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AN EVALUATION OF THE RELATIVE NURSERY VALUE OF SANDY SHORE SURF ZONES AND ESTUARY MOUTHS IN TROPICAL NORTH QUEENSLAND, AUSTRALIA

Thesis submitted by

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in July 1995

for the degree of Doctor of Philosophy

in the Department of Marine Biology

James Cook University of North Queensland

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21 July 1995

(Vachira Lheknim)

An evaluation of the relative nursery value of Sandy Shore Surf Zones and Estuary Mouths in Tropical North Queensland, Australia

ABSTRACT

This study attempts to assess the relative nursery value of tropical intertidal habitats. A new definition of a nursery habitat is proposed, based on persistence, growth and survival. Based on this definition, this thesis examines the relative nursery value of two intertidal habitats based on analyses of temporal and spatial abundance patterns, feeding success and growth rates. The relative value of these parameters for determining nursery area value is also evaluated.

Fishes were sampled bimonthly with seine nets (5 mm mesh) in three selected sandy shore surf zones and three estuary mouths from the summer of 1992 to the winter of 1994. The presence of the juvenile stage of 126 species in intertidal collections from both habitats indicated that these areas are potentially important habitats for young fishes. Nested ANOVAs for species richness, total abundance and total fish biomass revealed no significant differences between sandy shore surf zones and estuary mouths. However, marked seasonal differences between summer and winter assemblages were apparent, with higher total abundance and species richness in early summer which were likely to be related to recruitment episodes. Cluster analysis suggested there were relatively strong similarities between sandy shore surf zones and estuary mouths, with little similarity between seasons.

Four selected species which occur at both habitats were selected for detailed analyses of abundance, biomass, feeding success and growth rate determination: *Stolephorus nelsoni, Sillago analis, Leiognathus splendens* and *Valamugil seheli*. Analysis of variance detected no significant differences in numbers of individuals or biomass of each species between sandy shore surf zones and estuary mouths.

The stomach contents of *S. nelsoni, S. analis* and *L. splendens* were examined. For all species, estuary mouth fishes had a relatively high proportion of stomachs which contained food, and a greater gut fullness than fishes taken from sandy shore surf zones. It is suggested that there may be a potential for food limitation or sub-optimal feeding conditions in sandy shore surf zones.

Age-length relationships for *S. nelsoni, S. analis, L. splendens* and *V. seheli* were determined by using otolith increment counts. Daily deposition was validated in *S. analis, L. splendens* and *V. seheli* and assumed for *S. nelsoni.* A similar age at length relationship in both estuary mouths and sandy shore surf zones was evident in all selected species. This suggests that habitat differences may not account for growth rate in these selected species.

In conclusion, for the study species examined, estuary mouths have a relatively higher nursery value than sandy shore surf zones. The relative value of nursery habitats in the tropics is likely to be species and age specific. Food accessibility may influence the value of nursery areas, but alone it is a poor predictor of nursery function.

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STATEMENT ON SOURCES
DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given

21 July 1995

(Vachira Lheknim)

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CHAPTER 1

MOTIVATION AND APPROACH

MOTIVATION

Intertidal sandy shore surf zones, muddy beaches and mangrove-lined estuary habitats mark the line of contact between land and sea. These areas constitute a transition zone otherwise referred to as "an ecotone", that is inhabited by an abundant variety of vegetation and animal life (Whittaker, 1975). It has been hypothesised that these habitats are nursery areas for various fishes and decapod crustaceans. For example, Boesch and Turner (1984) have pointed out in their review article that coastal wetlands, especially estuaries as well as mangrove and seagrass beds, are important nursery sites for juvenile fish and crustaceans; whilst Bennett (1989), Whitfield (1989), Brown and McLachlan (1990) and Romer (1990) have proposed that sandy shore surf zones are also nursery grounds. Recently, Blaber *et al.* (1995) have suggested that the shallow inshore zone of the Gulf of Carpentaria acts as a nursery area for many fish species. However, the value of these habitats as a nursery ground remains unclear as few studies have measured their value in a comparative manner.

Over the last two decades, a rapid increase in coastal development and degradation of tropical marine environments has led scientists to develop an expanding awareness of the importance of coastal habitats (see review in Hatcher *et al.*, 1989). As the demand for the use of coastal areas in socioeconomic development increases, estuaries, sandy shore surf zones, seagrass and mangrove habitats will be highly susceptible to direct human influences such as aquaculture, resorts, fishing ports and settlements (Hatcher *et al.*, 1989). Increasing development of shorelines and drainage areas causes the destruction of natural habitats, such as estuaries and mangroves, which in turn, may result in the loss of vital nursery grounds for many commercial species (Orth *et al.*, 1984; Robertson and Duke, 1987; Hatcher *et al.*, 1989; Robertson and Klump, 1993).

WHAT ARE NURSERY AREAS ?

Ecologists generally recognise nursery areas *sensu lato* as "the selected places for production and rearing of the young" (Heape, 1931; cited in Harden-Jones, 1968), a definition based on the cod, herring, and flounder nurseries of Europe. These species spawn within a narrow time frame at precise locations, and the developing larvae spend long periods in the nursery areas (Cushing, 1969; Iles & Sinclair, 1982). A classical interpretation of this definition is that these locations are selected to maximise the availability of food for their larvae and juveniles over spatial and temporal scales (Cushing, 1975, 1990). For example, areas that contain large numbers of suitable food species are able to support a correspondingly greater diversity of fish than similar areas with fewer numbers of food species. Thus, areas which provide good feeding conditions for young fish are likely to contribute a greater proportion of fish to the offshore stock than other less favourable areas.

The shallow inshore coastal habitats, including the sandy shore surf zones and estuaries, are often considered as nursery areas, since the early life stages of many fish species and crustaceans can be found in these habitats (Pearcy and Myers, 1974; Haedrich, 1983; Kennish, 1990; Brown and McLachlan, 1990). Several factors are believed to contribute to the quality of shallow coastal areas that act as habitats for juveniles. Joseph (1973) was probably the first to clarify nursery area conditions and suggested that these areas provided (1) abundant food sources to facilitate the rapid growth of juveniles, (2) suitable environments for physiological adaptation, and (3) a considerable degree of protection from predation. While the role of coastal habitats nurseries is widely accepted, few studies have evaluated the importance of nursery habitats relative to adjacent habitats, the exception being mangrove swamps (Robertson & Duke, 1987; Thayer et al., 1987; Laegdsgaard & Johnson, 1995). Currently, the reasons/ criteria for establishing tropical mangrove estuaries as nursery grounds are as follows: high turbidity for reducing the effectiveness of visual predators, food availability, and structurally complex shelters for predator avoidance (Robertson and Blaber, 1992).

Problems of determination/ interpretation

With regards to the criteria used to determine nursery grounds, several studies have used or modified Joseph's criteria (1973) to establish and evaluate nursery areas. Some investigations have suggested that the relationship between the size of organisms in an area and salinity be used as an indicator of nursery function (Dahlberg, 1972; Copeland & Bechtel, 1974). This relationship is not a simple one as it is difficult to assess the actual size of the area and the factors controlling salinity (Lankford and Targett, 1994). Reid (1957), Simmons (1957) and Reid & Hoese (1958) have also noted that interactions of organisms with food supplies, substratum characteristics, and other physical and chemical factors dictate the preferred zone for nursery utilisation. It is possible that habitats that show the potential to support a high number of juveniles or larvae, are in fact not capable of supporting such numbers because physical and biological characteristics of the habitat are of paramount importance (Poxton *et al.*, 1982).

Most workers have used larval and small juvenile occurrence and abundance to distinguish nursery habitats (e.g. Hughes, 1966; Pearcy and Myers, 1974; Modde, 1980; Modde and Ross, 1981; Lasiak, 1983, 1984a, 1984b, 1986; Ruple, 1984; Ross *et al.*, 1987; Robertson and Duke, 1987; Bennett, 1989; Heck *et al.*, 1989; Whitfield, 1989; Bolle *et al.*, 1994; Blaber *et al.*, 1995). There are however, several basic factors which are frequently overlooked in the assessment of nursery function, these include responses such as growth rate and survivorship. Nixon (1980) has reviewed the literature on the value of nurseries in estuaries and has found that despite a widespread belief that fisheries productivity depends on the amount of outwelling from estuaries, this relationship is not clear, because estuarine-dependent species may simply require shallow protected habitats. Based on available evidence, Boesch and Turner (1984) have attempted to determine the relative importance of trophic function and physical refuge for supporting estuarine fishes and concluded that estuarine function was inadequate to identify the relative importance of food production and refuge provisions. Recently, the importance of natural mortality processes in the early life history of fish has been recognised in fishery management (Bergman *et al.*, 1988; Jones, 1989; Van der Veer *et al.,* 1990). These processes include 1) abiotic sources of mortality (disturbance); 2) encounter rates with predators, and vulnerability to predation; 3) competitive interaction with other residents; and 4) availability of food, shelter sites, and other resources (including partners in mutualism). These processes are likely to affect both the mortality and recruitment rate of fish to a given population and the subsequent growth rate of that population. Bergman *et al.* (1988), Houde (1989) and Jones (1989) have demonstrated that natural mortality, which may be either density-dependent or density-independent or both, may exert its greatest influence during the early life stages of fishes in the nursery areas.

Why do nursery areas exist ?

In the course of evolution, species will evolve alternative strategies which maximise the number of off-spring produced within given habitats (Stearns, 1991). Since conditions within habitats vary over time, the evolution of reproductive strategies may be viewed from both a temporal and spatial scale (Southwood, 1977; Stearns, 1991). Southwood (1977) suggested that at each of these scales the habitats may be considered to offer a level of favourableness for survival and reproductive success. Habitats may be heterogeneous in nature, so that patches within habitats may be characterised on their degree of favourability. The favourability within each patch will also vary and this spatial variation will contribute to an individual's survival and reproductive success. Consequently, most organisms in the natural environment need to adapt their behavioural strategies for gathering food and migration ranges to match those of survival and reproductive success. The favourability of a habitat can be defined in terms of the mean rate of increase in survival and reproductive success, which is in turn, dependent on the level of resources available, number of natural enemies present, and density of total number of organisms in the habitats. The favourability of these habitats will of course be influenced by local events that may make the habitat more or less favourable and thus will have an effect on the population dynamics. By defining habitats in terms of favourability, comparisons on the favourability of habitats or nursery grounds for early life history stage can be made.

The literature, however offers little evidence to indicate the benefit of living in a nursery area. Moreover, most authors have used the term "nursery" without stating whether such categorisation refers to a richness or paucity in abundance, diversity, or 'quality of life' in terms of growth, survival, reproductive potential in nursery versus adjacent habitats, thereby limiting the value of their statements. Most evaluations of nursery areas in the past have relied on rather tentative assumptions including the abundance of presumed food sources and relatively lower occurrence of piscivorous species while overlooking the importance of inter-and intraspecific interactions.

Working definition of nursery areas

A detailed knowledge of factors influencing fish in inshore habitats is essential if we are to answer the broad question of if and why these habitats provide an important nursery function. Thus, the definition of a "nursery area" based on the quality of resources and the environment, as used previously in the literature, should be reconsidered. In reality, these factors are not sufficient to determine the function of a nursery as the life history of the individual can be thought of as a continual compromise between food gathering and survival (Jones, 1989; Walters and Juanes, 1993). In this context, most scientists have paid little attention to growth, survival or other early life history information. However, survival rate and success of recruitment to parent stocks, how fish respond to a selected habitat, and the length of time they spend in such habitats can not be predicted. High numbers of larvae within an area do not necessarily prove that it is a nursery area, as they may grow faster, survive longer (Van Horne, 1983) and be more abundant in other areas (Van Horne, 1983; Suthers *et al.*, 1989; Bolle *et al.*, 1994).

Thus it would appear that this is an appropriate time to question the use and meaning of the term "nursery area" in the context of biological and ecological approaches. A nursery area should be thought of as an area that makes it possible to maintain a population of early life stages for maximum potential growth, with a high survival rate and successful recruitment to juvenile/ adult populations. Inclusion of "survival rate" and "growth" factors in the nursery area definition should now be considered (Gibson, 1994). Permanent persistence of a species or populations owing to reliable geographical localisation within limited areas, along with a possible lack of competition or co-existence among sympatric species should also be considered. There should be a wide variety of factors to determine nursery area quality, and the importance of these various factors may vary between species. For example, food conditions often control growth, however, at present no accurate growth estimates are available for comparison between or among nursery habitats. This concept of a nursery area itself is only useful if it helps to transmit knowledge and clarify complex scientific problems. With this point in mind, it would be helpful to differentiate nursery areas into different functions such as feeding and spawning areas, while at the same time allowing for a whole range of interesting comparative studies among or between habitats, especially in tropical regions.

In order to ensure that this concept has a broad utility, this thesis suggests that a working definition for nursery areas should be "*Areas where young are able to persist whilst achieving high growth and survival rates*". This approach would be more preferable than the previous traditional habitat-based fishery definitions, as all measurements are based on quantitative aspects of the fish *per se* and provide a functional perspective, especially growth rates, which are more appropriate to the evaluation of a nursery area. Basically, this definition can be used to evaluate each species, since one habitat may be of a low or medium nursery quality for certain species and high for others, even if they are sympatric. This research will extend the work on the species area management approach for critical species.

Growth rates of fish during the early stage of their life histories is an excellent criterion for assessing the adequacy of feeding conditions in the environment (Osenberg et al., 1988; Theilacker, 1987; Van der Veer and Witte, 1993). A rapid growth rate should indicate a high probability of survival and successful recruitment to the subsequent adult population (Shepherd and Cushing, 1980; Houde, 1987; Jones, 1989). Another benefit of rapid growth is a decreasing vulnerability to predators. Individuals that grow quickly will spend less time in vulnerable size ranges, thus increasing their survival as mortality decreases with increasing size (Brett, 1979; Shephard and Cushing, 1980; Calow, 1985; Kiørboe *et al.*, 1988; McGurk, 1986; Ware, 1975; Werner and Gilliam, 1984; Jones, 1989). Relatively fast growth rates which result from utilisation of nursery areas may carry benefits through to adulthood in terms of subsequent survival and competitive advantages.

As yet there is no experimental evidence to support this proposed definition of nursery function in the tropics. The goal of this thesis is to determine the relative value of nurseries in the mouth of tropical estuaries and sandy shore surf zones by applying a part of the proposed nursery function concept to these habitats. I will use abundance, feeding success and growth rate to assess the relative value of the two areas in terms of possible nursery function.

APPROACH

This thesis focuses on biological parameters of juvenile fish as a means of testing the role of two dominant tropical coastal habitats, sandy shore surf zones and estuary mouths, as possible nursery areas. Given that several tropical mangrove estuaries, especially in South East Asia, are currently being destroyed to some extent by shrimp farming, comparisons between sandy shore surf zones and estuary mouths is of particular interest. These areas were selected as they are also widespread and represent two of the primary habitats available in tropical regions of Northern Australia. Fish species associated with sandy shore surf zones and estuary mouths in two major areas of tropical North Queensland (the east coast of Australia and the Gulf of Carpentaria) have received considerable attention. However, the majority of data available from the east coast of Australia are species lists, with some biological studies of fish in mangrove areas in Townsville by Penridge (1971), Beumer (1978), Robertson and Duke (1987, 1990a, 1990b), Molony (1993), Sheaves (1992, 1993, 1995) and Trinity Inlet in Cairns by Blaber (1980). Several studies related to fish abundance, biomass and some biological aspects from the Gulf of Carpentaria were undertaken by Blaber (1986), Blaber *et al.* (1989, 1990a, 1990b).

This thesis will assess the relative value of sandy shore surf zones and estuary mouths as nursery areas using three types of data: 1) temporal and spatial variation in abundance, 2) feeding and 3) growth. There were several reasons for choosing the estuary mouth and not the whole estuary as a study site. First, it is very difficult to define and locate specific ecological regions within estuaries. The estuary mouth is relatively well defined as a fixed spatial position. Second, although estuary mouths are influenced by estuarine factors including freshwater input, organic input, shelters etc., they still permit the use of one type of gear (i.e. seine nets), while higher up or outer parts of an estuary need other methods. Difficulties with employing different sampling methods in different environments often precluded comparative studies and has perpetuated the speculative debate on the most appropriate habitat for a particular juvenile species. Thirdly, the estuary mouth at the lower reach of the estuary is recognised as an area of relatively high species diversity and biomass (Blaber *et al.*, 1989).

Temporal and spatial variations in the distribution and abundance of intertidal fishes will be examined to determine the degree of natural variation in the assemblages between habitats. Ross (1986), however, suggested that such information becomes less relevant to understanding the role of habitat in life history than biological interactions. Subsequently, the remaining parts of this thesis have been directed towards quantitative evaluation of resource use and 'quality of life' with the goal of evaluating the differences in the relative value of nursery areas in sandy shore surf zones and estuary mouths for fish. Both univariate (Chapter 3) and multivariate (Chapter 4) techniques are used to analyse and describe the abundance and distribution patterns of the fish assemblages. The relative nursery value of the two habitats is based primarily on feeding and growth parameters. This focuses on 4 species: *Stolephorus nelsoni* (Wongratana, 1987), *Sillago analis* (Whitley, 1943), *Leiognathus splendens* (Cuvier, 1829) and *Valamugil seheli* (Forsskål, 1775). These species represent different phylogenetic groups (Clupeiformes, Perciformes and Mugiliformes) and have different life histories and trophic status. Therefore, any common patterns are more likely to reflect broad habitat-associated trends rather than specific adaptations. In addition, these species were selected as they occurred in large numbers, cover a wide size range, and were present in both study habitats.

Somatic growth in juveniles is typically varied and related primarily to food resources (Theilacker, 1987). Many fish species in natural habitats sequentially exploit a series of food types throughout their lifetime (Helfman, 1978; Livingston, 1982). Knowledge of the feeding habits of juveniles is necessary for understanding the role of diet in the recruitment process of these selected species. In Chapter 5, the diets of juveniles of the four selected species will be examined qualitatively and quantitatively. Differences in diets between habitats will be used for assessing the potential relationship between habitat and growth rates.

Jones (1989) suggested that growth rates during the juvenile stage tend to be particularly variable and that this may be the result of the nature of the immediate habitat. Growth rates of each selected species will be determined by using age-length relationships. Length-at-age, age-specific-growth, and size-specific-growth from sandy shore surf zone and estuary mouth habitats will be compared by means of stepwise multiple regressions (Chapter 6). The ‘bigger is better concept’ (Shepard and Cushing, 1980; Leggett and Deblois, 1994) will be used to compare habitats. Differences between habitats will also be interpreted in relation to stomach content analyses. Thus, the combination of feeding data and growth data will be used as a basis to provide a qualitative evaluation of the relative nursery value of the two habitats (Chapter 7).

CHAPTER 2

STUDY SITES, GENERAL METHODS AND INTRODUCTION TO SELECTED SPECIES

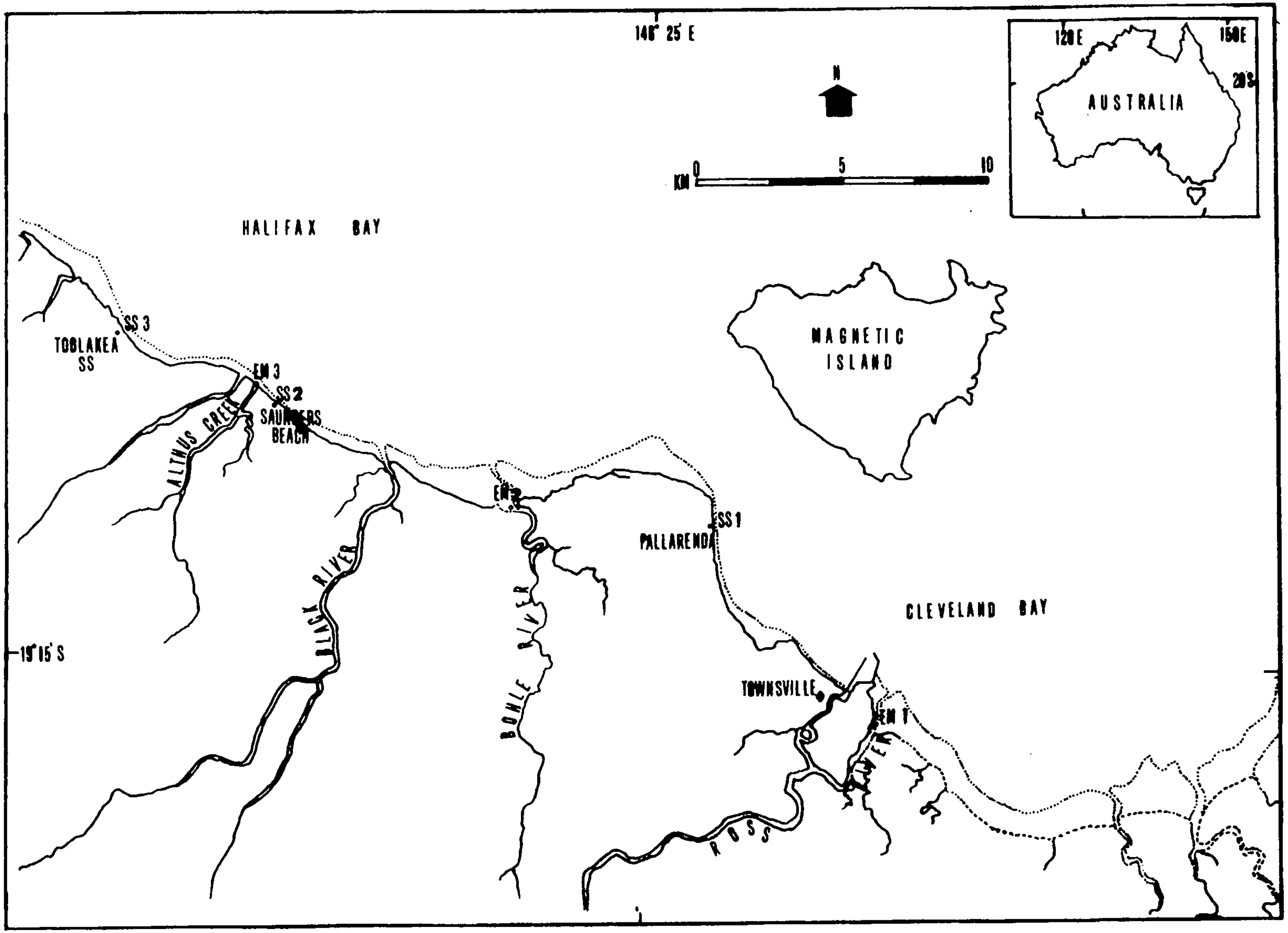
STUDY AREAS

The study area is located in tropical North Queensland, approximately midway along the eastern coast of the state of Queensland, between 18° 50′ and 19° 20′ S and 146° 00′ and 146° 30′ E. The area is part of an archipelago, and is influenced by a tropical climate. The sampling sites, Halifax Bay and Cleveland Bay, are located on the landward margin of the Great Barrier Reef lagoon (Fig. 2.1). Terrigenous mud and quartz sand with low carbonate concentrations are the main sedimentary characteristics of this region (Belperio, 1983). These sediments are found in a narrow band along the entire coast.

