromous species

3.4. Data treatment and analysis

Sample sites were categorised into salinity zones based on an adaptation of the Venice system (Strydom *et al*. 2003) (Table 2.2). Homogeneity of variance and normality tests were completed for physical and biological data, using a Levene's Test and normal probability plot. Square-root transformations were also used. The data did not conform to parametric test assumptions and therefore non-parametric tests were used.

Larval fish density was assessed for differences between seasons, sites and salinity zones using the non-parametric Kruskal-Wallis test and between years using the Mann-Whitney U-Test. Seasonal differences between salinity, temperature and turbidity were also assessed using the Kruskal-Wallis test. Multiple linear stepwise regression for parametric data, was used to determine the relationship between environmental variables and larval fish density. A reduced significance level of $P < 0.01$ was used for this analysis.

PRIMER statistical software package v5.2.9 (Clarke & Warwick 1994) was used to conduct community analysis and to calculate diversity indices (Marglef's species richness and Shannon-Wiener diversity). These were compared between seasons, sites and salinity zones. Larval fish density data were Log_{10} (x + 1) transformed prior to community analysis. A separation was made between estuarine resident species (category I) and marine-spawned, estuarine dependent and catadromous species (categories II, III, V) and a Bray-Curtis similarity matrix was generated for each of these data groups. ANOSIM was used to detect differences between groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity between groups assigned. A significance level of $P < 0.05$ was used.

Table 2.2: Adaptation of the Venice system for the classification of South African salinity zones in estuaries (Strydom *et al*. 2003).

Salinity zone	Salinity range (psu)
Fresh	0 - 0.49
Oligohaline	0.5 - 4.9
Mesohaline	5.0 - 17.9
Polyhaline	18.0 - 29.9
Euhaline	30.0 - 35.9
Hypersaline	≥36

4. RESULTS

4.1. Environmental variability

Seasonal physico-chemical variability was apparent in the Sundays Estuary. No significant difference was found in mean salinity between seasons (H = 2.69; P = 0.44). Salinity ranged from 1.5 - 33.7 in summer, 1.7 - 32.6 in autumn, 1.9 - 36.5 in winter and 2.0 - 32.9 in spring. Salinity stratification was evident, with stratification most prominent in summer and autumn at lower estuary sites. A significant difference (H = 97.86; $P < 0.01$) was found in mean water temperature between all seasons except spring and autumn. Water temperature ranged from 20.2 - 26.8°C in summer, 18.0 - 23.0°C in autumn, 11.6 - 15.8°C in winter and 20.1 - 22.5°C in spring. Stratification of water temperature was weak, occurring at lower sites in summer and autumn. A significant difference (H = 41.72; $P < 0.01$) in water transparency (k) was also found between summer and winter, autumn and winter, autumn and spring and winter and spring (Figure 2.2).

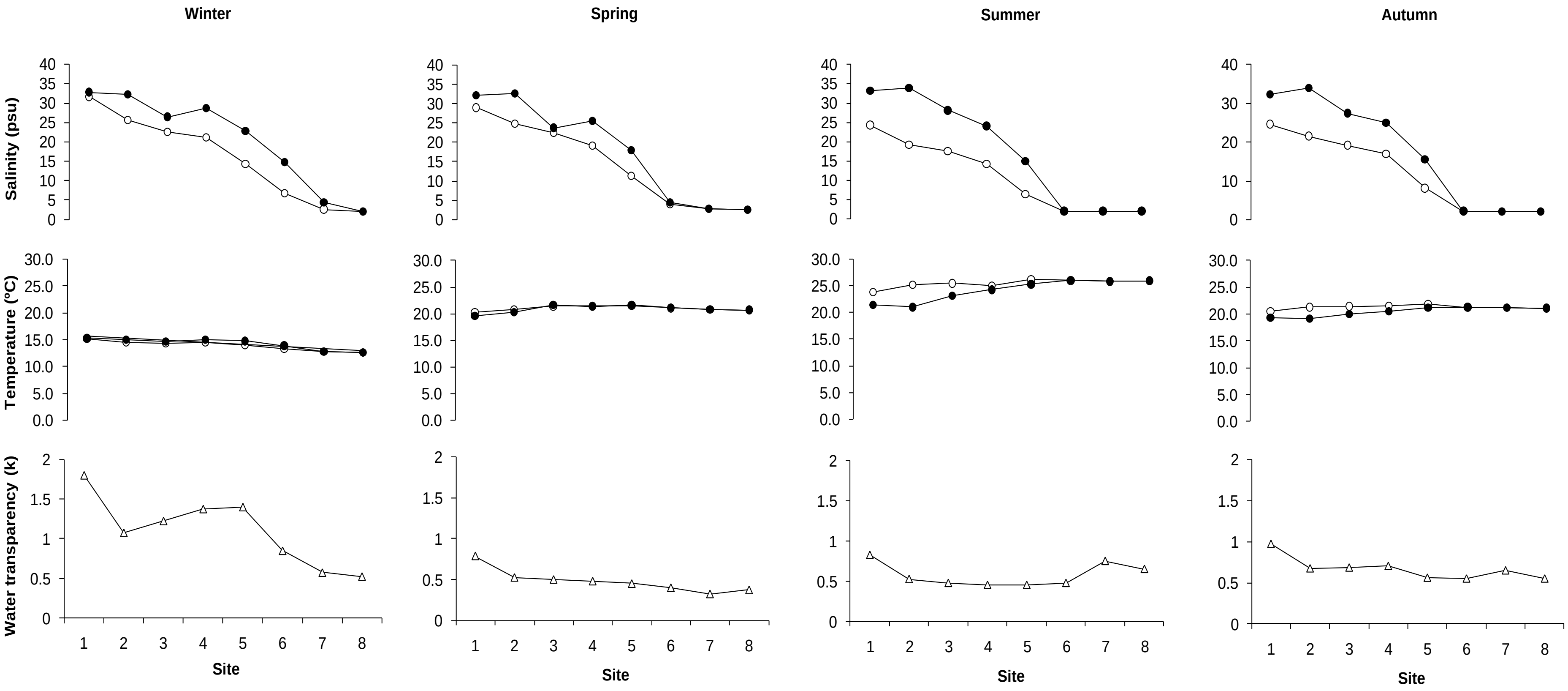

Figure 2.2: Mean surface (o) and bottom (●) salinity values and temperatures and water transparency (two sample sessions per season) for all seasons, at sites in the Sundays Estuary recorded between 2007 and 2009.

4.2. Temporal and spatial trends in species composition and estuary association

A total of 8 174 larval and early juvenile fishes were caught, representing 12 fish families and 23 species. *Gilchristella aestuaria*, the only representative species of the Clupeidae family, dominated the catch, comprising 59.2%. Gobiidae, contributed a further 22.0% with *Caffrogobius gilchristi* (19%) making the largest species contribution to the family catch. *Omobranchus woodi* (family Blenniidae) contributed 10% of the total catch. *Liza dumerilii* and *Myxus capensis* of the family Mugilidae (6.7%) comprised 4.3% and 2.1% of the total catch respectively. All other fish family contributions were less than 1% (Table 2.3).

The family Clupeidae dominated throughout the study with highest percentage contribution in summer 2008 and 2009 (12.4% and 13.2% respectively). The families Blenniidae, Gobiidae and Mugilidae also had their highest percentage contribution in summer 2009 (6.8, 13.0 and 2.5% respectively) (Figure 2.3). The largest portion of the catch (91%) was comprised of estuary-resident species (Category I). Marine dependents (Category II) and Catadromous species (Category V) followed contributing 6% and 2% of the total catch respectively.

Table 2.3: Species composition, mean density (range), total catch, body length, developmental stages and estuary association of larval fishes caught in the Sundays Estuary between 2007 to 2009. Pr = preflexion, F = flexion, Po = postflexion, Ej = early juvenile.

Family	**Species**	**Mean density (range) (no. per 100m^3)**				**Total catch**		**Body length (mm)**	**Dev. stage**	**Est. assoc.**
		Winter	**Spring**	**Summer**	**Autumn**	**No.**	**%**	**Mean Range**		
Ambassidae	*Ambassis natalensis*	0.1 (0 - 4.0)	0	0	0	1	<1	20.5	Ej	Ib
Anguillidae	*Anguillid* sp.	0	0.1 (0 - 4.4)	0.1 (0 - 3.9)	0	2	<1	45.7 (43.7 - 47.7)	Glass eel	V
Blenniidae	*Omobranchus woodi*	0	1.2 (0 - 18.5)	128.8 (0 - 855.0)	0	773	10.0	3.2 (1.5 - 17.9)	Pr, F	Ia
Clupeidae	*Gilchristella aestuaria*	135.9 (0 - 1194.0)	14.6 (0 - 188.7)	333.6 (0 - 2614.4)	288.6 (0 - 2443.6)	5339	59.2	16 (1.9 - 29.9)	Pr, F, Po, Ej	Ia
Cyprinidae	Cyprinid 1	0	0	0	0.1 (0 - 3.8)	1	<1	11.7	Po	IV
Elopidae	*Elops machnata*	0	0.3 (0 - 4.2)	1.3 (0 - 30.9)	0	6	<1	26.3 (23.0 - 28.9)	F, Po	IIa
Gobiidae	*Caffrogobius gilchristi*	0.1 (0 - 3.8)	63.8 (0 - 763.9)	162.2 (0 - 1772.1)	21.9 (0 - 190.2)	1112	19.0	2.4 (1.1 - 12.9)	Pr, F	Ib
	Glossogobius callidus	0	0	24.1 (0 - 526.0)	14.5 (0 - 300.9)	50	3.0	4.3 (2.8 - 9.6)	Pr, F	Ib
	Psammogobius knysnaensis	0.2 (0 - 4.0)	0.8 (0 - 9.9)	7.7 (0 - 85.9)	1.8 (0 - 27.6)	70	<1	2.3 (1.3 - 6.0)	Pr	Ib
	Unidentified Goby	0	0	0.8 (0 - 24.5)	0	4	<1	10.5 (6.7 - 13.1)	F	
Haemulidae	*Pomadasys commersonnii*	0.3 (0 - 7.2)	0	0	5.9 (0 - 95.5)	52	<1	18.6 (14.1 - 25.4)	Po, Ej	IIa
	Pomadasys olivaceum	0	0	0.2 (0 - 6.1)	0	1	<1	25.0	Ej	III
Monodactylidae	*Monodactylus falciformis*	0.9 (0 - 23.8)	0	0.1 (0 - 4.1)	0	8	<1	19.5 (6.5 - 29.3)	F, Po, Ej	IIa
Mugilidae	*Crenimugil crenilabis*	0	0.4 (0 - 13.4)	0	0.1 (0 - 3.6)	3	<1	17.6 (13.0 - 25.4)	Po, Ej	IIb
	Liza sp.	0.1 (0 - 4.0)	0.2 (0 - 6.1)	0.1 (0 - 3.6)	0	3	<1	10.2 (8.9 - 11.7)	Pr, F	
	Liza dumerilii	0.1 (0 - 4.0)	0.2 (0 - 6.7)	32.2 (0 - 465.9)	23.9 (0 - 336.4)	510	4.3	13.7 (8.3 - 28.1)	Pr, F, Po, Ej	IIb
	Liza richardsonii	0	0	0.1 (0 - 3.6)	0	1	<1	13.6	Po	IIc
	Liza tricuspidens	0	0	1.5 (0 - 33.1)	0	11	<1	17.8 (13.4 - 21.8)	Po, Ej	IIb
	Mugil cephalus	0.8 (0 - 7.1)	0.1 (0 - 4.2)	0	0	8	<1	20.1 (15.3 - 22.4)	Po, Ej	IIa
	Myxus capensis	0	24.5 (0 - 231.4)	1.3 (0 - 12.4)	2.1 (0 - 27.4)	178	2.1	14.6 (8.9 - 23.2)	F, Po, Ej	V
Soleidae	*Solea turbynei*	0	0	0.4 (0 - 12.3)	0	2	<1	7.3 (7.1 - 7.4)	F	IIb
Sparidae	*Diplodus capensis*	0	0	1 (0 - 24.5)	0	5	<1	7.7 (6.8 - 8.6)	F	IIc
	Rhabdosargus holubi	1.8 (0 - 28.6)	3.6 (0 - 24.4)	0.4 (0 - 4.1)	0.5 (0 - 16.4)	35	<1	12.1 (4.3 - 20.2)	Pr, F, Po, Ej	IIa

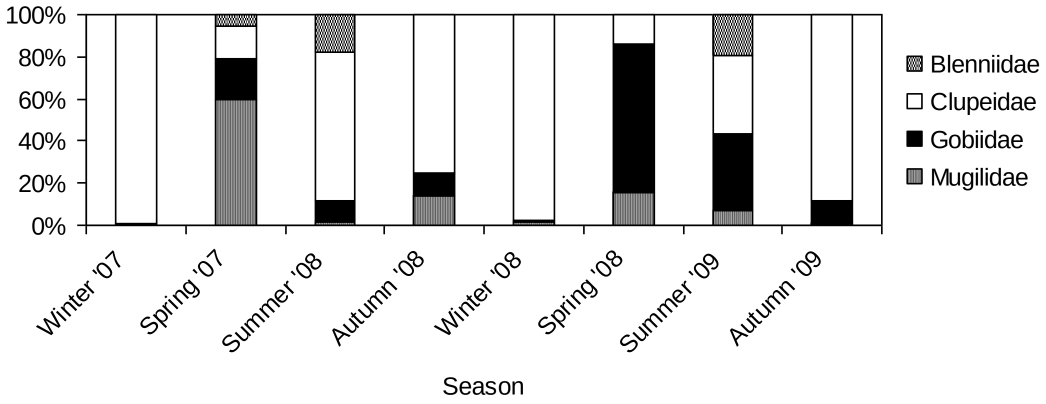

Figure 2.3: Family composition (percentage contribution) of larval fishes for all seasons in the Sundays Estuary during the study (2007-2009). ’07 = 2007, ’08 = 2008, ’09 = 2009. Families contributing < 2% to overall catch are excluded.

Spatial differences in the species contribution of larval fishes were noted, with a clear shift in larval fish species density between lower and upper reaches (Figure 2.4). *Omobranchus woodi* (category Ia) and *C. gilchristi* (category Ib) dominated the lower four sites near the mouth; however *C. gilchristi* also occurred at site 8 in the upper reaches. *Gilchristella aestuaria* (category Ia) showed highest densities at sites 3, 5, 6 and 7. *Glossogobius callidus* (category Ib), *L. dumerilii* (category IIb) and *M. capensis* (category V) occurred in highest densities in the upper reaches (site 5 - 8).

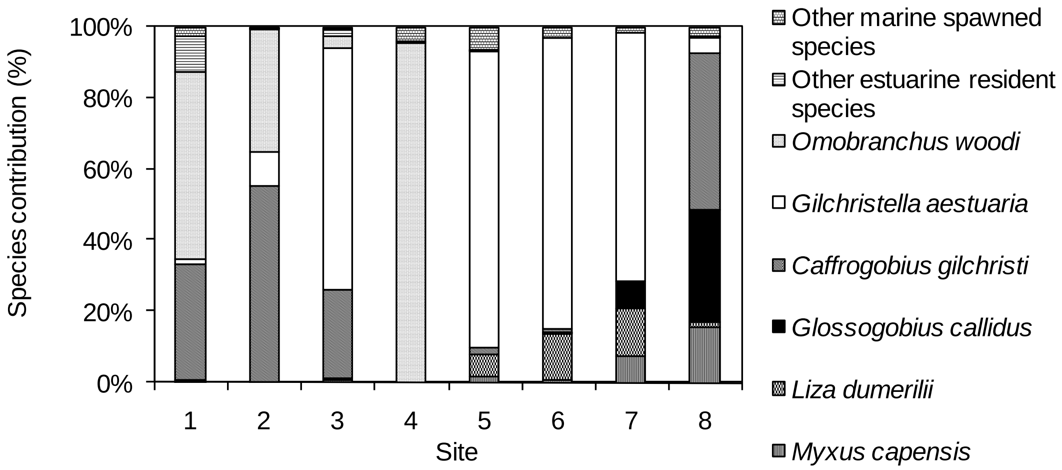

Figure 2.4: Percentage contribution of larval fish species at sites along the length of the Sundays Estuary between 2007 and 2009. Only species which contributed over 2% individually to the total catch were included. Rare species contributing less than 2% were grouped as other marine spawned or estuarine resident species as their contribution to overall catch was negligible. Site 1 occurs at the mouth of the estuary.

Species specific variations in seasonal occurrence were present during the study (Figure 2.5). The estuarine resident species *G. aestuaria*, *C. gilchristi* and *Psammogobius knysnaensis* and the marine spawned *L. dumerilii* and *Rhabdosargus holubi* occur throughout the year. Marine spawned species that only occurred in the summer season include Unidentified goby, *Pomadasys olivaceum*, *L. richardsonii, L. tricuspidens*, *Solea turbynei* and *Diplodus capensis*. Estuarine resident species (Category I) were present every season (2007-2009) and at all sites. Estuarine dependents (Category II) on the other hand were most abundant at sites 5, 6 and 8 and were also present every season (2007-2009). Marine stragglers (Category III) and the freshwater migrant (Category IV) were only present during summer 2008 at site 1 and autumn 2008 at site 6 respectively. Catadromous species (Category V) were absent in the winter seasons and showed highest densities at site 7 (Table 2.4).

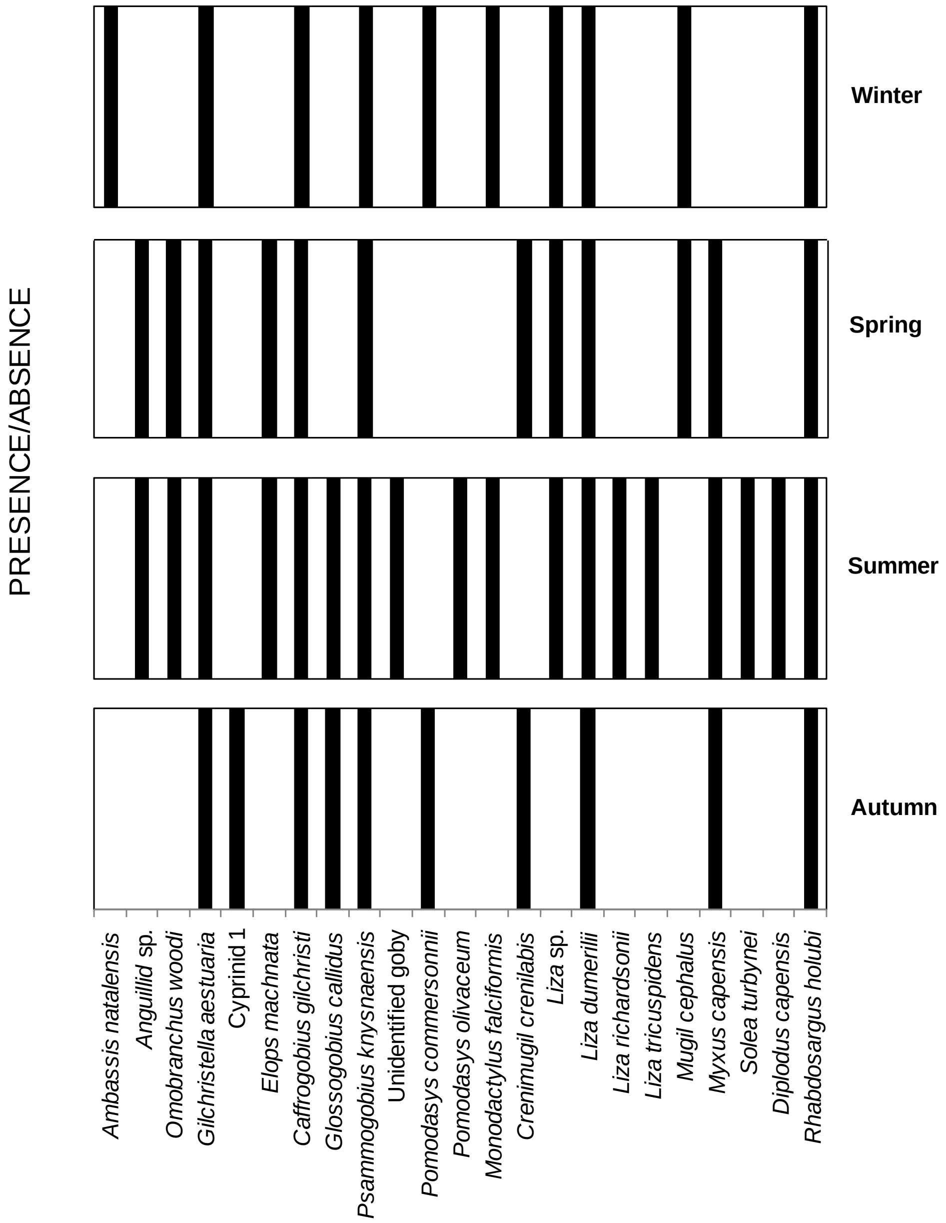

Figure 2.5: Seasonal presence and absence of all species caught in the Sundays Estuary between 2007 and 2009. Note bars indicate presence.

Table 2.4: Seasonal presence or absence of larval fishes in various estuary dependent categories (Whitfield 1998) at all sites sampled in the Sundays Estuary (2007-2009). Sp = spring, Su = summer, Au = autumn, Wi = winter. ’07 = 2007, ’08 = 2008, ’09 = 2009.

		Site							
		1	2	3	4	5	6	7	8
Estuarine residents	Wi '07		X	X	X	X	X	X	X
Category I	Sp '07	X	X	X	X	X			
	Su '08	X	X	X	X	X	X	X	X
	Au '08	X	X	X	X	X	X	X	
	Wi '08		X	X	X	X	X	X	X
	Sp '08	X	X	X	X		X	X	
	Su '09	X	X	X	X	X	X	X	X
	Au '09	X	X	X	X	X	X	X	X
Estuarine dependents	Wi '07				X	X	X		X
Category II	Sp '07			X		X	X	X	X
	Su '08	X		X		X	X	X	X
	Au '08			X	X	X	X	X	
	Wi '08	X	X	X	X	X	X		X
	Sp '08				X	X	X	X	X
	Su '09	X		X	X	X	X	X	X
	Au '09						X		
Marine stragglers	Wi '07								
Category III	Sp '07								
	Su '08	X							
	Au '08								
	Wi '08								
	Sp '08								
	Su '09								
	Au '09								
Freshwater species	Wi '07								
Category IV	Sp '07								
	Su '08								
	Au '08						X		
	Wi '08								
	Sp '08								
	Su '09								
	Au '09								
Catadromous species	Wi '07								
Category V	Sp '07	X		X		X	X	X	X
	Su '08		X	X	X			X	
	Au '08		X	X		X	X	X	
	Wi '08								
	Sp '08			X		X		X	X
	Su '09							X	
	Au '09								X

A weak positive regression relationship was evident between all taxa, dominant species and environmental variables. Larval fish density, in the Sundays Estuary showed a significant relationship with temperature ($P < 0.01$). At the community level, salinity and water transparency did not show any significant relationship with larval fish density. At the species level, *Caffrogobius gilchristi* and *Omobranchus woodi* were significantly influenced by salinity and temperature ($P < 0.01$). Salinity also had a positive relationship with *Liza dumerilii* and *Glossogobius callidus* ($P < 0.01$) (Table 2.5).

Table 2.5: Multiple linear regression statistics for the relationship between larval fish density and environmental variables (salinity, temperature and water transparency) for all taxa combined and the dominant species in the Sundays Estuary. r^2 = Coefficient of determination; r = correlation coefficient; F = F-statistic; Sa = salinity; Te = temperature. Significance level = $P < 0.01$

Taxon	r^2	r	F	Significant variable
All taxa	0.10	0.32	4.80	Te*
Dominant species				
Gilchristella aestuaria	0.04	0.19	1.59	
Caffrogobius gilchristi	0.13	0.37	6.36	Sa*, Te*
Omobranchus woodi	0.15	0.39	7.31	Sa**, Te*
Liza dumerilii	0.10	0.31	4.51	Sa*
Glossogobius callidus	0.11	0.33	5.07	Sa*

Significance levels: * = $P < 0.01$, ** = $P < 0.001$

4.3. Temporal and spatial trends in larval fish density, richness and diversity

A significant inter-annual difference in larval fish density was found between winter 2007 and summer 2009, spring 2007 and summer 2009, autumn 2008 and winter 2008 and winter 2008 and summer 2009 ($P < 0.01$) (Figure 2.6). Similarly, a significant difference in larval fish densities occurred between seasons. Greatest variability occurred between summer and winter, summer and spring and autumn and winter (H = 30.28; $P < 0.01$). Highest mean larval fish density occurred in summer of 2008 with 464 larvae per 100m^3 (range: 6 - 2625) and 2009 with 928 larvae per 100m^3 (range: 47 - 3171). Lowest mean larval fish density occurred in spring 2007 with 43 larvae per 100m^3 (range: 0 - 113) and winter 2008 with 49 larvae per 100m^3 (range: 0 - 207) (Table 2.6). No significant difference was found between different sites and larval fish density (H = 14.62; *P* > 0.05) (Figure 2.7).

The euhaline zone had the highest mean density of larval fishes (627 larvae per 100m^3). This was followed by the mesohaline, oligohaline and polyhaline zones (378, 299 and 263 larvae per 100m^3 respectively) (Table 2.6). No significant difference between larval fish densities and salinity zone was found (H = 10.15; *P* > 0.05). SIMPER analysis revealed that *Caffrogobius gilchristi* (in spring 2008, summer 2009 and autumn 2009), *Gilchristella aestuaria* (in autumn 2009) and *Omobranchus woodi* (in summer 2009) at the preflexion stage of development contributed to the high density of larval fish in the euhaline zone.

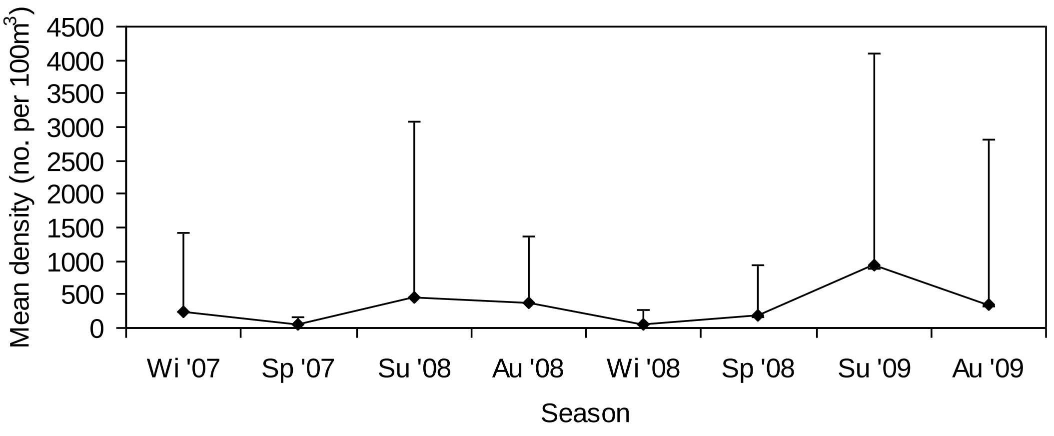

Figure 2.6: Mean larval fish density recorded consecutively per season between 2007 and 2009 in the Sundays Estuary. Sp = spring, Su = summer, Au = autumn, Wi = winter. ’07 = 2007, ’08 = 2008, ’09 = 2009. Bars indicate range.

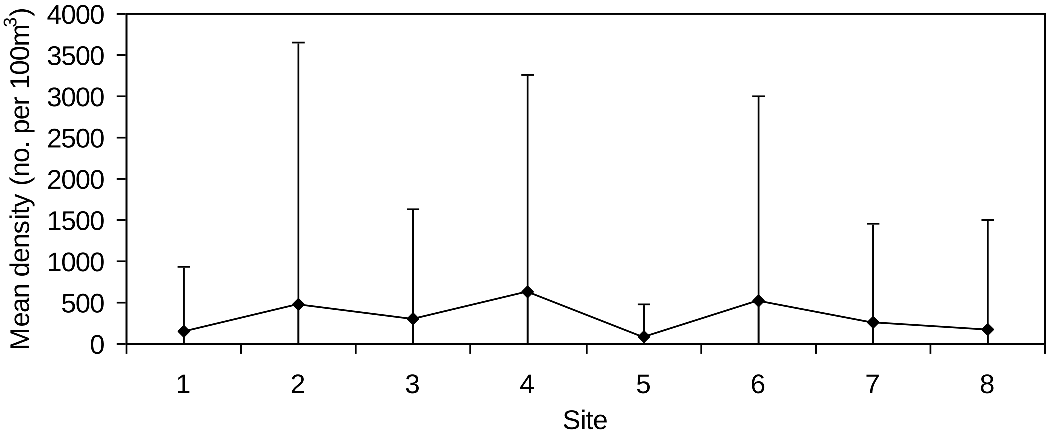

Figure 2.7: Mean larval fish density at all sites along the Sundays Estuary between 2007 and 2009. Bars indicate range.

Table 2.6: Mean, median and range of larval fish density recorded in the different seasons and salinity zones in the Sundays Estuary between 2007 and 2009.

	Density (no. per 100m^3)		
	Mean	Median	Range
Season			
Winter '07	232	27	0-1194
Spring '07	43	29	0-113
Summer '08	**464**	**145**	**6-2625**
Autumn '08	373	211	0-996
Winter '08	49	32	0-207
Spring '08	177	130	20-764
Summer '09	**928**	**782**	**47-3171**
Autumn '09	346	153	28-2476
Salinity Zone			
Euhaline	**627**	**311**	**28-3171**
Polyhaline	263	62	0-1316
Mesohaline	378	155	4-2625
Oligohaline	299	82	0-2476

Species richness (d) of 2.80 and species diversity (H') of 1.34 were obtained for the Sundays Estuary (Table 2.7). Species richness and diversity were highest in summer of 2008 and 2009 respectively. Also evident was a spatial difference in species richness and diversity. Highest species richness occurred at site 1 near the mouth and highest species diversity occurred at site 8 in the upper reaches (Table 2.8). Compared with other salinity zones, the oligohaline zone showed highest species richness and diversity followed by the polyhaline zone.

Table 2.7: Seasonal species richness index (d) and species diversity index (H') for the larval fish assemblage in the Sundays Estuary between 2007 and 2009.

	No. of species	Species richness (d)	Species diversity (H')
Season			
Winter '07	6	0.92	0.08
Spring '07	9	2.13	1.41
Summer '08	**16**	**2.44**	1.01
Autumn '08	9	1.35	0.90
Winter '08	9	2.05	0.60
Spring '08	9	1.55	0.99
Summer '09	10	1.32	**1.44**
Autumn '09	6	0.86	0.47
Entire Estuary	**23**	**2.80**	**1.32**

Table 2.8: Species richness index (d) and species diversity index (H') at sampling sites and salinity zones for the larval fish assemblage in the Sundays Estuary between 2007 and 2009.

	Species richness (d)	Species diversity (H')
Sites		
1	**2.40**	1.20
2	0.81	0.96
3	1.75	0.90
4	1.40	0.24
5	1.98	0.72
6	1.60	0.67
7	1.81	1.01
8	1.55	**1.34**
Salinity zone		
Euhaline	0.93	0.97
Polyhaline	2.51	1.08
Mesohaline	1.52	0.24
Oligohaline	**2.63**	**1.38**

The Sundays Estuary showed similar species richness for autumn, winter and spring, however highest species richness occurred in the summer seasons. Evenness was higher in spring and autumn, whereas winter was dominated by *Gilchristella aestuaria* (Figure 2.8).

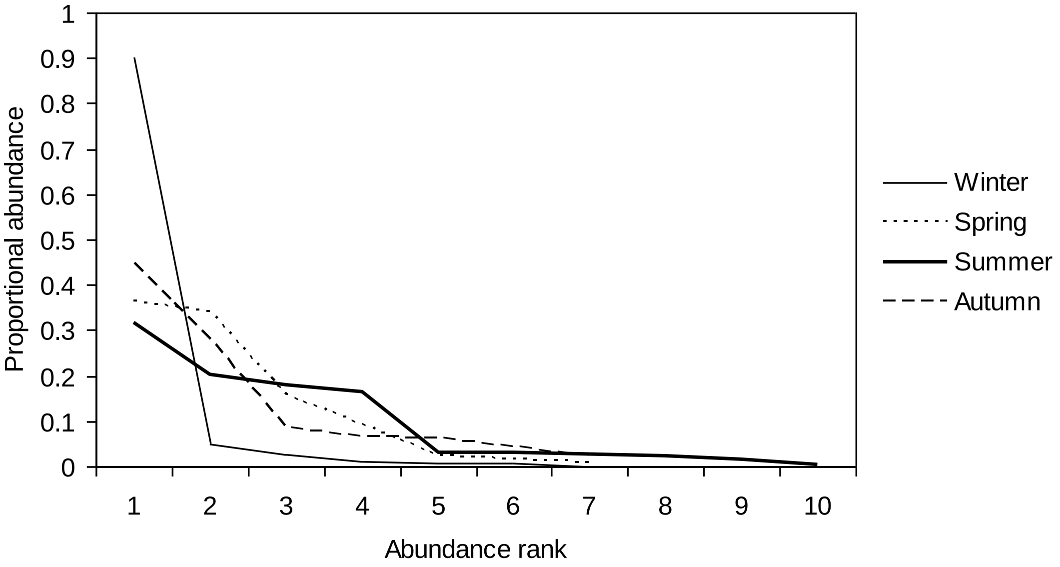

Figure 2.8: Rank abundance curve representing larval fish species richness (d), diversity (H') and evenness (J) for the Sundays Estuary in summer, autumn, winter and spring between 2007 and 2009.

4.4. Temporal and spatial variation in development stage and body length

The larval fish assemblage in the Sundays Estuary was dominated by preflexion larvae. Summer showed highest percentage of preflexion and flexion larvae. Postflexion larvae and early juveniles increased in autumn and winter (Figure 2.9). On a spatial scale, lower estuary sites (1-4) were dominated by preflexion larvae. Site 5 showed greatest percentage of flexion and postflexion larvae. Early juvenile fishes increased in abundance with distance up the estuary (Figure 2.10). Size ranges for larval fishes collected in the Sundays Estuary are shown in Table 2.9.

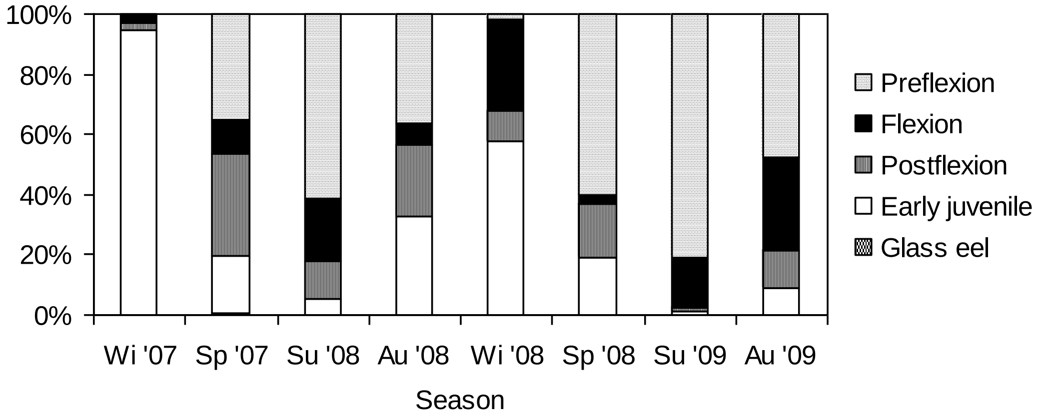

Figure 2.9: Temporal trends in larval fish development stages present in the Sundays Estuary between 2007 and 2009. Sp = Spring, Su = Summer, Au = Autumn, Wi = Winter. '07 = 2007, '08 = 2008, '09 = 2009. Due to low numbers of the glass eel developmental stage these are not visible on the figure.

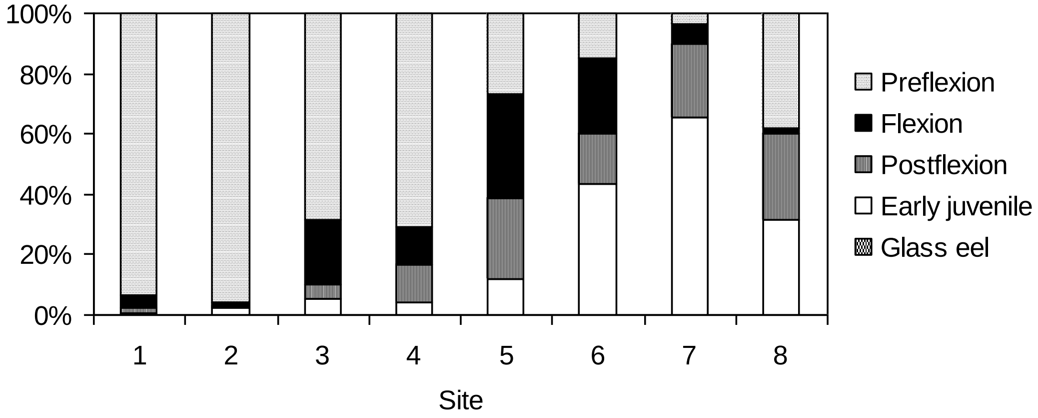

Figure 2.10: Spatial variation of larval fish developmental stages at all sites in the Sundays Estuary between 2007 and 2009. Due to low numbers of the glass eel developmental stage these are not visible on the figure.

4.5. Community analysis

Cluster analysis grouping indicated that for both estuarine residents and marine spawned species there were no clear patterns associated with selected factors (Figure 2.11a and 2.11b). Groups formed at 50% similarity, generally contained a variety of seasons and sites. Group 5 however mainly contained summer and spring samples. MDS plots were excluded as these showed similar patterns to the cluster analysis, thereby not adding any value to the community analysis.

Species composition by seasons and sites using density data was investigated using a community analysis approach (Table 2.10). SIMPER analysis revealed that the estuarine residents *Gilchristella aestuaria* and *Caffrogobius gilchristi* were the dominant contributing species to dissimilarity between seasons and sites (Table 2.10). Other estuarine resident species contributing to this dissimilarity include *Psammogobius knysnaensis*, *Omobranchus woodi* and *Glossogobius callidus*. The marine spawned *Myxus capensis*, *Rhabdosargus holubi* and *Liza dumerilii* were the dominant contributing species to dissimilarity between seasons and sites (Table 2.10). *Mugil cephalus*, *Liza tricuspidens* and *Pomadasys commersonnii* also contributed to this dissimilarity.

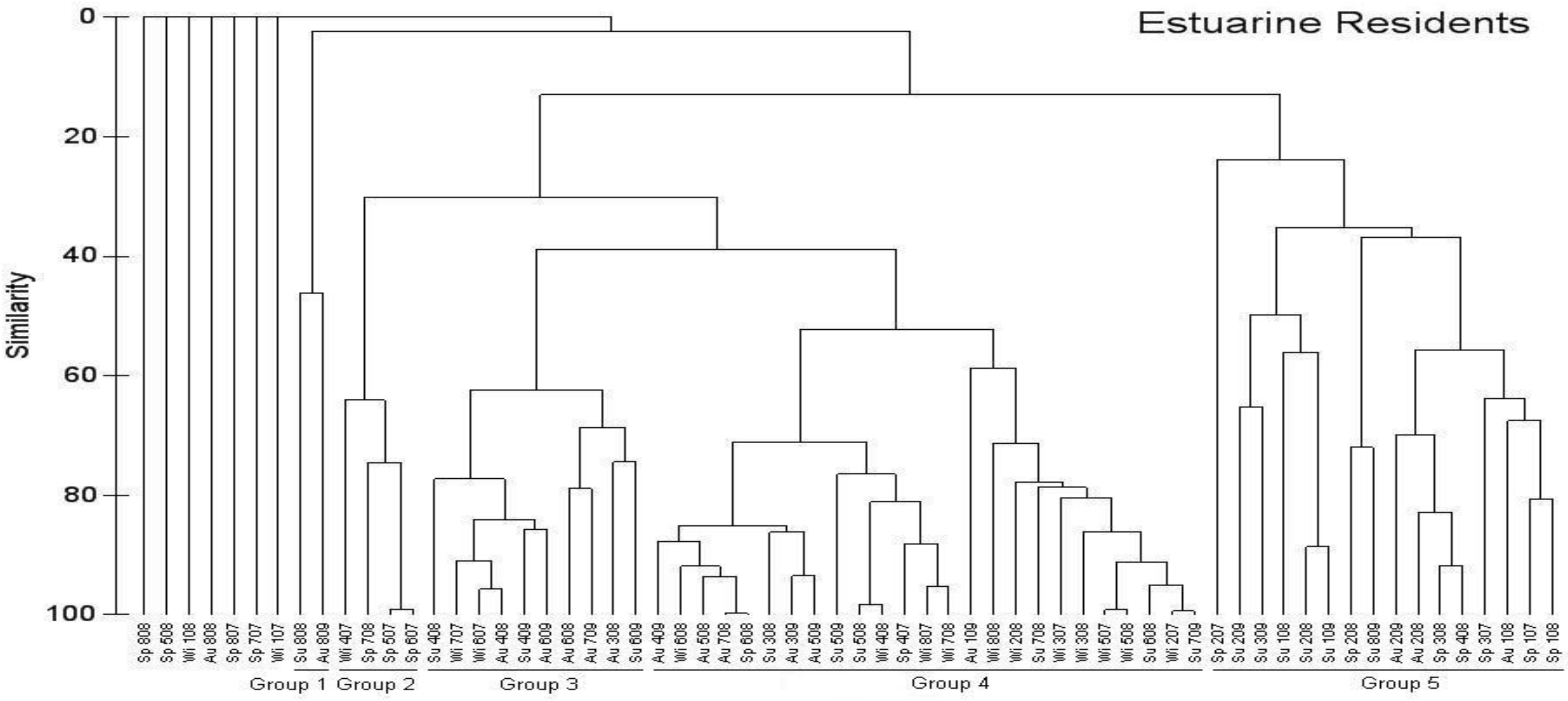

Figure 2.11a: Bray-Curtis dendogram showing percentage similarity measured by density of estuarine residents (category I) in the Sundays Estuary in 2007-2009. Each sample is represented by the season (Sp = Spring, Su = Summer, Au = Autumn, Wi = Winter), followed by a two letter code; the first letter is the site code (1-10), the second is the year code ('07 = 2007, '08 = 2008, '09 = 2009).

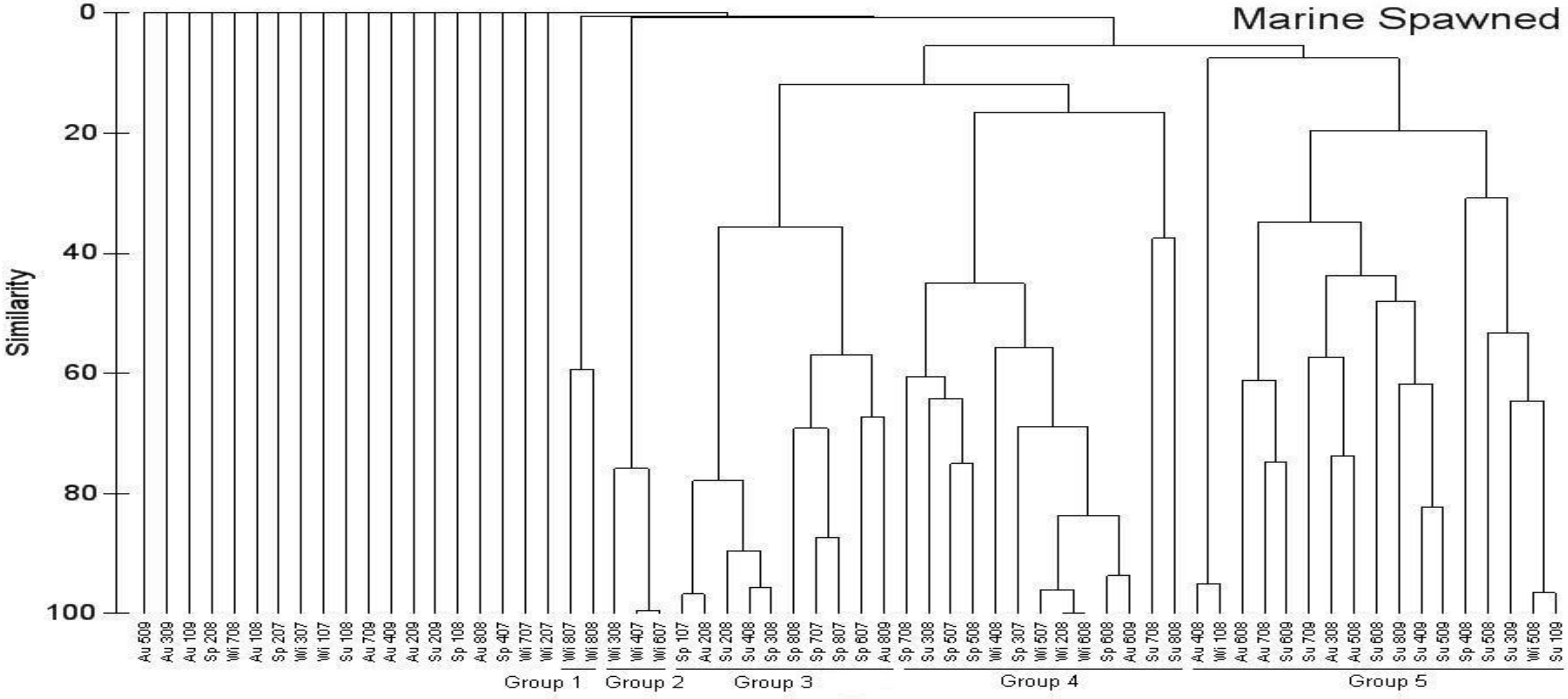

Figure 2.11b: Bray-Curtis dendogram showing percentage similarity measured by density of marine spawned species (categories II, III, IV and V) in the Sundays Estuary in 2007-2009. Each sample is represented by the season (Sp = Spring, Su = Summer, Au = Autumn, Wi = Winter), followed by a two letter code; the first letter is the site code (1-10), the second is the year code (’07 = 2007, ’08 = 2008, ’09 = 2009).

Table 2.9: ANOSIM and SIMPER test results for estuarine resident and marine spawned species in the Sundays Estuary.

Factor	**ANOSIM**		**SIMPER**	
Seasons	*P*	R - Statistic	Estaurine resident species (% contribution)	Marine spawned species (% contribution)
Winter - Spring	<0.01	0.39	*Gilchristella aestuaria* (34.0) *Caffrogobius gilchristi* (22.3) *Psammogobius knysnaensis* (2.67)	*Myxus capensis* (18.9) *Rhabdosargus holubi* (8.0) *Mugil cephalus* (2.5)
Winter - Summer	<0.01	0.26	*Gilchristella aestuaria* (32.8) *Caffrogobius gilchristi* (16.1) *Omobranchus woodi* (14.3)	*Liza dumerilii* (10.1) *Liza tricuspidens* (3.5) *Rhabdosargus holubi* (2.8)
Winter - Autumn	<0.01	0.21	*Gilchristella aestuaria* (48.7) *Caffrogobius gilchristi* (15.7) *Glossogobius callidus* (7.6)	*Liza dumerilii* (6.7) *Pomadasys commersonnii* (4.5) *Myxus capensis* (3.6)
Spring - Summer	<0.01	0.22	*Gilchristella aestuaria* (27.9) *Caffrogobius gilchristi* (19.8) *Omobranchus woodi* (13.1)	*Myxus capensis* (10.0) *Liza dumerilii* (8.6) *Rhabdosargus holubi* (3.8)
Spring - Autumn	<0.01	0.22	*Gilchristella aestuaria* (38.3) *Caffrogobius gilchristi* (19.9) *Glossogobius callidus* (6.1)	*Myxus capensis* (13.4) *Liza dumerilii* (5.6) *Rhabdosargus holubi* (4.8)
Summer - Autumn	>0.05	0.06	*Gilchristella aestuaria* (34.0) *Caffrogobius gilchristi* (17.1) *Omobranchus woodi* (12.8)	*Liza dumerilii* (10.5) *Myxus capensis* (3.1) *Liza tricuspidens* (2.5)

5. DISCUSSION

Water temperature showed seasonal variation and had the greatest influence on the larval fish assemblage of the estuary probably as a result of warmer temperatures coinciding with the breeding season for most coastal fishes. Larval fish densities and species diversity was highest in the summer seasons. This pattern is characteristic for South African estuaries (Strydom *et al*. 2003, Montoya-Maya & Strydom 2009) and estuaries worldwide (Neira *et al*. 1992, Ramos *et al*. 2006). Summer peaks in catches coincide with peaks in primary and secondary production and with peaks in recruitment for most fish species (Whitfield & Marais 1999, Hagan & Able 2003).

Salinity zones play an important role in the structuring of species density in estuaries (Strydom *et al*. 2003). In the present study, highest mean density occurred in the euhaline zone. This is predominantly due to the high densities of the estuarine residents *Gilchristella aestuaria, Omobranchus woodi* and *Caffrogobius gilchristi*.

Typically, highest mean densities of larval fish occur in the mesohaline zone of most estuaries due to its association with the river-estuary interface (REI), this being an area of high primary and secondary productivity (Wooldridge & Bailey 1982, Jerling & Wooldridge 1991, Snow *et al*. 2000, Strydom *et al*. 2003). This anomalous finding of highest larval fish density in the euhaline zone may be related to water quality problems in the low salinity waters of the estuary as has been highlighted in recent studies (N. Strydom pers. comm.). High mean larval fish density in the euhaline zone also corresponds with highest mean zooplankton density (primarily due to the copepod *Acartia longipatella*) that was found in this salinity zone.

Catches of larval fishes in this study (23 taxa representing 12 fish families) was slightly higher than that recorded in the estuary by Harrison & Whitfield (1990) (18 taxa representing 10 fish families). In other warm-temperate estuaries including the Kromme Estuary (Strydom & Whitfield 2000) and Breede Estuary (Montoya-Maya & Strydom 2009) 29 and 27 taxa were recorded. Typically a decrease in the number of taxa is found in cool-temperate estuaries, noted by Montoya-Maya & Strydom (2009) in the Olifants Estuary where 12 taxa were recorded. The number of taxa typically increases along the east coast of South Africa with an example of 40 taxa recorded in the Nxaxo-Ngqusi Estuary on the subtropical-warm temperate boundary (Wasserman *et al*. 2010) South African estuaries are typically characterized by having low species diversity and a dominance by relatively few species (Whitfield 1994b). Similar trends were found for the larval fish assemblage in the Sundays Estuary in the present study. The families Clupeidae, Gobiidae and Blenniidae dominated the estuary together contributing for 92% of the total catch. Analogous family dominance has been found in estuaries worldwide (Neira & Potter 1992, Marques *et al*. 2006). The three dominant taxa, *G. aestuaria* (59.2%), *C. gilchristi*

(19%) and *O*. *woodi* (10%) together comprised more than 88% of the Sundays Estuary larval fish community. This high dominance of estuary-resident species of larval fish is typical for permanently open estuaries in South African and temperate Australia (Melville-Smith & Baird 1980, Harrison & Whitfield 1990, Neira *et al*. 1992, Harris & Cyrus 2000, Strydom *et al*. 2003). The dominant family of estuarine-dependents was Mugilidae, also found in the Kowie and Great Fish estuaries by Whitfield *et al*. (1994) and in the south and west coast estuaries by Montoya-Maya & Strydom (2009). In the Sundays Estuary this family was primarily represented by the species *Liza dumerilii*. Other species contributing to the catch are *Myxus capensis*, *Psammogobius knysnaensis*, *Pomadasys commersonnii*, *Glossogobius callidus* and *Rhabdosargus holubi* also found by Harrison & Whitfield (1990) and Strydom *et al*. (2003).