The region experiences marked seasonality with wet summers (November-April) and dry winters (May-October). Mean annual rainfall recorded at Townsville from 1871-1988 (Pringle, 1989) was 1147 mm, however the overall pattern of rainfall is highly variable. Rain is concentrated between December and March, with moderate rainfall occurring in November and April. Changes in temperature patterns between seasons occur slowly without any sharp variations. As recorded in Pickard *et al.* (1977) and Oliver (1978), mean monthly air temperature reaches its maxima in December and January (31.5^{o}C) and minima in July or August (22.5^{o}C). Stream flow and run off patterns in this region are mainly dependent on rainfall intensity and duration of rainfall in mainland areas (Oliver, 1978; Mitchell *et al.*, 1991).

Tides within the study areas are predominantly semidiurnal with pronounced diurnal inequality. Mean maximum tidal range is 3.8 m, with high tide extending from 2.3 m to an extreme of 4.2 m from the lowest tide water mark (Department of Defence, 1995).

Figure 2.1. Cleveland Bay and Halifax Bay, North Queensland, Australia showing the study sites (SS1, SS2, SS3= sandy shore surf zone sites 1, 2 and 3; EM1, EM2, EM3= estuary mouth sites 1,2 and 3).


146° 25' E
N
0
5
10
KM
120E
150E
20S
AUSTRALIA
HALIFAX BAY
MAGNETIC ISLAND
SS 3
TOOLAKEA SS
EM 3
SS 2
SAUNDERS BEACH
ALTHUS CREEK
BLACK RIVER
EM 2
SS 1
PALLARENDA
BOHLE RIVER
CLEVELAND BAY
19°15'S
TOWNSVILLE
EM 1
ROSS
AWER
CR

Extreme tidal ranges result in significant exposures of intertidal habitats. The coastline in the area is protected from the oceanic swell of the south-west Pacific Ocean by the Great Barrier Reef system.

At least three common types of coastal areas occur on the east coast of tropical North Queensland. Rocky shorelines are associated with headlands and are found on most capes, while sand and cobble beaches occur between capes. Mangroves, mud flats, estuary mouths and estuaries also occur, and develop mainly in the vicinity of river systems. In this study, two different habitats along the coast, sandy shore surf zones and estuary mouths, will be investigated.

Sandy shore surf zones have no clear cut boundaries and cover the dynamic area between the sea and shore, without any clear cut boundaries. In the present study these areas are represented by the sandy coast from high water mark to the outer limit of surf circulation cells at low tide. The major substratum types consist of various sizes of sand.

Estuary refers to shallow marine waters which are defined as semi-enclosed bodies of water with a free connection to the ocean. Estuaries contain sea water measurably diluted by periodical freshwater run-off, they are affected by tides, and are usually shallower than 20 m (Kjerfve and Magill, 1989). In this present study a part of the estuarine system, the estuary mouth, was investigated. The estuary mouth is defined here as the region where rivers and creeks open into the sea. These areas were generally open throughout the year but freshwater input only during occurred wet periods. These estuary mouths were subjected to regular and strong tidal movements. In the present study, samples were taken from the shallow sloping intertidal sandy mud beach within 300-500 m of the estuary mouth. The major component of the sediment of the estuary mouth was silt and small amounts of fine sand.

STUDY SITES

The details of the present study were carried out at the following sites:

Cleveland Bay

Cleveland Bay is approximately 27 km wide and covers an area of approximately 400 km^2. The bay is shallow, reaching a maximum depth of 15 m at its seaward edge, and is sheltered from the dominant southeasterly trade winds by Cape Cleveland, which forms the southern margin of the bay. Water circulation within the bay is dominated by the effects of southeasterly-generated waves and semi-diurnal tidal currents (Carter and Johnson, 1987). Tidal currents rotate in an anticlockwise direction with south and south-southeasterly flood currents and north-northeasterly ebb currents. The tidal current patterns result in preferential sediment accumulations on the eastern side of the bay. The three major sources of direct run-off into the bay are from Ross River, Alligator Creek and Crocodile Creek. Pringle (1989) has suggested that the amount of discharge from the Burdekin River to the south may also have some influence on the hydrological patterns and chemical properties of Cleveland Bay.

Mangroves occur along the edge of creeks and form dense forests adjacent to the coast. Behind these are areas of salt-pan. *Rhizophora stylosa*, *Avicennia marina* and *Ceriops tagal* are the dominant mangrove species within this area (Robertson and Duke, 1987). Within the bay, seagrass beds occur in intertidal and subtidal areas with soft mud. These beds are mostly comprised of *Cymodocea serrulata, Halophila ovalis* and *Halodule uninervis* (Pringle, 1989).

Two study sites were selected from Cleveland Bay, Pallarenda Beach (a sandy shore surf zone) and the mouth of Ross River. Thus both habitat types are represented at this study site.

Halifax Bay

Halifax Bay lies to the north of Cleveland Bay. The Bohle, Alice and Black Rivers are the main sources of run-off into the southernmost region of the Bay, while some small tidal creeks such as Deep, Althus and Bluewater also flow into the bay. Southeasterly trade winds generate a strong northerly longshore current and carry terrigenous sediment north-eastward along the coast. This sediment is deposited on sandbanks or forms sandbars along the entire coast. There is no distinct mangrove vegetation or seagrass beds in these intertidal areas, except for areas along the bank of the river mouths and tidal creeks. *R. stylosa* and *A. marina* are still the main mangrove in these areas.

At this site, Saunders and Toolakea Beaches were selected as being representative of sandy shore surf zone habitats, while the mouth of the Bohle river and Althus Creek were selected to represent estuary mouth habitats. Both are easily accessible by road.

Pallarenda Beach (SS1, Figs 2.1 and 2.2A)

Pallarenda Beach is an exposed ocean beach facing east north-east. Its littoral zone extends over a width of up to 350 m. A narrow upper beach of relatively coarse sand adjoins the sand dune in Rowes Bay. Below this is a series of irregular sand bars which are generally arranged parallel to the coast and exposed at low tide. Medium and fine sand are the major substratum components. Seagrass beds occur at the low water mark edge (Pringle, 1989).

Ross River Mouth (EM1, Figs. 2.1 and 2.2B)

The Ross River site, located at the mouth of Ross River, is a sheltered area bordered by mangroves, and has a coastline consisting of sandbanks, mudflats and sand ridges. Due to land reclamation on the western shore of the mouth of Ross River, there are

Figure 2.2
Study locations at low tide (approximately 0.22 above the lowest tide mark).
A) Pallarenda Beach (SS1).
B) Ross River Mouth (EM1).

only a few colonies of the pioneer mangrove species, *Avicennia marina* and *Rhizophora stylosa*, on this bank. The littoral zone in this area extends for some distance (up to approximately 500 m) with silt and clay forming the major substratum constituents.

Saunders Beach (SS2, Figs. 2.1 and 2.3A)

Saunders Beach faces the north-eastern part of Halifax bay and is directly exposed to southeasterly trade winds. The littoral zone extends over a distance of approximately 200 m. Fine sand and clays are the principal substratum components.

Toolakea Beach (SS3, Fig. 2.1 and 2.3B)

Toolakea Beach is a small and steep, coarse sandy beach, extending from the highest astronomical tide level (3.98 m) to approximately 0.6 m above low tide water mark. Beyond this, a 200 m wide medium-coarse sand platform extends to the lowest tide water mark. No mangrove areas or seagrass beds exist in the intertidal zones of this beach.

Bohle River Mouth (EM2, Figs. 2.1 and 2.4A)

The Bohle River site is a large tidal mud flat at the mouth of the Bohle River. Coastline patterns are similar to those of the mouth of Ross River, with sandbanks, sand ridges, mud flats and mangrove areas. The tidal sandy mud flat extends over 750 m, with *Avicennia marina, Rhizophora stylosa* and other members of Rhizophoraceae being abundant along the coastal margin.

Althus Creek Mouth (EM3, Figs. 2.1 and 2.4B)

Althus Creek is a small creek with a sandbar and delta situated at the mouth of the creek. These features protect the opening from strong winds and waves. *Rhizophora stylosa* and other members of the Rhizophoraceae are abundant, along almost the entire bank.

Figure 2.3
Study locations at low tide (approximately 0.22 m above the lowest tide mark).
A) Saunders Beach (SS2).
B) Toolakea Beach (SS3).

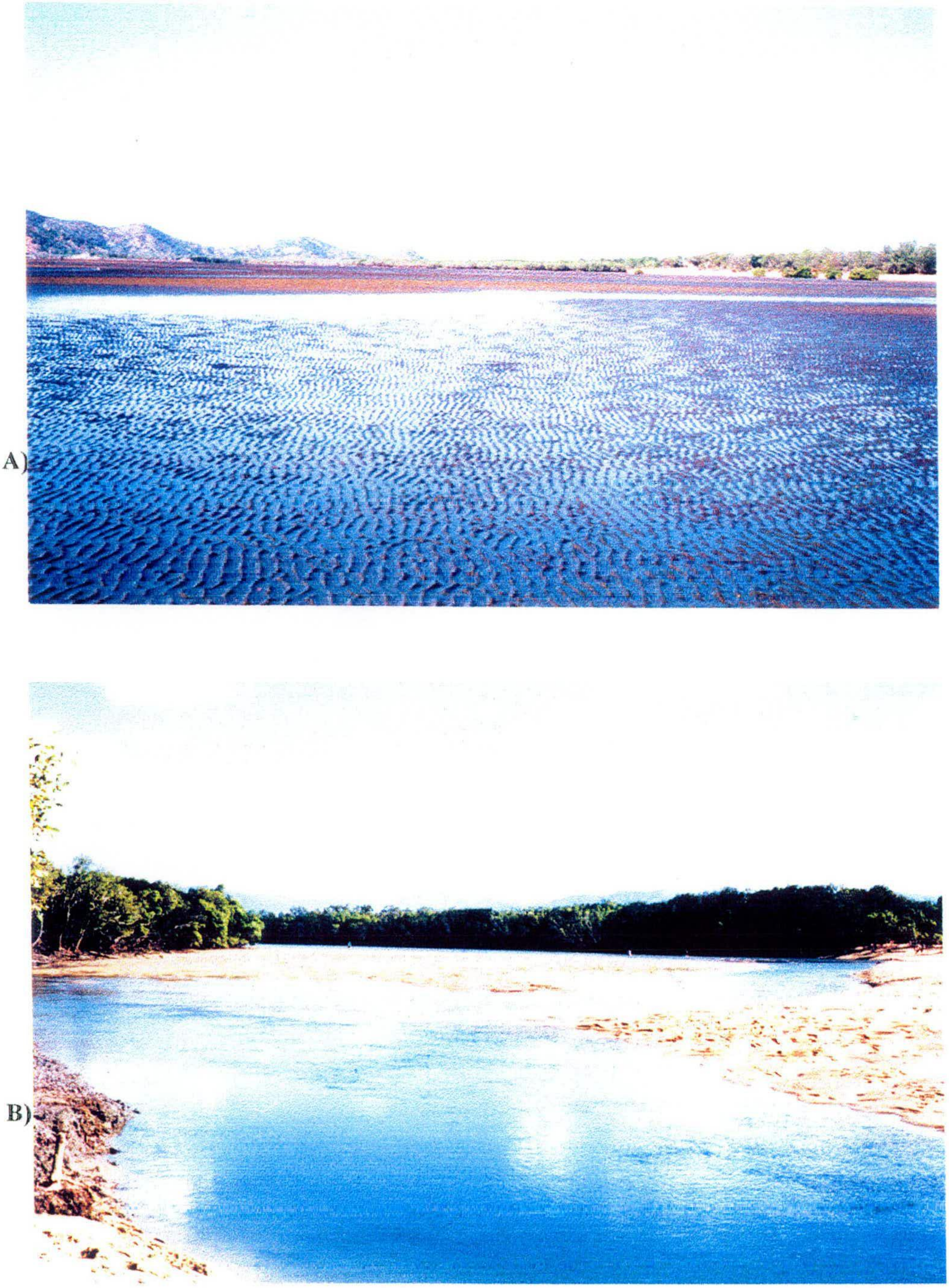


Figure 2.4
Study locations at low tide (approximately 0.22 m above the lowest tide mark).
A) Bohle River Mouth (EM 2).
B) Althus Creek Mouth (EM 3).

Substratum Assessment

As would be expected, sediment in sandy shore surf zones locations were generally coarser, with sand contents exceeding more than 80 %, whereas in estuary mouth locations sand contents were always below 60 % (Table 2.1). Coarse sand with diameter greater than 2000 μ was negligible to non existence in all locations. The organic content was also generally greater in estuary mouths. While the diameter of grain size of Althus Creek Mouth overlapped with sandy shore surf zone's particles, it still had the proportion of sand and organic matter characteristic of estuary mouths; therefore, it was grouped with estuary mouth habitats.

Table 2.1. Comparison of median grain size, percent of silt and clay, percent of sand and organic matter in substratum of all studied sites

Locations	Size	%Silt+Clay	%Sand	%OM
Pallarenda Beach	556.67±53.64	2.24±0.31	97.76±0.31	0.67±0.05
Saunders Beach	306.67±13.33	2.62±0.76	97.37±0.76	0.64±0.03
Toolakea Beach	946.67±207.95	0.29±0.04	99.71±0.04	0.48±0.06
Ross River Mouth	140.00±17.32	17.70±4.04	82.30±4.04	2.22±0.2
Bohle River Mouth	83.33±14.53	41.65±4.46	58.35±4.46	1.77±0.03
Althus Creek	123.33±8.82	50.04±18.91	59.52±19.04	1.23±0.15

SAMPLING METHODS

Fish were collected using a 15m x 2m beach seine net made of knotless 5 mm stretched mesh netting, with a 1.5 m purse bag in the middle. The net was operated approximately 15 m from the shoreline, at a depth of 1-1.5 m. The operation of the net required two people, each person holding a pole clipped to the end of the net whilst dragging the net perpendicularly towards the shoreline. The area sampled by the net was approximately 225 m^2.

The sampling program was carried out on a bi-monthly basis from January 1992. Due to time limitations and the distance between locations, the sampling program was split into two consecutive days according to their location. On the first day, samples were obtained from Saunders Beach, Althus Creek and Toolakea beach. The remaining locations were sampled on the second day, or vice versa. Prior to the decision to split the sampling program a pilot study was undertaken which indicated that there was no significant difference detected between consecutive days for numbers of species or individuals. In order to minimise tidal effects, sampling was conducted during the new moon at peak high tide in the early morning of each sampling day. The sample sites were always exposed during preceeding low tides, and covered by 1.0-1.5 m water during collections. Sampling time occurred within about 2 hours before and after peak tide.

TREATMENT OF SAMPLES

All specimens from each sampling haul were immediately preserved in separate plastic bags with 10% neutral formalin and transported to the laboratory where they were sorted according to taxa, counted and weighed. Specimens were then identified according to the lowest possible taxon, by using the available taxonomic literature (including Allen and Swainston, 1988; Fischer and Whitehead, 1974; Fischer and Bianchi, 1984; Munro, 1967; Smith and Heemstra, 1986; and Gloerfelt-Trap and Kailola, 1985). This information will be used for determination of temporal and spatial variation in abundance and biomass of whole fish communities (Chapter 3) and fish assemblage patterns (Chapter 4).

Four main species, details given below, were separated and measured to the nearest 0.1 mm and stored in 70% alcohol within 3 days of collection for further stomach contents analysis (Chapter 5), and age and growth information from otolith studies (Chapters 5 and 6 respectively).

SOME EARLY LIFE HISTORY BIOLOGY DEFINITIONS

Definitions and terms for early life history biology and developmental stages vary considerably depending on the investigators and the species involved. For consistency, the following terminology has been used throughout the present study.

Juvenile is defined as the stage starting when larvae achieve the minimum adult fin-ray complement and ending with the acquisition of the adult body form and sexual maturity (Heath, 1992).

Recruitment refers to the arrival and residence of juveniles in the intertidal habitats.

Duration of residence refers to the period of time that juveniles remain in intertidal habitats (as estimated by modal progression analyses).

Size at first recruit is defined as the smallest juveniles/post larvae which were captured in intertidal habitats by the seine net.

INTRODUCTION TO SELECTED SPECIES

In this study, the main focus is on the abundance, growth rates and diets of 4 selected species: *Stolephorus nelsoni* Wongratana, 1987 (Clupeiformes: Engraulidae), *Sillago analis* Whitley, 1943 (Perciformes: Sillaginidae), *Leiognathus splendens* (Cuvier, 1829) (Perciformes: Leiognathidae), and *Valamugil seheli* (Forsskål, 1775) (Mugiliformes: Mugilidae). These four species have been selected because they are common within both habitat types and occur in abundance nearly all the year round.

Stolephorus nelsoni Wongratana, 1987 (Fig. 2.5A)

This stolephorid anchovy is a small (approximately 80 mm S.L.), schooling clupeoid fish which inhabits coastal regions throughout the tropical Indo-West Pacific. Wongratana's (1987) original description of this species, which includes two paratypes from Cleveland Bay, provides an identification key to all 18 *Stolephorus* spp. occurring in this region. Hoedt (1984) found that *S. nelsoni* was one of the

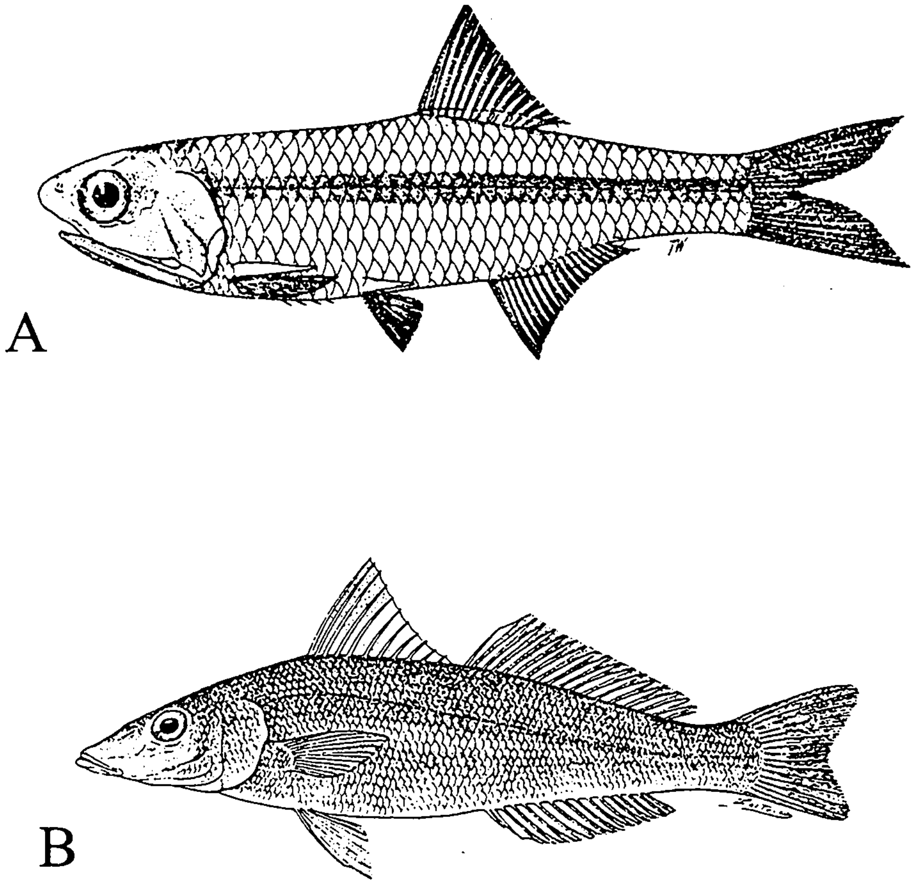


Figure 2.5 General morphology of selected species

A) *Stolephorus nelsoni* Wongratana, 1987 (From Wongratana, 1987)

B) *Sillago analis* Whitley, 1943 (From Grant, 1972) commonest anchovies and that these species spawn throughout the year in nearshore waters of Townsville. In a later study, Hoedt (1994) found that *S. nelsoni* was the most common anchovy of the catch in this area.

Diagnostic characteristics: *S. nelsoni* has a moderately deep compressed body, and distinctive long pelvic fins with tips terminating vertically through the first quarter of the dorsal fin. There is no predorsal spine or interpelvic scute.

Distinguishing characteristics of other local *Stolephorus*: *S. carpentariae* is one of the most common species in this area, however, this species has relatively short pelvic fins with tips terminating vertically through the dorsal fin origin. It has a series of prominent diagonal black spots at the anal fin bases. *S. insularis* occur in the winter season and have relatively short pelvic fins that are characterised by a series of posterior dorsal double pigmented lines. *S. commersonii* is another common species, it has relatively long pelvic fins that are characterised by a series of double pigmented lines before the dorsal fin origin. It also has an anal fin that is inserted vertically below the mid-dorsal.

Sillago analis Whitley, 1943 (Fig. 2.5B)

S. analis is a member of the family Sillaginidae. This family is widely distributed with 31 species spread throughout the Indo-West Pacific Ocean. It is well-represented in Australian waters with 13 species (McKay, 1992). In Australia, sillaginids (whiting) are among the most favoured recreational fishing species found in most sandy beaches and estuaries. They have an elongate body with a conical snout which facilitates burrowing in the soft substratum for foraging or escaping predators. Sillaginids inhabit open sandflats and muddy substratum, including estuaries and near shores along beaches subject to moderately strong wave action. Benthic and epibenthic fauna (principally polychaete worms, small shrimps, small crabs, bivalves and fish) are commonly reported as their main diet (Munro, 1967; Gunn and Milward, 1985; McKay, 1992).

Diagnostic characteristics : Similar external morphology among species has led to confusion in species identification. Fin ray counts, lateral line scale numbers and body pigmentation patterns are the most useful features for identifying sillaginids occurring in the study areas. A series of black spots and bars occur along the mid-lateral section and above the body of fish less than 100 mm. There are no black spots on the pectoral fin bases.

Distinguishing characteristics of other local species : Three sillaginids species have been found in the study sites: *S. sihama, S. ciliata* and *S. analis*. In the field, *S. sihama* is more slender than *S. analis* and lacks body pigmentation patterns. It also has a higher number of dorsal fin rays, 21-22 compared with 18 in *S. analis*. *S. ciliata* has more black spots on the body than *S. analis*. *S. ciliata* also has black spots at the pectoral fin bases, which are either few or absent in *S. analis*.

Leiognathus splendens (Cuvier, 1829) (Fig. 2.6 A)

Leiognathid are small fishes with moderate to strongly compressed bodies. Protractile mouthparts and the presence of a nuchal spine with a bony ridge at the top of the head make this genus unique (Gloerfelt-Trap and Kailola, 1984; Jones, 1985). These fishes consume a wide range of food items from benthic flora, benthic fauna and plankton. The family is widely distributed throughout the entire tropical and subtropical coastal Indo-West Pacific region and forms the main catch component in many trawled fisheries (Gloerfelt-Trap and Kailola, 1984; James, 1975; Jones, 1985).

In a revision of the taxonomy of this family, Jones (1985) reported at least 15 leiognathid species in Australian waters, 12 of which belong to the genus *Leiognathus*.