Seasonal fluctuations in larval fish species density and diversity was recorded in the Sundays Estuary, with highest mean density and diversity occurring in summer. *Gilchristella aestuaria*, *C*. *gilchristi*, *O*. *woodi*, *L*. *dumerilii* and *G*. *callidus* were most abundant in summer. Harrison & Whitfield (1990) also measured highest densities of *G*. *aestuaria* in summer, corresponding to the peak in the main spawning period for this species. These peaks in productivity are associated with lower salinities which trigger spawning of this species (Strydom *et al*. 2002). Past studies have found that high densities of *G*. *aestuaria* are found in areas of low salinity and in freshwater rich systems (Strydom *et al*. 2002, Pattrick *et al*. 2007). In the Swartkops Estuary, Melville-Smith (1978) recorded *C*. *gilchristi* in spring, with large numbers occurring throughout the summer season. Similarly, *C*. *gilchristi* was found to be most abundant in early spring to late summer in the present study. *Rhabdosargus holubi* occurred in highest densities in summer (Harrison & Whitfield 1990) in the Sundays

Estuary with a decline in densities in winter in the Swartkops Estuary (Melville-Smith 1978). However, in the present study, highest densities (although not highly abundant) of *R*. *holubi* were recorded in spring.

Zooplankton standing stock in the Sundays Estuary attains highest biomass in summer (Wooldridge & Bailey 1982). This is primarily due to the abundance of the dominant copepods *Acartia longipatella* and *Pseudodiaptomus hessei* (see chapter 3). Therefore, the seasonal fluctuations positively correlate to copepod abundance, increasing potential growth and survival of larval fish (Harrison & Whitfield 1990).

Highest larval fish diversity was found in the oligohaline zone and in the upper reaches of the estuary (site 8). SIMPER revealed that this high diversity was attributed to high densities of *G*. *aestuaria*, *G*. *callidus*, *M*. *capensis* and *L*. *dumerilii*. Hilmer and Bate (1990) recorded chlorophyll-*a* and nitrate maxima not only in the mesohaline but also in the oligohaline zone of the Sundays Estuary. Maximum primary productivity in these regions results in elevated zooplankton productivity, particularly copepods (Wooldridge & Bailey 1982, Jerling & Wooldridge 1991). High densities of the copepod *P*. *hessei* were recorded in the upper reaches of the estuary (see chapter 3). Therefore high larval fish diversity in the oligohaline zone may be explained through feeding implications for larval fish such as *G*. *aestuaria*, *G*. *callidus*, *M*. *capensis* and *L*. *dumerilii*.

Gilchristella aestuaria spawn in the upper reaches of open estuaries and larvae extend down into the estuary as they develop. This explains the dominance of *G*. *aestuaria* in the middle stations 3 and 5 and upper reaches (stations 6 and 7) in the Sundays Estuary. Similar spatial distribution of *G*. *aestuaria* was found by Melville-

Smith (1978) and Whitfield (1989b) in the Swartkops and Swartvlei estuaries. Harrison & Whitfield (1990) found largest abundance of *O*. *woodi* and *C*. *gilchristi* in the lower reaches of the estuary. Similar results were found in the present study; however *C*. *gilchristi* also occurred in higher densities in the upper estuary (site 8).

Estuarine resident species (category I) comprised the largest portion of the larval fish assemblage in the Sundays Estuary. The dominance of estuarine resident species in open estuaries was also noted by Strydom *et al*. (2003) and Montoya-Maya & Strydom (2009). The trend of freshwater species being restricted to the upper reaches and marine stragglers to the lower reaches as found by Pattrick *et al*. (2007) in the intermittently open Mngazi Estuary was not as clear in the Sundays Estuary. Estuarine dependent and catadromous species occurred throughout most of the estuary.

A high dominance of preflexion larvae in summer coincides with peaks in spawning of most species. This suggests a high degree of local production occurring in the Sundays Estuary. Highest densities of early juveniles occurred in winter, which may be attributable to grow-out of estuarine resident species (e.g. *G*. *aestuaria*) that make use of the estuary throughout their life cycle. Preflexion larval fish dominated the lower reaches of the estuary, mainly attributable to *C*. *gilchristi* and *O*. *woodi*. There is evidence that these species, which have a marine larval phase, show synchronized hatching that coincides with strong ebb tidal currents in order to be carried into the sea (Whitfield & Marais 1999). A trend of expansion into the middle and upper estuary as larvae develop, is seen. Similar trends were noted by Strydom (2003) where postflexion larvae make their way up into the estuary through active migration and flood tidal movement.

In conclusion, the Sundays Estuary plays an important role as a nursery area in the early life history of many fish species, including marine species as well as estuarine resident species. It is an area of high primary production and an assessment of the larval fish assemblage occurring in the Sundays Estuary facilitates a holistic understanding of the plankton in this estuarine system. An important finding in the present study is the reduction in larval fish density in areas predicted to be high and an increase in larval fish density in the lower reaches of the estuary. Such anomalous findings may be related to water quality problems in the low salinity waters and warrants further study.

6. ACKNOWLEDGEMENTS

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CHAPTER 3

COMPOSITION, ABUNDANCE, DISTRIBUTION AND SEASONALITY OF ZOOPLANKTON IN THE SUNDAYS ESTUARY, SOUTH AFRICA

1. SYNOPSIS

The zooplankton assemblage was studied in the permanently open Sundays Estuary on the south-east coast of South Africa. Seasonal samples were collected between winter 2007 and autumn 2009 at ten sites along the estuary by means of boat-based plankton tows using two modified WP2 nets. Salinity ranged from 1.5 - 36.5 and temperature ranged from 11.6 - 26.8ºC during the study period. A total of 19 taxa were recorded, comprising two phyla, three classes and seven orders. The copepod *Pseudodiaptomus hessei* numerically dominated the zooplankton. The copepods *Acartia longipatella* and *Halicyclops* sp. also contributed significantly to the zooplankton assemblage. Mysids were dominated by *Mesopodopsis wooldridgei* and *Rhopalopthalmus terranatalis*. Among the brachyura, *Hymenosoma orbiculare* larvae and *Paratylodiplax edwardsii* larvae, were prevalent in the estuary. Zooplankton density varied significantly with season, site and salinity zone. Zooplankters were most abundant in summer, with a mean of 3331 ind. m^{-3} in 2008 and 8031 ind. m^{-3} in 2009. Highest densities of the copepod *A. longipatella* occurred in the lower estuary (sites 1 - 3) and *P. hessei* densities peaked in the upper estuary (Sites 8 - 10). Highest zooplankton density occurred in the euhaline zone largely due to the high density of *A. longipatella*. The site closest to the mouth (site 1) supported the highest diversity of zooplankton. These patterns in zooplankton density and diversity were the result of the combined influence of salinity, temperature, freshwater inflow and possibly chlorophyll-*a* concentrations in the Sundays Estuary.

2. INTRODUCTION

The distribution of zooplankton in estuaries is spatially and temporally heterogeneous due to the highly dynamic conditions occurring in these systems (Downing *et al*. 1987, Schlacher & Wooldridge 1995, Kibirige & Perissinotto 2003). Due to this heterogeneity in community structure longer term studies are required to adequately assess community dynamics of zooplankton in estuarine systems.

Zooplankton dynamics in estuarine, as well as other systems, have for many years been the focus of research worldwide because of the importance of this group as primary consumers in aquatic habitats (Jeffies 1964, Johnston & Lasenby 1981, Coetzee 1981, Fulton 1984, Jerling & Wooldridge 1995a). Internationally, zooplankton studies have focused on distribution and community structure (Fulton 1984, Franz *et al*. 1991), body size patterns (Dodson 1979), behaviour in response to lunar cycles (Gliwiez 1986), diet and predation (Murtaugh 1981, Bremer & Vijverberg 1982, Fenton 1996), mating (Titelman *et al*. 2007) and the effects that zooplankton biomass has on their predators (larval fish) (Thayer *et al*. 1974, Townsend 1983). Likewise, local studies have focused on similar dynamics, including community responses to physical factors such as salinity, sediment type and freshwater inflow (Wooldridge & Callahan 2000, Bursey & Wooldridge 2003, Teske & Wooldridge 2004), feeding studies (Web & Wooldridge 1989, Froneman 2000, Froneman 2001) and the effects of anthropogenic changes on zooplankton communities (Jerling & Cyrus 1999, Jerling 2003, Kruger *et al*. 2005).

One of the most important anthropogenic changes is that of freshwater input into estuaries. The nutrients provided by freshwater is essential for the sustainability of primary and secondary production (Wooldridge & Bailey 1982, Baird & Heymans

1996). Freshwater is one of South Africa's most limited natural resources, which has given rise to the alteration of river flow regimes such as inter-basin water-transfers. Freshwater quality and quantity input seems to be more important than individual environmental variables *per se* in structuring zooplankton communities in cool temperate South Africa (Montoya-Maya & Strydom 2009a). Grange *et al*. (2000) indicated that considerably lower zooplankton biomass occurred in estuaries with a weak salinity gradient compared to estuaries having pronounced salinity gradients. It has been suggested that temporal zooplankton abundance patterns do not necessarily follow a seasonal cycle but are linked to frequency in inflow of freshwater pulses into an estuary (Wooldridge 1999).

In the Sundays Estuary, Day (1981) regarded the estuary as supporting an impoverished fauna. Day's (1981) studies however focus mainly on the intertidal fauna with limited sampling of the invertebrate community in the water column. Numerous biological studies following Day's (1981) work focused on the distribution, abundance, and feeding patterns of the mesozooplankton (Jerling & Wooldridge 1995a; Jerling & Wooldridge 1995b), trophic relationships within the zooplankton community (Wooldridge & Bailey 1982), predator-prey relationships between the mysid *Rhopalophthalmus terranatalis* and *Mesopodopsis wooldridgei* (Wooldridge & Webb 1988), copepod succession (Wooldridge & Melville-Smith 1979) and the utilization of tidal currents by the zooplankton community (Wooldridge & Erasmus 1980). Zooplankton research in the Sundays Estuary to date has shown that the copepods *Acartia longipatella*, *A. natalensis* and *Pseudodiaptomus hessei* and the mysid shrimps *Mesopodopsis wooldridgei*, *Rhopalophthalmus terranatalis* and *Gastrosaccus brevifissura* are the most common species recorded in the Sundays

Estuary (Wooldridge & Melville-Smith 1979, Wooldridge & Bailey 1982, Jerling & Wooldridge 1995a).

The objective of this study was to describe the spatio-temporal dynamics of the zooplankton assemblage in the Sundays Estuary over a two year period. The specific aims were to identify the species composition, abundance, distribution and seasonality of the zooplankton community in the Sundays Estuary and relate this to the physico-chemical variability within the system.

3. MATERIALS AND METHODS

3.1. Study area

The Sundays Estuary located on the south-east coast of South Africa is a permanently open system. The estuary is part of the Addo Elephant National Park (AENP) rising in the Karoo (south central South Africa). The Sundays Estuary drains a catchment area of 20 729 km^2 before flowing in to Algoa Bay (33 04 3'S, 25 05 1'E) (Beckley 1984). The estuary is approximately 800 m at its widest point near the mouth and narrows at the head of the estuary to approximately 20 m wide (Marais 1981, Whitfield & Harrison 1996). Along the 21 km length of the estuary depth varies from 5 m in the lower and middle reaches to less than 2 m in the upper reaches (Wooldridge & Erasmus 1980, Whitfield & Harrison 1996). Salt marshes and large mud flats are absent (Beckley 1984) and the estuary is characterized by steep banks (about 3-4 m high) with limited marginal vegetation. A small bed of *Zostera capensis* sometimes establishes itself near the mouth and benthic algae dominate the middle reaches (Harrison & Whitfield 1990). High chlorophyll-*a* levels were recorded by Hillmer (1990) in the middle and upper reaches extending into the lower reaches of the estuary during summer. This is due to intense agricultural practices along the river contributing to generally high nutrient levels (Emmerson 1989).

The mean annual rainfall in the region is 323 mm with a mean annual runoff of approximately 200 X 10^6 m^3 (Whitfield & Harrison 1996). The estuary has continuous freshwater inflow (Jerling & Woodridge 1995) supplemented by an inter-basin water-transfer scheme (Perch *et al*. 1995). Linked to the inter-basin water-transfer scheme the estuary displays a full salinity gradient and return flows from the citrus farming practices above the estuary (Wooldridge & Bailey 1982, MacKay & Schumann 1990). Due to the permanent connection with the ocean salinity levels are highest near the mouth of the estuary. Spring tidal range is about 1.2 - 1.5 m and at neap tide 0.1 - 0.3 m (Harrison & Whitfield 1990). Water temperatures range from 13ºC in winter to 26ºC in summer (Jerling & Wooldridge 1991).

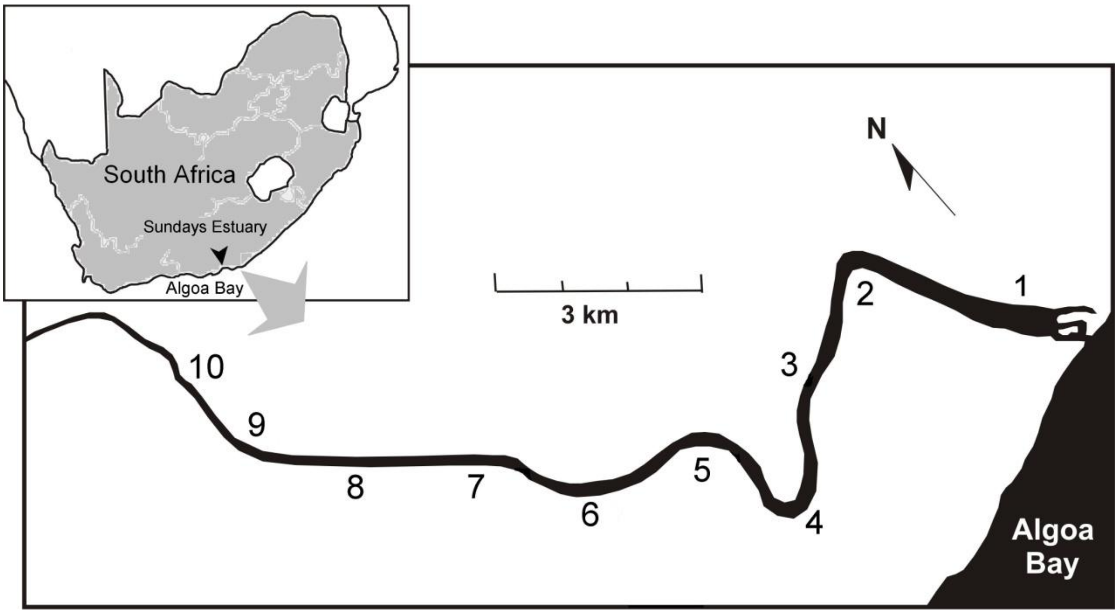

Figure 3.1: Geographical position of the Sundays Estuary showing location of zooplankton sampling stations used in the study.

3.2. Field sampling

Two slightly modified WP2 plankton nets (570 mm mouth diameter and 0.2 µm mesh aperture size) fitted with Kahlsico 005 WA 130 flowmeters (Strydom *et al*. 2003) were used for plankton tows at 8 GPS-fixed sites along the length of the Sundays Estuary. Tows took place at seasonal intervals during July 2007 and 2008, October 2007 and 2008, January 2008 and 2009 and April 2008 and 2009. Nets were simultaneously lowered ca 30 min after nightfall on the new moon and towed alongside the boat for 3 min at a speed of 1-2 knots sampling the subsurface layer (Strydom *et al*. 2003). Samples were preserved on site in 10% buffered formalin and after each tow, flowmeter readings were taken to determine the water volume filtered.

A YSI 6600 multi-parameter instrument was used to obtain vertical temperature (ºC) and salinity (expressed as practical salinity units) profiles at each site. Recordings were conducted at intervals of 0.5 m between the surface and bottom of the water column (Strydom & Whitfield 2000). For analyses integrated values were used. A Secchi disc was used to measure water transparency at each site. All Secchi disc depth measurements were converted into an extinction coefficient (k) using methods described by Dawes (1981) where k = 1.7/D (Secchi depth in cm) (Strydom *et al*. 2003).

3.3. Zooplankton identification

In the laboratory, zooplankton samples were diluted by the addition of freshwater to a predetermined volume (up to 2 L on average). Three sub-samples were drawn off from each well agitated sample using a wide-mouthed pipette (Wooldridge & Melville-Smith 1979). Samples were placed on a tray for counting and identification using a stereo dissecting microscope. Zooplankton abundance was then expressed as the number of individuals of each species per cubic meter of water (Wooldridge & Erasmus 1980).

3.4. Data treatment and analysis

Sample sites were categorised into salinity zones based on an adaptation of the Venice system (Strydom *et al*. 2003). Homogeneity of variance and normality tests were completed for physical and biological data, using a Levene's Test and normal probability plot. Square-root transformations were also used. The data did not conform to parametric test assumptions and therefore non-parametric tests were used.

Zooplankton density was assessed for differences between seasons, sites and salinity zones using the non-parametric Kruskal-Wallis test and between years using the Mann-Whitney U-Test. Seasonal differences between salinity, temperature and turbidity were also assessed using the Kruskal-Wallis test. Multiple linear stepwise regression for parametric data, was used to determine the relationship between environmental variables and zooplankton density. A reduced significance level of $P < 0.01$ was used for this analysis.

PRIMER statistical software package v5.2.9 (Clarke & Warwick 1994) was used to conduct community analysis and to calculate diversity indices (Marglef's species richness and Shannon-Wiener diversity). These were compared between seasons, sites and salinity zones. Zooplankton density data were Log_{10} (x + 1) transformed prior to analysis. A Bray-Curtis similarity matrix and non-metric multi-dimensional scaling (MDS) plot was generated for each dominant copepod and mysid species. Clusters in a dendogram format were assessed using group average hierarchical sorting, and ANOSIM was used to detect differences between groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity between groups. A significance level of $P < 0.05$ was used.

4. RESULTS

4.1. Environmental variability

Seasonal variations in physico-chemical parameters was apparent in the Sundays Estuary. No significant difference was found in mean salinity between seasons (H = 5.60; $P = 0.13$). Salinity ranged from 1.5 - 33.7 in summer, 1.7 - 32.6 in autumn, 1.9 - 36.5 in winter and 2.0 - 32.9 in spring (Figure 3.2). Salinity stratification was evident, with stratification most prominent in summer and autumn at lower estuary sites. A significant difference (H =124.09; $P < 0.01$) was found in mean water temperature between all seasons except spring and autumn. Water temperature ranged from 20.2 - 26.8°C in summer, 18.0 - 23.0°C in autumn, 11.6 - 15.8°C in winter and 20.1 - 22.5°C in spring. Stratification of water temperature was weak, occurring at lower sites in summer and autumn. A significant difference (H = 56.60; $P < 0.01$) in water transparency (k) was found between summer and winter, autumn and winter, autumn and spring and winter and spring (Figure 3.2).

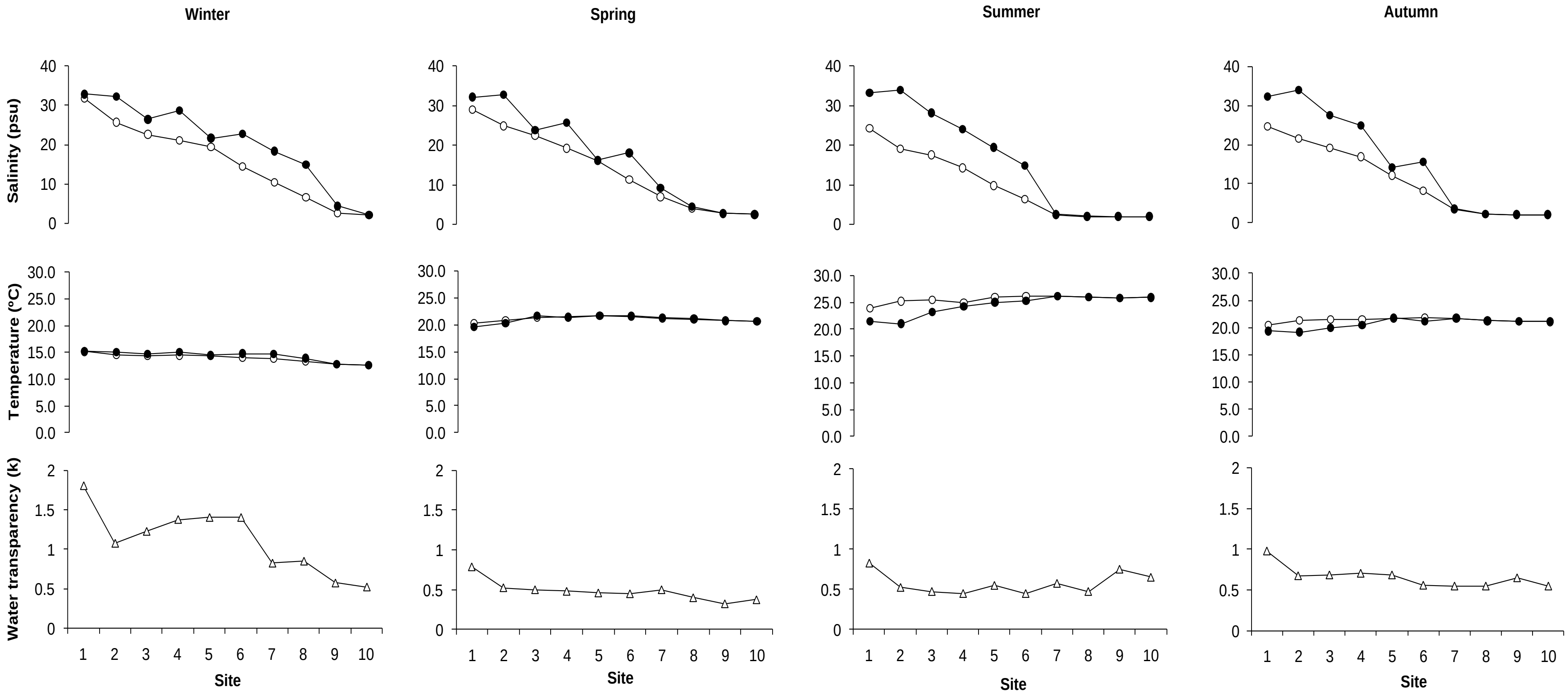

Figure 3.2: Mean surface (o) and bottom (●) salinity values and temperatures and water transparency (two sample sessions per season) for all seasons, at sites in the Sundays Estuary recorded between 2007 and 2009.

4.2. Temporal and spatial trends in species composition

A total of 19 taxa (comprising two phyla, three classes, and seven orders), were represented in the Sundays Estuary. The Copepoda contributed the largest percentage (85.6%) to the zooplankton community in terms of numerical abundance. *Pseudodiaptomus hessei* dominated the assemblage, comprising 35.7%. Other dominant species included the copepods *Acartia longipatella* (32.9%) and *Halicyclops* sp. (17.0%). Mysidacea contributed 7.5% to the community with *Mesopodopsis wooldridgei* dominating (6.5%) this group. Brachyuran species such as *Paratylodiplax edwardsii* larvae (3.3%) and *Hymenosoma orbiculare* (2.5%) larvae also made a noticeable contribution to the overall catch (5.8%) (Appendices I-VIII).

Copepoda were the most important contributors to the summer 2008 (10.7%), summer 2009 (26.9%) and autumn 2009 (23.4%) assemblages. Mysidacea showed highest contribution in spring of 2007 and 2008 (1.9% and 2.0% respectively). Brachyura had the highest contribution to catches in autumn 2008 (2.0%) and autumn 2009 (1.5%) (Figure 3.3).

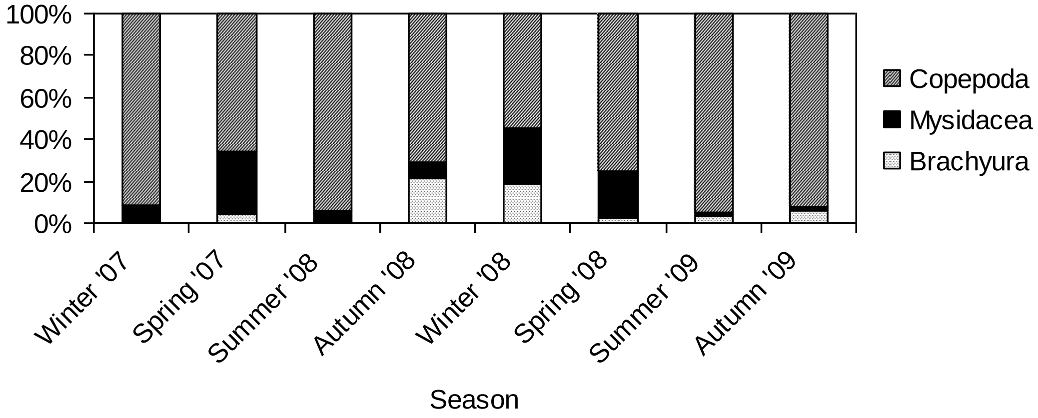

Figure 3.3: Class and order composition (percentage contribution) of zooplankton for all seasons in the Sundays Estuary during the study (2007-2009). ’07 = 2007, ’08 = 2008, ’09 = 2009. Classes and orders contributing < 2% to overall catch are excluded.

Spatial variation in the dominant species contribution to the zooplankton within the estuary was noted, with different species dominating different reaches of the estuary (Figure 3.4). The brachyuran, *P. edwardsii* larvae showed highest percentage contribution in the lower estuary (site 1, 2 and 3). This species was replaced by another brachyuran, *H. orbiculare* larvae in the middle and upper reaches of the estuary (site 4-10). The mysid, *M. wooldridgei* occurred mostly in the lower and middle reaches of the estuary (site 1-6). The copepod, *P. hessei* occurred at all sites with percentage contribution to total zooplankton abundance increasing up the estuary. A clear switch in dominance occurred between *A. longipatella* in the lower estuary (site 2-4), and *Halicyclops* sp., occurring in the upper estuary (site 7-10).

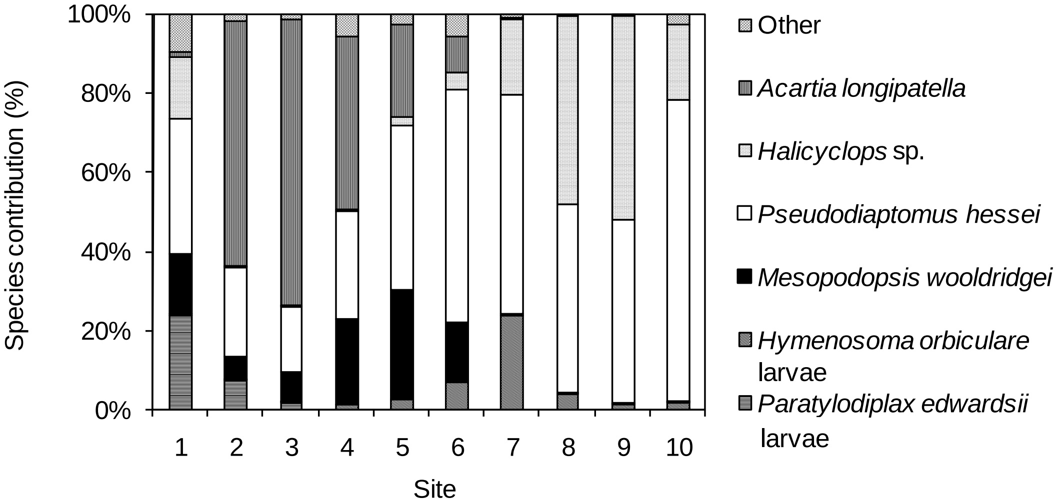

Figure 3.4: Percentage contribution of zooplankton species at sites in the Sundays Estuary between 2007 and 2009. Only species contributing over 2% to the total catch were included. Rare species contributing less than 2% were grouped as "other" as their contribution to overall catch was negligible.

A weak positive regression relationship was evident between all taxa, dominant species and environmental variables. Zooplankton density in the Sundays Estuary showed a significant relationship with temperature ($P < 0.01$). At the community level, salinity and water transparency did not show a significant relationship with zooplankton density. At the species level, *Pseudodiaptomus hessei* was significantly influenced by temperature (*P* < 0.01). *Acartia longipatella*, *Halicyclops* sp., *Mesopodopsis wooldridgei* and *Paratylodiplax edwardsii* larvae had a positive relationship with salinity (*P* < 0.001). Turbidity also showed a significant relationship with *Halicyclops* sp. (*P* < 0.001) (Table 3.1).

Table 3.1: Multiple linear regression statistics for the relationship between zooplankton density and environmental variables (salinity, temperature and water clarity) for all taxa combined and the dominant species in the Sundays Estuary. r^2 = Coefficient of determination; r = correlation coefficient; F = F-statistic; Sa = salinity; Te = temperature, Tu = turbidity (water transparency). Significance level = P < 0.01.

Taxon	r^2	r	F	Significant variable
All taxa	0.74	0.27	4.16	Te*
Dominant species				
Pseudodiaptomus hessei	0.08	0.29	4.76	Te*
Acartia longipatella	0.11	0.33	6.45	Sa**
Halicyclops sp.	0.14	0.37	8.50	Sa***, Tu**
Mesopodopsis wooldridgei	0.18	0.42	11.41	Sa***
Paratylodiplax edwardsii larvae	0.15	0.39	9.45	Sa***

Significance levels: * = *P* < 0.01, ** = *P* < 0.001, *** = *P* < 0.0001

4.3. Temporal and spatial trends in zooplankton density, richness and diversity

Copepod species dominated the zooplankton assemblage. *Pseudodiaptomus hessei* had the highest mean density of 1261 ind. m^{-3}, with *Acartia longipatella* and *Halicyclops* sp. following with 1164 and 601 ind. m^{-3} respectively (Table 3.2). A significant inter-annual difference in zooplankton density was found. This was mainly between autumn 2008 and winter 2008, winter 2008 and autumn 2009 (*P* < 0.01). Similarly, a significant difference in zooplankton density occurred between seasons. Greatest variability occurred between summer and winter and autumn and winter (H = 23.96; *P* < 0.01).

Highest mean zooplankton density occurred in the summer seasons of 2008 with 3331 ind. m^{-3} and again in 2009 with 8031 ind. m^{-3}. Lowest mean zooplankton density occurred in the winter of 2007 with 1484 ind. m^{-3} and in 2008 with 1096 ind. m^{-3} (Table 3.3). A significant difference was found between different sites and zooplankton density ($H = 27.83$; $P < 0.01$). Greatest variability occurred between the lower estuary (site 2, 3) and middle estuary (site 6). Highest density of *A. longipatella* occurred in summer 2009 in the lower estuary (sites 1 - 3). Highest density of *P. hessei* occurred in summer 2008 in the upper estuary (sites 8 -10) (Table 3.3; Figure 3.5). Density of *Mesopodopsis wooldridgei* peaked in spring 2007 in the lower (sites 1 - 3) and middle reaches (sites 4 - 7) of the estuary. Highest density of *Rhopalophthalmus terranatalis* occurred in spring 2008 in the middle reaches (sites 4 - 7) of the estuary (Table 3.3 and Figure 3.6).

The euhaline zone had the highest mean density of zooplankton (10805 ind. m^{-3}) largely due to the high density of *A. longipatella*. This was followed by the oligohaline, polyhaline, mesohaline and hypersaline zones (4163, 3540, 854 and 40 ind. m^{-3} respectively) (Table 3.3). A significant difference between zooplankton densities and salinity zone was found ($H = 38.46$; $P < 0.01$), particularly between the mesohaline and polyhaline, mesohaline and oligohaline and mesohaline and euhaline zones.

Table 3.2: Overall density of the most abundant zooplankton taxa collected in the Sundays Estuary between 2007 and 2009. Species listed constitute 99.8% of the total abundance of all taxa present.

Taxa	Mean density (no. per m^{-3})	Max density (no. per m^{-3})	Percentage of total
Copepoda			
Acartia longipatella	1164	63763	32.9
Halicyclops sp.	601	17951	17.0
Pseudodiaptomus hessei	1261	14109	35.6
Mysidacea			
Gastrosaccus brevifissura	2	106	0.1
Mesopodopsis wooldridgei	231	2522	6.5
Rhopalophthalmus terranatalis	32	436	0.9
Isopoda			
Corallana africana	10	271	0.3
Anomura			
Upogebia africana stage 1	27	940	0.8
Brachyura			
Hymenosoma orbiculare larvae	87	2440	2.4
Paratylodiplax edwardsii larvae	118	2690	3.3

Table 3.3: Mean zooplankton density and maximum density of dominant taxa recorded in different seasons and salinity zones in the Sundays Estuary between 2007 and 2009.

	Density (no. per m^{-3})				
	Mean	Max density *Acartia longipatella*	Max density *Pseudodiaptomus hessei*	Max density *Mesopodopsis wooldridgei*	Max density *Rhopalophthalmus terranatalis*
Season					
Winter '07	1484	6262	1008	402	43
Spring '07	1759	108	3053	2522	261
Summer '08	3331	236	14109	810	58
Autumn '08	2808	52	3889	809	66
Winter '08	1096	387	1735	913	339
Spring '08	2590	8334	4561	1813	436
Summer '09	8031	63763	9228	656	106
Autumn '09	7211	13772	8402	433	79
Salinity Zone					
Hypersaline	40	3	26	6	9
Euhaline	10805	63763	9228	1690	106
Polyhaline	3540	19231	3053	1813	436
Mesohaline	854	108	1891	2522	261
Oligohaline	4163	11	14109	11	5

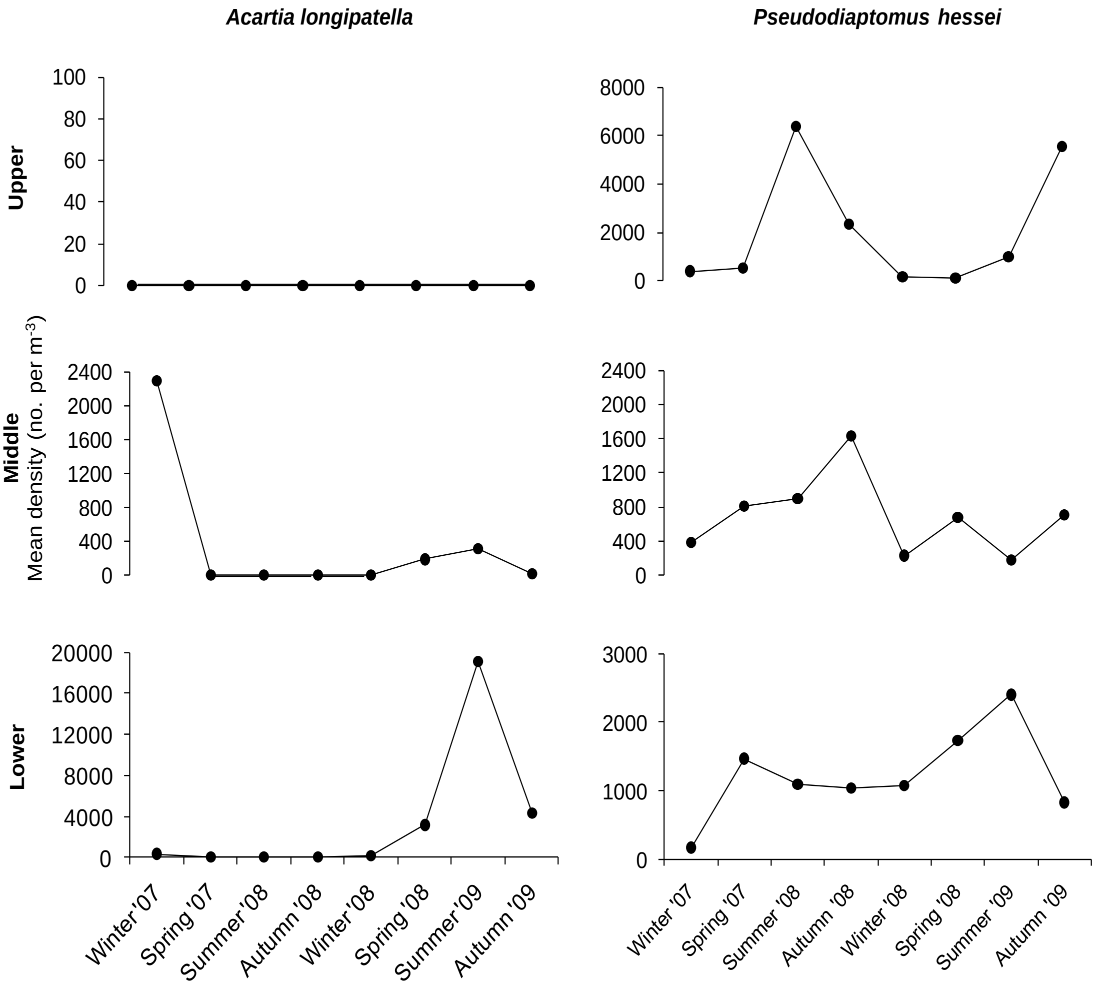

Figure 3.5: Mean density of dominant copepod species *Acartia longipatella* and *Pseudodiaptomus hessei* recorded in different seasons in the lower (sites 1 - 3), middle (sites 4 - 7) and upper (sites 8 - 10) estuary. Note the difference in scale on the y-axis between species. Also note an absence of *A. longipatella* in the upper estuary.

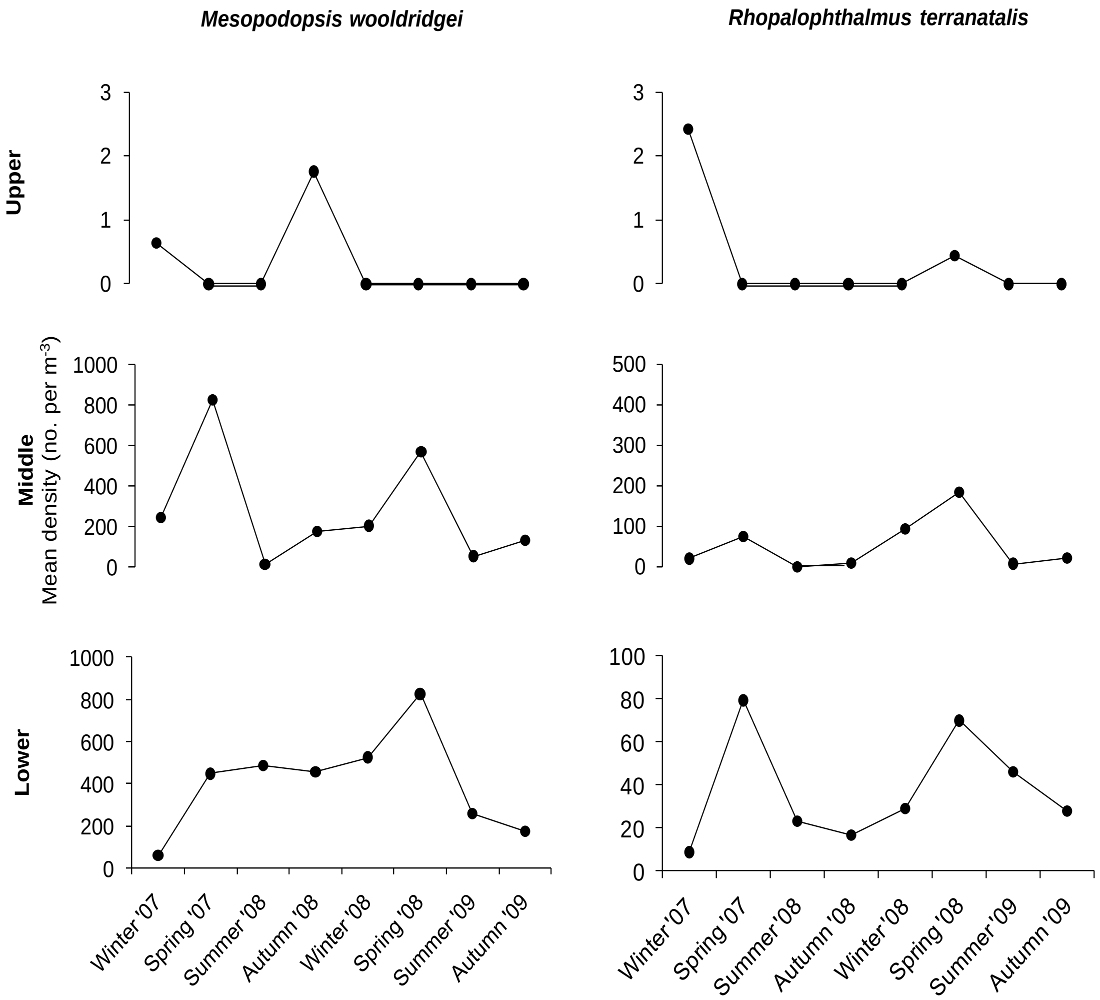

Figure 3.6: Mean density of dominant mysids *Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis* recorded in different seasons in the lower (sites 1 - 3), middle (sites 4 - 7) and upper (sites 8 - 10) estuary. Note the difference in scale on the y-axis between species.

The number of species occurring in the Sundays Estuary ranged from between 11 and 15, with maximum occurring in spring 2007 (15 species) and minimum in the summer and autumn of 2009 (11 species). Also evident was a spatial difference in species richness and diversity. Highest species richness and diversity occurred at site 1 near the mouth (Table 3.4). Compared with other salinity zones, the polyhaline zone (present near the mouth region for the most part of the study) showed highest species diversity followed by the mesohaline zone.

Table 3.4: Species richness index (d) and species diversity index (H’) at sampling sites and salinity zones for the zooplankton assemblage in the Sundays Estuary between 2007 and 2009.

	Species richness (d)	Species diversity (H')
Sites		
1	**2.18**	**1.70**
2	1.31	1.09
3	1.03	0.89
4	1.05	1.29
5	1.19	1.34
6	1.51	1.34
7	1.34	1.09
8	1.05	0.87
9	0.71	0.79
10	1.06	0.73
Salinity zone		
Hypersaline	2.21	1.83
Euhaline	1.88	1.70
Polyhaline	**3.03**	**2.03**
Mesohaline	2.63	1.91
Oligohaline	2.73	1.48

4.4. Community analysis

Cluster analysis grouping indicated a clear pattern associated with the lower, middle and upper reaches of the estuary (Figure 3.7). At 50% similarity two groups were formed. Group 1 contained sites occurring in the lower and middle reaches and group 2 contained sites occurring in the upper reaches of the estuary. The MDS plot showed similar patterns to the cluster analysis, indicating the similarity between the lower and middle estuary sites and the dissimilarity of the upper sites to that of the lower and middle (Figure 3.8).

Species composition of dominant copepods (*Acartia longipatella* and *Pseudodiaptomus hessei*) and mysids (*Mesopodopsis wooldridgei* and *Rhopalophthalmus terranatalis*) in lower, middle and upper reaches using density data was investigated using a community analysis approach (Table 3.5). A significant difference was found between lower and middle and middle and upper reaches of the estuary (ANOSIM). SIMPER analysis revealed high dominance of *A. longipatella* in the lower reaches and *P. hessei* in the upper reaches of the estuary. *Mesopodopsis wooldridgei* contributed to the dissimilarity between lower and upper reaches of the estuary. *Rhopalophthalmus terranatalis* contributed to the dissimilarity between the middle and upper reaches of the estuary (Table 3.5).

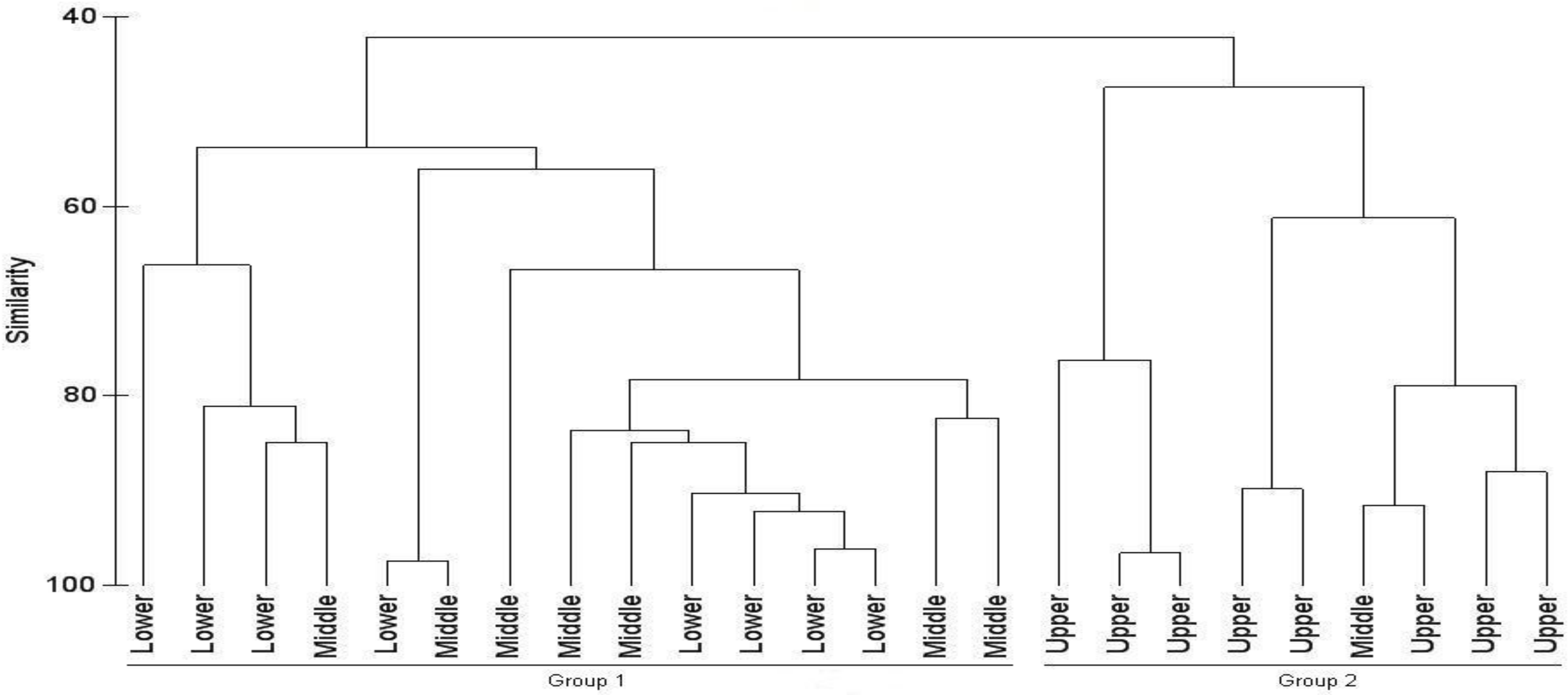

Figure 3.7: Bray-Curtis dendogram showing percentage similarity based on dominant copepod and mysid species composition and abundance in the lower, middle and upper reaches of the Sundays Estuary in 2007-2009.

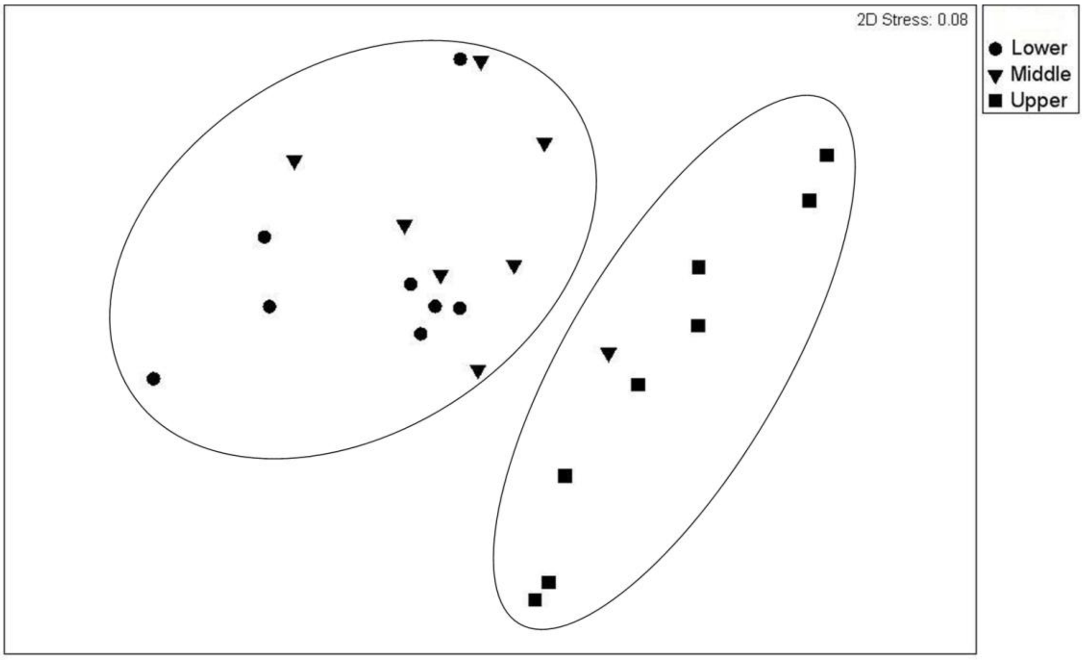

Figure 3.8: Multi-dimensional scaling plot of dominant copepod and mysid species in the lower, middle and upper reaches of the Sundays Estuary (2007-2009).

Table 3.5: ANOSIM and SIMPER test results for dominant copepod and mysid species in the Sundays Estuary.

Factor	**ANOSIM**		**SIMPER**
Sites	*P*	R - Statistic	Dominant species (% contribution)
Lower - Middle	>0.05	0.04	*Acartia longipatella* (51.6) *Pseudodiaptomus hessei* (23.4) *Mesopodopsis wooldridgei* (18.0)
Lower - Upper	<0.01	0.66	*Acartia longipatella* (38.6) *Pseudodiaptomus hessei* (28.4) *Mesopodopsis wooldridgei* (25.8)
Middle - Upper	<0.01	0.50	*Pseudodiaptomus hessei* (39.9) *Mesopodopsis wooldridgei* (28.8) *Acartia longipatella* (19.9) *Rhopalopthalmus terranatalis* (11.4)

5. DISCUSSION

Species of copepods, mysids and the brachyurans numerically dominated the zooplankton assemblage of the Sundays Estuary. The copepods *Pseudodiaptomus hessei*, *Acartia longipatella*, *Halicyclops* sp., the mysids *Mesopodopsis wooldridgei* and *Rhopalopthalmus terranatalis* were common in the catches. These species are also dominant in the zooplankton assemblages of other estuaries in South Africa (Grindley 1981, Wooldridge 1999, Montoya-Maya & Strydom 2009a). Similar reports on copepod community structure from other estuarine systems around the world have been made (Lee & McAlice 1979, Greenwood 1981, Ambler *et al*. 1985).

At a community level, water temperature had the greatest influence on the zooplankton assemblage in the Sundays Estuary. The correlation between temperature and zooplankton production in Eastern Cape estuaries is well documented with the highest values recorded during warmer summer months (Jerling & Wooldridge 1991, Froneman 2001). As in this study, Wooldridge (1999) indicated that in South African estuaries zooplankton density exhibits winter minima and summer maxima. Froneman (2001) and Montoya-Maya & Strydom (2009a) also found peak densities of zooplankton in summer in the Kariega Estuary and selected west coast estuaries respectively. Despite variability in species density across seasons, little variation in the composition of the zooplankton assemblage was found in the present study. Similar findings were made in the Bot Estuary (Coetzee 1985). Grindley (1981) suggested that in general, South African estuaries tend to show little variability in zooplankton composition, due to well-established estuarine populations, except during periods when there is a change in freshwater inflow resulting in shifts in the contribution of marine or estuarine species.