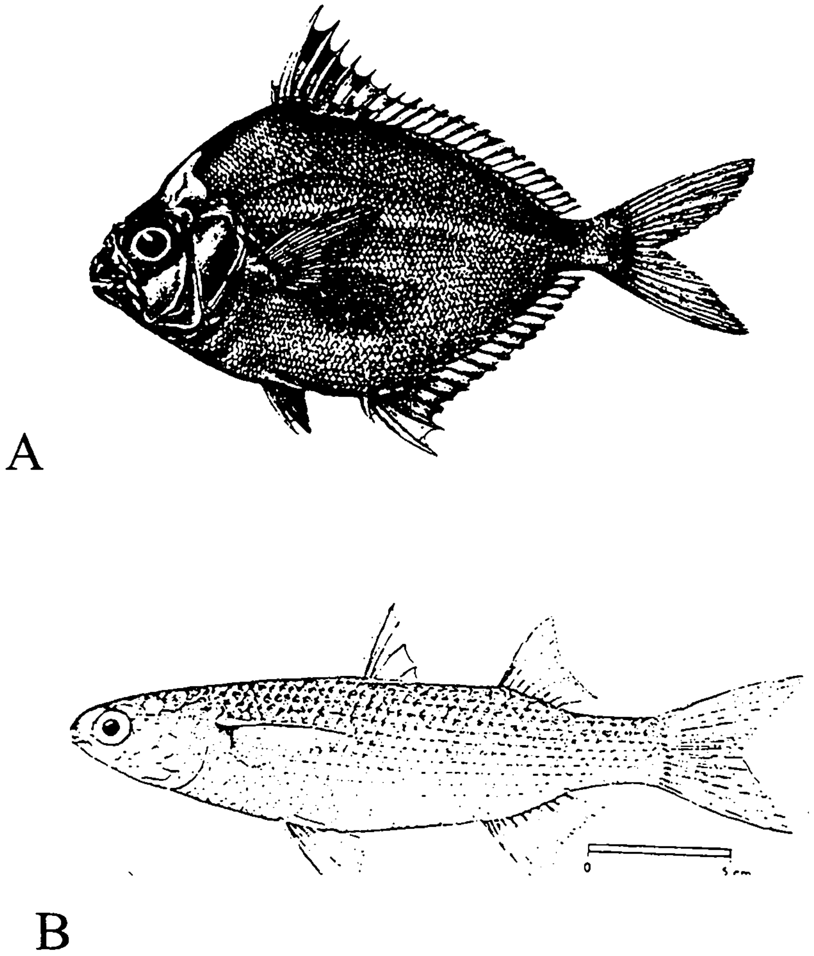


Figure 2.6 General morphology of selected species

A) *Leiognathus splendens* (Cuvier, 1829); (From Day, 1899)

B) *Valamugil seheli* (Forsskal, 1775); (From Thomson and Luther, 1984)

Diagnostic characteristics: *L. splendens* is oblong in body shape with a scaled breast and protracted mouth directed downwards. A distinct black blotch on the outer half of the spinous dorsal fin, and wavy vertical lines on the upper half of the body have been identified as consistent and distinctive characteristics of *L. splendens* (Jones, 1985).

Distinguishing characteristics of other local species: Several Leiognathids occur in the target study areas, namely *L. bindus, L. decorus, L. moretonensis, L. equulus, Secutor rucornis* and *Gazza minuta*. *Leiognathus* spp. differ from other genera because of their downwards protracted mouthparts. Within the genus *Leiognathus*, *L. equulus, L. decorus, L. moretonensis* and *L. splendens* are the only species that have their chest partially or totally covered with scales. *L. splendens* is the only species which has a fully-scaled chest and a conspicuous black blotch on the outer half of the dorsal fin (Jones, 1985).

Valamugil seheli (Forsskål, 1775) (Fig. 2.6 B)

V. seheli is a member of the mullet family Mugilidae. Mullets are littoral species of commercial value for both human consumption and as baitfish (Munro, 1967). Mullets are abundant, usually forming large schools in coastal waters and estuaries, and are able to tolerate great changes in salinity. *V. seheli* were selected for this study, due to their abundance and the fact that they are easy to distinguish from other mullets in the study area.

Diagnostic characteristics: Mullets belonging to the genera *Valamugil* have a moderately robust body with a wide, dorsally-flattened head and well-developed pectoral axillary scales. In *V. seheli*, the second dorsal fin originates vertically through the anal fin origin. The hind end of the maxilla extends vertically between the posterior nostrils and the anterior margin of the eye. The adipose eyelids are only slightly developed, mainly around the rim of the eye. There are 38 - 42 scales along the lateral series while the origin of the second dorsal fin origin is opposite the 26th - 28th scale of the lateral series.

Distinguishing characteristics of other local species: In other mullet species, the pectoral fins are relatively short and do not extend to the vertical position from the origin of the first dorsal fin. Within the genus *Valamugil*, other species have less than 37 scales in the lateral series, except for *V. speigleri* which has 37-40 scales. However, unlike *V. seheli* this species has a well developed adipose eyelid over the iris. *V. buchanani* is a close relative of *V. seheli* and has the same second dorsal fin position, but fewer lateral scales (32 - 36).

CHAPTER 3

SPATIAL AND TEMPORAL VARIATIONS IN ABUNDANCE AND BIOMASS OF INTERTIDAL FISH ASSEMBLAGES BETWEEN SANDY SHORE SURF ZONES AND ESTUARY MOUTHS

INTRODUCTION

Estuaries and coastal waters have long been recognised as important areas supporting the early life history stages of various marine fish species of recreational and commercial value (Bell *et al.*, 1984; Boesch and Turner, 1984; Blaber and Milton, 1990; Blaber *et al.*, 1985; Robertson and Duke, 1987).

Many recent studies have provided qualitative descriptions and basic quantitative information on the total numbers and/or biomass of the most common taxa in these areas. In most cases however, these studies have been conducted over limited spatial or temporal scales only. Often the data has been collected on one occasion or if collected over time, restricted to one habitat at a specific site. Alternatively, where sampling has occurred at more than one site, the sampling has been limited to one bay or to one estuary from one particular area, such as Lasiak (1986), Modde (1980), Ross *et al.* (1987), Ruple (1984) and Whitfield (1989). Thus these studies have provided only limited information on habitat variability or on possible population changes through time. In order to overcome these problems, Green (1979), Underwood (1981) and Andrew and Mapstone (1987) have recommended the use of nested sampling designs, whereby each series of successively smaller spatial or temporal scales is nested within the above larger scales. Nested sampling designs provide estimates of the contribution of each scale to the total variation among samples within the analysis.

Coastal fish communities are highly dynamic because they tend to be dominated by a variety of migratory species which enter inshore habitats from open waters at certain periods of their life cycles, especially as larvae and juveniles (Haedrich, 1983; Kennish, 1990). Different species migrate to these areas at different times, producing "episodic recruitment" (Lasiak, 1984b; Allen and Barker, 1990; Kennish, 1990; Houde, 1994). This dynamic nature of coastal fish assemblages influences quantitative analysis, and complicates studies of factors affecting such communities.

No comparative information on the abundance and diversity of juvenile fish species between intertidal areas of sandy shore surf zones and estuary mouths are currently available for North Queensland in particular, or for the tropical Indo-West Pacific region in general. Little information on the fish fauna in Indo-Pacific estuaries and sandy shore surf zones has been published. Although there are several key studies, few are of a comparative nature e.g. Ponggol estuary in Singapore (Chua, 1973), Trinity estuary in North Queensland (Blaber, 1980), mangrove creeks and inshore areas, Dampier, Western Australia (Blaber *et. al.*, 1985), mangrove creeks, Townsville, Queensland (Penridge, 1971; Robertson and Duke, 1990a, 1990b; Sheaves, 1992, 1993, 1995), Leanyer swamp and the Norman River estuary in the Northern Territory (Davis, 1988; Russell and Garrett, 1983; respectively). Cabanban (1991) has reported seasonal variations and abundances of *Leiognathus* spp. and coastal fish communities in the Cleveland Bay region.

The main aims of this chapter are to quantify differences in ichthyofaunal abundance and biomass between intertidal areas of sandy shore surf zones and mangrove-lined estuary mouths. These data will provide a long term baseline study of abundance and biomass of juvenile fishes for tropical sandy shore surf zones and estuary mouths, areas that have received little attention to date. This study focuses primarily on juvenile fish and investigates whether their contribution to total abundance and biomass differs between sandy shore surf zones and estuary mouth habitats. The principal question of this study is: Do sandy shore surf zones support a greater diversity and abundance of fish fauna than estuary mouth habitats over large spatial and temporal scales? Temporal and spatial variations in abundance and biomass of the dominant species in the intertidal assemblages will also be examined.

MATERIALS AND METHODS

Care was taken in the sampling designs to gain an adequate understanding of variation in abundance with time and space.

Sampling designs

Spatial variation: Sandy shore surf zones and estuarine habitats are the major habitats found along the North Queensland coast (Fig. 2.1). In order to eliminate confounding factors, the sampling design (Fig. 3.1) incorporates four spatial levels: hauls, sites, locations and habitats. Three replicate locations within each habitat were spaced approximately 4-10 km apart. At each location, three replicate sites were established, 100-500 m apart. Three replicate hauls were taken at each site. In this design, locations and sites within locations were defined as being fixed, as the same locations and the same sites were visited on all occasions.

Temporal variations: A hierarchical design for temporal variations of abundance and biomass was classified into three levels, years, seasons and trips (Fig. 3.1). The study was conducted over a period of three years with bimonthly sampling. The three replicate trips for each season were intended to provide greater generality to the year, season and habitat results.

Statistical analysis

Data from the entire survey period for total species abundance, total species number, total species biomass and selected species abundance and biomass were analysed by using mixed model ANOVAs. Fish samples were divided into summer (November-April) and winter (May-October) seasons. Trips (T) were considered as random factors nested in

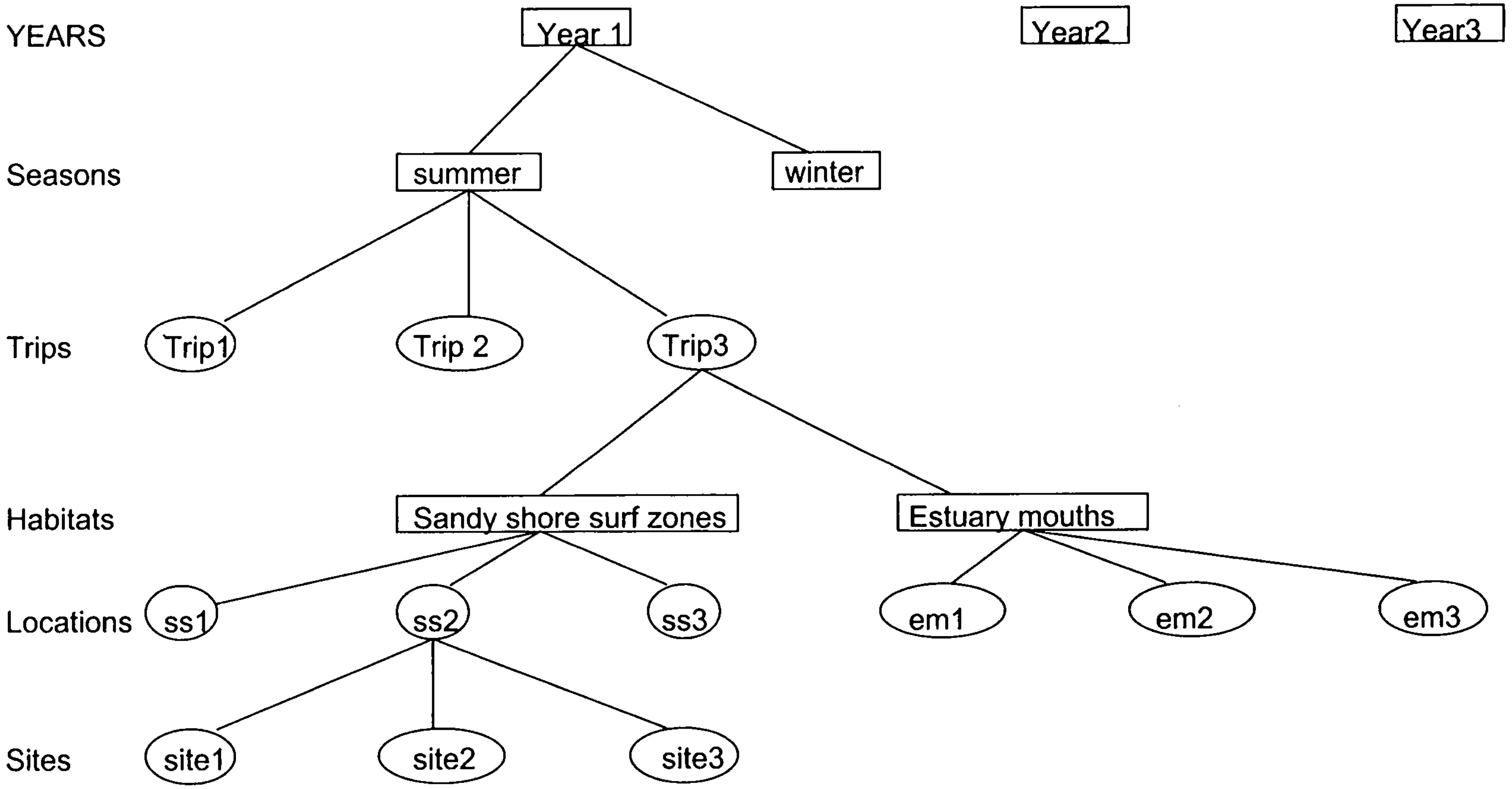


Figure 3.1. Multistage sampling design showing main sampling levels and relationships. Three replicate hauls were randomly taken at each site. Location abbreviations are given in Chapter 2.

interactions of years (Y) and seasons (S), while sites and locations were fixed factors although they appeared as random factors to represent the variations within locations (L) and habitats (H) of sampling designs respectively (Fig. 3.1). In contrast, years, seasons and habitats were treated as fixed factors.

Due to the patchiness of species in the samples, there were numerous zero values in the data set and consequently it did not produce homogeneous variances. Mean densities for each species at each site were therefore calculated and used, instead of the original values. The final ANOVA model (Equation 1) used was a simplified version of the original since no significant differences were detected at the replicate haul, site and location levels. Consequently, mean abundance and biomass for each trip at a given site were used as dependent variables . The following is the analysis of variance model used:

$$\mathrm{E}(\mathrm{Y}_{\mathrm{ijklm}}) = \mu + Y_i + S_j + H_k + YS_{ij} + YH_{ik} + SH_{jk} + YSH_{ijk} + T(YS)_{l(ij)} + TH_{kl(ij)} + \varepsilon \qquad \text{(Equation 1)}$$

Mean-squares estimates for the four factor analyses are shown in Appendix 1.

Homogeneity of variances for dependent variables was tested using the scatter plot of studentised residuals (Sokal and Rohlf, 1981). All dependent variables were transformed to improve normality and homogeneity of variances. For the purpose of this study, standard log-transformations ($log\ x+c$) were applied. Berry (1987) has suggested that the addition of a constant (c) in log-transformation for ANOVAs should be appropriate for data with lots of zero and that it would not affect the test statistic, or at least there would only be minimal effects to symmetrical residuals. This method would also minimise skewness and improve kurtosis. As recommended by Box (1953), ANOVA is fairly robust to departures from homogeneity of variances when sample sizes are equal. Therefore ANOVA was employed for this particular study even where heterogeneity or non-normality of variance existed. In order to compensate for this problem and increase the likelihood of minimising significant differences due to Type I error, these analyses were interpreted by the use of conservative $\alpha = 0.01$ significant levels, instead of the more popular $\alpha = 0.05$ (Underwood, 1981). It is important to note that differences among years, seasons and habitats are not testable unless interactions among them are non-significant. In this study, Ryan-Einst-Gabriel-Welsch multiple range test was used to detect the differences between the means of main factors (Day and Quinn, 1989; SAS Institute Inc., 1990).

In the early stages of this study, the author was only able to take samples during the mid and late periods of the first summer season (1992). The problem was overcome by using an unbalanced design mixed model ANOVA instead of the usual balanced designs (SAS Institute Inc., 1990). The degrees of freedom for this analysis are affected by the unbalanced design, especially for the denominator of year and season, and the interaction between year and season (change from 10 to 9), due to missing locations in trip one of year one. This approach provides a conservative analysis.

RESULTS

A total of 126 fish species were collected (Appendix 2). For the purposes of this study, total species abundance, total species number, total species biomass and selected species abundance and biomass are used in ANOVAs to detect temporal and spatial trends. The complete data set will be analysed using multivariate analysis in Chapter 4.

Great variability in the proportion of dominant species and major taxonomic groups between seasons, years and habitats were apparent (Tables 3.1 and 3.2, respectively). Such differences, which are reflections of the relative abundance of various species at different habitats as well as seasonal and yearly influences on density, biomass and species numbers, will be considered in greater detail in a subsequent section.

Table 3.1. Number of individuals and biomass (Kgs) of dominant species and major taxonomic groups caught by beach seine netting from intertidal zones of sandy shore surf zones and estuary mouths of tropical North Queensland between January 1992 and September 1994. Data are based on pooled values for each species from all replicates for each habitat. Percentage frequency occurrence (% Freq) were based on the number of locations in which a species was collected as a proportion of the sum of total locations visited.

TAXA	Total contributions					Sandy Shore Surf Zones					Estuary Mouths				
	Abundance	%	Biomass	%	%Freq	Abundance	%	Biomass	%	%Freq	Abundance	%	Biomass	%	%Freq
TOTAL	181,988		209.96			131,114		125.12			50,874		84.84		
Escualosa thoracata	14,964	8.22	3.18	1.52	27.78	12,947	9.87	29.24	2.34	37.04	2,017	3.96	0.26	0.31	18.52
Sardinella gibbosa	51,156	28.11	26.28	12.52	50.00	45,057	34.36	18.41	14.71	57.41	6,099	11.99	7.88	9.29	42.59
Stolephorus nelsoni	15,212	8.36	12.03	5.73	69.44	12,081	9.21	10.07	8.05	79.63	3,131	6.15	1.96	2.31	59.26
Sillago analis	3,760	2.07	16.94	8.07	91.67	1,894	1.44	9.73	7.77	90.74	1,866	3.67	7.21	8.50	92.59
Leiognathus splendens	24,513	13.47	5.82	2.77	62.04	18,395	14.03	4.98	3.98	64.81	6,118	12.03	0.84	1.00	59.26
Valamugil seheli	12,223	6.72	16.76	7.98	89.81	5,015	3.82	1.64	1.31	85.19	7,208	14.17	15.12	17.83	94.44
Major Taxonomic Groups															
Clupeoids	94,034	51.67	55.25	26.31		80,783	61.61	42.73	34.15		13,251	26.05	12.52	14.76	
- Clupeids	67,591	37.14	32.64	15.55		58,882	44.91	23.33	18.64		8,709	17.12	9.32	10.98	
- Engraulids	26,448	14.53	22.50	10.72		21,901	16.70	19.30	15.43		4,547	8.94	3.20	3.77	
Atherinomorpha	11,565	6.35	40.58	19.33		2,050	1.56	16.71	13.36		9,515	18.70	23.87	28.14	
Ambassis spp	6,459	3.55	7.06	3.34		1,598	1.22	2.29	1.83		4,861	9.55	4.72	5.56	
Sillago spp.	5,699	3.13	21.80	10.38		3,317	2.53	13.02	10.40		2,382	4.68	8.78	10.35	
Carangids	6,286	3.45	12.39	5.90		6,021	4.59	10.74	8.58		265	0.52	1.64	1.94	
Leiognathids	29,924	16.44	8.98	4.28		23,367	17.82	7.83	6.26		6,557	12.89	1.15	1.36	
Mugilids	15,445	8.49	31.70	15.10		5,770	4.40	5.25	4.19		9,675	19.02	26.45	31.17	

Table 3.2. Number of individuals and biomass (KgFW) of dominant species and major taxonomic groups caught by beach seine netting from intertidal zones of sandy shore surf zones and estuary mouths of tropical North Queensland between January 1992 and September 1994. Data are based on actual pooled values for each species from all replicates for each year and season. Percentage frequency occurrence (%Freq) were based on the number of locations in which a species was collected as a proportion of the sum of total locations visited.

TAXA	Abundance			Biomass (Kg fresh weight)			Summer Season					Winter Season				
	1992	1993	1994	1992	1993	1994	Abundance	%	Biomass	%	%Freq	Abundance	%	Biomass	%	%Freq
TOTAL	44,531	38,777	98,680	67.74	53.32	88.90	145,131		151.66			36,857		58.30		
E. thoracata	3,892	465	10,607	0.32	0.46	2.39	11,115	7.66	3.00	1.98	33.33	3,849	10.44	0.18	0.31	22.22
S. gibbosa	1,589	5,440	44,127	4.82	2.76	18.71	51,014	35.15	25.63	16.90	81.48	142	0.39	0.66	1.13	18.52
S. nelsoni	10,418	3,171	1,623	6.42	2.35	3.25	14,595	10.06	10.68	7.04	85.19	617	1.67	1.35	2.31	53.70
S. analis	2,794	521	445	9.62	2.81	4.50	2,640	1.82	12.45	8.21	92.59	1,120	3.04	4.48	7.69	90.74
L. splendens	5,255	8,245	11,013	1.29	1.88	2.65	20,560	14.17	4.60	3.04	83.33	3,953	10.73	1.22	2.09	40.74
V. seheli	5,414	5,173	1,636	6.56	5.05	5.16	2,858	1.97	10.51	6.93	88.89	9,365	25.41	6.25	10.72	90.74
Major Taxonomic Groups																
Clupeoidei	19,033	12,078	62,923	15.51	9.35	30.39	87,253	60.12	49.64	32.73		6,781	18.40	5.61	9.63	
- Clupeids	5,588	6,401	55,602	5.82	4.04	22.78	63,483	43.74	30.86	20.35		4,108	11.15	1.79	3.07	
- Engraulids	13,451	5,676	7,321	9.65	5.25	7.61	23,777	16.38	18.78	12.38		2,671	7.25	3.72	6.38	
Atherinomorpha	2,291	3,901	5,373	9.03	12.52	19.03	5,992	4.13	23.12	15.25		5,573	15.12	17.46	29.95	
Ambassis spp.	3,153	2,008	1,298	2.45	2.77	1.78	3,019	2.08	3.21	2.12		3,440	9.33	3.80	6.51	
Sillago spp.	3,346	1,394	959	10.09	5.27	6.44	3,349	2.31	14.89	9.82		2,350	6.38	6.91	11.85	
Carangids	,356	480	5,450	6.35	2.27	3.77	6,153	4.24	9.47	6.24		133	0.36	2.92	5.00	
Leiognathids	6,305	8,568	15,051	2.04	2.13	4.82	25,841	17.81	7.56	4.99		4,083	11.08	1.42	2.44	
Gerres spp.	1,042	2,276	1,521	0.76	0.74	0.78	4,303	2.96	1.75	1.15		536	1.45	0.53	0.91	
Mugilids	6,498	6,023	2,924	11.60	9.00	11.09	4,589	3.16	19.04	12.56		10,856	29.45	12.65	21.70	

General Description of Major Fish Composition

The total number of specimens collected was 181,988, of which 44,531 were collected in 1992, 38,777 in 1993 and 98,680 in 1994 (Table 3.2). Similarly, total biomass for each year was 67.74 (1992), 53.32 (1993) and 88.90 (1994) Kg FW (Table 3.2). Greater abundance and biomass were evident in 1994 due to the large catches of clupeids, especially *Escualosa thoracata* and *Sardinella gibbosa*. The distribution of these two species of clupeoids was very patchy owing to their schooling behaviour and movement along the coast. *Escualosa thoracata* and *S. gibbosa* occurred in 135 and 222 hauls respectively, out of a total of 972 hauls. In the case of *E. thoracata*, an unusually large catch of more than 8000 specimens of 30 -40 mm SL was recorded at one site at Saunders Beach in the early 1994 summer season, the normal catch at this site ranged from 300 - 500. Similarly, an extremely large catch of *S. gibbosa* (more than 16,000 specimens, 30 - 40 mm in length), were collected at this particular site and sampling time. The normal catch collected at this site for *S. gibbosa* ranged from 600 - 800 specimens.

The five most abundant taxa over the period of this study were *Sardinella gibbosa*, *Leiognathus splendens*, *Stolephorus nelsoni*, *Escualosa thoracata* and *Valamugil seheli* (Table 3.1). *Sillago analis*, one of the largest contributors to total biomass (8.07%), was not among the five most abundant, while *S. gibbosa*, *S. nelsoni* and *V. seheli* were among the largest contributors to biomass as well as being among the most abundant. This phenomenon can be explained by differences in the size structure of these species. There was a considerable number of small *L. splendens* and *E. thoracata* collected while a greater proportion of large *S. analis* were caught. Fluctuations in overall abundance and biomass (across all taxa) were evident over the temporal scale examined (Figure 3.2B).

Overall, higher numbers of clupeids, engraulids, *Sillago* spp., carangids, leiognathids and gerreids were found in sandy shore surf zones while the remaining groups, namely

Figure 3.2. Mean ± 1SE of number of taxa, abundance (No. Individuals / haul) or biomass (g FW / haul) for each trip from sandy shore surf zone samples (◊) and estuary mouth samples (Δ) from January 1992 to September 1994.
A) Total Species Numbers
B) Total Individuals Abundance and Biomass
C) Total Adjusted Abundance and Total Adjusted Biomass

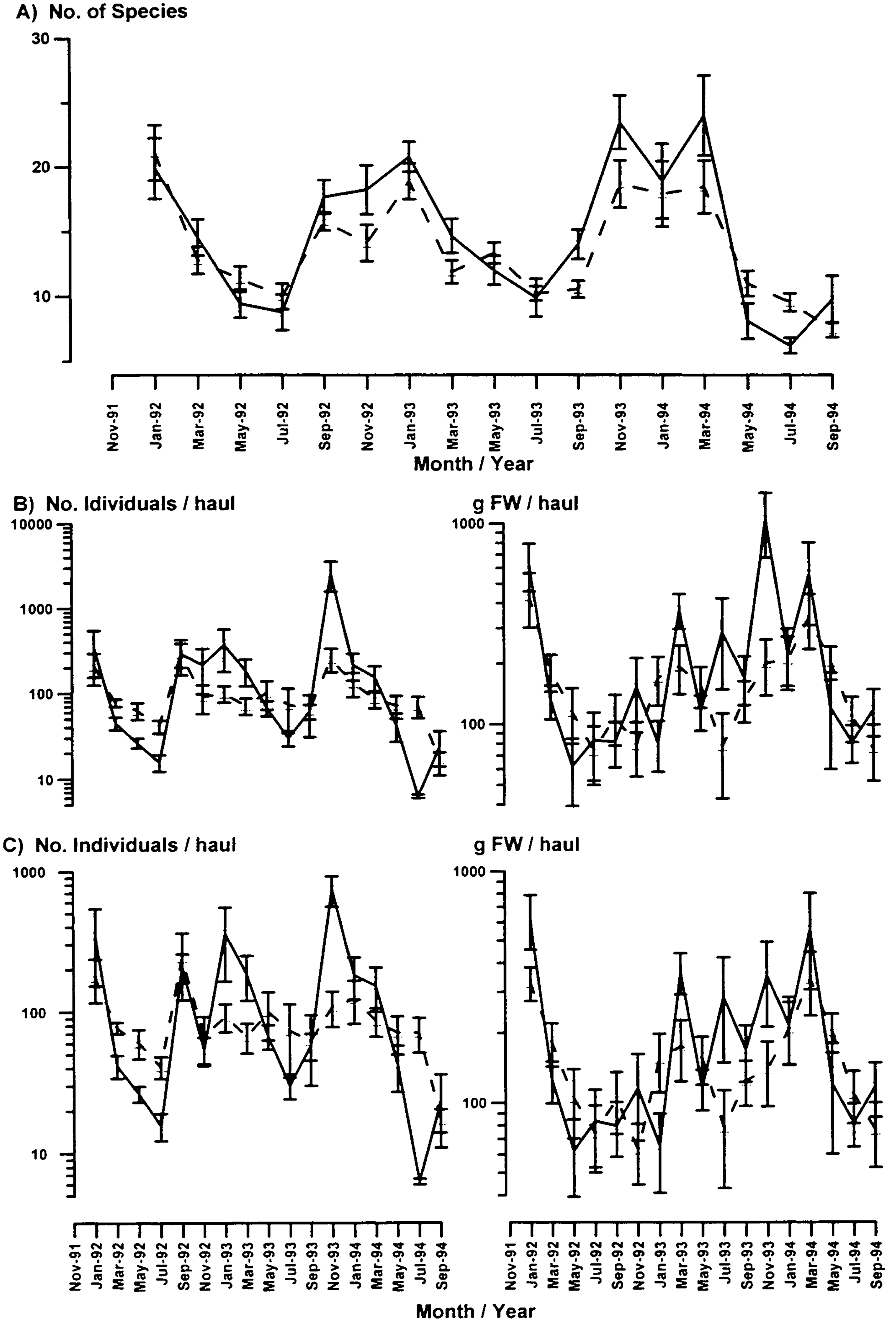

A) No. of Species
30
20
10
Nov-91
Jan-92
Mar-92
May-92
Jul-92
Sep-92
Nov-92
Jan-93
Mar-93
May-93
Jul-93
Sep-93
Nov-93
Jan-94
Mar-94
May-94
Jul-94
Sep-94
Month / Year
B) No. Idividuals / haul
10000
1000
100
10
g FW / haul
1000
100
C) No. Individuals / haul
1000
100
10
g FW / haul
1000
100
Month / Year

Fig. 3.2

Atherinomorpha, *Ambassis* spp. and mugilids were shown to be located predominantly in estuary mouth habitats (Table 3.1).

Variations in Mean Numbers of Species

Mean numbers of species in sandy shore surf zones and estuaries appear to fluctuate consistently revealing similar trends through time (Fig. 3.2A). There was no significant difference in the total numbers of species among sampling years between sandy shore surf zones and estuary mouths habitats (Table 3.3). Mean total species numbers were significantly greater however in the summer season than in winter, averaging 9.97 and 5.69 species haul^{-1} respectively ($F_{1,9}$=22.39, $p < 0.01$; Tables 3.3 and 3.4 and Fig. 3.3A). There were also variations in species numbers between habitats within seasons as indicated by a significant interaction term (H x S, $F_{1,281}$=8.97, $p < 0.01$; Table 3.3 and Fig 3.3B). In general, sandy shore surf zones had significantly greater mean numbers of species than estuary mouths in summer while almost the same numbers in winter (Fig. 3.2A).

Variations in Mean Abundance

Abundant species with patchy distributions as found in this study (Table 3.1 and Fig. 3.2B) can interfere with total abundance analyses of assemblage patterns. Thus in the following analyses of Total Abundance, the results are presented with and without the most variable species, *E. thoracata* and *S. gibbosa*.

Total Individual Abundance

For sandy shore surf zones, mean abundance for each sampling trip ranged from extremely low (5.3 - 14.7 individuals haul^{-1} in July 1994 and July 1992 respectively) to extremely high (2547 individuals haul^{-1} in November 1993). For estuary mouths, the range in mean abundance from individual sampling trips was less dramatic. The lowest recorded was 16.2 individuals haul^{-1} in September 1994 and the highest was 255.0 and 294.0 individuals haul^{-1} in November 1993 and September 1992 respectively (Fig. 3.2).

Table 3.3. Summaries of F-value from the analysis of variance for Total Species Numbers, Total Abundance and Biomass, Abundance and Biomass of dominant species caught in beach seines from sandy shore surf zones and estuary mouths (See also Appendix 1). F-ratio values are rounded to two decimal places. (*: $p < 0.05$; ** : $p < 0.01$; for variables indicated with # a critical value of $p < 0.01$ is proposed because the variable did not meet the homogeneity of variance criteria.)

TAXA	Main effects			2-way interactions			3-way interactions
	Year (Y)	Season (S)	Habitat (H)	Y x S	Y x H	H x S	Y x H x S
	2/9	1/9	1/2	2/9	2/281	1/281	2/281
Total Species Numbers	0.33	**22.39****	<0.001	2.55	1.38	**8.97***	1.83
ABUNDANCE							
Total Abundance	0.03	**8.06***	0.05	2.05	0.17	**32.59****	1.55
Adjusted Abundance [1]	0.04	**7.81***	0.45	2.20	0.12	**23.70***	3.26
Major Taxa							
Stlephorus nelsoni	0.94	**6.99***	3.20	0.31	**10.12****	**11.62****	**4.37***
Sillago analis	**5.92***	1.22	1.29	2.33	0.19	1.06	0.17
Leiognathus splendens#	0.06	7.09	1.07	1.65	1.32	**18.39****	3.88
Valamugil seheli	1.70	0.85	3.29	1.10	0.004	0.12	**3.86***
BIOMASS							
Total Biomass #	0.83	**11.55****	0.20	1.00	0.49	5.78	1.23
Adjusted Biomass # [2]	0.77	5.28	3.22	1.20	0.29	183	1.74
Major Taxa							
Stlephorus nelsoni	0.38	4.21	2.64	1.38	**6.77***	3.43	2.07
Sillago analis	**5.61***	4.41	0.20	**5.59***	0.27	**7.75****	3.69
Leiognathus splendens #	0.50	8.09	6.58	1.47	2.01	**16.98****	2.54
Valamugil seheli	0.77	2.16	**42.69***	0.004	0.09	0.25	3.04

1) Adjusted Abundance = Total Abundance - No. of individuals *Escualosa thoraca*
- No. of individuals *Sardinella gibbosa*

2) Adjusted Biomass =Total Biomass - Biomass of *Escualosa thoraca*
- Biomass of *Sardinella gibbosa*

Figure 3.3. Mean ± 95% CI of significant dependent variables from Analyses of Variances in Table 3.3

A) Mean ± 95% CI of Total Numbers of Species between summer and winter;

B) Mean ± 95% CI of Total Numbers of Species from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ)habitats in summer and winter;

C) Mean ± 95% CI of Total Abundance between summer and winter;

D) Mean ± 95% CI of Total Abundance from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats in summer and winter;

E) Mean ± 95% CI of Total Adjusted Abundance between summer and winter;

F) Mean ± 95% CI of Total Adjusted Abundance from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats in summer and winter.

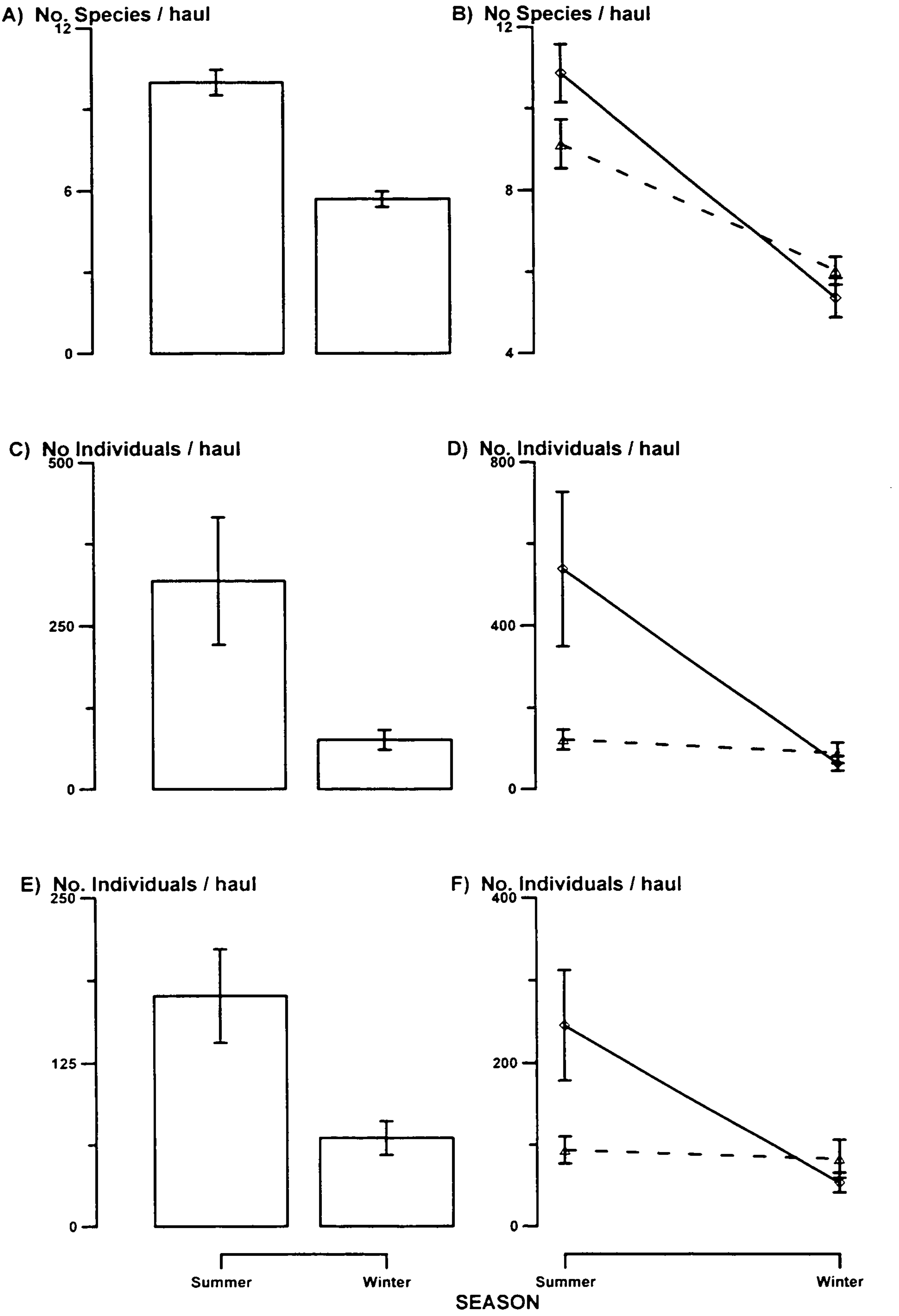

A) No. Species / haul
12
6
0
B) No Species / haul
12
8
4
C) No Individuals / haul
500
250
0
D) No. Individuals / haul
800
400
0
E) No. Individuals / haul
250
125
0
F) No. Individuals / haul
400
200
0
Summer
Winter
SEASON
Summer
Winter

Fig. 3.3

There was no significant difference detected in abundance among study years nor between habitats (Table 3.3), while there was a clear significant seasonal difference ($F_{1,9}$=8.06, $p < 0.05$; Fig 3.3C). Multiple comparisons of the means using the Ryan-Einst-Gabriel-Welsch multiple range test (Table 3.4) suggest a trend for greater abundance in summer than in winter, with an average of 318.28 and 75.84 individuals haul^{-1} respectively (See also Fig. 3.3C). A total of 145,131 (~80%) specimens was caught in the summer seasons between 1992 and 1994 while only 36,857 (~20%) were caught in winter seasons (Table 3.2). Two thirds of all major groups, namely clupeids, engraulids, carangids, leiognathids and gerreids yielded higher catches in summer than in winter, except for the Atherinomorpha and *Ambassis* spp. which were caught in almost consistent numbers over both seasons, and for mugilids which yielded higher numbers in winter (Table 3.1).

A significant interaction between habitats and season was also detected (H x S, $F_{1,281}$= 32.59, $p < 0.01$; Table 3.3 and Fig 3.3D). Higher average abundance in sandy shore surf zones than in estuaries occurred in summer, whereas slightly higher or equal abundance levels were recorded in winter for estuary mouths as compared to sandy shore surf zones.

"Adjusted Abundance": Abundance without *E. thoracata* and *S. gibbosa*

When *E. thoracata* and *S. gibbosa* are excluded from the analysis, about half of the highest amplitude of catch per haul in November 1993 is clearly reduced, while the rest follow the same trend as found in Total Individual Abundance (Figs. 3.2C and 3.2B respectively). Abundance was still dependent on seasons alone ($F_{1,9}$=7.81, $p < 0.05$; Table 3.3 and Fig 3.3E) and the interaction between habitat and season ($F_{1,281}$ = 23.70, $p < 0.05$; Table 3.3 and Fig 3.3F). As shown for Total Individual Abundance, results from the Ryan multiple range test for Adjusted Abundance indicated a higher catch in summer than in winter (175.64 and 67.62 individual haul^{-1} respectively; Table 3.4 and Fig. 3.3E). Similarly, the

H x S interaction for Adjusted Abundance was due to higher winter abundances in the sandy shore surf zones as compared to estuary mouths (Fig. 3.3F).

Variations in Abundance of Dominant Species

Stolephorus nelsoni, Sillago analis, Leiognathus splendens and *Valamugil seheli* were caught in sufficient numbers during the study periods to enable each to be examined separately. Overall patterns are presented in Figure 3.4. There was, however, no consistent pattern in abundance for any of these taxa.

Stolephorus nelsoni abundance peaked in the summer for sandy shore surf zones (170.81, 98.81 and 49.48 individuals haul^{-1} for January 1992, March 1993 and 1994 respectively, Fig. 3.4A), while individuals numbers were extremely low or zero in winter catches. Average numbers of *S. nelsoni* in estuary mouths were high in January 1992, where 49.74 individuals haul^{-1} were caught, after that the average number of *S. nelsoni* caught from estuary mouths never reached more than 10 individuals haul^{-1}(Fig. 3.4A).

Sand Whiting, *Sillago analis*, showed a year round distribution in both sandy shore surf zones and estuary mouths. Highest numbers of *S. analis* per haul were 33 and 17 individuals haul^{-1} in sandy shore surf zones and estuary mouths respectively for January 1992 (Fig. 3.4B). Later, catches of sand whiting from both habitats were low averaging 1-5 individuals haul^{-1}.

Leiognathus splendens numbers peaked in summer and declined in winter during the study period in sandy shore surf zone habitats. The peaked abundances were 20.41, 266.44 and 269.44 individuals haul^{-1} in January 1992, 1993 and 1994 respectively (Fig. 3.4C). In comparison, the peak abundance for this species in estuary mouths did not occur in the summer of 1992 but in the late winter of 1992 and early summer of 1993 (September 1992), with 131.11 individuals haul^{-1} being caught. The number of *L. splendens* caught in

Figure 3.4. Mean ±1 SE abundance (No. Individuals / haul) or biomass (g FW / haul) of each trip from sandy shore surf zone samples (◊) and estuary mouth samples (Δ) from January 1992 to September 1994.

A) Total *Stolephorus nelsoni* Abundance and Biomass
B) Total *Sillago analis* Abundance and Biomass
C) Total *Leiognathus splendens* Abundance and Biomass
D) Total *Valamugil seheli* Abundance and Biomass

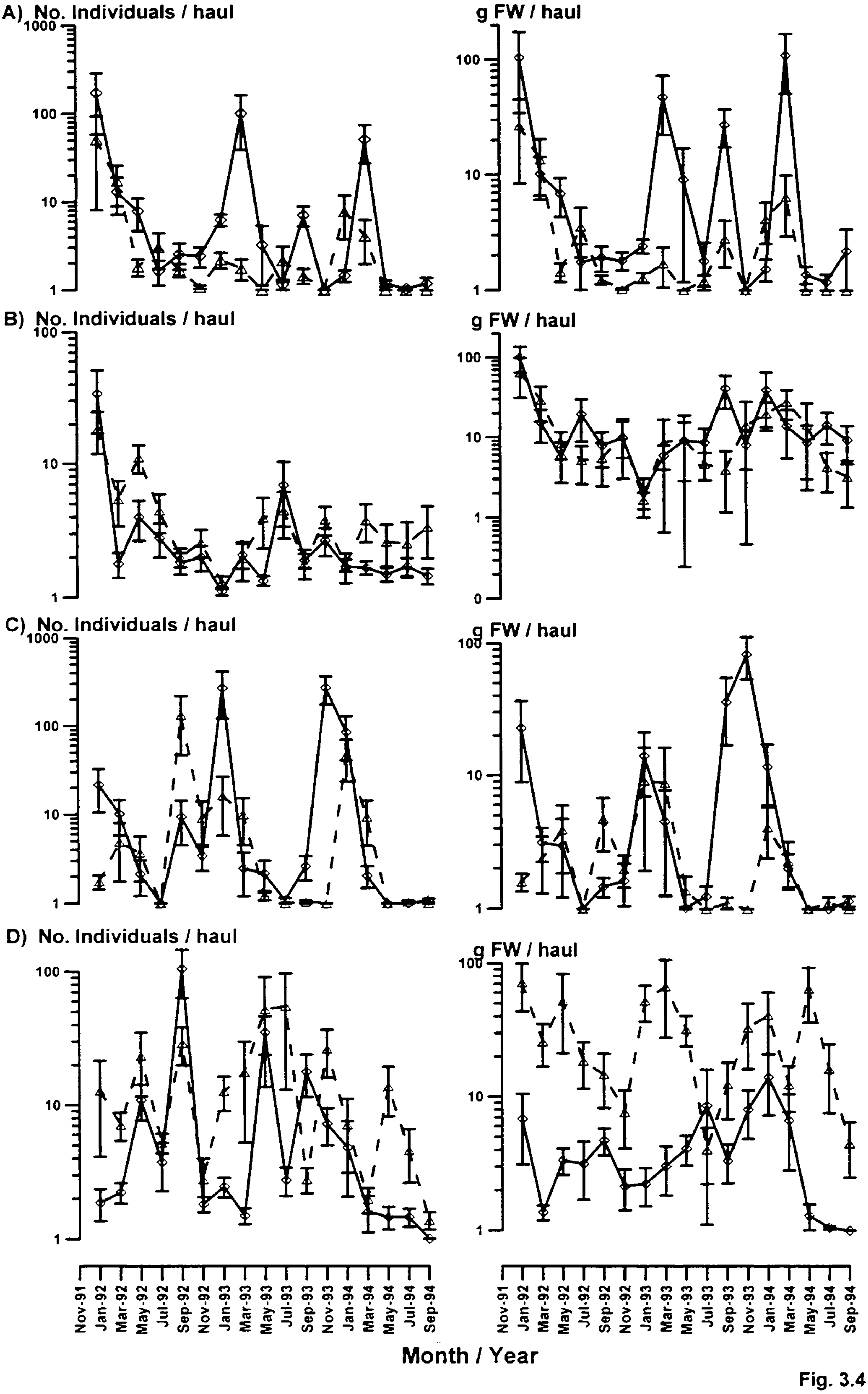

A) No. Individuals / haul
g FW / haul
B) No. Individuals / haul
g FW / haul
C) No. Individuals / haul
g FW / haul
D) No. Individuals / haul
g FW / haul
1000
100
10
1
0
Nov-91
Jan-92
Mar-92
May-92
Jul-92
Sep-92
Nov-92
Jan-93
Mar-93
May-93
Jul-93
Sep-93
Nov-93
Jan-94
Mar-94
May-94
Jul-94
Sep-94
Month / Year

Fig. 3.4

January 1994 was again high, being 45.2 individuals haul^{-1}. Numbers of *L. splendens* caught over winter ranged from 1 to 10 individuals haul^{-1} (Fig. 3.4C).