Clear seasonal and spatial variations between the dominant copepods *A*. *longipatella* and *P*. *hessei* was evident in the present study. *Acartia longipatella* has previously been found to be most abundant in winter and spring (Wooldridge & Bailey 1982). Similar trends were found in the early periods of this study with highest densities of *A*. *longipatella* occurring in winter 2007. However, maximum density recorded during the present study occurred in summer 2009. Spatially *A*. *longipatella* showed similar distribution to that recorded by Wooldridge & Melville-Smith (1979), with highest densities occurring in the lower estuary where higher salinities occur. Therefore the temporal and spatial distribution of *A*. l*ongipatella* is regulated largely by temperature (low) and salinity (high), resulting in seasonal succession, also noted by Wooldridge & Callahan (2000). When suitable conditions are present, such as those mentioned above, dormant eggs of *A*. *longipatella* present in the substrate hatch resulting in density peaks (Wooldridge & Callahan 2000). At least 24 taxa are known to produce resting eggs (Greenwood 1981, Grice & Marcus 1981, Marcus 1984, Uye 1985, Sullivan & McManus 1986, Ianora & Santella 1991). *Pseudodiaptomus hessei* was present during all seasons and showed highest density in summer in the upper reaches of the estuary. Wooldridge & Bailey (1982), found *P*. *hessei* to be present in high numbers during all seasons and Jerling & Wooldridge (1995a) found densities of this species peaked in summer. It has been argued that the change in season has no obvious effect on *P*. *hessei* population abundance, but rather that, river flow, in some way, regulates temporal abundance patterns (Wooldridge 1999). Although lowest population densities are linked to periods of low freshwater inflow, abundance levels also decline sharply due to floods. Population recovery is rapid (weeks), increasing again to very high levels following a freshwater pulse event. Peaks in the distribution of chlorophyll-*a* in the Sundays Estuary have been found to correspond with phytoplankton blooms (Jerling & Wooldridge 1995a). Chlorophyll-*a* has been shown to play an important role in the distribution of *P*. *hessei* due to this species feeing on phytoplankton occurring in these regions of high production (Jerling & Wooldridge 1995a). Distinct hydrodynamic regions of differing chlorophyll-*a* levels were identified by MacKay & Schumann (1990) and Hilmer & Bate (1990), showing low values near the mouth and high values in the middle and upper reaches of the Sundays Estuary. Therefore, chlorophyll-*a* displayed a clear salinity-related distribution also found by Wooldridge & Callahan (2000) in the Kromme Estuary. In the present study highest *P*. *hessei* densities were found to correspond with these high chlorophyll-*a* regions, increasing in density towards the upper estuary.

Acartia natalensis was not found in the present study. However, in previous studies, this species was not abundant in the estuary and only occurred occasionally (Wooldridge & Melville-Smith 1979, Wooldridge & Bailey 1982). *Halicyclops* sp. was found in high densities in summer and autumn 2009 in the lower salinity zone in the upper estuary. This species was not found at high densities in any other study conducted in the Sundays Estuary. The spatial patterns shown between *A*. *longipatella* and *Halicyclops* sp. were similar to that seen in previous studies between *A*. *longipatella* and *A*. *natalensis* (Wooldridge & Melville-Smith 1979, Wooldridge & Bailey 1982, Jerling & Wooldridge 1995a). Together with the absence of *A*. *natalensis* in the present study, this may be evidence that this species may have been replaced by *Halicyclops* sp in the system.

In previous studies, mysids rarely contributed less than 70% and in most cases exceeded 90% of the total standing stock of the zooplankton in the Sundays Estuary (Wooldridge & Bailey 1982). In the present study, biomass values were not assessed however mysid abundance levels suggest that the correspondent biomass values would be less than 70% of the total. This may be explained by the sampling technique used during the study whereby only the near surface waters were sampled, where mysids showed relatively low densities (Wooldridge 1999), in comparison to subsurface and mid-depth waters sampled in previous studies (Jerling & Wooldridge 1995a, Wooldridge & Bailey 1982). *Mesopodopsis wooldridgei* was the most abundant mysid species in the Sundays Estuary, occurring in high densities during spring in the lower and middle reaches of the estuary. The largest mysid encountered in southern African estuaries, *R. terranatalis*, showed similar seasonal and spatial trends to *M. wooldridgei*, with highest abundance also occurring in spring in the middle reaches of the estuary. Wooldridge (1999) stated that these mysid species do occur in discrete but overlapping zones along estuarine axial gradients and that salinity *per se* does not appear to be the major factor regulating spatial zonation. Other factors noted by Wooldridge (1999) such as predation, play an important role and is the major factor leading to high densities of *M. wooldridgei* occurring nearer to the tidal inlet of the Sundays Estuary compared to *R. terranatalis* in the present study. Predation by *R. terranatalis* (particularly adults) is largely on newly emerged *M. wooldridgei* juveniles from the brood pouch and this leads to low recruitment into the *M. wooldridgei* population where *R. terranatalis* is abundant (Wooldridge & Webb 1988). Jerling & Wooldridge (1995a), found evidence of overlap in abundance in the middle reaches of the estuary, leading to resource partitioning between *M. wooldridgei* and *R. terranatalis*. *Gastrosaccus brevifissura* was not found in high densities in the estuary. Similarly, Jerling & Wooldridge (1995a) found *G. brevifissura* to seldom exceed 10 individuals per m^3. The brachyurans, *Hymenosoma orbiculare* larvae and *Paratylodiplax edwardsii* larvae, made a considerable contribution to the zooplankton assemblage of the Sundays Estuary. Both species occurred in highest densities in autumn. Large spatial differences were found between these two brachyuran species, with *P*. *edwardsii* larvae occurring in highest densities in the lower estuary, being replaced by *Hymenosoma orbiculare* larvae in the middle and upper reaches.

In the present study, highest mean density of zooplankton occurred in the euhaline zone. Typically highest mean densities of zooplankton occur in the oligohaline and mesohaline zones (Wooldridge 1999, Montoya-Maya & Strydom 2009a) due to its association with the river-estuary interface (REI) region (Bate *et al*. 2002). This is a highly productive zone (Hilmer & Bate 1990) supporting rich phytoplankton (Snow & Adams 2006) and high densities of larval fishes (Strydom *et al*. 2003, Montoya-Maya & Strydom 2009b). However, in the present study the high densities of zooplankton in the euhaline zone may be explained by high densities of *A*. *longipatella* in this zone and the relatively low densities of mysids sampled from the mesohaline zone in comparison to previous studies (Wooldridge & Bailey 1982, Jerling & Wooldridge 1995a). However water quality problems associated with eutrophication in the low salinity waters of the estuary, as found by N. Strydom (pers. comm.) may also explain this deviation from previous studies.

In conclusion, the Sundays Estuary shows strong seasonal and spatial trends in zooplankton species density and diversity. These trends are regulated by temperature, salinity and freshwater inflow. Due to the high seasonal and spatial heterogeneity in the zooplankton community, longer term studies are required to adequately assess the trends in zooplankton community dynamics in the estuary. In addition the assessment of the zooplankton assemblage occurring in the Sundays Estuary facilitates a holistic understanding of the primary consumer tier of this estuarine ecosystem.

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CHAPTER 4

LARVAL FISH DIET, FEEDING GUILDS AND ZOOPLANKTON PREY SELECTION IN THE SUNDAYS ESTUARY, SOUTH AFRICA

1. SYNOPSIS

The zooplankton and larval fish dynamics were investigated in the permanently open Sundays Estuary on the south-east coast of South Africa. Seasonal samples were collected between winter 2007 and autumn 2009 at eight sites along the estuary by means of boat-based plankton tows using two modified WP2 nets. Salinity ranged from 1.5 - 36.5 and temperature ranged from 11.6 - 26.8ºC. Mean density of both larval fishes and zooplankton showed similar seasonal and spatial trends. Gut contents analyses were performed on five larval fish species namely *Gilchristella aestuaria* (estuarine resident species), *Pomadasys commersonnii*, *Monodactylus falciformis*, *Rhabdosargus holubi* (estuarine dependent species) and *Myxus cap*ensis (catadromous species). Methods used were percentage frequency of occurrence (%F), percentage numerical occurrence (%N) and percentage volume (%V). A total of 296 stomachs were examined, 271 of which contained food. Copepod eggs constituted the largest volume of the prey consumed by *G*. *aestuaria*. The copepod *Pseudodiaptomus hessei* was frequently eaten in large numbers and formed the largest volume of *P*. *commersonnii's* diet. For both *M*. *falciformis* and *M*. *capensis*, chironomid larvae were often eaten in large numbers and constituted the largest volume of the diet. The most numerous prey item and that which formed the largest volume in the diet of *R*. *holubi* was the amphipod *Corophium triaenonyx*, with *P*. *hessei* been the most frequently consumed prey item. Seasonal and spatial variability in the diet of larval fish occurred in the estuary. Larval fish also showed changes in diet at different stages of development and different salinity zones. An analysis of feeding guilds indicated that pelagic prey species constituted the largest

volume of the diet of *G*. *aestuaria* and *P*. *commersonnii*. *Monodactylus falciformis*, *M*. *capensis* and *R*. *holubi* consumed large volumes of bentho-pelagic prey species. Larval fish prey selection of pelagic prey species indicated that all larval fish species selected for *P*. *hessei*. *Myxus capensis* and *R*. *holubi* also selected for the copepod *Halicyclops* sp. *Myxus capensis* and *R*. *holubi* showed the largest diversity in diet. The majority of the larval fish species showed diversity in their diet. However, for all species only a few prey items provided the bulk of the diet.

2. INTRODUCTION

Specific larval fish diet is initiated by the nutritional status of the mother through the influences of the chemical composition of the yolk sac material which serves as endogenous food for the metamorphosing larvae (Dabrowski 1984). After the yolk reserves are practically exhausted, larvae start exogenous feeding in order to continue development and growth (Parra & Yufera 2000). “First feeding” has a large influence on total growth and development of the larval fish. The primary sources of mortality in larval fish are starvation and predation (Hunter 1972) with the small larval stages being the most vulnerable (Newton 1996). Parra (2000) indicated that prey availability affects the duration of the transition period before growth commences, causing delays in the onset of growth. Therefore prey concentration affects growth rate and consequently, the duration of the larval period when vulnerability to predators is high (Houde & Schekter 1980). Therefore good prey patches for first feeding larvae is vital. Lower growth rates, poor condition and consequently high mortalities of larvae are a consequence of inadequate and inappropriate prey organisms in the vicinity of the larvae (Cushing & Horwood 1994, Welker *et al*. 1994, Puvanendran & Brown 1999).

Larval fish make extensive use of zooplankton species during at least one of their life-history stages (Thayer *et al*. 1974) mostly due to the nutritional value of the fatty acids contained in the zooplankton (Dabrowski 1984). When compared to benthic invertebrate groups, zooplankton often contain a higher energy content (Whitfield 1985). Therefore zooplankton often form an important link in the transfer of energy from producers to aquatic carnivores (Thayer *et al*. 1974). Most larval fish species feed on similar prey (nauplii and early copepodite stages of calanoid copepods) throughout much of the larval phase (Houde & Taniguchi 1979; Whitfield 1985; Pepin & Penney 2000). Protozoa and diatoms can be important prey items when prey availability may limit growth and survival, particularly for first feeding larvae, (Houde & Schekter 1980).

The diet of larval fishes has been particularly well studied in marine (Houde 1978, Houde & Schekter 1980, Cahu & Zambonino Infante 2001) and estuarine environments worldwide (Thayer *et al*. 1974, Kjelson *et al*. 1975, Townsend 1983). Many of these studies have focused specifically on the diet of individual species of larval fish (Puvanendran & Brown 1999, Parra & Yufera 2000), prey selection (Rajasilta & Vuorinen 1983), larval fish feeding and the impact on zooplankton density (Pepin & Penney 2000), and physical functioning required for larval fish during first feeding and early growth (Dabrowski 1984, Osse *et al*. 1997). In South Africa, a number of fish dietary studies have been undertaken (Masson & Marais 1975, Whitfield & Harrison 1996, Talbot & Baird 1985, Hecht & Van der Lingen 1992, Schlacher & Wooldridge 1996, Froneman & Vorwerk 2003). However, very few studies have focused on larval fish diet or prey selection. Whitfield (1985) studied the role of zooplankton in the feeding ecology of fish fry and Wooldridge & Bailey (1982) conducted a study on the euhaline zooplankton of the Sundays Estuary with notes on trophic linkages with larval fish of some species. Besides these two works, there is a lack of larval fish dietary studies in South Africa. An investigation into the feeding of larvae of important fish species in the Sundays Estuary was necessary for understanding of overall resource utilization within the estuary. The specific aims of the study were to assess the relationship between the two major components of the plankton through abundance and distribution trends and information on diet, guild feeding and prey selection of selected larval fishes in the estuary. Larvae of *Gilchristella aestuaria* (Clupeidae), *Pomadasys commersonnii* (Haemulidae), *Monodactylus falciformis* (Monodactylidae), *Rhabdosargus holubi* (Sparidae) and *Myxus capensis* (Mugilidae) were used for these analyses.

3. MATERIALS AND METHODS

3.1. Study area

The Sundays Estuary rises in the Karoo (south central South Africa), draining a catchment area of 20 729 km^2 before flowing in to Algoa Bay (33 04 3’S, 25 05 1’E) (Beckley 1984). It is a permanently open system on the south-east coast of the country. The Sundays Estuary forms part of the Addo Elephant National Park (AENP) and is characterized by steep banks (about 3-4 m high) with limited marginal vegetation. Salt marshes and large mud flats are absent (Beckley 1984) and a small bed of *Zostera capensis* sometimes establishes itself near the mouth and benthic algae dominate the middle reaches (Harrison & Whitfield 1990). Submerged macrophytes such as *Potamogeton crispus* occur at the head of the estuary while *Phragmites australis* occurs in the upper reaches. The estuary is approximately 800 m at its widest point near the mouth and narrows at the head of the estuary to approximately 20 m wide (Marais 1981, Whitfield & Harrison 1996). The estuary is channel-like along the majority of its 21 km length with a depth variation from 5 m in the lower and middle reaches to less than 2 m in the upper reaches (Wooldridge & Erasmus 1980, Whitfield & Harrison 1996). Hilmer (1990) recorded high chlorophyll-*a* levels in the middle and upper reaches extending into the lower reaches of the estuary during summer. This is due to intense agricultural practices along the river contributing to generally high nutrient levels (Emmerson 1989).

The Sundays Estuary displays a full salinity gradient linked to the inter-basin water-transfer scheme and return flows from the citrus farming practices above the estuary (Wooldridge & Bailey 1982, MacKay & Schumann 1990). The estuary has continuous freshwater inflow (Jerling & Wooldridge 1995) supplemented by an inter-basin water-transfer scheme (Pech *et al*. 1995). The mean annual rainfall in the region is 323 mm with a mean annual runoff of approximately 200 X 10^6 m^3 (Whitfield & Harrison 1996). Salinity levels are highest near the mouth of the estuary due to the permanent connection with the ocean. Water temperatures range from 13ºC in winter to 26ºC in summer (Jerling & Wooldridge 1991). Spring tidal range is about 1.2 - 1.5 m and at neap tide 0.1 - 0.3 m (Harrison & Whitfield 1990).

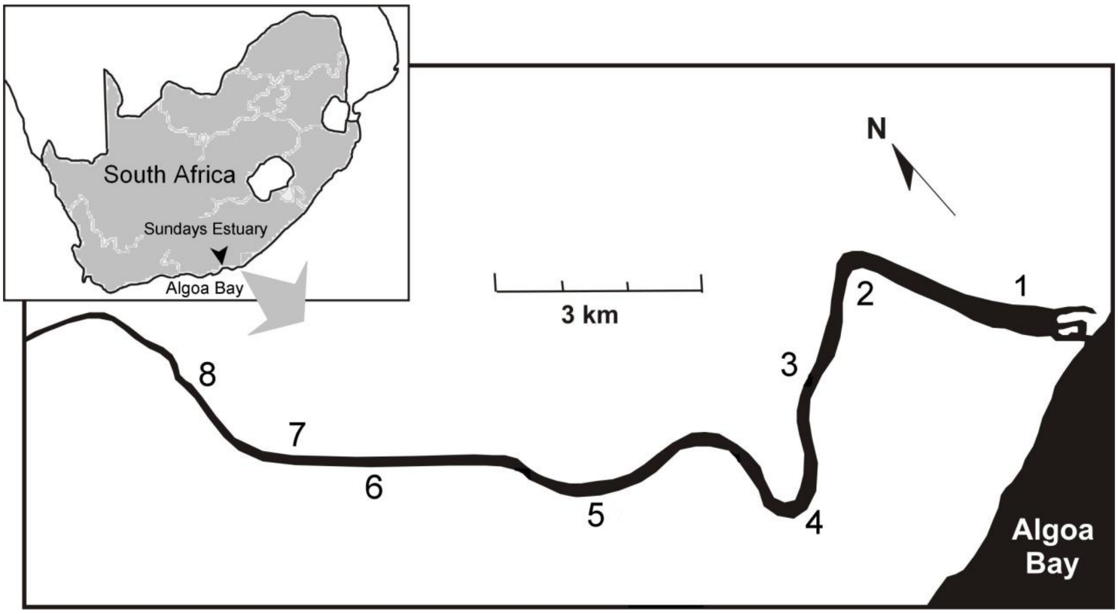

Figure 4.1: Geographical position of the Sundays Estuary showing location of the sampling stations used in the study.

3.2. Field sampling

Sampling commenced ca 30 min after nightfall on the new moon using two slightly modified WP2 plankton nets (570 mm mouth diameter and 0.2 µm mesh aperture size) fitted with Kahlsico 005 WA 130 flowmeters (Strydom *et al*. 2003). Plankton tows took place at 8 GPS-fixed sites along the length of the Sundays Estuary at seasonal intervals during July 2007 and 2008, October 2007 and 2008, January 2008 and 2009 and April 2008 and 2009. Nets were simultaneously lowered and towed alongside the boat for 3 min at a speed of 1-2 knots sampling the subsurface layer (Strydom *et al*. 2003). Samples were preserved on site in 10% buffered formalin and after each tow, flowmeter readings were taken to determine the water volume filtered.

A Secchi disc was used to measure water transparency at each site and these measurements were converted into an extinction coefficient (k) using methods described by Dawes (1981) where k = 1.7/D (Secchi depth in cm) (Strydom *et al*.

2003). Vertical temperature (ºC) and salinity (expressed as practical salinity units) profiles were obtained at each site using a YSI 6600 multi-parameter instrument. Recordings were conducted at intervals of 0.5 m between the surface and bottom of the water column (Strydom & Whitfield 2000).

3.3. Laboratory and gut content analysis

In the laboratory, zooplankton samples were diluted by the addition of freshwater to a predetermined volume (up to 2 L on average). Three sub-samples were drawn off from each well agitated sample using a wide-mouthed pipette (Wooldridge & Melville-Smith 1979). Samples were placed on a tray for counting and identification using a stereo dissecting microscope. Zooplankton abundance was then expressed as the number of individuals of each species per cubic meter of water (Wooldridge & Erasmus 1980).

Larval fishes were first sorted from plankton samples. Identification was completed to the lowest possible taxon using Smith & Heemstra (1986), Neira *et al*. (1998) and Leis & Carson-Ewart (2000) amongst others. Larvae were measured to the nearest 0.1 mm body length (BL) using a eyepiece micrometer for larvae <10 mm and Vernier callipers for larger specimens. This represents notochord length in preflexion and flexion larvae, and standard length in postflexion larvae (Neira *et al*. 1998). Larvae that were positively identified were grouped into estuary-dependence categories as defined by Whitfield (1998).

Specimens for gut content analysis were obtained from a two year plankton survey in the Sundays Estuary (Chapters 2 and 3). Gut content analysis was performed on postflexion stages of *Gilchristella aestuaria* (category Ia) due to the difficulty in dissection of younger stages, *Pomadasys commersonnii*, *Monodactylus falciformis*, *Rhabdosargus holubi* (category IIa) and *Myxus capensis* (category V). All available specimens for each of the above species were analysed, except for the more abundant species (*G. aestuaria* and *M. capensis*) where a maximum of 20 individuals per season (where possible) were dissected and analysed.

Stomachs were removed and opened under a dissecting microscope into a 1 mm deep tray with marked blocks of 1 mm X 1 mm. The food items were then sorted into taxonomic groups, identified to the lowest possible taxon, counted and measured (using a eyepiece micrometer). From this data, a percentage frequency of occurrence (%F = the number of stomachs in which each prey item occurred, expressed as a percentage of the total number of stomachs examined) (Hyslop 1980) and percentage numerical occurrence (%N = the number of individuals of a particular food item in all stomachs, expressed as a percentage of the total number of food items recorded) was determined (Hyslop 1980). The food was then flattened in the tray with a microscope slide and the number of blocks occupied by the food items were counted. From this data a percentage volume (%V = the volume of the consumed item, given as a percentage of the total volume of stomach contents) of prey items was determined (Hyslop 1980, Cyrus *et al*. 1993).

3.4. Data treatment and analysis

Sample sites were categorised into salinity zones based on an adaptation of the Venice system (Strydom *et al*. 2003). Seasonal differences between salinity, temperature and turbidity were assessed using the Kruskal-Wallis test. Descriptive statistics were used to assess trends in zooplankton and larval fish mean densities between seasons, sites and salinity zones. Descriptive statistics were also used to show differences in %V in each species of larval fish diet between seasons, sites, developmental stage and salinity zones. Prey items were then placed into two guilds (bentho-pelagic and pelagic), dependent on where that species of prey occurs most abundantly (Wooldridge 1999). A percentage volume of each guild was calculated per species of larval fish. A category for unidentifiable prey items was also included.

Prey selection by larval fish was calculated for pelagic species only. This is because the method used during the study sampled the subsurface layer of the water column, therefore only pelagic zooplankton prey species data was available for statistical analysis. After values had been converted to a percentage, each pelagic zooplankton species available was subtracted from the corresponding pelagic prey species found in the gut of each larval fish. Differences in prey selection by each larval fish species was then assessed using a one-way ANOVA. The total percentage selection value for each pelagic zooplankton species by each larval fish species was also calculated. Differences between each pelagic prey species selected by each larval fish species was calculated using a Tukey significant difference test. A significance level of $P < 0.05$ was used for all tests.

4. RESULTS

4.1. Environmental variability

Seasonal salinity, temperature and water transparency readings are summarized in Table 4.1. Seasonal physico-chemical variability was apparent in the Sundays Estuary. No significant difference was found in mean salinity between seasons ($H = 2.69$; $P = 0.44$). Salinity ranged from 1.5 - 33.7 in summer, 1.7 - 32.6 in autumn, 1.9 -

36.5 in winter and 2.0 - 32.9 in spring. Salinity stratification was evident, with stratification most prominent in summer and autumn at lower estuary sites. A significant difference (H = 97.86; $P < 0.01$) was found in mean water temperature between all seasons except spring and autumn. Water temperature ranged from 20.2 - 26.8°C in summer, 18.0 - 23.0°C in autumn, 11.6 - 15.8°C in winter and 20.1 - 22.5°C in spring. Stratification of water temperature was weak, occurring at lower sites in summer and autumn. A significant difference (H = 41.72; $P < 0.01$) in water transparency (k) was also found between summer and winter, autumn and winter, autumn and spring and winter and spring.

Table 4.1: Mean (range) surface and bottom salinity, temperature and water transparency values for all seasons (two samples sessions per season) at sites in the Sundays Estuary recorded between 2007 and 2009 (Sp = spring, Su = summer, Au = autumn, Wi = winter)
.