Valamugil seheli was another common species that occurred year-round in both sandy shore surf zones and estuary mouths. There was no general trend detected in *V. seheli* abundance for the two habitats. For sandy shore surf zones, the first abundance peak recorded was 103.33 individuals haul^{-1} in September 1992. In contrast, only 28.03 individuals haul^{-1} of this species were collected from estuary mouths in September 1992. The second peak in numbers for *V. seheli* was evident in May and July 1993 with 53.74 and 33.92 individuals haul^{-1} sampled from estuary mouths and sandy shore surf zones respectively (Fig. 3.4D).

Interspecific differences were detected among catches between years and season. For example, there was a significant difference among annual catches in *S. analis* ($F_{2,9}$= 5.92, $p < 0.05$; Table 3.3), where the total number of individuals caught in 1992 were significantly higher than in 1993 and 1994 (2794, 521 and 445 respectively; see also Table 3.4, Fig. 3.5A). *Stolephorus nelsoni* showed a significant seasonal difference in numbers caught ($F_{1,9}$= 6.99, $p < 0.05$) where catches were greater in summer than in winter (Table 3.4 and Fig. 3.5B). Significantly higher numbers of *S. nelsoni* were caught in sandy shore surf zones than from estuary mouths every sampling year (Y x H interaction, $F_{2,281}$= 10.12, $p < 0.01$; Table 3.3 and Fig. 3.5C). Higher abundance of *S. nelsoni* and *L. splendens* were found in sandy shore surf zones in summer than in estuary mouths, while the abundance in both habitats were quite similar during the winter season (H x S interaction, $F_{2,281}$= 16.12, $p < 0.05$; $F_{2,281}$= 18.39, $p < 0.01$ respectively; Table 3.3; Figs. 3.5D and 3.5 E respectively). *Stolephorus nelsoni* and *V. seheli* had a significant habitat by season by year interaction (Y x H x S interaction, $F_{2,281}$= 4.37, $p < 0.05$ and $F_{2,281}$= 3.86, $p < 0.05$ respectively; Table 3.3, Fig. 3.6E). Relatively higher abundances of *S. nelsoni* were found

Table 3.4. A posteriori comparisons of mean values of abundance (No. of idividuals haul^{-1}) and biomass (g FW haul^{-1}) of significant main effect factors in analyses of variances for Total Species Number, Total Abundance and Biomass, dominant species abundance and biomass. These comparisons are based on the Ryan-Einst-Gabriel-Welsch multiple range test. Means of untransformed data are presented. Underlined means were found not to differ significantly.

TAXA	YEARS			SEASONS		HABITATS	
	1992	1993	1994	SUMMERS	WINTERS	SSSZ	ESTUARIES
Total Species Numbers				27.52	> 16.09		
ABUNDANCE							
Total Abundance				298.61	> 75.84		
Adjusted Abundance				170.78	> 67.62		
Stolephorus nelsoni				30.02	> 1.27		
Sillago analis	8.63 >	1.61	1.37				
Leiognathus splendens							
Valamugil seheli							
BIOMASS							
Total Biomass				312.06	> 119.99		
Adjusted Biomass							
Stolephorus nelsoni							
Sillago analis	29.71 >	8.67	13.11				
Leiognathus splendens							
Valamugil seheli						3.73	< 30.93

Figure 3.5.

A) Mean ± 95% CI of Annual Abundance of *Sillago analis* between 1992 and 1994;

B) Mean ± 95% CI of Abundance of *Stolephorus nelsoni* between summer and winter;

C) Mean ± 95% CI of Annual Abundance of *Stolephorus nelsoni* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats between 1992 and 1994;

D) Mean ± 95% CI of Seasonal Abundance of *Stolephorus nelsoni* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats;

E) Mean ± 95% CI of Seasonal Abundance of *Leiognathus splendens* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats;

F) Mean Abundance of *Stolephorus nelsoni* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats in summer (open symbols) and winter (close symbols) between 1992 and 1994; and

G) Mean Abundance of *Valamugil seheli* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats in summer (open symbols) and winter (close symbols) between 1992 and 1994.

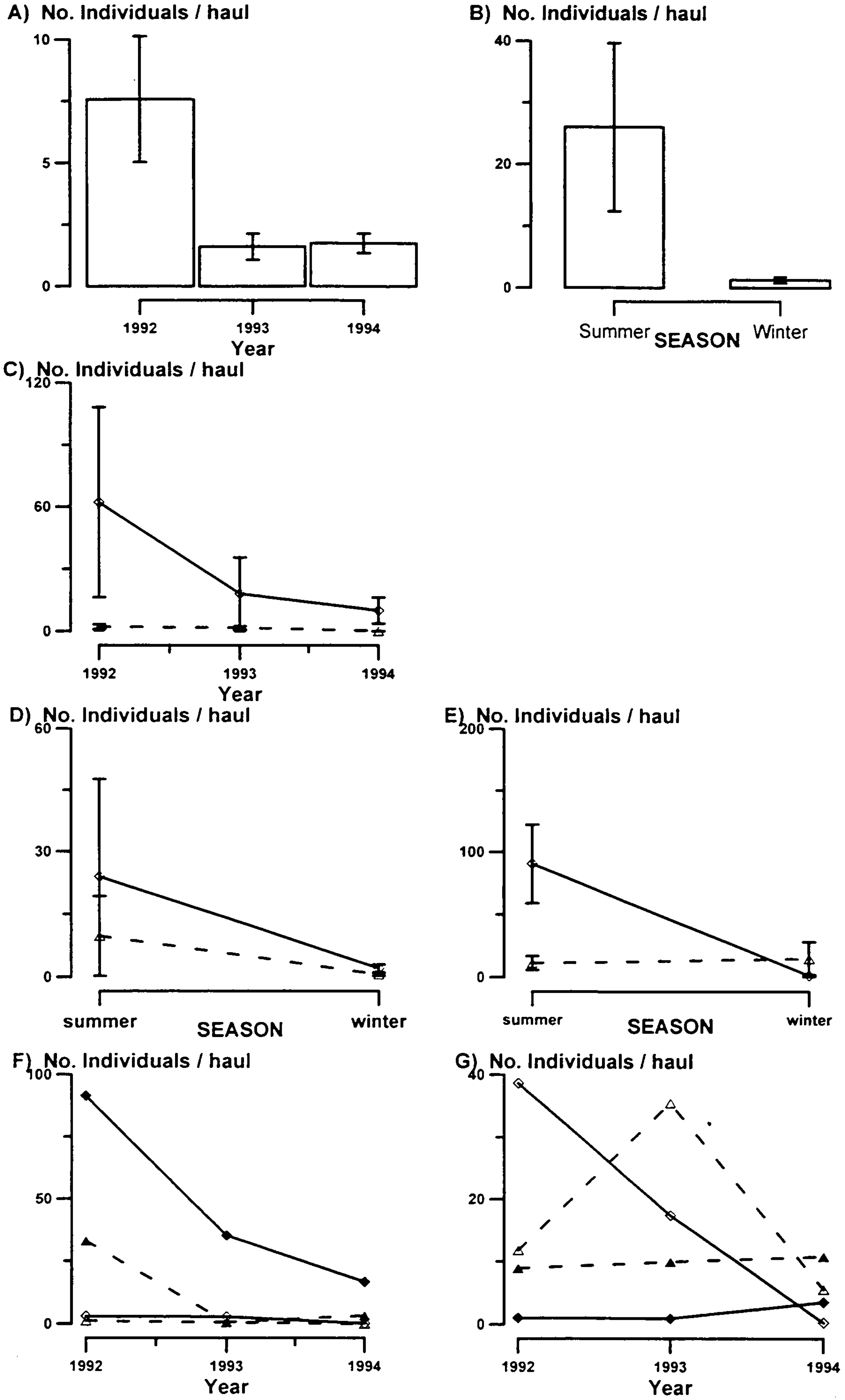

A) No. Individuals / haul
10
5
0
1992
1993
1994
Year
B) No. Individuals / haul
40
20
0
Summer
SEASON
Winter
C) No. Individuals / haul
120
60
0
1992
1993
1994
Year
D) No. Individuals / haul
60
30
0
summer
SEASON
winter
E) No. Individuals / haul
200
100
0
summer
SEASON
winter
F) No. Individuals / haul
100
50
0
1992
1993
1994
Year
G) No. Individuals / haul
40
20
0
1992
1993
1994
Year

Fig. 3.5

in sandy shore surf zones in summer for each sampling year while only the summer samples of 1992 from estuary mouths had a comparable number. Consistently lower numbers of *S. nelsoni* were collected in both habitats in winter for each sampling year (Fig. 3.5F). For *V. seheli*, individual numbers found in summer catches of every sampling year in both habitats were similar, while abundance varied considerably in both habitats over winter for each sampling year (Fig. 3.5G).

Total Biomass

Mean total biomass for each sampling trip ranged from 61.1 g FW haul^{-1} in June 1992 to 1050.4 g FW haul^{-1} in November 1993 for sandy shore surf zones, and from 72.8 g FW haul^{-1} in August 1992 to 432.9 g FW haul^{-1} in February 1992 for estuary mouths (Fig. 3.2B). These biomass distribution patterns appeared to follow consistent trends throughout the study years. Most temporal variations were due to seasonal influences. There was a significant difference between seasons ($F_{1,9}$= 11.15, $p < 0.01$; see Table 3.3 and Fig. 3.6A), with a mean summer catch of 312.1 g FW haul^{-1} versus a mean winter catch of 120.0 g FW haul^{-1}(Table 3.4). No significant differences were detected among study years, habitats or their possible interactions.

"Adjusted Biomass": Total Biomass without *E. thoracata* and *S. gibbosa*

There were no distinct spatial trends in adjusted biomass from 1992 to 1994. Biomass was highest in the summer of 1992, with 620.0 and 326.8 g FW haul^{-1} for sandy shore surf zones and estuary mouth habitats respectively, it then decreased to 78.6 and 72.8 g FW haul^{-1} respectively in mid winter (Fig. 3.2C). However, with respect to overall annual patterns, there were no significant differences in Adjusted Biomass among study years and between seasons as demonstrated in the previous Total Biomass analysis (Table 3.3).

Variations in biomass of selected species

General patterns of biomass for all the selected species followed a similar trend to that of abundance (Fig. 3.4A-3.4D). The biomass for most species clearly peaked in the summer season of each year. Biomass was high for *S. nelsoni* in January 1992, March 1993 and 1994 for sandy shore surf zones (103.60, 46.60, and 109.59 g FW haul^{-1} respectively), while it peaked in January 1992 and March 1994 for estuary mouth habitats (25.9 and 5.4 g FW haul^{-1} respectively; Fig. 3.4A). Over the 3 year study period, the biomass of *S. nelsoni* ranged from 0-109.6 and 0-25.0 g FW haul^{-1} from sandy shore surf zones and estuary mouths respectively. The range outside of peak periods for this species was 0-3.0 g FW haul^{-1}. Only one clear peak was recorded for the biomass of *S. analis,* the peak occurred in January 1992 and was 103.6 and 65.2 g FW haul^{-1} for sandy shore surf zones and estuary mouths respectively. No obvious peaks were observed in the following years (Fig. 3.4 B). The range of biomass recorded was 0-103.6 and 0.5- 65.2 g FW haul^{-1} for sandy shore surf zones and estuary mouths respectively, while off-peak periods yielded 5.0 - 20.0 g FW haul^{-1} from both habitats. Three clear peaks of *L. splendens* biomass from sandy shore surf zones were recorded in January 1992 & 1993 and November 1993 (21.69, 13.04 and 81.94 g FW haul^{-1} respectively), while only one large peak was evident in estuary mouths. This peak occurred in January 1993 with a biomass of 8.06 g FW haul^{-1} (Fig. 3.4C). The range in biomass recorded for *L. splendens* was 0 - 82.0 and 0 - 8.0 g FW haul^{-1} for sandy shore surf zones and estuary mouths respectively. The biomass of *V. seheli* in estuary mouths was higher than for sandy shore surf zones (Fig. 3.4D). The biomass of *V. seheli* ranged from 0- 15.0 g FW haul^{-1} for sandy shore surf zones with a clear peak occurring in January 1994. On the other hand, *V. seheli* from estuary mouths showed three clear peaks, in January 1992 and 1993 and May 1994, recording a biomass of 70.5, 51.4 and 63.4 g FW haul^{-1} respectively (Fig. 3.4D).

Sillago analis was the only species that showed a significant difference in biomass among annual catches ($F_{2,9}$= 5.61, $p < 0.05$; Table 3.3). The Ryan-Einst-Gabrial-Welsch multiple range test indicated a significantly lower biomass in 1993 than in 1992, while the biomass for 1994 was intermediate between 1992 and 1993 values (Table 3.4 and Fig. 3.6B). The remaining selected species did not show any significant differences in biomass among annual catches. Additionally, the biomass of *Stolephorus nelsoni, Sillago analis, Leiognathus splendens* and *Valamugil seheli* were not significantly different between summer and winter (Tables 3.3). There were no significant differences in biomass between sandy shore surf zones and estuarine embayment habitats for *S. nelsoni, S. analis* and *L. splendens*, while there was a significantly higher biomass recorded in estuary mouths than sandy shore surf zones for *Valamugil seheli* (ANOVA, $F_{1,2}$= 42.69, $p < 0.05$; Tables 3.3 and 3.4 and Fig. 3.6C).

Biomass varied among seasons and years for *S. analis* (ANOVA, Y x S, $F_{2,9}$= 5.59, $p <$ 0.05; Table 3.3, Fig. 3.6D). This interaction was due to a higher winter biomass in 1993. The biomass for *S. nelsoni* was clearly greater in sandy shore surf zones than estuary mouth samples in 1992 and 1994 (H x Y interaction, $F_{2,281}$= 6.77, $p < 0.01$; Table 3.3 and Fig. 3.6E). The biomass of *S. analis* was relatively higher for estuary mouths in summer while in sandy shore surf zones, its biomass was higher in winter ($F_{1,281}$= 7.75, $p < 0.01$ respectively; Table 3.3; Fig. 3.6F). On the other hand, the biomass for *L. splendens* was distinctly greater for sandy shore surf zones than estuary mouths in summer, while biomass was relatively high and similar for both habitats in winter ($F_{1,281}$= 16.98, $p < 0.01$ respectively; Table 3.3; Fig. 3.6G). For *S. analis* biomass varied between habitats, years and seasons (ANOVA, Y x H x S, $F_{2,281}$= 3.69, $p < 0.05$; Table 3.3). This complex interaction was due to the relatively high biomass recorded for both habitats in the summer

Figure 3.6.

A) Mean ± 95% CI of Total Biomass between summer and winter;

B) Mean ± 95% CI of Annual Biomass of *Sillago analis* between 1992 and 1994;

C) Mean ± 95% CI of Biomass of *Valamugil seheli* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats;

D) Mean ± 95% CI of Seasonal Biomass of *Sillago analis* between 1992 and 1994 (open symbol:winter, close symbol: summer);

E) Mean ± 95% CI of Biomass of *Stolephorus nelsoni* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats between 1992 and 1994;

F) Mean ± 95% CI of Seasonal Biomass of *Sillago analis* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats;

G) Mean ± 95% CI of Seasonal Biomass of *Leiognathus splendens* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats; and

H) Mean Biomass of *Sillago analis* from Sandy Shore Surf Zone (◊) and Estuary Mouth (Δ) habitats in summer (open symbols) and winter (close symbols) between 1992 and 1994.

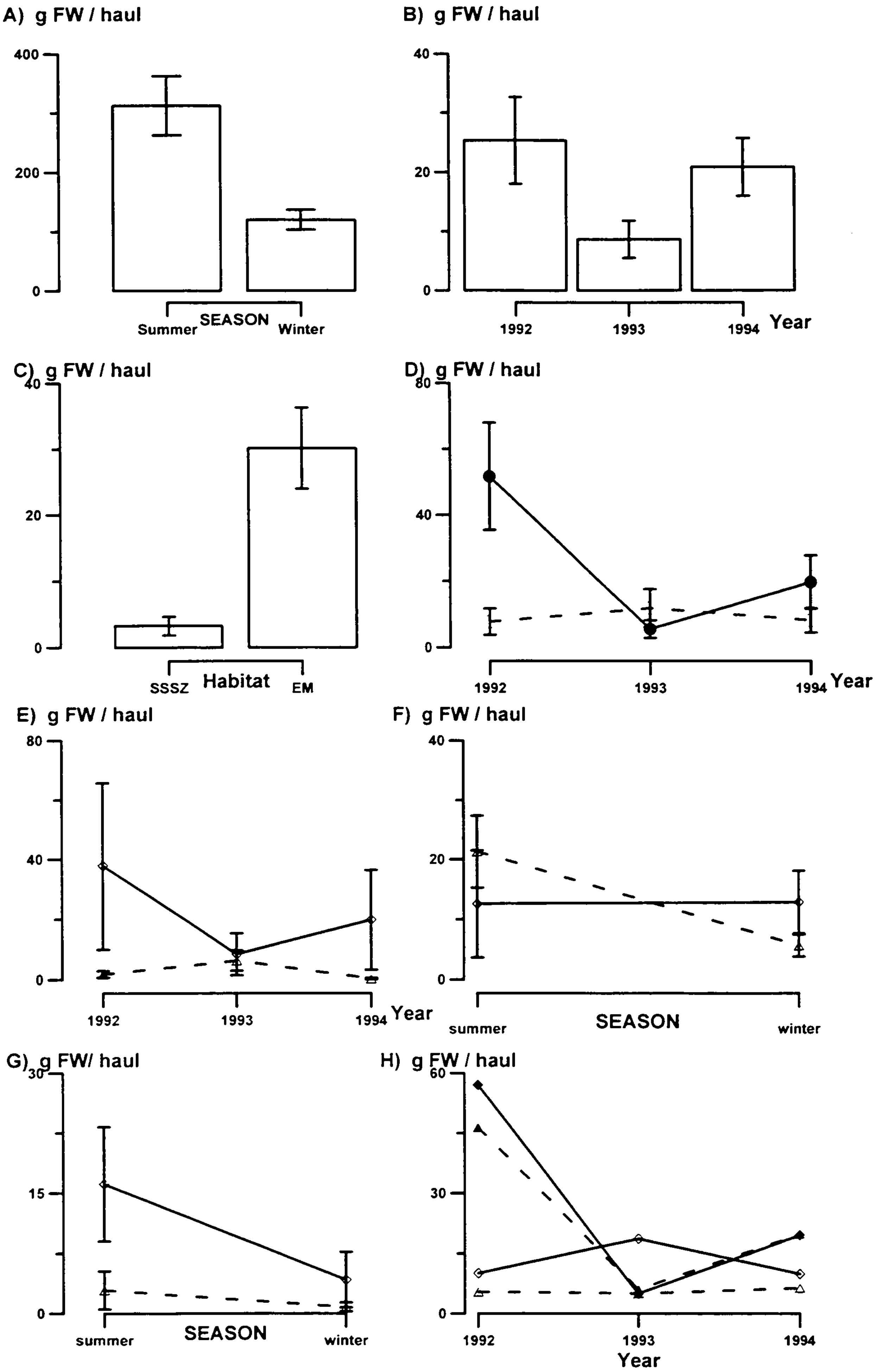

A) g FW / haul
400
200
0
Summer
SEASON
Winter
B) g FW / haul
40
20
0
1992
1993
1994
Year
C) g FW / haul
40
20
0
SSSZ
Habitat
EM
D) g FW / haul
80
40
0
1992
1993
1994
Year
E) g FW / haul
80
40
0
1992
1993
1994
Year
F) g FW / haul
40
20
0
summer
SEASON
winter
G) g FW/ haul
30
15
0
summer
SEASON
winter
H) g FW / haul
60
30
0
1992
1993
1994
Year

Fig.3-6

of 1992, and a lower biomass for the winter of 1992 and the remainder of seasons in 1993 and 1994 for both habitats (Fig. 3.6H).

DISCUSSION

Species Diversity

The diversity of fish species found in estuary mouths is relatively lower than in sandy shore surf zones, with 31 and 14 species found only in sandy shore surf zones and estuary mouths respectively, and 81 species found in both habitats (see also Fig. 3-2). The juveniles in these two habitats are characterised by a few dominant species that are present in large numbers. This pattern is quite a common characteristic of sandy shore surf zones and estuaries (Modde and Ross, 1981; Lasiak, 1984; Robertson and Duke, 1987; Ross *et al.*, 1987; Romer, 1990; Robertson and Blaber, 1992). In the present study, juveniles in both habitats were dominated by tropical marine visitors, these visitors accounted for the large number of taxa recorded. Thus, the connectedness of both habitats to the open sea is probably the major determination of fish species and abundance (Lasiak, 1984; Whitfield, 1989; Bennett, 1989; Romer, 1990). In the following chapter, species composition will be examined by multivariate analysis techniques (Chapter 4).

Not only is species diversity different between sandy shore surf zones and estuary mouths, but so is species composition. For example, Robertson and Blaber (1992) have listed 15 species and 2 unidentified gobies from mangrove habitats at Alligator Creek, Townsville. In contrast, the present study recorded only five species of gobies, of which, four were different from those recorded by Robertson and Duke (1987) and Robertson and Blaber (1992).

ABUNDANCE: Temporal and Spatial Variations

The answer to the question "Do sandy shore surf zones support a greater diversity and abundance of fish fauna than estuary mouths over large spatial and temporal scales?" is complex. The diversity and abundance of fish fauna vary, depending on the variables chosen to measure use of such habitats. Large and inconsistent differences in individual species are prominent features of this study. Despite such fluctuations, many species also show consistent patterns of abundance and/ or biomass over spatial and/or temporal scales. The following section will deal with the contribution of each spatial and temporal scale to variations in species number, abundance and biomass.

Seasonal Variability

The data presented provides overwhelming evidence that recruitment of various groups into a habitat is highly seasonal, and occurs predominantly in summer (Table 3.2 and Figs. 3.2 & 3.3). Total Species Number (Fig. 3.3A), Total and Adjusted Abundance (Figs. 3.3 C&E), Abundance of *Stolephorus nelsoni* (Figs.3.5 B&D) and *Leiognathus splendens* (Fig. 3.5E) all show a consistent decline from summer to winter.

In this study, seasonal peaks in abundance appeared between November and March but were slightly variable between years (Figs. 3.2B and 3.2C). Recruitment episodes and immigration-emigration to intertidal habitats are the processes regarded as capable of causing similar seasonal changes among Total Number of Species, Total and Adjusted Abundance, Abundance of *S. nelsoni* and *L. splendens* in abundance (Lasiak, 1983, 1984b; Doherty and Williams, 1988). Thus, the high abundance of fish that occurred in habitats in early summer in this particular study corresponds to the recruitment of juveniles to inshore habitats. In addition, *S. nelsoni* and *L. splendens* were rarely caught or absent from the catch in the inshore habitats during the winter season (Figs. 3.4A, 3.4C and 3.5B). This result suggests that most of these fish move away from intertidal habitats during winter.

Most seasonality studies in temperate zones have reported temperature as a major determining factor in fish abundance, with salinity, turbidity and wind patterns of secondary importance (Senta and Kinoshita, 1985; Ross *et al.*, 1987). Gibson *et al.* (1993)

suggested that, even though fluctuations in abundance and species richness may concurrently occur with changes in temperature and salinity, seasonal cycles are the result of recruitment and mortality rather than of immigration and emigration in response to physical factors. It seems that most previous studies have attempted to identify a single cause for variability in the composition of sandy shore surf zone fishes. Pauly and Navaluna (1983) have suggested that the recruitment pulses of several species in the Philippines sea match seasonal monsoon wind patterns. The marked seasonality in the total abundance of juveniles in the present study parallels quite closely the trends suggested by Pauly and Navaluna (1983). It has been observed that the majority of juvenile recruitment to intertidal zones, particularly the species selected for the purposes of this study, occurs in approximate synchrony with the late winter and early summer season, September- November. From the above data, it can be postulated that all selected species spawn year round and their larvae subsequently recruit to coastal habitats. It is only then that they enter the shallow areas of sandy shore surf zones and estuarine systems, especially in summer.

The large seasonal changes in Total Number of Species, and Total and Adjusted Abundance can be related to habitats (H x S; Table 3.3, Figs. 3.3B, 3.3D and 3.3E respectively). Total Number of Species, and Total and Adjusted Abundance were significantly higher in sandy shore surf zones than estuary mouths during summer, while abundances for both habitats were relatively similar in winter. This implies that seasonal factors within each habitat are important to intertidal fish assemblages. Moreover, such a significant interaction reveals the tendency for each habitat to support different numbers of species in certain seasons. Within the same year, greater exposure of sandy shore surf zones to off-shore environments, which was largely coupled with the effects of wind, may also increase the chance for recruitment to sandy shore habitats as compared with the more sheltered river mouths (Lasiak, 1984b).

Annual Variability

There were no annual differences in Total and Adjusted Abundance while only a significant difference in abundance was found for *Sillago analis* within selected taxa (Table 3.3 and Fig. 3.5A). This finding indicates that the annual consistency of Total and Adjusted Abundance and abundance of the most dominant taxa may reflect actual observed differences in the structure of natural habitats among years.

Consistent patterns in annual abundance of tropical fish have been recorded in several studies. For example, a seven-year study of fish inhabiting a rocky tidal pool in the northern part of the Gulf of California showed that fish abundance and diversity varied little from year to year (Thomson and Lachner, 1976). A long-term study of other intertidal organisms by Coull (1985) and Coull and Dudley (1985) have also found that typically, consistent inter-annual stability patterns persist.

Annual fluctuations in abundance in the present study may be regulated by several factors that were not measured. Biological characteristics of species assemblages including body size, population growth rate and trend cycle, density-dependence, dispersal patterns and size of geographical range, and extrinsic factors like habitat/ environmental temporal variability and predator abundance, may all modify animal abundance (Gaston and McArdle, 1994). In natural habitats, body size can interact with the measured variability due to selectivity of sampling gear, and sample unit size as mentioned by Green (1979), Blaber *et al.* (1989) and Hook (1991). Populations with higher growth rates are able to track the carrying capacity more closely and hence fluctuate more widely, while populations with low growth rates will tend to remain stable (Krebs, 1985), thus suggesting the possibility of increasing variability in the interaction between population growth rates and temporal and spatial abundance. Consistent annual trends in total and adjusted abundance of *Stolephorus nelsoni, Leiognathus splendens* and *Valamugil seheli* in this study are likely to be influenced by the large variability among sampling trips, and probably the population growth rate and carrying capacity of these coastal habitats.

Sillago analis was the only selected species which demonstrated significant annual variations in abundance, with catches being at least five times higher in 1992 than in the other years of the study. High densities of *S. analis* in 1992 can be related to the large annual differences in the level of recruitment of this species, and particularly to specimens smaller than 60 mm. The causes of variability in recruitment may be explained by any one of several factors (Jones, 1989; De Lafontaine, 1992). Jones (1989) proposed several environmental factors that could influence recruitment. Among those factors, hydrographic conditions associated with *El Niño* are known to affect recruitment of the Peruvian anchovy (Longhurst and Pauly, 1987). Climate and other environmental anomalies may have also contributed to the annual variations in abundance for *S. analis* in this study. Continual monitoring of physical factors (including atmosphere and hydrosphere) and faunal characteristics of these tropical habitats is essential in order to understand how fluctuating physical factors affect intertidal fish abundances.

Habitat Variability and Abundance

Species numbers and abundance of total juveniles fish and selected species were relatively higher at sandy shore surf zones than in estuary mouths during summer (Figs. 3.2 and 3.4). Concomitant decreasing numbers in winter and increasing numbers in summer reflect the pattern of seasonal recruitment episodes into both sandy shore surf zones and estuary mouths habitats. As many temporary species occurred in sandy shore surf zones and estuary mouths, both habitats experience a wide variation in abundance.

The abundance of catches in both sandy shore surf zone and estuary mouth habitats may be affected by many factors not measured during this study, such as depth, substratum type, habitat structure and to some extent meteorological parameters (Lasiak, 1984b). Habitat structure was shown by Robertson and Duke (1987), Thayer *et al.* (1987) and Laegdsgaard and Johnson (1995) to be one of the factors affecting tropical and subtropical shallow fish distributions. Substratum types, such as mud and sand are associated with particular depths and have been found closely correlated with several shallow demersal fish in the Gulf of Carpentaria (Blaber *et al.,* 1995). For juvenile plaice, burying ability was determined by the substratum type, thus influencing their distribution patterns (Gibson and Robb, 1992; Rogers, 1992). Wave energy gradients within habitats is another factor that may determine species composition patterns in sandy beaches (Romer, 1990). These factors may therefore strongly influence the distribution of small juvenile fishes in sandy shore surf zone and estuary mouth habitats and could provide a key to understanding the primary links in the food webs for these two study habitats.

BIOMASS: Temporal and spatial variability

Few biomass estimates for tropical intertidal assemblages are available, thus making it one of the most difficult areas for comparative productivity studies (Hellier, 1962; Whitfield, 1993). This is probably because of different habitat samples, seasonality, sampling design, short sampling periods, few replicated habitats and sampling gear specifications. According to Whitfield (1993) most previous studies have either combined the data or sampled on only one occasion.

In this study, biomass of fish taken from sandy shore surf zones and estuaries was separated and as a result, it became apparent that the magnitude of biomass between these two habitats was similar. Mean biomass for each trip varied from trip to trip, ranging from 0.31 ± 0.08 to 5.25 ± 1.16 g FW m^{-2} for sandy shore surf zones and 0.36 ± 0.09 to 2.16 ±

0.51 g FW m^{-2} for estuary mouths. Published comparisons of fish biomass in coastal systems around the world (reviewed in Whitfield, 1993) indicate that fish biomass from the sandy shore surf zones and estuary mouths in the current study were at the lower end of expected ranges (0.1 - 104.0 gm^{-2}). The differences in estimation of biomass in this study and others are large, and are probably due to the type of fishing gear and mesh size employed. Other studies have used a range of gear from rotenone, drop nets, trap nets, gill nets, cast nets, seine nets, and trawls.

Robertson and Duke (1990a) reported an approximate 10.9 g FWm^{-2} of fish biomass from mangrove estuaries in the vicinity of Townsville. This value is about five-times higher than that found in this study. Blaber *et al.* (1990b) suggested that comparisons with neighbouring areas should be made with caution because of differences in fishing effort and sampling gear. For instance, Blaber *et al.* (1989) used a wide range of gears, including large mesh gill nets, up to 150 mm mesh size, seine nets, beam trawls, stake nets and rotenone to assess species composition and biomass in Embley estuary in the Gulf of Carpentaria. The large estimate of biomass by Blaber *et al* (1989) is probably due to the capture of large fishes, including sharks and rays. Robertson and Duke (1990a) used trap nets, with a mesh size of 3 mm, which are far more efficient than seine nets, especially in terms of the capture of mobile species moving in or out of the creeks with the tides. In conjunction with efficiency, the relatively higher biomass in mangrove creeks is probably primarily related to appropriate complex micro-habitats. Moreover, mangrove ecosystems may be functionally different from estuarine embayments. Habitats within mangroves may provide better protection and food supplies than those in estuary mouths (Robertson and Duke, 1987; Robertson and Blaber, 1992; Thayer *et al*, 1987).

Annual and Seasonal Variability and Biomass

Seasonal variations in total biomass were influenced primarily by the biomass of dominant species, such as the patchy occurrences of *Escualosa thoracata* and *Sardinella gibbosa* (Figs 3.2 B and C). However, the exclusion of *E. thoracata* and *S. gibbosa* from the analysis still resulted in the same pattern with biomass being high in summer and low in winter. Mean annual biomass of *Sillago analis* varied over the three year study period. This annual variability followed the same trend as the abundance data.

Seasonal biomass patterns of the dominant species follow the same trends as found for the abundance data i.e. high biomass in summer as compared with winter. This difference reflects the fact that larger individuals were collected in summer versus winter.The only exception is *Stolephorus nelsoni* which did not show a significant seasonal difference in biomass.

Habitat Variability and Biomass

Mean Total and Adjusted Biomass between sandy shore surf zones and estuary mouths were similar while an examination of dominant species revealed a significantly higher biomass in estuaries for *Valamugil seheli.* These results suggest that there are different life history requirements between species and habitat preferences. Preliminary observations on the size frequency distribution for *V. seheli* showed that small juveniles (SL < 60 mm) are more abundant in sandy shore surf zones, whilst larger individuals are found in estuarine habitats. These findings are similar to those of Blaber (1987) and Vieira (1991), who suggested that individuals move from sandy shore surf zones to estuaries. Several studies have also shown that the substratum in most estuaries is rich in organic matter and has a high biomass of benthic animals (reviewed in Kennish, 1990; see also Table 2.1). It is probable that the large biomass of *V. seheli* in estuary mouth habitats is permitted only by the large resource of energy contained in the substratum (Blaber, 1987).

Other Factors Influencing Variability in Abundance and Biomass

There appear to be some mechanisms by which juveniles become concentrated inshore which are above and beyond a merely random hydro-dynamical phenomena, such as tides or currents. Behavioural and physiological responses to hydro-dynamical processes associated with seasons have been proposed to explain this association (Boehlert and Mundy, 1988; Miller, 1988).

The sandy shore surf zone environment is a hydrodynamically active site and physical activity apparently diversifies microhabitats in such a way as to support relatively higher juvenile numbers than an estuarine embayment environment which is much less active hydrodynamically (Brown and McLachlan, 1990; Kennish, 1990). Whilst this may help explain the higher abundance and biomass of individuals in sandy shore surf zones in the present study other factors must be considered.

The pattern of higher abundance in the summer season is readily apparent within both sandy shore surf zones and estuaries. Abundance and biomass in both sandy shore surf zones and estuaries showed strong seasonal variations in comparison with other tropical habitats (e.g. Robertson and Duke, 1987; Whitfield, 1993). However, these trends have been influenced largely by changes in the abundance and biomass of a few dominant species. How well these reflect the broader community patterns will be addressed in the next chapter.

CHAPTER 4

ASSEMBLAGE COMPOSITIONS AND PATTERNS OF JUVENILE FISHES IN SANDY SHORE SURF ZONES AND ESTUARY MOUTHS

INTRODUCTION

The ecological patterns and processes relating to assemblage persistence and stability are dynamic, with the abundance and taxonomic organisation of species varying over both spatial and temporal scales (Connell and Sousa, 1983; Krebs, 1985; Rahel, 1990). Persistence refers to the continuing presence of certain species over time. Stability is the relative constancy of assemblage abundances over time, despite disturbances. Persistence and stability in nature may result from regulatory processes by means of resistance to potential destructive forces or by resilience. Resilience is defined as the ability of an assemblage to rapidly bounce back from disturbances in order to maintain their relative constancy of structure (Krebs, 1985). Factors influencing persistence and stability are unknown and opinions are divergent (Grossman, 1982; Grossman *et al.*, 1982; Beckley, 1985; Ross *et al.*, 1985; Collette, 1986; Thorman and Wiederholm, 1986; Yoshiyama *et al.*, 1986; Meffe and Minckley, 1987; Mahon and Mahon, 1994; Ross and Doherty, 1994).

Several principal variables play a role in the distribution patterns of fish assemblages in these sandy shore surf zones and estuary mouths including temperature (Blaber *et al.*, 1985), salinity (Blaber *et al.*, 1985; Weinstein, 1979), wind speed and direction (Modde and Ross, 1981; Lasiak, 1984; Romer, 1990), depth (Weng, 1986; Gibson, 1994), turbidity (Blaber, 1980; Cyrus and Blaber, 1987), and substrate characteristics (Gibson, 1994). Protection from predators (Werner *et al.*, 1983), competition (Grossman, 1982), food availability (Ross *et al.*, 1987) and seasonal climate variation (Quinn, 1980) are also thought to influence the utilisation of habitats by fish species or assemblages.

Fish that inhabit intertidal areas are more directly influenced by seasonal climate changes than those living in subtidal or shallow waters of the ocean (Gibson, 1982, 1993). Davis (1988) studied temporal changes in fish fauna entering tropical tidal swamps in the Northern Territory. He suggested that the seasonal patterns in abundance of species found there was determined by breeding patterns and the dispersal ability of fishes rather than by environmental parameters such as temperature or salinity. Recent studies by Ross and Doherty (1994) have also indicated seasonal trends in abundance and species diversity in the coastal habitat of Florida because of recruitment patterns.

In recent years, increased scientific effort has been focused on the role of near shore marine environments in determining the distribution of fish assemblages. These areas are believed to fulfil the role of nursery areas for larvae and juveniles (Blaber and Blaber, 1980; Weinstein et al., 1980; Livingston, 1982; Robertson and Duke, 1987, 1990; Brown and McLachlan, 1990; Robertson and Blaber, 1992). Little information is available on the seasonal variation in the composition of fish fauna in sandy shore surf zones and estuary mouths in tropical Indo-Pacific regions (Blaber, 1980; Gibson, 1982), and even less is known about their assemblage patterns.

Fish faunas associated with these areas are dominated by a few numerically abundant species. Use of these regions by these fishes can be seasonal or opportunistic (Lasiak, 1981, 1984; Romer, 1990; Ayvazian and Hyndes, 1995). Typically sandy shore surf zones and estuary mouths are influenced by temporal and spatial instability from physical features such as tides, winds and wave energy, and these in turn affect the dynamics of the fish assemblage.

Several studies have shown that intertidal fish assemblages in the tropics can be highly diverse (Gibson, 1982; Mahon and Mahon, 1994). However, studies of temporal and spatial variations in abundance (Chapter 3) are limited and permit little understanding of the dynamics of these assemblages because it is not known whether or not the abundance or the composition of assemblages undergo significant changes. The aim of this chapter is to examine temporal and spatial variations in the abundance of juvenile fishes in sandy shore surf zones and estuary mouths. Unlike chapter 3 which examined numerical data for total species numbers, total numbers of individuals of selected species, and total individuals caught, this chapter will examine the assemblage as a whole. Information gained from the analysis will address the following questions:

1) Are assemblages in sandy shore surf zones and estuary mouth habitats persistent over long or short terms? (ie. are individual taxa retained over time);

2) Are assemblages stable? (ie. is the number of individuals of each taxa stable over time).

MATERIALS AND METHODS

Data Collection

A multistage sampling design was employed to collect the samples for the present study. Samples were taken at approximately 2 month intervals from January 1992 to September 1994. Analyses of data for this chapter is based on seine catch abundance data from sandy shore surf zone and estuarine surveys as outlined in Chapters 2 and 3.

Data Analyses

A multivariate approach to data analysis was selected for this study in order to avoid the criticisms raised by Rahel *et al.* (1984) and Rahel (1990), such as sensitivity, poorly known mathematical backgrounds, and subjective definitions that can actually hide data features that are being sought while using a species diversity index. Multivariate statistical analyses have been used to explore fish assemblage changes because of their advantages over analyses based on simpler measures of similarity indices (James and McCulloch, 1990; Grossman *et al.*, 1991; Scheiner, 1993).

Stability and Variations in Assemblage Pattern

Stability is the relative constancy of abundances in an assemblage over time. Stability of the intertidal fish assemblages in the near-shore waters of Townsville were examined by using a multivariate analysis of variance (MANOVA; Meffe and Minckley, 1987; James and McCulloch, 1990).

A total of 126 fish species were caught from sandy shore surf zones and estuary mouths . No attempt was made to analyse the entire assemblage due to the number of rare species. In order to examine the factors contributing to the abundance patterns of fishes in sandy shore surf zones and estuary mouths, the data was examined with a multivariate analysis of variance (MANOVA). This procedure is best carried out with a reduced number of variables to allow a clearer interpretation of trends in the data (Scheiner, 1993). Initially, only species that were present each year over the 3 year sampling period were selected and included in the analysis, species which did not meet this requirement were classified as rare. Consequently, 60 species were eliminated from the analysis. Sixty-seven common species were retained (Table 4.1). However, preliminary analysis of these common species by MANOVA revealed that there were insufficient degrees of freedom for testing interpretation. This called for a further reduction in the number of species analysed. To achieve this reduction, any species that did not constitute at least 1% of the total catch was removed. Consequently, 23 abundant species were retained for further analysis by

Table 4.1 Abundance of each "common species" for all samples collected from sandy shore surf zones (SSSZ) and estuary mouth habitats across season from North Queensland, between January 1992 and September 1994.

TAXA	Abbreviation	Summer		Winter	
		SSSZ	EM	SSSZ	EM
Sardinella gibbosa	SGI	44082	5336	4	138
Leiognathus splendens	LSP	15398	1212	333	3620
Escualosa thoracata	ETH	10512	545	2414	1438
Stolephorus nelsoni	SNE	9124	1920	479	138
Trachinotus blochii	TBL	5135	9	70	0
Stolephorus insularis	SIN	2255	120	456	0
Encrasicholina devisi	EDE	1492	0	284	0
Gerres oblongus	GOB	1487	657	258	99
Stolephorus commersonii	STC	1272	99	19	0
Thryssa hamiltoni	THA	1192	20	64	15
Secutor rucornis	SRU	1116	73	48	0
Sillago analis	SAN	1049	859	385	735
Gerres oyena	GOY	869	615	25	95
Gazza minuta	GMI	824	36	0	3
Ambassis vachelli	AVA	784	2049	738	2622
Stolephorus carpenteriae	SCR	670	433	828	388
Hyporhamphus quoyi	HQU	591	1004	57	186
Sardinella brachysoma	SBR	573	23	21	36
Terapon jarbua	TJA	478	319	40	41
Sillago sihama	SSI	418	113	881	296
Arrhamphus sclerolepis	ASC	400	1433	214	1043
Liza subviridis	LSB	340	43	391	298
Valamugil seheli	VSE	326	2344	4567	4798
Chelonodon patoca	CPT	297	97	43	16
Rhynchorhamphus georgii	RGE	297	346	203	465
Selenotoca multifasciatus	SMU	274	39	0	3
Leptobrama mulleri	LMU	256	25	89	4
Lactarius lactarius	LLA	196	0	0	0
Scomberoides tol	STO	193	117	20	17
Liza vaigensis	LVA	185	797	97	578
Eleuteronema tetradactylum	ETE	181	4	242	5
Lagocephalus lunaris	LLU	103	0	0	0
Gerres filamentosus	GFI	72	138	8	47
Atherinomorus endrachtensis	AEN	55	1738	20	3306
Drepane punctata	DPU	54	3	4	0
Sphyraena jello	SJE	46	16	0	0
Strongylura leiura	SLE	46	83	47	28
Carangoides headlandensis	CHE	33	6	3	1
Herklotsichthys koningsbergeri	HKO	33	58	6	9
Nematalosa come	NCO	32	407	2	0
Ambassis nalua	ANA	28	101	54	26
Terapon theraps	TTH	25	7	1	2
Scomberoides commersonnianus	SCC	23	55	7	5
Trixiphichthys weberi	TWE	15	1	12	0
Dactyloptena ?orientalis	DOR	14	1	8	0
Caranx bucculentus	CBU	12	0	1	0
Paraplagusia bilineata	PBI	12	1	72	0
Sillago ciliata	SCI	10	34	6	47
Platycephalus fuscus	PFU	8	10	62	4
Silhouettea evanida	SEV	8	398	21	174
Leiognathus equulus	LEQ	5	96	1	33
Lutjanus russelli	LRU	5	27	0	1
Platycephalus endrachtensis	PEN	4	2	0	4
Arothron manillensis	AMA	3	4	2	1
Valamugil buchanani	VBU	3	300	1	9
Herklotsichthys castelnaui	HCA	2	1	10	25
Siganus canaliculatus	SCN	2	38	0	0
Valamugil speigleri	VSP	2	105	32	15
Tetractenos hamiltoni	TQH	1	4	1	11
Acanthopagrus berda	ABE	0	5	0	5
Butis butis	BBU	0	2	1	7
Gerres poeti	GPO	0	13	0	4
Nemipterus sp.	NEM	0	0	4	2
?Pelates sp.	PEL	0	1	1593	574
Platax teira	PTE	0	2	0	0
Tylerius spinosissimus	TSP	0	4	1	2
Valamugil cunnensius	VCU	0	45	4	41
Leiognathus decorus	LDE	0	0	2141	78

MANOVA. Before conducting the MANOVA, the raw data were log(x+1) transformed to reduce heterogeneity of variances.

To examine the stability of assemblage abundance, a three-factor unbalanced MANOVA was used to test for overall significant differences in the mean number of individuals of the assemblage among years, seasons and habitat groups in the data matrix. The statistical hypothesis tested by MANOVA was that year, season, habitat and interaction combinations had no effect on total assemblage abundance of common species. Pillai's Trace was used as the multivariate test statistic because it is robust and unlikely to involve Type I errors (Green, 1979; Johnson and Field, 1993; Scheiner, 1993). In the present study, analysis of variances (ANOVAs) were used as *post hoc* tests to detect the differences in the means of main factors. It is important to note that study years in the present analysis were randomly selected to detect only annual variation in patterns. Due to limited data on physical and biological factors related to distribution, no attempt was made to explain assemblage patterns related to these factors.