		Sites	1	2	3	4	5	6	7	8
Salinity (psu)										
	Wi	Surface	31.7 (26.9-36.4)	25.7 (22.4-29.0)	22.6 (18.7-26.5)	21.1 (16.1-26.1)	14.4 (12.4-16.4)	6.7 (4.9-8.5)	2.6 (2.3-2.9)	2.0 (1.9-2.2)
		Bottom	32.8 (29.0-36.7)	32.3 (29.9-34.7)	26.4 (25.7-27.2)	28.6 (25.4-31.9)	22.8 (22.4-23.2)	14.8 (14.4-15.3)	4.4 (2.4-6.5)	2.0 (1.9-2.2)
	Sp	Surface	29.0 (25.2-32.9)	24.9 (19.3-30.5)	22.5 (16.6-28.3)	19.2 (13.0-25.4)	11.3 (5.0-17.5)	4.0 (2.3-5.8)	2.8 (2.1-3.4)	2.5 (2.0-3.0)
		Bottom	32.1 (31.3-33.0)	32.7 (28.9-36.6)	23.7 (18.5-29.0)	25.6 (25.2-26.0)	18.0 (16.1-20.0)	4.4 (2.3-7.0)	2.8 (2.1-3.6)	2.5 (2.0-3.0)
	Su	Surface	24.3 (15.7-33.0)	19.2 (11.6-27.0)	17.5 (11.1-24.0)	14.3 (6.8-21.8)	6.4 (2.1-10.7)	2.0 (1.5-2.5)	2.0 (1.5-2.4)	2.0 (1.6-2.4)
		Bottom	33.2 (31.5-35.0)	34.0 (31.0-37.0)	28.1 (28.0-28.3)	20.0 (22.5-25.6)	14.9 (12.1-17.7)	2.0 (1.5-2.5)	2.0 (1.5-2.4)	2.0 (1.6-2.4)
	Au	Surface	24.6 (19.8-29-5)	21.6 (17.3-25.9)	19.2 (13.7-24.7)	16.9 (11.4-22.4)	8.2 (4.4-11.9)	2.2 (1.8-2.7)	2.1 (1.7-2.5)	2.1 (1.7-2.5)
		Bottom	22.3 (29.8-34.9)	34.0 (30.1-37.3)	27.5 (27.0-27.9)	25.0 (24.6-25.3)	15.6 (15.3-15.9)	2.2 (1.8-2.6)	2.1 (1.7-2.5)	2.1 (1.7-2.5)
Temperature (ºC)	Wi	Surface	15.2 (14.4-15.9)	14.6 (14.3-14.8)	14.4 (14.2-14.5)	14.5 (14.4-14.6)	14.0 (13.5-14.5)	13.4 (12.5-14.3)	12.8 (11.6-14.0)	12.6 (11.6-13.6)
		Bottom	15.3 (14.7-15.9)	15.1 (14.5-15.7)	14.7 (14.7-14.7)	15.0 (14.8-15.2)	14.8 (14.4-15.1)	13.9 (13.5-14.3)	12.8 (11.7-14.0)	12.6 (11.6-13.6)
	Sp	Surface	20.3 (20.1-20.5)	20.8 (20.3-21.2)	21.4 (20.6-22.2)	21.4 (20.6-22.3)	21.5 (20.8-22.2)	21.1 (20.5-21.7)	20.7 (20.3-21.2)	20.7 (20.2-21.2)
		Bottom	20.0 (19.0-20.1)	20.3 (19.8-20.9)	21.6 (20.7-22.6)	21.3 (20.8-21.8)	21.7 (21.0-22.4)	21.2 (20.6-21.8)	20.8 (20.3-21.3)	20.7 (20.2-21.2)
	Su	Surface	23.9 (23.3-24.4)	25.2 (24.8-25.7)	25.5 (24.9-26.1)	25.0 (24.2-25.9)	26.2 (25.8-26.6)	26.0 (25.5-26.5)	25.8 (25.4-26.3)	25.9 (25.6-25.2)
		Bottom	21.5 (18.5-24.5)	21.0 (18.0-24.1)	23.2 (21.4-25.0)	24.3 (22.6-26.0)	25.3 (23.9-26.7)	26.0 (25.6-26.5)	25.9 (25.4-26.3)	26.0 (25.7-26.3)
	Au	Surface	20.5 (19.4-21.6)	21.3 (20.2-22.4)	21.5 (20.5-22.4)	21.5 (20.6-22.4)	21.8 (20.5-23.1)	21.3 (20.3-22.3)	21.2 (20.3-22.1)	21.1 (20.1-22.1)
		Bottom	19.4 (17.5-21.4)	19.2 (17.3-21.0)	20.0 (17.8-22.2)	20.5 (18.8-22.2)	21.2 (19.6-22.9)	21.3 (20.3-22.3)	21.1 (20.2-22.1)	21.1 (20.2-22.1)
Turbidity (k)	Wi		1.8 (1.1-2.5)	1.1 (0.9-1.3)	1.2 (1.0-1.5)	1.4 (1.0-1.8)	1.4 (0.8-2.1)	0.9 (0.8-1.0)	0.6 (0.3-0.9)	0.5 (0.4-0.7)
	Sp		0.8 (0.6-1.0)	0.5 (0.5-0.6)	0.5 (0.5-0.5)	0.5 (0.5-0.5)	0.5 (0.4-0,5)	0.4 (0.3-0.5)	0.3 (0.3-0.4)	0.4 (0.3-0.5)
	Su		0.8 (0.8-0.9)	0.5 (0.5-0.6)	0.5 (0.4-0.6)	0.5 (0.3-0.6)	0.5 (0.3-0.6)	0.5 (0.4-0.6)	0.8 (0.8-0.8)	0.7 (0.6-0.7)
	Au		1.0 (1.0-1.0)	0.7 (0.6-0.8)	0.7 (0.7 -0.7)	0.7 (0.7-0.7)	0.6 (0.4-0.7)	0.6 (0.4-0.7)	0.7 (0.4-0.9)	0.6 (0.4-0.7)

4.2. Temporal and spatial trends in zooplankton and larval fish density

Mean density of larval fish showed similar trends to zooplankton between seasons, generally increasing during spring and summer. However, larval fish density decreased from winter 2007 to spring 2007, which is unusual and the same trend was not seen in the zooplankton assemblage (Figure 4.2). Highest mean larval fish density occurred in the summer of 2008 with 464 larvae per 100m^3 (range: 6 - 2625) and again in summer 2009 with 928 larvae per 100m^3 (range: 47 - 3171). Highest mean zooplankton densities occurred in the summer seasons of 2008 with 3591 ind. m^{-3} (range: 216 - 15615) and 2009 with 9810 ind. m^{-3} (268-75276) (Table 4.2).

Similarly, zooplankton and larval fish density mirrored spatial trends along the length of the estuary (Figure 4.3). However the larval fish assemblage showed an increase in mean density from site 3 to site 4, which is not the same trend exhibited by the zooplankton assemblage. Zooplankton and larval fish density showed peaks in mean density at site 2 (9408.5 ind. m^{-3} and 488.1 larvae per 100m^3 respectively) and site 6 (5212.0 ind. m^{-3} and 518.5 larvae per 100m^3 respectively).

The euhaline zone had the highest mean density of larval fishes (627 larvae per 100m^3) (Figure 4.4). This was followed by the mesohaline, oligohaline and polyhaline zones (378, 299 and 263 larvae per 100m^3 respectively) (Table 4.2). Similarly, the euhaline zone had the highest mean density of zooplankton (10805 ind. m^{-3}) (Figure 4.4). This was followed by the oligohaline, polyhaline and mesohaline zones (4543, 3559 and 697 ind. m^{-3} respectively) (Table 4.2).

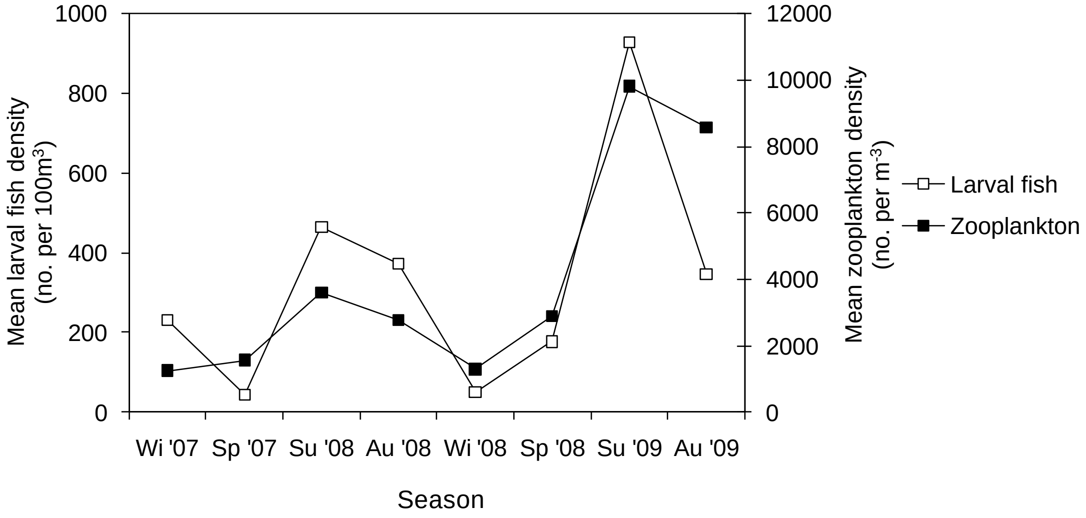

Figure 4.2: Mean seasonal changes in larval fish and zooplankton density between 2007 and 2009 in the Sundays Estuary. Sp = spring, Su = summer, Au = autumn, Wi = winter. ’07 = 2007, ’08 = 2008, ’09 = 2009.

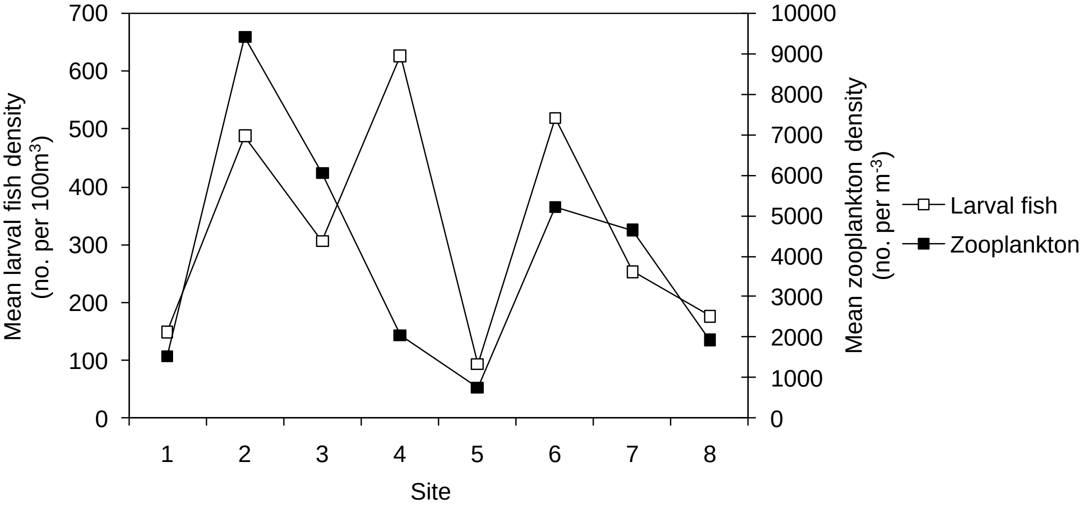

Figure 4.3: Spatial changes in larval fish and zooplankton density at all sites along the Sundays Estuary between 2007 and 2009.

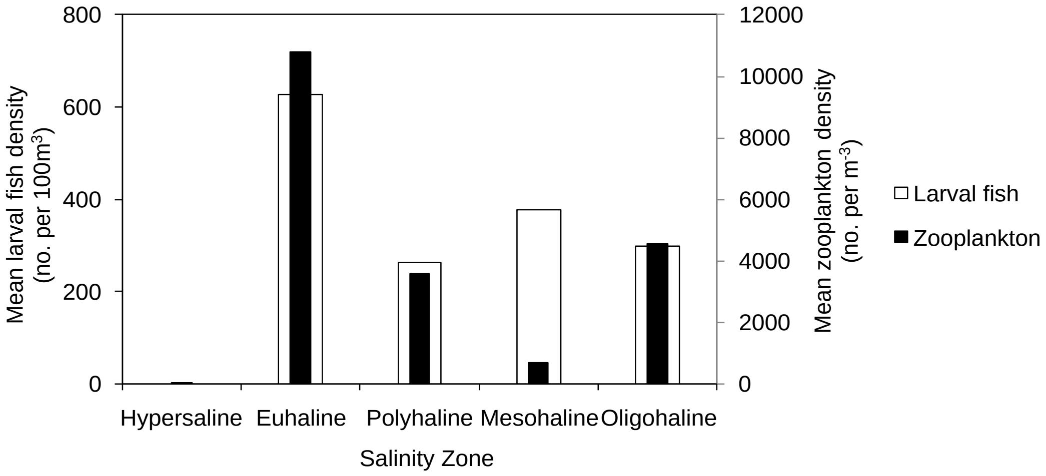

Figure 4.4: Mean spatial changes in larval fish and zooplankton density at salinity zones along the Sundays Estuary between 2007 and 2009.

Table 4.2: Mean, median and range of larval fish and zooplankton density recorded in the different seasons and salinity zones in the Sundays Estuary between 2007 and 2009.

	Larval fish			Zooplankton		
	Density (no. per m^3)			Density (no. per m^{-3})		
	Mean	Median	Range	Mean	Median	Range
Season						
Winter '07	232	27	0-1194	1245	778	20-6803
Spring '07	43	29	0-113	1567	1291	640-3763
Summer '08	464	145	6-2625	3591	1051	216-15615
Autumn '08	373	211	0-996	2772	2876	905-5271
Winter '08	49	32	0-207	1295	557	18-4487
Spring '08	177	130	20-764	2902	1869	30-15001
Summer '09	928	782	47-3171	9810	1741	268-75276
Autumn '09	346	153	28-2476	8576	5246	219-26766
Salinity Zone						
Hypersaline	0	0	0	40	40	20-61
Euhaline	627	311	28-3171	10805	2272	356-75276
Polyhaline	263	62	0-1316	3559	2450	107-20875
Mesohaline	378	155	4-2625	697	321	30-2381
Oligohaline	299	82	0-2476	4543	1505	18-26766

4.3. Diet of the larval fish assemblage in the Sundays Estuary

A total of 296 stomachs from five species of larval fish (*Gilchristella aestuaria*, *Pomadasys commersonnii*, *Monodactylus falciformis* and *Rhabdosargus holubi* and *Myxus capensis*), were examined during the course of this study, 271 of which contained food (Table 4.3). The size range of larval fishes examined for gut content was from 6.5 – 30.0 mm for all species combined. *Monodactylus falciformis* consisted of the largest size range of all five species examined. Considering the total number of guts examined for each species, *M. falciformis* and *M. capensis* consumed the largest number of prey items. The size range of the prey items analyzed from the larval fish guts ranged from 0.2 – 6.0 mm for all species combined. *Pomadasys commersonnii* consumed the largest prey size range of all five species examined.

The volumetric percentage, frequency of occurrence and numerical occurrence of each of the prey items found in the guts of each species are presented in Table 4.4. From this table it is apparent that the majority of species consumed a wide variety of prey items, however for all species, only a few prey items provided the bulk of the diet. The greatest volume of prey consumed by G. aestuaria were copepod eggs. The most frequent prey item in the diet was the copepod *Pseudodiaptomus hessei* with chironomid larvae being the most numerous in the stomachs of *G. aestuaria*. *Pseudodiaptomus hessei* was the most frequent, most numerous and formed the largest volume of *P. commersonnii*'s diet. *Monodactylus falciformis* and *M. capensis* indicated chironomid larvae as their most frequently eaten prey item. Chironomid larvae was also the most numerous prey item and composed the largest volume of these two species' diet. Not including unidentifiable matter, the amphipod *Corophium triaenonyx* was the most numerous prey item and constituted the largest volume for

R. *holubi*. *Pseudodiaptomus hessei* was the most frequently consumed prey item for *R*. *holubi*.

4.3.1. Temporal and spatial trends in the diet of larval fish

Seasonal variability in the diet of larval fish occurred in the Sundays Estuary (Figure 4.5). The estuarine resident (category Ia) *Gilchristella aestuaria* consumed a large volume of copepod eggs throughout the study period, especially over the winter seasons. Largest diversity in *G*. *aestuaria* diet occurred in autumn 2008, summer and autumn 2009. The copepod, *Pseudodiaptomus hessei* was consumed from spring to autumn, with *Halicyclops* sp., chironomid larvae and Ostracoda appearing in the diet in summer and autumn 2009.

Larval fish of the estuarine dependent species (category IIa) were only analysed for seasons of capture since larvae were not available all year round. *Pomadasys commersonnii* were only caught in autumn and winter 2008. The autumn and winter diets were dominated by *P*. *hessei* and *Mesopodopsis wooldridgei* respectively. In winter 2007 and summer and winter 2008, *Monodactylus falciformis* (category IIa) revealed a dominance of chironomid larvae in their diet. In summer 2008, *P*. *hessei* and *Halicyclops* sp. were primarily consumed. The catadromous species (category V), *Myxus capensis* and the estuarine dependent species (category IIa), *Rhabdosargus holubi*, showed the largest diversity in diet. For both species, *P*. *hessei* and chironomid larvae constituted the greatest volume of the summer 2008 and autumn 2009 diet respectively. *Halicyclops* sp. and insect larvae were also consumed in large volumes by *M*. *capensis*. *Rhabdosargus holubi* spring diet constituted large volumes of the bentho-pelagic amphipod, *Corophium triaenonyx* (Figure 4.5).

Similarly, larval fish diet varied spatially in the Sundays Estuary (Figure 4.6). This spatial variability in diet can be compared with the percentage contribution of zooplankton sampled along the length of the estuary during the study (Figure 4.7). Copepod eggs were consumed by *G. aestuaria* throughout the estuary, with highest diversity in diet occurring at sites 6 and 7. *Pseudodiaptomus hessei* composed the largest volume to the diet of *P. commersonnii* at most sites, with the exception of sites 3 and 4 where the mysid, *M. wooldridgei* made a strong contribution to the diet. Figure 4.7 indicates the higher percentage contribution of *M. wooldridgei* at these sites. *Monodactylus falciformis* consumed large volumes of *P. hessei* and *Halicyclops sp.* at site 6 (Figure 4.7), where the percentage contribution of these copepod species was high. A shift in the diet at site 8 in the upper reaches was noted by an increase in chironomid larvae. *Myxus capensis* diet at lower estuary sites (sites 2 - 4) composed large volumes of copepod species (copepod eggs, *P. hessei* and *Halicyclops* sp.). *Pseudodiaptomus hessei* was present at these sites but with lower percentage contributions when compared to upper estuary sites (Figure 4.7). Insect larvae, chironomid larvae and Ostracoda increased in the volume of the diet towards the upper reaches of the estuary (sites 7 and 8). Similarly, copepod species (*Copepod* sp., *P. hessei* and *Halicyclops* sp.) constituted greatest volumes to the diet of *R. holubi* at sites 3 and 4, with insect larvae and chironomid larvae being consumed at site 7. *Corophium triaenonyx* showed greatest volumetric contribution to the diet at sites 5 and 6.

Table 4.3: Total number of larval fish per species examined for gut contents, total number with food, larval fish size range, total number of prey items and size range in the Sundays Estuary between 2007 and 2009.

Family	Species	Estaurine association catergory	Total no. of guts	Total no. with food	Size range of fish (mm)	Total no. of prey	Size range of prey (mm)
Clupeidae	*Gilchristella aestuaria*	Ia	142	131	15.7-30.0	1242	0.3-4.1
Haemulidae	*Pomadasys commersonnii*	IIa	50	50	14.1-25.4	12084	0.2-6.0
Monodactylidae	*Monodactylus falciformis*	IIa	8	8	6.5-29.3	161	0.4-2.3
Sparidae	*Rhabdosargus holubi*	IIa	34	29	9.6-20.2	141	0.3-3.9
Mugilidae	*Myxus capensis*	V	62	53	8.9-19.7	666	0.3-3.8

Table 4.4: Diet of selected larval fish in the Sundays Estuary between 2007 and 2009. Length range and n = total number of larval fish examined for gut contents is given below species names. %V is the volumetric percentage (the volume of the consumed item, given as a percentage of the total volume of stomach contents). %F is the frequency of occurrence (the number of stomachs in which each prey item occurred, expressed as a percentage of the total number of stomachs examined). %N is the numerical occurrence (the number of individuals of a particular food item in all stomachs, expressed as a percentage of the total number of food items recorded).

	Gilchristella aestuaria 15.7-30.0 mm n=142			*Pomadasys commersonnii* 14.1-25.4 mm n=50			*Monodactylus falciformis* 6.5-29.3 mm n=8			*Rhabdosargus holubi* 9.6-20.2 mm n=34			*Myxus capensis* 8.9-19.7 mm n=62		
Prey item	%V	%F	%N	%V	%F	%N	%V	%F	%N	%V	%F	%N	%V	%F	%N
Copepoda															
Copepod eggs	**51.5**												2.0		
Copepod sp.							0.9	12.5	1.9	0.4	2.9	1.4	0.2	1.6	0.9
Halicyclops sp.	1.4	7.0	17.2	3.5	20.0	1.7	1.5	37.5	8.1	4.1	14.7	12.8	3.4	22.6	16.7
Pseudodiaptomus hessei	5.0	**26.8**	25.8	**81.1**	**96.0**	**97.7**	10.8	75.0	22.4	11.2	**41.2**	27.7	7.0	27.4	17.1
Mysidacea															
Mysid sp.										2.6	5.9	3.5	0.1	1.6	0.2
Mesopodopsis wooldridgei				5.5	10.0	0.2									
Rhopalophthalmus terranatalis										1.5	2.9	0.7			
Isopoda															
Isopod sp.				0.2	2.0					1.1	8.8	2.8	0.6	4.8	1.4
Corallana africana										0.7	2.9	1.4			
Amphipoda															
Amphipod sp.													0.1	1.6	0.2
Corophium triaenonyx	0.1	1.4	0.3	4.2	32.0	0.3				**24.2**	14.7	**29.8**	7.6	6.5	6.8
Anomura															
Upogebia africana				0.1	2.0										
Brachyura															
Paratylodiplax edwardsii		1.4	0.2										0.3	3.2	0.5
Insecta															
Insect lavae	0.1	1.4	0.2							1.9	2.9	0.7	23.8	30.6	7.5
Chironomid larvae	3.2	7.7	**50.6**	0.9	12.0		**49.4**	**87.5**	**57.8**	17.5	11.8	17.7	**26.6**	**35.5**	**38.0**
Ostracoda	1.0	8.5	5.6	0.2	6.0		2.4	50.0	9.9	0.7	5.9	1.4	3.9	24.2	11.0
Unidentified															
UnID plant matter							0.6						4.3		
UnID matter	37.5			4.4			34.4			**34.2**			20.2		

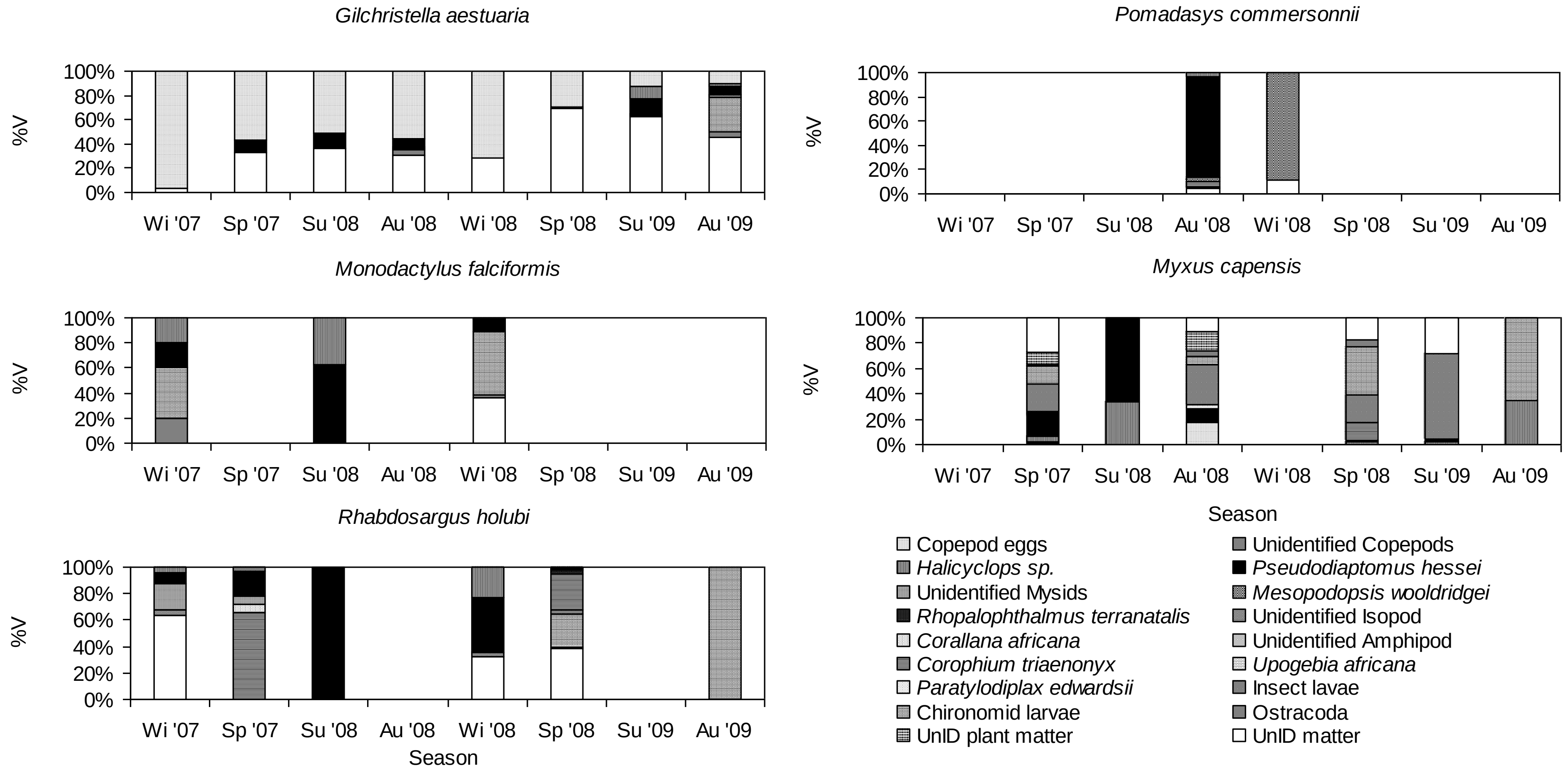

Figure 4.5: Seasonal contribution (%V) of prey species in the diet of larval fish species examined. Sp = spring, Su = summer, Au = autumn, Wi = winter. ’07 = 2007, ’08 = 2008, ’09 = 2009. Blank areas represent no larvae caught during that season. Refer to Table 4.4 for class and order divisions.