Species Assemblage Patterns and Spatial Groupings

To determine the pattern of spatial groups and characteristic species of sandy shore surf zones and estuary mouths, a correspondence analysis (CA) was used. Correspondence analysis is a multivariate ordination technique that allows the detection of patterns between species and the surveys in which they are observed. The CA ordinates species according to trends in their occurrence within samples, and both species and samples are represented graphically according to their score on an axis. In the present study, CA was also used in association with a graphical display to interpret species assemblage patterns of fish from sandy shore surf zones and estuary mouths as described by Greenacre and Vrba (1984) and Greenacre and Hastie (1987). To reduce the problems associated with rare species, only the 67 common species were analysed (Table 4.1). Before analysis, abundance data for each species was log (x+1) transformed to minimise heterogeneity of variances.

Persistence of Assemblage Patterns

In order to examine persistence in these assemblages, the similarities in taxonomic compositions between habitat-season combinations were investigated with a hierarchical cluster analysis. Again, only data for the 67 common species were analysed (Table 4.1). Catches were averaged over each season and each habitat to give 4 habitat-season totals per year. The numbers of individuals were log (x+1) transformed to stabilise variances. Ward's minimum variance method (SAS Institution Inc., 1990) was selected to construct the dendrogram of the distance between observations because of its ability to recover clusters from a variety of data structures. Clusters of common species in habitat-season combinations between years indicate persistence of underlying assemblages whereas separate clusters of habitat-seasons between years will indicate a lack of persistence.

RESULTS

Species Composition and Relative Abundance

A total of 181,988 individuals from 48 fish families were collected from January 1992 to September 1994. The number of species sampled from sandy shore surf zones (112) and estuary mouths (93) were similar, and collectively produced a total of 126 species. Assemblages in sandy shore surf zones and estuary mouths were dominated by a few species that occurred in large numbers. *Sardinella gibbosa* was the most dominant species, constituting 29.50% of the total catch, followed by *Leiognathus splendens* (12.24%), and *Escualosa thoracata* (8.00%). These three species collectively constituted approximately 50% of the total catch, the other 50% being shared by 123 species (see also Appendix 2).

The species composition of the fish assemblage varied with season and habitat. The abundance of most species was lower in winter and higher in summer, with the exception of *Valamugil seheli*, *Ambassis vachelli*, *Leiognathus decorus*, *Atherinomorus endrachtensis* (Table 4.1). Individuals were generally more numerous in sandy shore surf zones than estuary mouths with the exception of *Ambassis vachellii, Hyporhamphus quoyi, Rhynchorhamphus georgii, Arrhamphus sclerolepis, Atherinomorus endrachtensis, Nematalosa come*, and all the mullets, such as *Valamugil buchanani, V. seheli*, and *Liza vaigensis*. The most abundant species in estuary mouths were *V. seheli* (4.25%), followed by *S. gibbosa* (3.25%), *A. endrachtensis* (3.00%), *L. splendens* (2.88%), *A. vachellii* (2.78%), *A. sclerolepis* (1.47%), *Stolephorus nelsoni* (1.22%) and *Escualosa thoracata* (1.18%). In contrast, *S. gibbosa* was the most abundant species in sandy shore surf zones (26.24% of the total catch) followed by *L. splendens* (9.36%), *E. thoracata* (7.69%), *S. nelsoni* (5.72%), *Trachinotus blochii* (3.10%), *V. seheli* (2.9%), *Stolephorus insularis* (1.61%), *Leiognathus decorus* (1.06%) and *Gerres oblongus* (1.04%).

Stability Variations in Assemblage Patterns

Assemblage abundance patterns of common species varied over years, seasons and habitats. Annual variation in assemblage abundance was evident for *Leiognathus splendens, L. decorus, Secutor rucornis, L. vaigensis, V. seheli, G. oblongus, G. oyena, S. insularis, S. nelsoni, S. carpentariae, Sillago analis, S. sihama, A. sclerolepis* and *Hyporhamphus quoyi* (MANOVA, $F_{46, 138} = 5.489$, $P < 0.01$; Table 4.2; and ANOVA, $p < 0.05$; Table 4.3). Similarly, abundance of individuals in both habitats between summer and winter was not consistent (MANOVA, $F_{23, 68} = 8.1081$, $p < 0.01$; Table 4.2), *L. splendens, Secutor rucornis, Sardinella gibbosa, Stolephorus nelsoni, S. insularis, S. commersonii, E. thoracata, Trachinotus blochii, Gerres oblongus, G. oyena, and Hyporhamphus quoyi* had a higher abundance in summer than winter (ANOVA, $p < 0.05$; Table 4.3). In contrast, a significantly higher abundance of *V. seheli*, and *Pelates* spp. was recorded in winter compared to summer (ANOVA, $p<0.05$; Table 4.3), while abundance was similar in summer and winter for *Sillago analis, S. sihama, Amabassis vachellii, Arrhamphus sclerolepis, Aterinomorus endrachtensis, Leiognathus decorus, Liza vaigensis, Stolephorus carpentariae, Encrasicholina devisi*, and *Thryssa hamiltoni* (ANOVA, $p> 0.05$; Table 4.3). There was also a significant difference in assemblage of abundant species between sandy shore surf zones and estuary mouths (MANOVA, $F_{23, 68} = 7.5828$, $p < 0.01$; Table 4.2). Individual abundances were 2-5 times higher in estuary mouths for the species *Valamugil seheli, Liza vaigensis, Ambassis vachellii, Atherinomorus endrachtensis, Arrhamphus sclerolepis*, and *Hyporhamphus quoyi* (ANOVA, $p< 0.05$; Tables 4.1 and 4.3), while *Stolephorus nelsoni, S. insularis, S. commersonii, Encrasicholina devisi, Thryssa hamiltoni* and *Secutor rucornis* were significantly more abundant in sandy shore surf zones (ANOVA, $p< 0.05$; Tables 4.1 and 4.3). The rest of the species occurred in similar abundance in both habitats (Table 4.3). Abundance varied between season and habitat (MANOVA, $F_{23, 68} = 1.7256$, $p < 0.01$; Table 4.2) due to the patterns of abundance of *Stolephorus commersonii* and *Trachinotus blochii* (ANOVA, $p< 0.05$; Table 4.3). Fish abundance between seasons was not consistent among study years (MANOVA, $F_{46, 138} = 4.7927$, $p < 0.01$; Table 4.2) with respect to the abundance of *Valamugil seheli, Gerres oyena, G. oblongus, Arrhamphus sclerolepis, Leiognathus decorus, Stolephorus carpentariae, Sillago sihama* and *Secutor rucornis* (ANOVA, $p< 0.05$; Tables 4.1 and 4.3).

Table 4.2. Summary table of results of MANOVA model testing for the effect of year, season, habitats and combined interactions of number of individuals of common species assemblages of intertidal habitats of tropical North Queensland. Test statistic used is Pillai's Trace.

Source of Variance	*F*-ratio	Numerator *df*	Denominator *df*	*P*-value
Year	5.4890	46	136	<0.001
Season	8.1081	23	68	<0.001
Year x Season	4.7927	46	138	<0.001
Habitat (Hab)	7.5828	23	68	<0.001
Year x Hab	1.3871	46	136	>0.05
Season x Hab	1.7256	23	68	<0.05
Year x Season x Hab	0.6612	46	138	>0.05

Table 4.3. Results from 3-way ANOVAs on 23 species used in the MANOVA. Results are only presented for the factors that are significant; F-values and their significance are indicated; **p<0.01, *p<0.05. Y: year; S: season; H: habitat (Locations and sites were omitted because they are nested within habitats, trips were also omitted as it nested in Y*S).

Species	Source						
	Y	S	Y*S	H	Y*H	S*H	Y*S*H
	df=2	df=1	df=2	df=1	df=2	df=1	df=2
Leiognathus splendens	6.26**	24.48**	-	-	-	-	-
Sardinella gibbosa	-	32.46**	-	-	-	-	-
Valamugil seheli	7.67**	4.79*	6.22**	15.41**	-	-	-
Stolephorus nelsoni	18.11**	29.74**	-	11.80**	-	-	-
Escualosa thoracata	-	-	-	-	-	-	-
Ambassis vachellii	-	-	-	4.71*	-	-	-
Trachinotus blochii	-	11.80**	-	24.92**	-	-	-
Atherinomorus endrachtensis	-	-	-	62.41**	-	-	-
Sillago analis	10.96**	-	-	-	-	-	-
Gerres oblongus	6.81**	9.77**	15.50**	-	-	-	-
Stolephorus insularis	5.93**	4.40*	-	5.76*	-	-	-
Arramphus sclerolepis	15.83**	-	3.65*	4.14*	5.28**	-	-
Leiognathus decorus	7.77**	-	12.12**	-	-	-	-
Pelates sp.	-	32.46**	-	-	-	-	-
Stolephorus carpenteriae	-	-	13.19**	-	-	-	-
Hyporhamphus quoyi	14.39**	53.48**	-	12.06**	-	-	-
Encrasicholina devisi	-	-	-	5.35*	-	-	-
Sillago sihama	3.32*	-	7.32**	-	-	-	-
Liza vaigensis	4.33*	-	-	17.36**	3.40*	-	-
Gerres oyena	5.62**	16.06**	11.14**	-	-	-	-
Stolephorus commersonii	-	31.50**	-	11.16**	-	-	-
Thryssa hamiltoni	-	-	-	6.60*	-	-	-
Secutor rucornis	3.26*	21.17**	3.86*	8.42**	-	-	-

Juvenile Species Assemblage Patterns and Spatial Groupings

Temporal and Spatial Patterns

Graphical displays from correspondence analysis are used to describe habitat and seasonal patterns. The major factor responsible for the assemblage structure of all juveniles in each year was season (CA, Fig. 4.1). Samples from summer and winter seasons were separated by the first axis along the right side and left side of Axis 1 respectively, especially in 1993 and 1994 (Figs. 4.1 B and C).

There were consistent differences between the total assemblage of common species associated with sandy shore surf zones and estuary mouths across all sampling years (Figs. 4.2 A, B and C). Samples taken from sandy shore surf zones were not completely distinct from estuary mouths as several species were common in both habitats. It is interesting to note that assemblage patterns over sandy shore surf zones were more variable than those of estuary mouths. Sample ordinations from both habitats across seasons yielded similar results to those found across sampling years (Table 4.2). Assemblage patterns from sandy shore surf zones were also more variable than those from estuary mouths, however, assemblage patterns in estuary mouths almost completely overlapped sandy shore surf zone patterns in winter (Figs. 4.3 A and B). The difference between sandy shore surf zones and estuary mouth assemblages were also clearly seen in scatter plots of every study season. Strong groupings of fish were evident for sandy shore surf zones and estuary mouths in summer, while assemblages within habitats overlapped in winter (Figs. 4.4 A, B and C).

Species Patterns

Species patterns were grouped by season (Axis 1, Fig. 4.5) and habitat (Axis 2, Fig. 4.5). In general, species occurring in summer were grouped on the right hand side of Axis 1. These species included *Eleuteronema tetradactylus* (ETE), *Lagocephalus lunaris* (LLU),

Figure 4.1. Scatter diagram of ordinated scores of summer (closed circles) and winter (open circles) seasons for Axes 1 and 2 using Correspondence Analysis, showing seasonal difference.

A) For 1992 catch

B) For 1993 catch

C) For 1994 catch

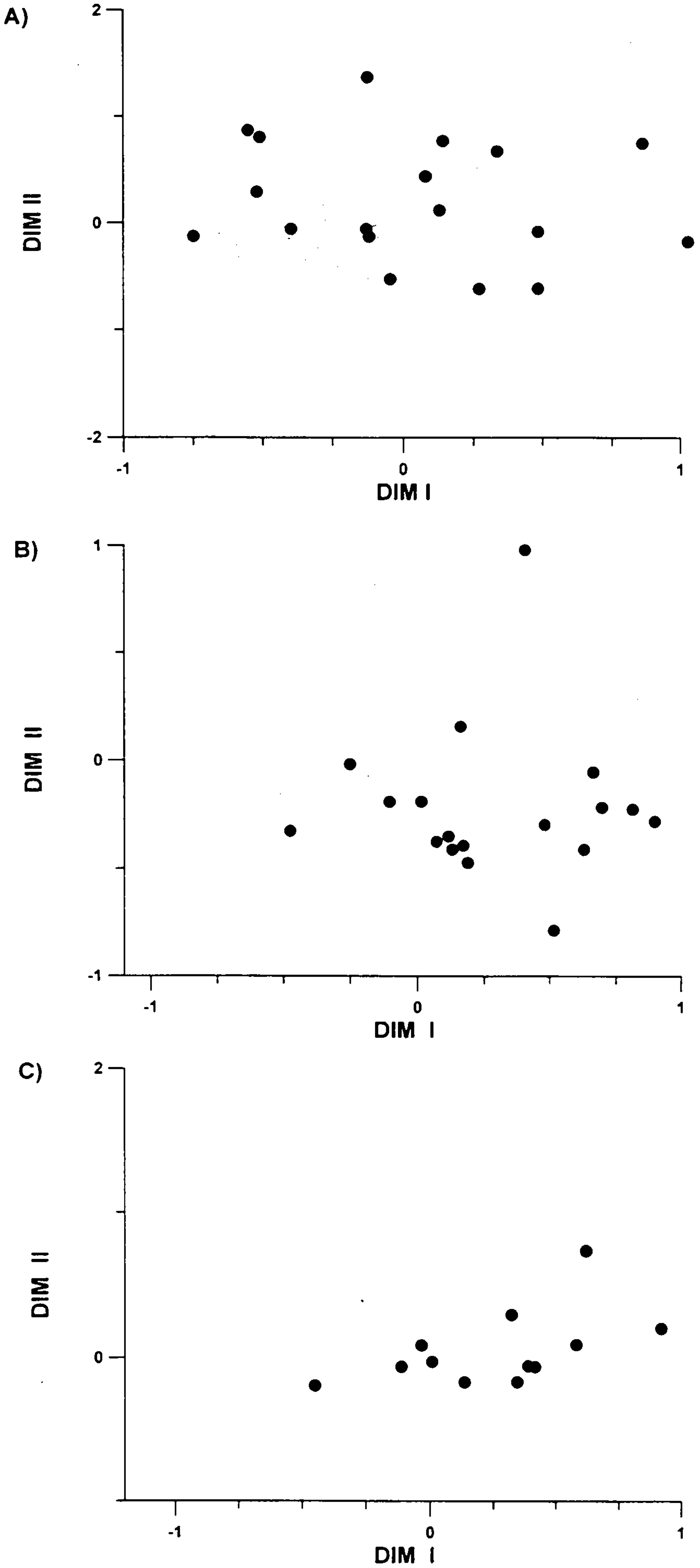


Fig. 4-1

Figure 4.2. Scatter diagram of ordinated scores of sandy shore surf zones (closed circles) and estuary mouths (open circles) on Axes 1 and 2 using Correspondence Analysis

A) For 1992 catch

B) For 1993 catch

C) For 1994 catch

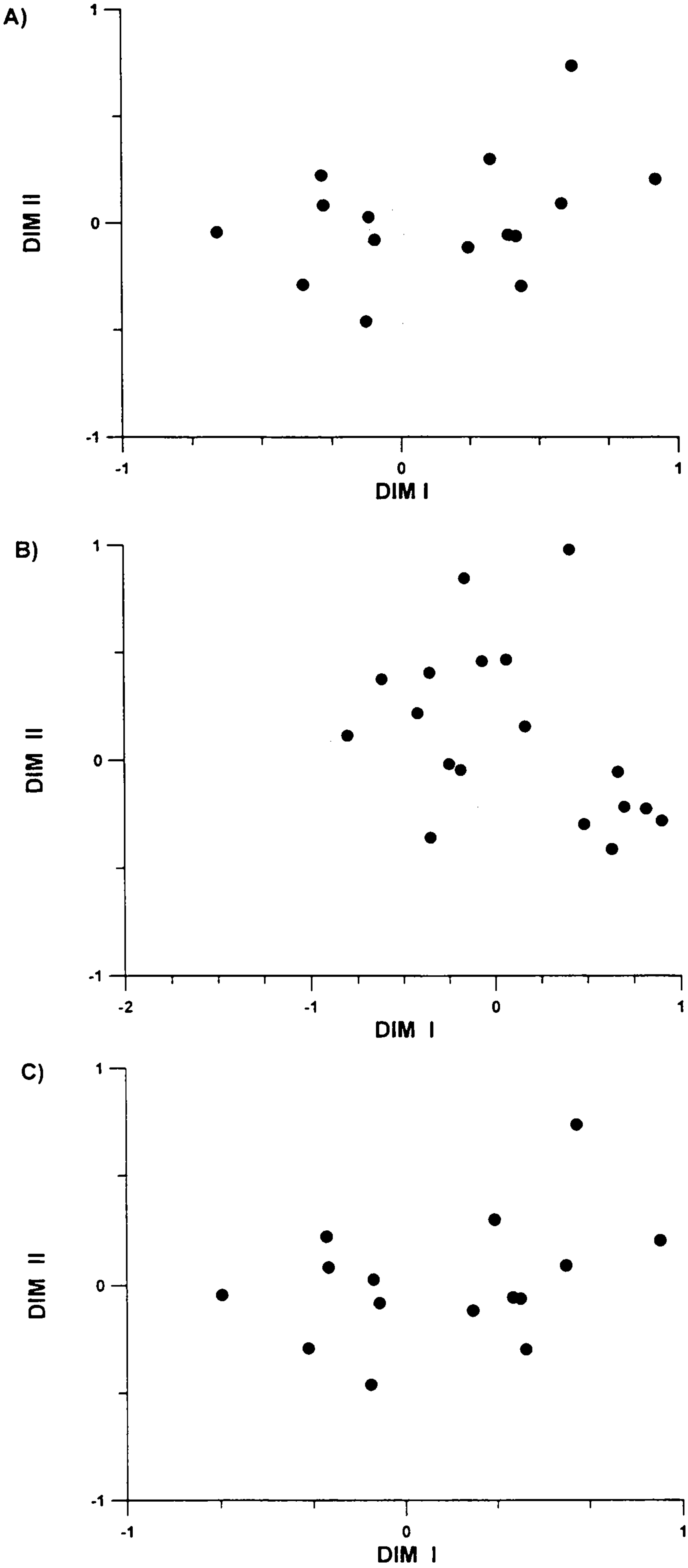
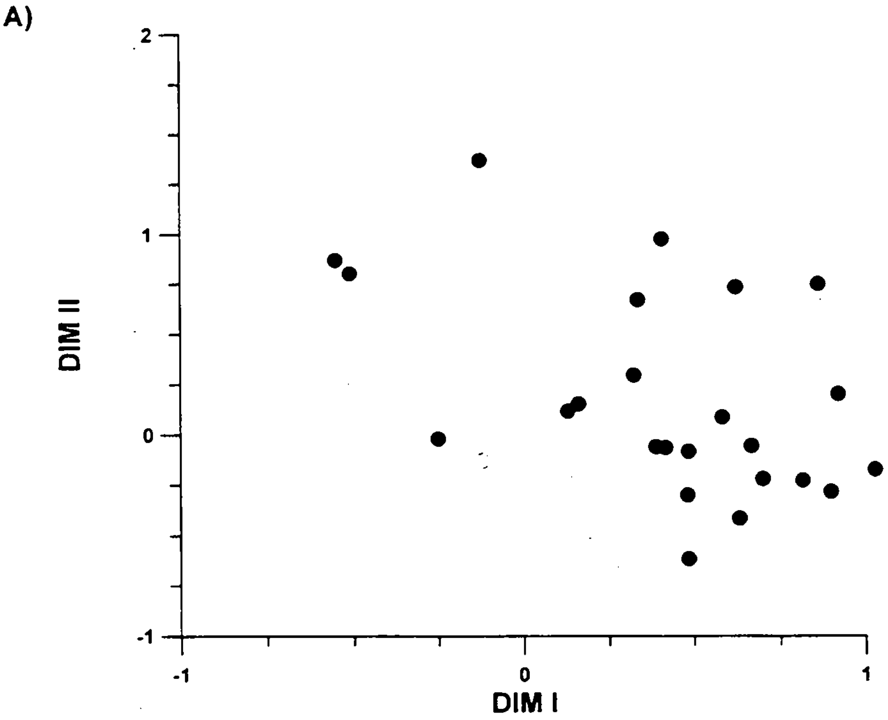


Fig. 4-2

Figure 4.3. Scatter diagram of ordinated scores of sandy shore surf zones (closed circles) and estuary mouths (open circles) on Axes 1 and 2 using Correspondence Analysis

A) Summer Season

B) Winter Season



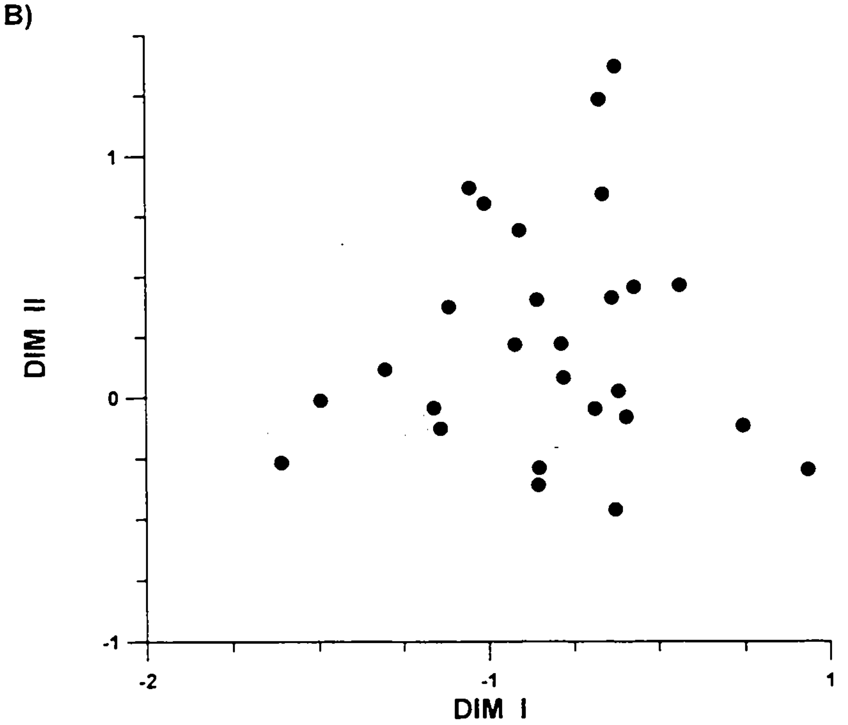


Fig.4-3

Figure 4.4. Scatter diagram of ordinated scores of total fish samples, showing habitat difference: sandy shore surf zones (closed circles) and estuary mouths (crosses)