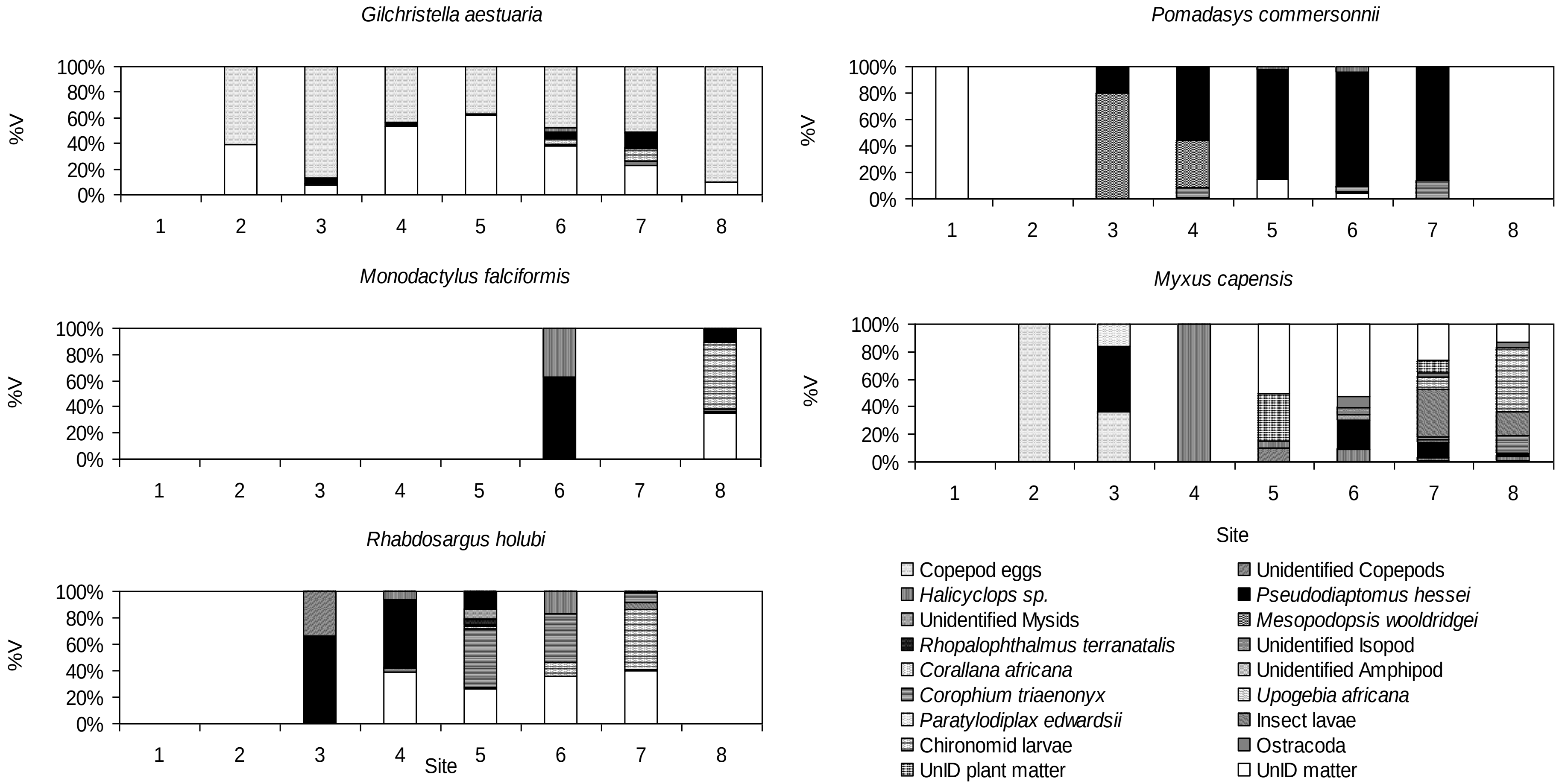

Figure 4.6: Spatial contribution (%V) of prey species in the diet of larval fish species examined. Blank areas represent no larvae caught at that site. Refer to Table 4.4 for class and order divisions.

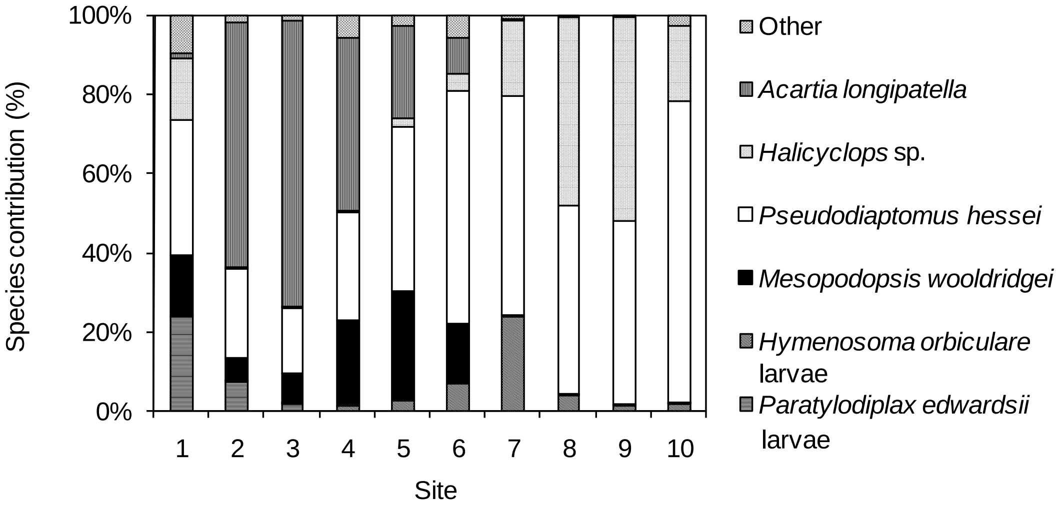

Figure 4.7: Percentage contribution of zooplankton species at sites in the Sundays Estuary between 2007 and 2009. Only species contributing over 2% to the total catch were included. Rare prey species contributing less than 2% were grouped as “other” as their contribution to overall catch was negligible.

4.3.2 The relationship between diet, developmental stage of larval fish and salinity zone

Larval fish showed changes in diet at different developmental stages (Figure 4.8). In terms of the estuarine resident species, *Gilchristella aestuaria* diet became less diverse with increasing size with copepod eggs, *Pseudodiaptomus hessei* and chironomid larvae being consumed during the postflexion stage and only copepod eggs and *P. hessei* being consumed during the early juvenile stage.

Pseudodiaptomus hessei composed the bulk of *Pomadasys commersonnii* diet through both developmental stages analysed. *Mesopodopsis wooldridgei* increased in the volume of the diet as *P. commersonnii* increased in size from the postflexion to the early juvenile stage. During the flexion stage, *Monodactylus falciformis* consumed primarily copepod species (*P. hessei* and *Halicyclops* sp.). Diversification of diet occurred at the postflexion and early juvenile stages, to include chironomid larvae and Ostracoda. A large diversity in the diet of *Myxus capensis* occurred in the flexion, postflexion and early juvenile stages. Copepod eggs were consumed at flexion stage and *P*. *hessei* and chironomid larvae were consumed at all stages analysed. A decrease in the volume of *Halicyclops* sp. and an increase in the volume of insect larvae is noted from the flexion to the early juvenile stage. Largest diversity in the diet of *Rhabdosargus holubi* occurred during the flexion stage. *Corophium triaenonyx* composed a large volume of the diet during the flexion and the early juvenile stages. *Pseudodiaptomus hessei* contributed to the flexion and postflexion larvae and insect larvae were consumed by both postflexion and early juvenile *R*. *holubi* (Figure 4.8).

From Figure 4.9 it is apparent that a change in diet occurred at different salinity zones for each species analysed. *Gilchristella aestuaria* consumed larger varieties of prey items such as copepod eggs, *Halicyclops* sp., *P*. *hessei*, chironomid larvae and Ostracoda at the oligohaline zone. However, copepod eggs constituted the bulk of the diet across salinity zones analysed. *Pseudodiaptomus hessei* was consumed in large volumes by *P*. *commersonni*i over all salinity zones were larvae were found. Chironomid larvae and *M*. *wooldridgei* increased in the volume of the diet in the polyhaline zone. *Monodactylus falciformis* diet was only analysed at the oligohaline salinity zone and indicated the consumption of *P*. *hessei*, Ostracoda and dominance of chironomid larvae in the diet. Largest diversity in the diet of *M*. *capensis* occurred at the oligohaline zone with *P*. *hessei*, chironomid larvae, insect larvae, *C*. *triaenonyx* and Ostracoda being consumed. A large volume of copepod eggs and *P*. *hessei* were consumed at the polyhaline zone. The brachyuran, *Paratylodiplax edwardsii* also appeared in the diet at this salinity zone. Chironomid larvae composed the largest volume to the diet of *R*. *holubi* in the oligohaline zone. *Pseudodiaptomus hessei* and *C*. *triaenonyx* increased in the volume of the diet at the mesohaline and polyhaline zones.

4.3.3. Diet of larval fish and feeding guilds

Gilchristella aestuaria consumed large volumes (58.0%) of pelagic copepod eggs and *Pseudodiaptomus hessei*. *Gilchristella aestuaria* also contained large volumes of well digested unidentifiable matter (37.5%). The diet of *Pomadasys commersonnii* consisted primarily of pelagic species (90.1%), attributable to the large consumption of the copepod *P. hessei*. Bentho-pelagic prey species constituted a large volume of *Monodactylus falciformis*, *Myxus capensis* and *Rhabdosargus holubi* diet (58.1, 62.5 and 46.1% respectively). This can be explained by the large volumes of chironomid larvae in the diet of all these larval fish species and the large volumes of insect larvae and *Corophium triaenonyx* in the diet of the latter two larval fish species. *Pseudodiaptomus hessei* was the most abundant pelagic prey item in the diet of *M*. *falciformis* (13.2%), *M*. *capensis* (12.9%) and *R*. *holubi* (19.7%) (Figure 4.10).

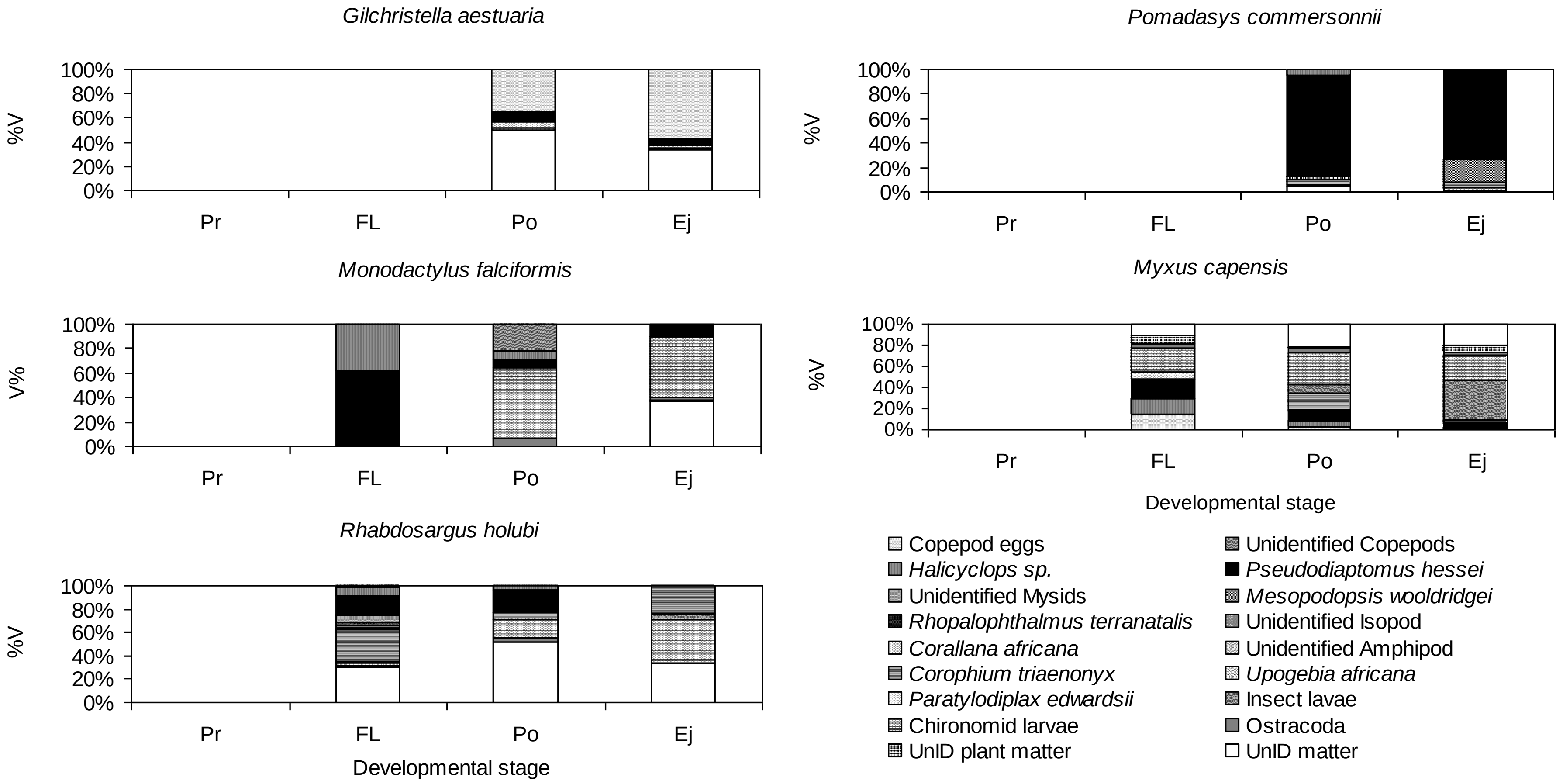

Figure 4.8: Relationship between contribution (%V) of prey species and developmental stage of larval fish species examined. Pr = preflexion, FL = flexion, Po = postflexion and Ej = early juvenile. Blank areas represent no larvae analysed at that developmental stage. Refer to Table 4.4 for class and order divisions.

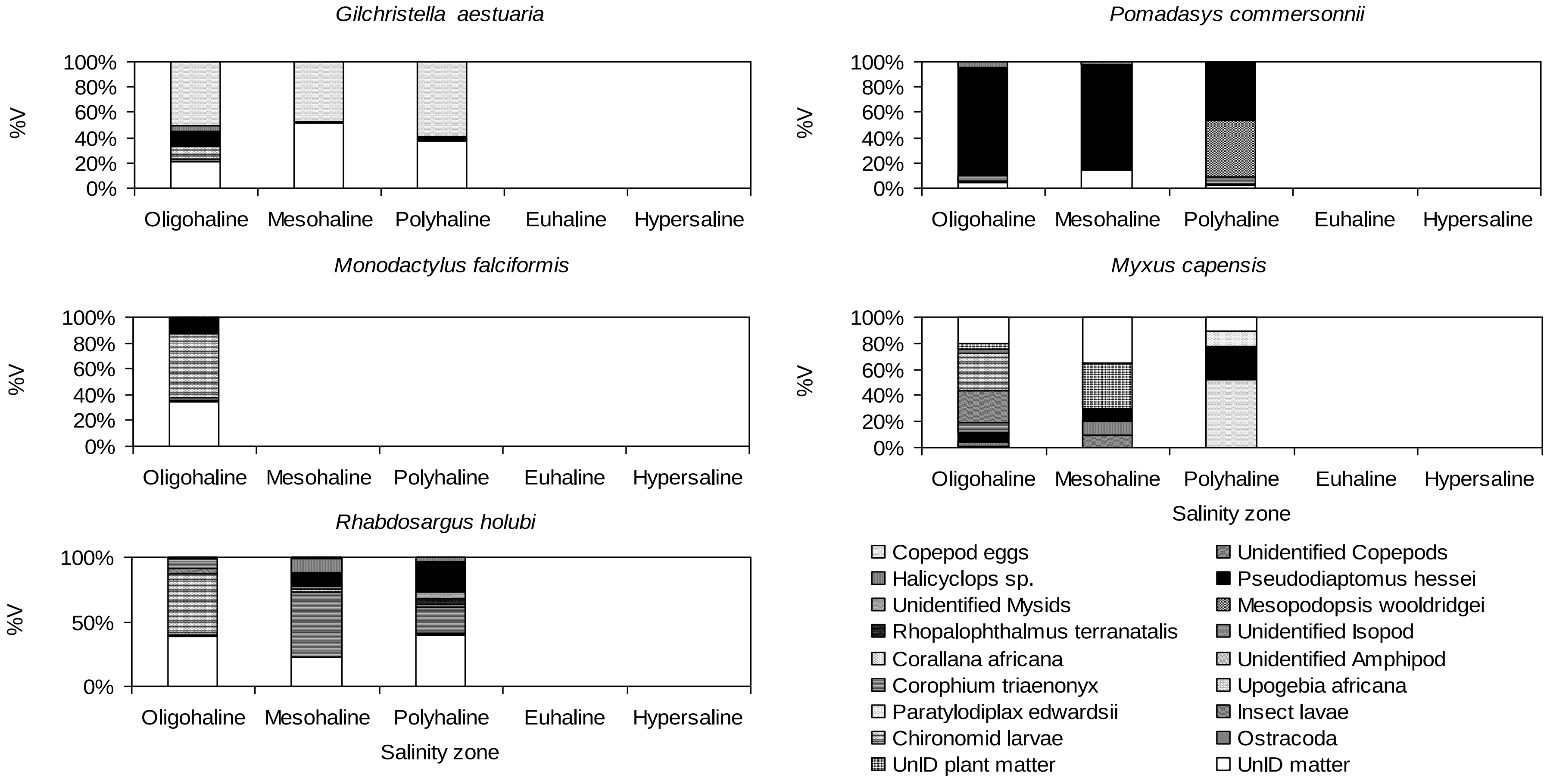

Figure 4.9: Relationship between contribution (%V) of prey species to larval fish species examined and salinity zone. Blank areas represent no larvae analysed at that salinity zone. Refer to Table 4.4 for class and order divisions.

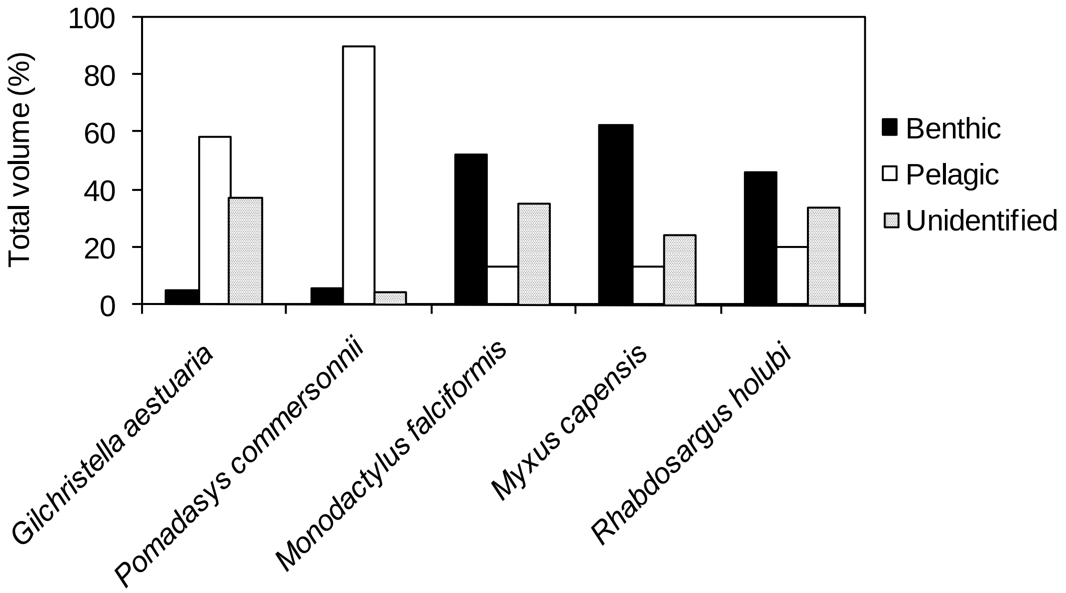

Figure 4.10: The total percentage volume of the diet of bentho-pelagic, pelagic and unidentifiable prey species for each larval fish species analysed for gut contents.

4.4. Prey selection of pelagic species by larval fish in the Sundays Estuary

Prey selection of pelagic species differed between larval fish species (Figure 4.11). *Gilchristella aestuaria* showed a significant difference between the selection of prey items ($P < 0.05$). Largest differences were found between all possible prey items and *Halicyclops* sp., and all possible prey items and *Pseudodiaptomus hessei*. This can be explained by the high selection for *P. hessei* and the low selection for *Halicyclops* sp. *Gilchristella aestuaria* also did not make use of *Acartia longipatella*, *Mesopodopsis wooldridgei* and *Hymenosoma orbiculare* larvae available.

Pomadasys commersonnii showed a similar selection pattern to *G. aestuaria,* also showing a significant difference ($P < 0.05$) between the selection of all possible prey items and *Halicyclops* sp. and all possible prey items and *P. hessei*. *Pomadasys commersonnii* also selected *Mesopodopsis wooldridgei* out of the pelagic zone. *Monodactylus falciformis* showed a similar selection pattern to both *G. aestuaria* and

P. *commersonnii*, also selecting for *P*. *hessei* and not making use of *Halicyclops* sp. and *Cladocera* sp. However, there was no significant difference found between the selection of prey items ($P = 0.43$). Similarly, no significant difference ($P = 0.25$) was found between the selection of prey items by *Myxus capensis*. *Halicyclops* sp. was the prey item primarily selected for. *Mesopodopsis wooldridgei* and *H. orbiculare* larvae were not selected for. *Rhabdosargus holubi* showed a significant difference ($P < 0.05$) between the selection of prey items. Largest differences occurred between all possible prey items and *M*. *wooldridgei* and *P*. *hessei* and all possible prey items, excluding *Halicyclops* sp. This can be explained by the selection for *P*. *hessei* and *Halicyclops* sp. and the low selection for *M*. *wooldridgei*. *Acartia longipatella*, *Rhopalophthalmus terranatalis* and *H*. *orbiculare* larvae were also not selected for by *R*. *holubi* (Figure 4.11).

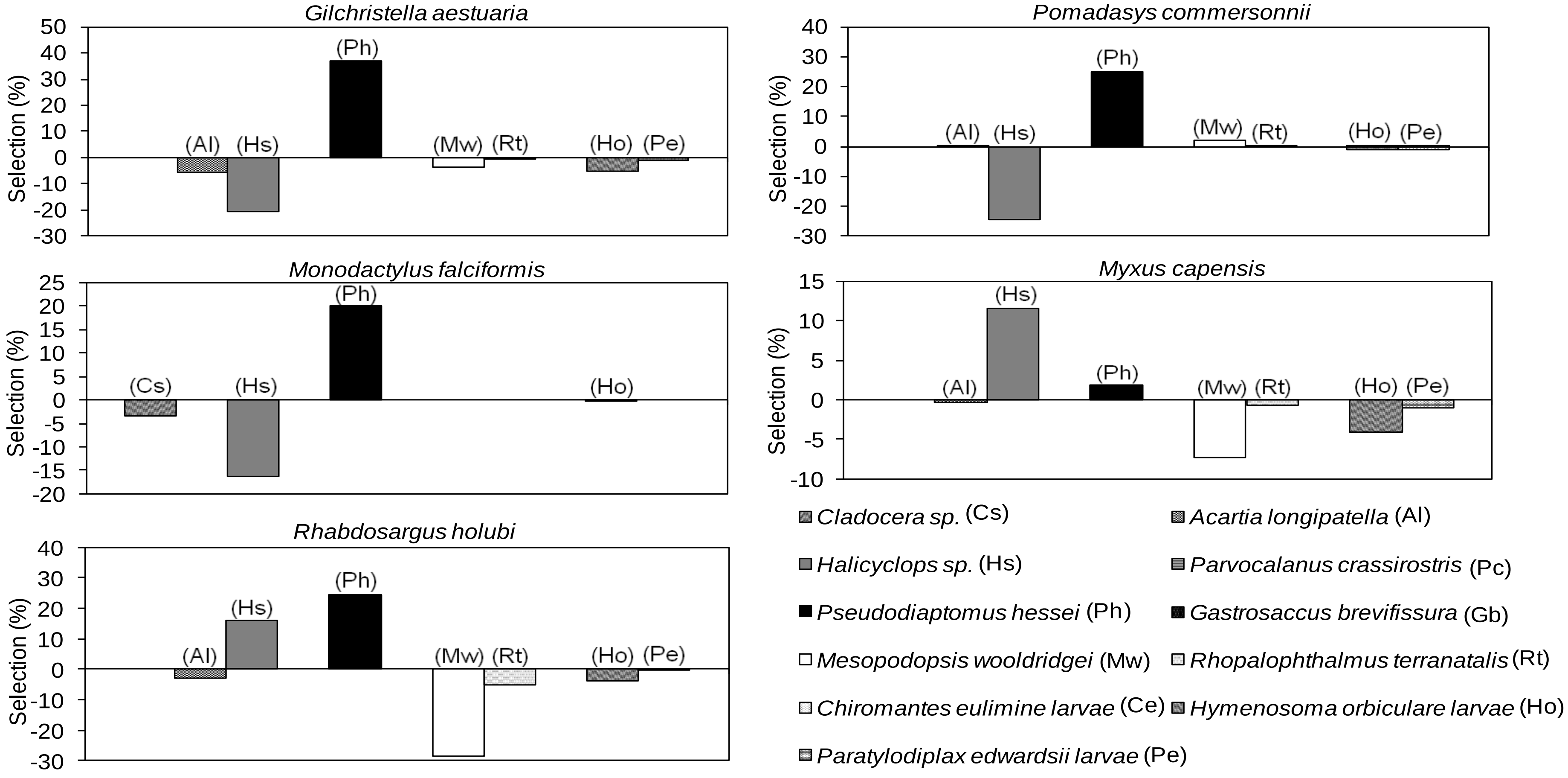

Figure 4.11: Prey selection (%) of pelagic species for each larval fish species analysed for gut contents. Refer to Table 4.4 for class and order divisions. Note the difference in scale on the y-axis between species.

5. DISCUSSION

Variability in zooplankton composition and biomass in South African estuaries is determined primarily by the effects of temperature, salinity and freshwater input (Wooldridge 1999). The zooplankton assemblage showed peaks in density in summer, coinciding with warmer water temperatures. Similarly, peaks in larval fish densities also occurred in summer, coinciding with warmer water temperatures, seasonal fish spawning and recruitment peaks for most fish species (Whitfield & Marais 1999). Therefore, the predator-prey interaction between larval fish and zooplankton plays an influential role in determining the demographics of a population or species (Rosel & Kocher 2002). The corresponding density trends of larval fish and zooplankton is not only evident on a seasonal scale but also spatially across the estuary. Typically, highest mean larval fish densities occur in the mesohaline zone of most estuaries due to the association with the river-estuary interface (REI), this being an area of high primary and secondary production (Wooldridge & Bailey 1982, Jerling & Wooldridge 1991, Snow *et al*. 2000, Strydom *et al*. 2003). However, in the present study, larval fish density was highest in the euhaline zone nearer the mouth, corresponding to highest mean zooplankton densities (primarily *Acartia longipatella*) also found in this salinity zone. This is an anomalous finding and may well be related to water quality problems in the low salinity waters of this estuary as has been highlighted in recent studies (N. Strydom, pers. comm.).

5.1. Larval fish diet and prey selection

5.1.1. Clupeidae: *Gilchristella aestuaria*

The estuarine resident, *Gilchristella aestuaria* is planktivorous during larval, juvenile and adult stages of development (Beckley 1984, Whitfield & Harrison 1996). In the Sundays Estuary, surprisingly, copepod eggs were consumed in large volumes and the most frequent prey item was the copepod *Pseudodiaptomus hessei*. The predominance of copepod species and other small crustaceans in the diet is common to the majority of zooplanktivorous clupeoids (Longhurst 1971). *Pseudodiaptomus hessei* was consumed in large volumes in summer in the upper reaches of the estuary during all developmental stages studied, coinciding with highest densities of this copepod species (Jerling & Wooldridge 1995, Whitfield & Harrison 1996). The copepod *Halicyclops* sp. also contributed to the diet in summer 2009 when abundance was high (see Chapter 3). The consumption of ostracods in the upper estuary was also noted by Wooldridge & Bailey (1982) in this region of the estuary. Chironomid larvae are usually most abundant in upper reaches of estuarine systems where lower salinity values occur (Blaber *et al*. 1984, Davies 1984). *Gilchristella aestuaria* spawn in the upper reaches of estuaries and extend down into the estuary as their larvae grow. Therefore a decrease in the consumption of chironomid larvae as *G*. *aestuaria* larvae grow corresponds with the distribution of larval fish at that developmental stage and the occurrence of chironomid larvae. *Gilchristella aestuaria* consumed largest volumes of pelagic prey, which is mainly attributable to the large abundance of *P*. *hessei* in the diet. *Pseudodiaptomus hessei* was largely selected for out of the plankton (Talbot & Baird 1985) and despite large abundance of *Halicyclops* sp., *Acartia longipatella* and the brachyuran, *Hymenosoma orbiculare* larvae, these species were not selected by this species. This may be attributable to the higher density (in comparison to other prey species available) of *P*. *hessei* throughout the year along the estuary (see chapter 2 and 3).

5.1.2. Haemulidae: *Pomadasys commersonnii*

The copepod *Pseudodiaptomus hessei* constituted the largest volume in the diet of the estuarine dependent, *Pomadasys commersonnii*. *Pseudodiaptomus hessei* was consumed in large volumes in autumn 2008, being replaced by the mysid *Mesopodopsis wooldridgei* in winter 2008. Wooldridge & Bailey (1982), also found *P*. *hessei* and *M*. *wooldridgei* in the diet of *P*. *commersonnii*. Spatial differences in the diet of *P*. *commersonnii* were also noted with *M*. *wooldridgei* being consumed in the lower estuary where this mysid was most abundant (Jerling & Wooldridge 1995). A switch in the diet to *P*. *hessei* in the middle and upper estuary again indicates the consumption of zooplankton species in areas where they are most prevalent. *Pomadasys commersonnii* indicated a switch in prey from *P*. *hessei* to *M*. *wooldridgei* as larvae developed from postflexion larvae (14 to 20 mm) to early juveniles (20 to 26 mm). This may be attributable to the larger size of *M*. *wooldridgei* and the increase in gape size in *P*. *commersonnii* (Hodson *et al*. 1981, Whitfield 1985). Like *G*. *aestuaria*, *P*. *commersonnii* feed primarily on pelagic prey species, selecting *P*. *hessei* (Wooldridge & Bailey 1982) and not making use of *Halicyclops* sp. that was also available. *Pseudodiaptomus hessei* is therefore the preferred copepod prey species.

5.1.3. Monodactylidae: *Monodactylus falciformis*

Bentho-pelagic prey species comprised the largest volume of the diet of the estuarine dependent, *Monodactylus falciformis*. This may be explained by the large volume of the bentho-pelagic chironomid larvae in the diet. However, *M*. *falciformis* also fed on the copepod species *Pseudodiaptomus hessei* and *Halicyclops* sp. in summer when these copepod species were most abundant (Whitfield 1985, Jerling & Wooldridge 1995). The addition of chironomid larvae and Ostracoda to the diet in winter in the upper estuary may be attributable to the lower copepod standing stock during this season (see chapter 3) . Copepod species made up the largest volumes of the diet of *M*. *falciformis* during flexion development (6 to 7 mm). Chironomid larvae and

Ostracoda occurred in the diet at postflexion (8 to 10 mm) and early juvenile stages (21 to 30 mm). Whitfield (1985), also noted the presence of insects in larger individuals of *Pomadasys commersonnii* (10 to 29 mm). Pelagic prey selection of *M. falciformis* was similar to that found by *G. aestuaria* and *P. commersonnii*.

5.1.4. Mugilidae: ***Myxus capensis***

The catadromous, *Myxus capensis* showed a highly diverse diet, however bentho-pelagic prey species comprised the bulk of the diet. *Pseudodiaptomus hessei* and *Halicyclops* sp. were consumed in summer when these copepod species were found to be highly abundant (see chapter 3). Blaber & Whitfield (1977), stated that *M. capensis* adjusted from consuming migratory zooplankton to meiobenthos between 10 and 20 mm length, this was followed by large quantities of mainly insects been taken from the surface of the water. In the Sundays Estuary, *M. capensis* consumed largest volumes of copepod species during postflexion development (10 to 15 mm) at lower estuary sites and the polyhaline salinity zone, with large volumes of insect larvae occurring in the diet of early juveniles (16 to 20 mm) in the upper reaches and oligohaline salinity zone of the estuary. The preference of *M. capensis* for feeding on insects may be linked to their preference for freshwater areas where meiobenthos may be scarcer than in the lower reaches of estuaries (Blaber & Whitfield 1977). *Myxus capensis* showed some selectivity for *P. hessei*, however greater selectivity occurred for *Halicyclops* sp. which may be explained by the catadromous nature of *M. capensis* and the large densities of *Halicyclops* sp. found during the zooplankton study in the upper reaches of the estuary (see Chapter 3).

5.1.5. Sparidae: *Rhabdosargus holubi*

The estuarine dependent, *Rhabdosargus holubi*, showed a very similar diet to that of *Myxus capensis*. A diverse diet with *Pseudodiaptomus hessei* being consumed in large volumes in summer in the lower and middle reaches of the Sundays Estuary as found by other researchers (Wooldridge & Bailey 1982, Whitfield 1985, Whitfield 1988). However, *R*. *holubi* also consumed a considerable volume of the amphipod, *Corophium triaenonyx*. This amphipod species is frequently found in sandy substrates where it constructs tubes on the surface of solid objects on the substratum, enabling it to exploit a great variety of habitats (Cyrus & Martin 1988, Teske & Wooldridge 2004). *Corophium triaenonyx* contributed to the largest percentage of the diet in the middle and upper estuary, in the mesohaline salinity zone. The pelagic *P*. *hessei* and *Halicyclops* sp. was selected for out of the water column. Despite large availability of mysids, *Mesopodopsis wooldridgei* and *Rhopalopthalmus terranatalis* these species were not selected for, this may be explained by the large abundance of bentho-pelagic species in their diet and therefore the consumption of mysids may be unnecessary.

In conclusion most of the larval fish species examined showed diversity in their diet however, for all species, only a few prey items provided the bulk of the diet. Factors affecting larval fish prey selection are seasonal and spatial availability of zooplankton species and larval fish body size. The present study provides insight into larval fish diet and prey selectivity for pelagic prey species. It is suggested that future studies on larval fish prey selection include analyses of bentho-pelagic prey species available. Such studies would contribute to the present description of bentho-pelagic prey species to further understand selection of prey items in estuaries.

6. ACKNOWLEDGEMENTS

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CHAPTER 5

SYNTHESIS AND CONCLUSIONS

The present study assessed the composition, abundance, distribution and seasonality of the larval fish and zooplankton assemblages of the Sundays Estuary. Furthermore, the dynamics of larval fish were related to zooplankton dynamics by assessing the diet, feeding guilds and prey selection of five larval fish species occurring in the study area. Such an investigation was necessary for the understanding of feeding dynamics and distribution of individual species, as well as an understanding of the overall resource utilization by larval fish within the estuary.

A total of 8 174 larval and early juvenile fishes were caught, representing 12 fish families and 23 species. Clupeidae, Gobiidae, Blenniidae and Mugilidae dominated catches. Dominant species included *Gilchristella aestuaria* (59.2%), *Caffrogobius gilchristi* (19%), *Omobranchus woodi* (10%), *Liza dumerilii* (4.3%) and *Myxus capensis* (2.1%). The larvae and early juveniles of estuary resident fishes dominated the catches (91%). Similar findings were made by Strydom *et al*. (2003) in other Eastern Cape estuaries and Montoya-Maya & Strydom (2009) in Western Cape systems and Harris & Cyrus (2000) in KwaZulu Natal. South African estuaries are characterized as having typically low species diversity and a dominance of relatively few species (Whitfield 1994a). This was evident in the Sundays Estuary, with *G. aestuaria* dominating the catch. Larval fish densities peaked in summer, coinciding with warmer water temperatures, seasonal fish spawning and recruitment peaks for most fish species (Whitfield & Marias 1999). Diversity was also shown to be highest in the summer season, attributable to peaks in coastal fish spawning and estuary-dependent fish recruitment (Whitfield 1998, Strydom *et al*. 2003). Spatial variation in larval fish densities was noted, with highest densities occurring in the lower and upper reaches of the estuary. A high dominance of preflexion larvae in the lower reaches of the estuary emphasized the movement of estuary dependent marine fishes into the marine environment where early development occurs (Beckley 1985, Whitfield 1989, Strydom 2003) and the expansion into the middle and upper reaches of the estuary as larvae grow is typical of estuary dependent marine fish (Strydom 2003).

A total of 19 zooplankton taxa, comprising two phyla, three classes, and seven orders were caught in the Sundays Estuary. Copepoda (85.6%) dominated the zooplankton community of the estuary, with mysidacea and brachyura only making a small contribution. Low densities of mysids was probably a reflection of the sampling strategy that focused on near surface waters where mysids are less abundant (Wooldridge 1999). Dominant species included *Pseudodiaptomus hessei* (35.7%), *Acartia longipatella* (32.9%), *Halicyclops* sp. (17.0%), *Mesopodopsis wooldridgei* (6.5%), *Paratylodiplax edwardsii* larvae (3.3%) and *Hymenosoma orbiculare* larvae (2.5%). The zooplankton density showed winter minima and summer maxima, similar to findings by Wooldridge (1999). Despite variability in species density across seasons, little variation in the composition of the zooplankton assemblage was found in the present study. Spatial variation in dominant copepods *A. longipatella* and *P. hessei* was noted, with clear dominance shifting between the former in the lower reaches and the latter in the upper reaches of the estuary. High summer densities of *P. hessei* in the upper reaches of the estuary may be explained by high chlorophyll-*a* concentrations, as noted by Grange *et al*. (2000). The mysids *M. wooldridgei* and *Rhopalopthalmus terranatalis* showed an overlap in high densities in the middle of the estuary in spring. *Mesopodopsis wooldridgei* also occurred in high densities in the lower reaches of the estuary. Similar spatial distributions caused by the predation of *R. terranatalis* on juvenile *M. wooldridgei* was made by Wooldridge (1999) where *M. wooldridgei* occurred nearer the tidal inlet. An absence of *Acartia natalensis* and presence of *Halicyclops* sp. occurred in the Sundays Estuary, differing from previous studies (Wooldridge & Melville-Smith 1979, Jerling & Wooldridge 1995). It was stated that there is evidence of the replacement of *A*. *natalensis* by *Halicyclops* sp. This was explained by the spatial patterns between *Halicyclops* sp. and *A*. *longipatella* in the present study showing similar patterns noted between *A*. *natalensis* and *A*. *longipatella* in previous studies (Wooldridge & Melville-Smith 1979, Wooldridge & Bailey 1982, Jerling & Wooldridge 1995).

Highest mean densities of larval fish occurring in the mesohaline zone, owing to the river-estuary interface (Wooldridge & Bailey 1982, Jerling & Wooldridge 1991, Snow *et al*. 2000, Strydom *et al*. 2003) did not emerge in the Sundays Estuary. Mean larval fish mean densities were highest in the euhaline zone, corresponding with the high mean zooplankton density in this zone. This was primarily due to high densities of the copepod *A. longipatella*. These anomalous findings in larval fish and zooplankton density in the euhaline zone may be related to water quality problems as a result of eutrophication in the low salinity waters of the estuary as has been highlighted in recent studies (N. Strydom pers. comm.).

Estuarine systems are important settlement, spawning and nursery areas for many fish species (Whitfield 1998, Harris & Cyrus 1995, Strydom *et al*. 2003). Fish species do not only use estuaries during and after their juvenile stages, but also during their larval stages (Beckley 1985, Whitfield 1994b, Strydom *et al*. 2003). Postflexion larvae of both estuarine-dependent marine species and of certain estuary-resident species recruit from the marine environment into estuarine nurseries (Strydom & Whitfield 2000). Newly recruited larval fish join the plankton assemblage of the estuaries and engage in predator-prey relationships. In estuaries, zooplankton distribution is spatially and temporally heterogeneous because of the highly dynamic conditions in these systems (Downing *et al*. 1987, Schlacher & Wooldridge 1995, Kibirige & Perissinotto 2003). Zooplankton are an important food resource for larval fish, transferring energy from primary producers to aquatic carnivores (Thayer *et al*. 1974, Whitfield & Harrison 1996). Zooplankton fatty acid content also ensures a high nutritional value for larval fish which feed on them (Dabrowski 1984).

Predator-prey interactions play an influential role in determining the demographics of the population and species (Rosel & Kocher 2002). Gut contents were analysed in the older developmental stages of *Gilchristella aestuaria*, *Pomadasys commersonnii*, *Monodactylus falciformis*, *Myxus cap*ensis and *Rhabdosargus holubi*. Each larval fish species showed differing diet and prey selection, however a general trend was evident in the Sundays Estuary, indicating diversity in the diet of larval fish species but a dominance of only a few prey items. *Gilchristella aestuaria* and *P*. *commersonnii* selected pelagic prey however *M*. *falciformis*, *M*. *capensis* and *R*. *holubi* mainly selected bentho-pelagic zooplankton species and these formed the bulk volume of the diet. A shift in diet from the planktonic to the hyperbenthos community has previously been explained by low zooplankton stocks of most South African estuaries (Blaber *et al*. 1981) relative to the zoobenthos resources (McLachlan & Grindley 1974, Whitfield 1980, Whitfield 1985).

A large number of studies on the diet and prey selection of larval fishes have been conducted worldwide (Puvanendran & Brown 1999, Rajasilta & Vuorinen 1983, Thayer *et al*. 1974, Kjelson *et al*. 1975, Townsend 1983). In South Africa, despite the large number of adult fish dietary studies undertaken (Whitfield & Harrison 1996, Hecht & Van der Lingen 1992, Schlacher & Wooldridge 1996, Froneman & Vorwerk 2003), few studies have focused on larval fishes. Studies on larval fish feeding dynamics are necessary for the understanding of trophic linkages and habitat choice, as well as overall resource utilization of larval fish within the estuary. The role of estuaries and the food source available in these nursery areas is crucial for the survival of the larval stage of fish populations. Therefore there is a need for future long term studies on larval fish diet and prey selection in South Africa.

In conclusion the Sundays Estuary, recently part of the Addo Elephant National Park under the authority of South African National Parks, has a high biomass of zooplankton and is therefore a vital nursery area for many fish species occurring along our coast. However, some water quality issues need to be resolved in order to understand the lack of high numbers of plankton in the low salinity waters of the estuary. The assessment of the zooplankton and larval fish assemblages and the trophic linkages between these two communities contributes to a holistic understanding of the dynamics occurring in the Sundays Estuary. The spatio-temporal distribution of larval fish and corresponding abundance level of zooplankton found in the present study highlights the importance of the Sundays Estuary as a conservation area that drives important biotic processes.

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Appendix I: Zooplankton abundance (ind. m^{-3}) sampled in winter 2007 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Winter '07									
Site	1	2	3	4	5	6	7	8	9	10
Branchiopoda										
Cladocera sp	0	0	0	0	0	0	0	0	0	92
Copepoda										
Acartia longipatella	3	995	1095	10071	7104	1101	20427	0	0	0
Halicyclops sp.	0	0	0	0	0	0	16	22	19	12
Pseudodiaptomus hessei	35	502	463	449	444	889	4028	303	1695	418
Mysidacea										
Mesopodopsis wooldridgei	6	35	314	727	655	419	2277	2	1	0
Rhopalophthalmus terranatalis	14	6	33	79	53	18	200	15	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	0	0	1	1	0	0	0
Corallana africana	0	3	1	2	13	1	21	1	3	4
Anomura										
Upogebia africana postlarvae	3	0	0	0	0	0	0	0	0	0
Upogebia africana juvenile	3	0	0	0	0	0	0	0	0	1
Brachyura										
Hymenosoma orbiculare larvae	0	1	0	0	0	0	1	6	0	10
Paratylodiplax edwardsii larvae	17	31	0	0	0	0	31	0	0	0

Appendix II: Zooplankton abundance (ind. m^{-3}) sampled in spring 2007 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Spring '07									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	0	149	144	46	0	0	0	0	0	0
Halicyclops sp.	22	22	8	46	74	95	337	839	1204	1208
Parvocalanus crassirostris	6	0	0	0	0	0	0	0	0	0
Pseudodiaptomus hessei	1316	5734	1747	440	3361	1421	1257	1379	1392	447
Mysidacea										
Gastrosaccus brevifissura	196	0	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	19	754	1909	2224	4192	173	0	0	0	0
Rhopalophthalmus terranatalis	2	133	341	478	9	106	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	5	0	0	0	0	0	0	0	0
Corallana africana	0	0	7	0	0	13	18	22	8	82
Amphipoda										
Amphipoda spp.	2	0	0	0	0	0	0	0	0	0
Caridea										
Palaemon peringueyi postlarvae	0	1	0	0	0	0	0	0	0	0
Anomura							0			
Upogebia africana stage 1	92	138	98	7	0	0	0	0	0	0
Brachyura										
Hymenosoma orbiculare larvae	22	5	52	76	9	271	849	85	7	0
Paratylodiplax edwardsii larvae	7	14	0	0	0	0	0	0	7	7
Megalopa larvae	39	1	0	0	0	0	0	0	0	0

Appendix III: Zooplankton abundance (ind. m^{-3}) sampled in summer 2008 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Summer '08									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	266	0	0	0	0	0	0	0	0	0
Halicyclops sp.	2202	0	0	9	381	178	1900	2660	785	271
Pseudodiaptomus hessei	3584	1874	1101	326	2093	307	4486	28033	9815	406
Mysidacea										
Gastrosaccus brevifissura	35	0	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	1143	945	831	99	0	0	0	0	0	0
Rhopalophthalmus terranatalis	4	35	99	3	0	0	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	22	20	7	3	0	0	0	0
Corallana africana	0	18	10	2	15	46	38	82	68	427
Eurydice longicornis	4	0	0	0	0	0	0	0	0	0
Anomura										
Upogebia africana stage 1	979	21	20	0	0	0	13	0	0	0
Brachyura										
Hymenosoma orbiculare larvae	12	36	7	10	161	163	71	220		10
Paratylodiplax edwardsii larvae	0	27	14	0	0	0	0	0	0	0
Megalopa larvae	2	0	0	0	0	0	0	0	0	0
Insecta										
Chironomid larvae	0	0	0	0	0	0	0	136	69	21

Appendix IV: Zooplankton abundance (ind. m^{-3}) sampled in autumn 2008 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Autumn '08									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	0	0	99	33	0	0	11	0	0	0
Halicyclops sp.	1212	0	10	15	84	76	388	1809	716	477
Parvocalanus crassirostris	259	0	0	0	0	0	0	0	0	0
Pseudodiaptomus hessei	2523	935	2737	4109	867	1674	6377	3298	3944	6763
Mysidacea										
Gastrosaccus brevifissura	2	0	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	23	1392	1319	982	240	171	0	0	0	11
Rhopalophthalmus terranatalis		66	35	16	22	29	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	9	0	6	22	7	0	0
Corallana africana	3	22	0	7	7	2	22	61	18	132
Anomura										
Upogebia africana stage 1	161	1348	200	0	0	5	11	14	0	0
Brachyura										
Hymenosoma orbiculare larvae	8	22	10	25	137	71	3593	54	0	0
Paratylodiplax edwardsii larvae	1296	4613	1428	0	8	0	0	0	0	12
Megalopa larvae	0	0	0	0	0	5	22	48	0	0
Insecta										
Chironomid larvae	0	0	0	0	0	0	0	0	0	23

Appendix V: Zooplankton abundance (ind. m^{-3}) sampled in winter 2008 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Winter '08									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	0	551	554	0	0	0	0	0	0	0
Halicyclops sp.	50	63	51	3	26	23	33	51	15	1289
Pseudodiaptomus hessei	67	3335	3056	882	701	195	53	37	30	922
Mysidacea										
Gastrosaccus brevifissura	0	13	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	38	1784	1328	1601	3	8	0	0	0	0
Rhopalophthalmus terranatalis	10	151	12	403	344	0	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	3	0	0	0	0	0	0
Corallana africana	7	0	0	0	18	5	13	28	0	12
Eurydice longicornis	0	0	0	0	0	2	12	0	0	0
Anomura										
Upogebia africana stage 1	5	0	25	0	3	0	0	0	0	0
Brachyura										
Hymenosoma orbiculare larvae	0	0	0	3	0	8	0	0	0	0
Paratylodiplax edwardsii larvae	936	2889	272	0	0	0	0	0	0	0

Appendix VI: Zooplankton abundance (ind. m^{-3}) sampled in spring 2008 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Spring '08									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	0	13514	5519	1525	0	0	0	0	0	0
Halicyclops sp.	287	0	0	26	13	13	123	31	283	516
Pseudodiaptomus hessei	277	8579	1522	1072	2051	2069	206	36	107	584
Mysidacea										
Gastrosaccus brevifissura	49	10	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	2386	2391	179	814	2721	989	20	0	0	0
Rhopalophthalmus terranatalis	38	66	315	847	211	410	0	3	0	0
Isopoda										
Corallana africana	0	0	0	0	0	0	0	18	3	46
Eurydice longicornis	0	0	0	0	0	13	0	0	0	0
Anomura										
Upogebia africana stage 1	263	423	13	0	0	0	0	0	0	0
Brachyura										
Chiromantes eulimine larvae	13	0	0	0	0	0	0	0	0	0
Hymenosoma orbiculare larvae	13	0	0	0	0	0	20	16	131	130
Paratylodiplax edwardsii larvae	773	76	13	0	0	0	0	0	0	0
Megalopa larvae	24	0	0	0	0	0	0	3	0	0

Appendix VII: Zooplankton abundance (ind. m^{-3}) sampled in summer 2009 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Summer '09									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	5	76751	38005	2547	0	0	0	0	0	0
Halicyclops sp.	19	20	0	0	7	95	1615	10438	1205	49
Pseudodiaptomus hessei	297	11359	2766	596	249	178	414	3700	1934	317
Mysidacea										
Gastrosaccus brevifissura	13	0	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	38	1142	370	169	182	60	0	0	0	0
Rhopalophthalmus terranatalis	59	156	62	25	33	0	0	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	0	21	4	5	0	0	0
Corallana africana	0	0	0	3	7	15	0	36	62	29
Anomura										
Upogebia africana stage 1	14	188	0	0	0	0	0	0	0	0
Brachyura										
Hymenosoma orbiculare larvae	36	0	11	197	394	263	735	860	280	164
Paratylodiplax edwardsii larvae	278	2064	73	0	0	0	0	0	0	0

Appendix VIII: Zooplankton abundance (ind. m^{-3}) sampled in autumn 2009 at all sites in the Sundays Estuary. Data represent the total of two replicates per site.

	Autumn '09									
Site	1	2	3	4	5	6	7	8	9	10
Copepoda										
Acartia longipatella	0	1289	24632	113	0	0	0	0	0	0
Halicyclops sp.	40	15	28	0	12	19	987	23960	35672	1974
Pseudodiaptomus hessei	258	2007	2715	1131	2950	413	1192	2923	16803	13619
Mysidacea										
Gastrosaccus brevifissura	0	5	0	0	0	0	0	0	0	0
Mesopodopsis wooldridgei	42	165	842	559	448	32	0	0	0	0
Rhopalophthalmus terranatalis	40	45	81	14	109	41	5	0	0	0
Isopoda										
Cirolana fluviatilis	0	0	0	0	0	0	21	0	0	0
Corallana africana	0	0	28	0	0	0	31	0	46	46
Anomura										
Upogebia africana stage 1	53	206	0	0	0	0	5	0	0	0
Brachyura										
Hymenosoma orbiculare larvae	0	15	12	0	0	33	1239	2158	826	321
Paratylodiplax edwardsii larvae	2471	1381	144	0	0	0	0	0	0	0