A) For 1992 catch

B) For 1993 catch

C) For 1994 catch

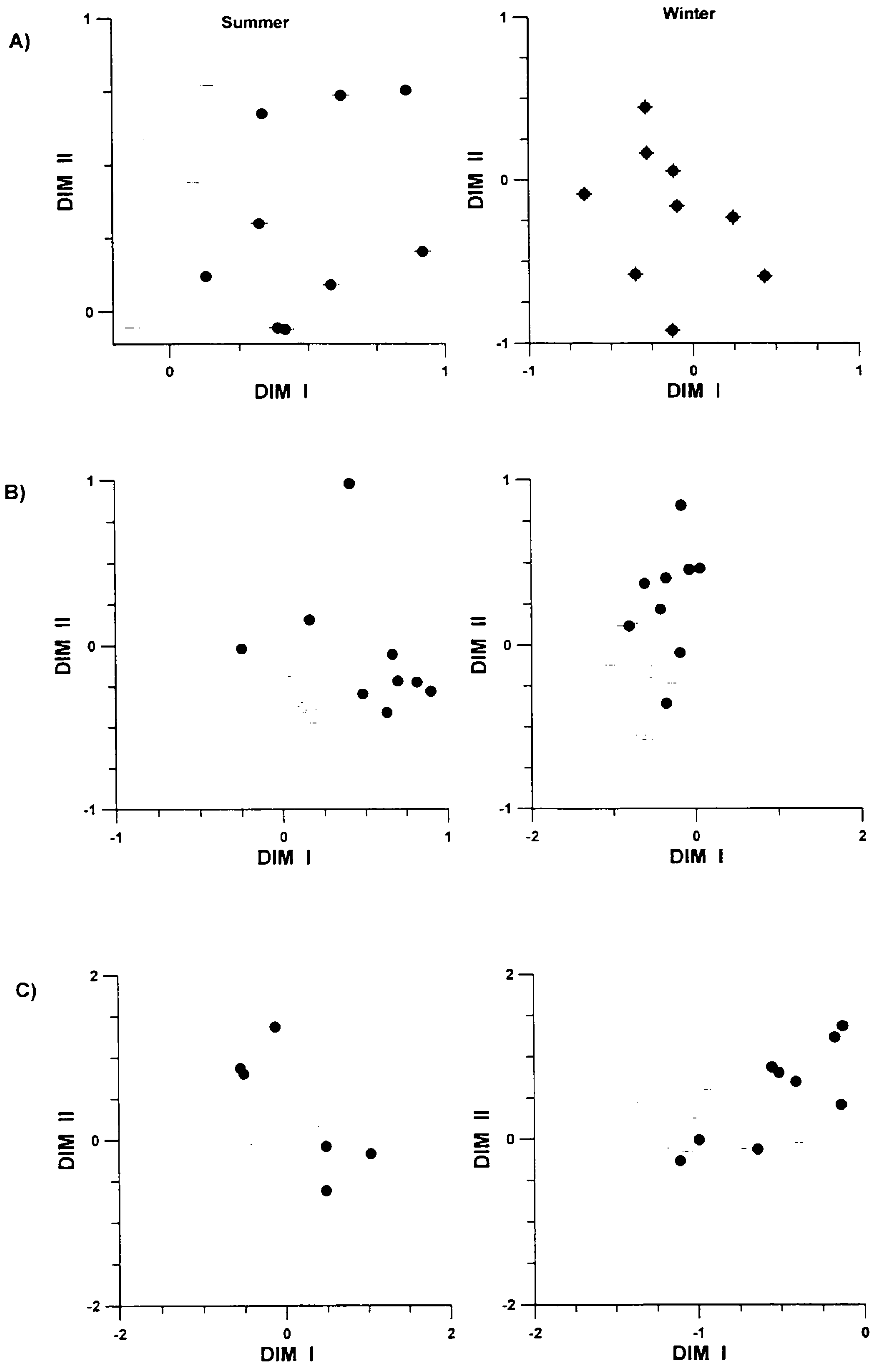

A)
Summer
Winter
B)
C)
DIM II
DIM I
1
0
-1
2
-2

Figure 4.5. Scatter diagram of ordinated scores for 67 species of total fishes from sandy shore surf zones and estuary mouths on Axes 1 and 2 using Correspondence Analysis. (Abbreviation codes for scientific names given in full in Table 4.1)

S1H1[●]: Sandy shore surf zone in summer;

S1H2[◆]: Sandy shore surf zone in winter;

S2H1[○]: Estuary mouth in summer, and

S2H2[◇]: Estuary mouth in winter)

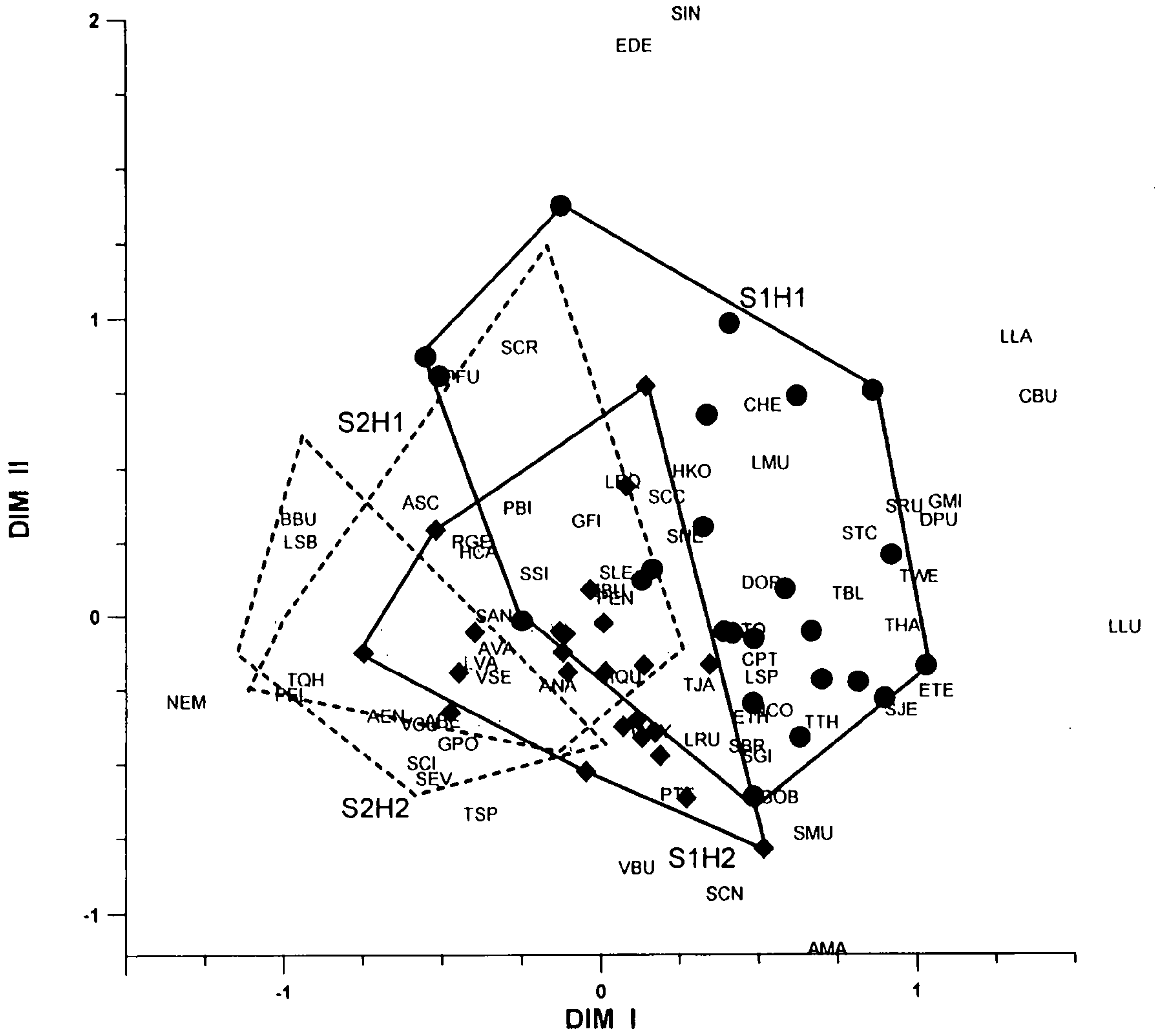

S1H1
S1H2
S2H1
S2H2
SIN
EDE
LLA
CBU
LLU
SCR
TFU
CHE
LMU
HKO
LEO
SCC
SNE
ASC
PBI
GFI
BBU
LSB
RGE
HCA
SSI
SLE
RBU
PEN
SRU
GMI
DPU
STC
TWE
DOR
TBL
THA
SAN
AVA
LVA
VSE
ANA
RQU
TJA
TTO
CPT
LSP
ETE
SJE
NEM
TQH
PEI
AEN
VGO
ABE
GPO
SCI
SEV
TSP
LRU
ETH
ECO
TTH
SBR
SGI
PTE
SOB
SMU
VBU
SCN
AMA
2
1
0
-1
DIM II
-1
0
1
DIM I

Fig. 4-5

Drepane punctata (DPU) and *Gazza minuta* (GMI). In contrast, species situated on the left hand side of Axis 1 are principally species caught in winter such as *Atheriomorus endrachtensis* (AEN), *Pelates* spp. (PEL), *Liza subviridis* (LSB) and *Torquigener hamiltoni* (TQH). Species located in the middle such as *Sillago analis* (SAN), *S. sihama* (SSI), *Ambassis vachellii* (AVA), and *Valamugil seheli* (VSE), have less affinity to season and appear in both summer and winter samples.

For Axis 2, species grouped in the mid to lower portion represent fish from estuary mouths. These species included *Valamugil cunnesis* (VCU), *Silhouettea evanida* (SEV), *Tylerius spinosissimus* (TSP), *Ambassis nalua* (ANA) and *Gerres poeti* (GPO). On the other hand, species from the mid to upper portion of Axis 2 were those caught from sandy shore surf zones. These species included *Stolephorus carpenteriae* (SCR), *S. insularis* (SIN), *Leptobrama mulleri* (LMU) and *Paraplagusia bilineata* (PBI). There is, however, some overlap among these general patterns, probably due to the interaction of diverse variables.

Intertidal fishes taken from sandy shore surf zones and estuary mouths were clarified by Ward's minimum variance linkage following Cluster Analysis of the abundance of common species (Fig. 4.6). The dendrogram indicates that assemblage similarity was dominated by season, and year and habitat are of minimal importance (Fig. 4.6). The biological basis for these clusters is more clearly seen in scatter plots from the correspondence analysis (Figs. 4.1 to 4.5). Two meaningful clusters are formed at level 1 of the dendrogram, and the results parallel those found by correspondence analysis. The first cluster (a) is formed by three season-habitat samples from sandy shore surf zones in the summer seasons of 1992, 1993 and 1994. The second cluster (b) is formed by samples

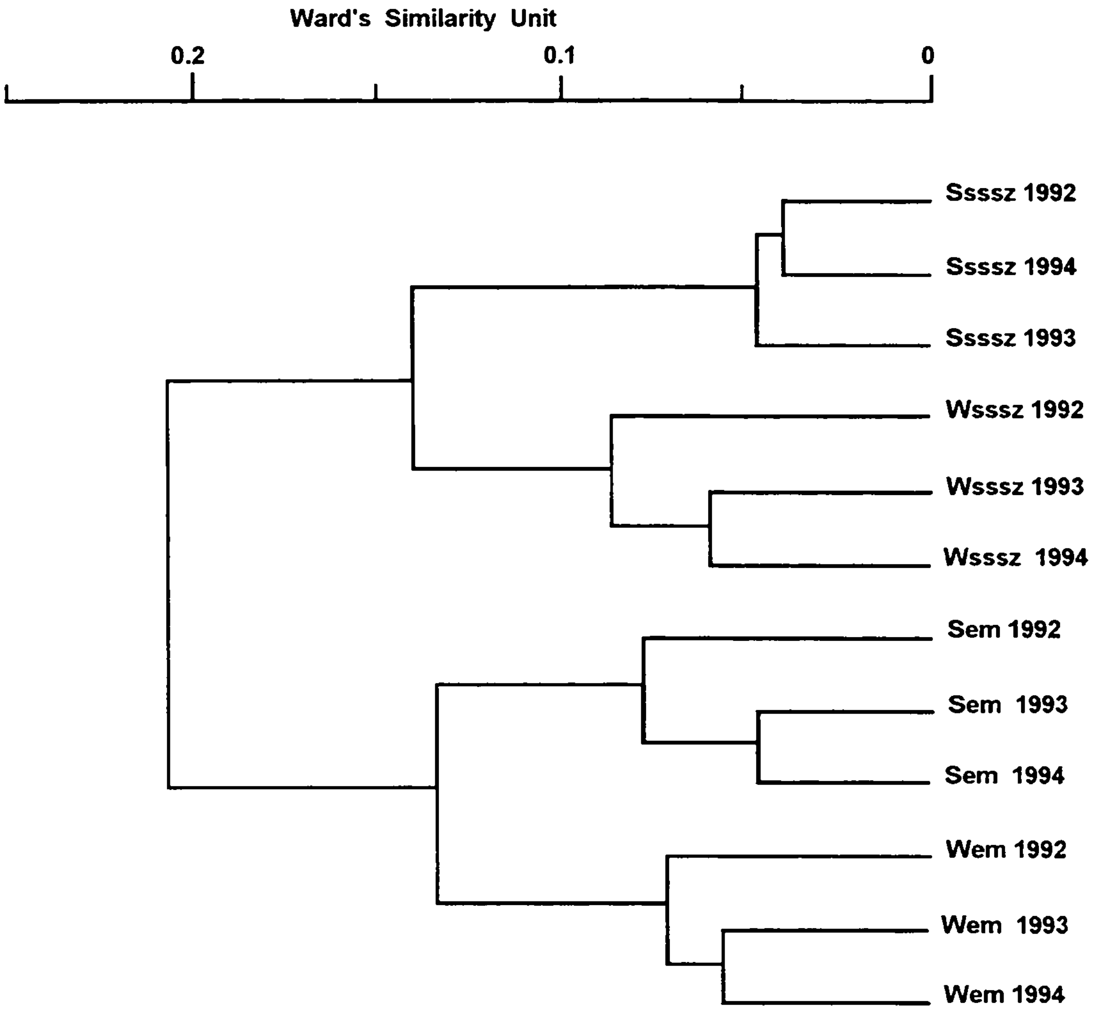


Figure 4.6. Hierarchical cluster dendrogram of intertidal fish assemblage data based on the number of individuals of common assemblage species for each habitat-season over a 3 year period. The dendrogram used Ward's minimum variance linkage method (sssz= sandy shore surf zones; em = estuary mouths; S = summer and W = winter).

taken between 1992 and 1994 in the summer and winter seasons of estuary mouths and a section of samples taken from sandy shore surf zones in winter.

DISCUSSION

Characteristics of Sandy Shore Surf Zones and Estuary Mouths Assemblages

The sandy shore surf zones and estuary mouths of tropical North Queensland, Australia, consist of a diverse ichthyofauna. A total of 112 species from 38 families and 93 species from 35 families were found in sandy shore surf zones and estuary mouths, respectively. There were around 5-10 numerical abundant species found in both habitats throughout the study. These trends are consistent with those exhibited in other sandy shore surf zones and estuarine assemblages, which have been characterised by a dynamic and diverse group of species, and dominated numerically by a few species (Modde and Ross, 1981; Lasiak, 1984 a, b; Ross et al, 1987; Romer, 1990; Tseng and Weng, 1993). The total number of species caught in the present study w greater than that recorded in previous studies in the estuarine habitat of Alligator Creek (Robertson and Duke, 1987) and may reflect the fact that this study incorporated a greater number of locations and covered a wider geographical range.

Sandy shore surf zones and estuary mouths are important habitats for many species since at least 30 families were shared between the habitats. Representative families included Clupeidae, Engraulididae, Mugilidae, Ambassidae, and Hemirhamphidae. The species belonging to these families were relatively abundant in both habitat assemblages (Table 4.1).

A greater number of species were recorded for sandy shore surf zones than estuary mouths. This pattern can probably be attributed to two factors. First, sandy shore surf zones are made up of more relatively complex and heterogeneous habitats than estuary mouths as a result of different beach and coast line morphologies, and the presence of other complex adjacent habitats such as coral reefs, rocky shores and seagrass beds. In some circumstances, the presence of nearshore seagrass and / or reef patches is likely to influence the fish assemblages in adjacent sandy shore surf zones by enhancing the numbers of microhabitats, providing refuges from predation and foraging areas, and moderating wave swell activity on beaches (Lasiak, 1984a, 1986; Bell and Pollard, 1989). The relatively greater habitat complexity in sandy shore surf zone habitats not only influences the number of species, but also the life stages of fishes present. This is best illustrated by *Valamugil seheli*, which was represented by a majority of post-larvae and juveniles in sandy shore surf zones, but larvae, juveniles and sub-adults were the predominant stages in estuary mouths. Second, the movement of a landward current from the outer continental shelf facilitates egg, larvae and juvenile dispersal and subsequent recruitment along sandy shore surf zones. This landward current has less effect in estuary mouths due to its relative distance from the continental shelf and the morphology of estuaries. Consequently, the recruitment of many species in estuary mouths is restricted.

Temporal Variations in Assemblage Abundance

Several temporal changes in the fish assemblages were evident in the present study. The common assemblage species in estuary mouths are either permanent or temporary residents (Bell and Pollard, 1989). The seasonal fluctuations in abundances of species in the present study could result from short-term or annual recruitment events (Lasiak, 1984a and 1984b; Gibson, 1993, 1996). Temporary residents are usually large, recruit seasonally, and move on after spawning. These species Carangids, Drepanids and Scombrids. For a selected species in the present study, *Sillago analis*, spawning areas of this species were expected to be in inshore areas, with recruitment to sandy shore surf zones and estuary mouths nearly year-round (See also Chapter 6). This species moves out of these habitats after approximately 6 months. Failure to catch larger fish in the present study can also probably be attributed to the small mesh size of nets as well as departure of these species.

There are 3 possible explanations for the large variability in abundance of juvenile fishes between seasons in sandy shore surf zones and estuary mouths. Firstly, a large part of the variation could be controlled by density-independent phenomena, which are believed to control the structure of some communities (Helfman, 1978). These probably include all of the physical environments in sandy shore surf zones and estuary mouths. Second, ecological heterogeneity within each habitat is relatively high because each location within the habitat significantly contributes to the variation of all the dependent variables (ANOVA/MANOVA, Tables 4.2 and 4.3). These significant differences could be due to both habitat and seasonal variability as postulated by Lasiak (1984) for sandy shore surf zones of South Africa. Third, other variables may also influence community structure including food availability, density of predators and several environmental factors (Lasiak, 1984; Falcon *et al.*, 1996). These variables were not examined in this study and highlight an area for further research (eg. temperature, number and size of refuges, local wind speed and direction, current velocity, distance between the habitats, water quality and fishing pressure).

Habitat Variation in Assemblage Abundance

The present study was limited to habitats at specific locations due to the principal aims and goals of the study. Sandy shore surf zones were characterised by a relatively large grain size and lower organic matter than estuary mouths.

The importance of sandy shore surf zones and estuary mouths to juveniles fishes is evident when both habitats are compared. Common species present in both sandy shore surf zones and estuary mouths included *Sardinella gibbosa, Escualosa thoracata,* *Valamugil seheli, Leiognathus splendens, Ambassis vachelli,* and *Arrhamphus sclerolepis* (Table 4.1; Fig. 4.2 and 4.3). However, the presence of species unique to the sandy shore surf zones in summer suggest that this habitat is the preferred habitat, and that sandy shore surf zones may have a particular function for these fishes during the summer season. Similar assemblage patterns between sandy shore surf zones and estuary mouths in winter may result from a more equitable temporal and spatial environment between sandy shore surf zones and estuary mouths during this season. While the number of shared species was high in both sandy shore surf zones and estuary mouths, the greater number of transient/ visitor species on sandy shore surf zones may be regulated by prevailing shore-ward currents.

The differences in fish assemblages between sandy shore surf zones and estuary mouths can also depend on the distance separating the two habitats (Whitfield, 1989). The differences in fish assemblages shown in the present study are clear even though the distances between estuary mouths and sandy shore surf zones varied widely. Distance to open water explained some of the pattern observed, especially for the distinct assemblages of sandy shore surf zones due to the extreme degree of connection to open water. While a number of species were present in both sandy shore surf zones and estuary mouths, over 15 species were recorded only from sandy shore surf zones, and 4 species were recorded exclusively from estuary mouths. These included several species such as *Nematalosa come, Hyporhamphus quoyi,* and *Triacanthus weberi* in sandy shore surf zones and *Acanthophagrus berda* and *Pelates* sp. in estuary mouths, which would therefore appear to display some degree of dependence on sandy shore surf zones and estuary mouths respectively. The greater diversity and overall greater abundance of fish over sandy shore surf zones than over estuary mouths was probably due to the structural complexity of sandy shore surf zones habitats and the abundance of larval supply (Ross and Doherty, 1994). The distinction between assemblage abundance in the two habitats was also probably due to many species consistently occurring in both habitats, but predominantly being caught in one habitat. In the present study, *Sardinella gibbosa, Leiognathus splendens, Escualosa thoracata*, and *Stolephorus nelsoni* were predominantly caught in sandy shore surf zones, whereas *Valamugil seheli, S. gibbosa, Atherionomus endrachtensis, Leiognathus splendens* and *Ambassis vachelli* were predominantly caught in estuary mouths. It is interesting to note that *Valamugil seheli* and other members of the Mugilidae were abundant in the present study but absent in a previous study of estuarine habitats by Robertson and Duke (1987).

In the present study, *Sardinella gibbosa, Leiognathus splendens, Escualosa thoracata*, and *Stolephorus nelsoni* are the most abundant species found in both habitats. Habitat breadth is one species-specific variable that could account for the variation in the distribution and abundance of species occurring in a variety of habitats. Unfortunately, habitat breadth was not measured in the present study, but in general the 5-8 most abundant species are tolerant of both habitat variations due to their concurrent occurrence.

Stability and Persistence of Species Assemblages

Menge and Sutherland (1987) suggested that sandy shore surf zones and estuary mouths both offer a stressful environment for associated organisms. Sandy shore surf zones are physiologically stressful due primarily to wave action (Ross *et al.*, 1987; Denny, 1995; Denny and Shibata, 1989). In contrast, the stress gradient in the estuary mouths is related primarily to salinity changes which is also physiologically challenging (Haedrich, 1983; Kennish, 1990). Thus, it is not surprising that the fish assemblages differ between habitats.

Some species are completely absent from estuary mouths, such as *Eleuteronema tetradactylum, Trachinotus blochii,* and *Gazza minuta*, while approximately a quarter of the abundant species were in high numbers in sandy shore surf zones but often found in relatively lower numbers in estuary mouths, such as *Lactarius lacterius, Secutor rucornis, Hyporhamphus quoyi* and *Nematalosa come* (Table 4.1). Such circumstances were likely influenced by a lack of successful recruitment or failure to recruit in particular intertidal habitats and preferential requirements in the life history of these fishes, as recorded in some species in the intertidal habitats of Florida (Ross and Doherty, 1994).

Correspondence ordinations based on distribution and abundance data of intertidal fish assemblages in this present study also indicated that species distribution patterns can be allocated according to particular habitat and seasonal combinations (Fig. 4.5). Sandy shore surf zones and estuary mouth habitats do not show the same degree of seasonal variation. Winter season assemblages of sandy shore surf zones and estuary mouth habitats are the most homogeneous and they are closely related (Fig. 4.6). On the other hand, summer season assemblages of both habitats are relatively different, thus implying that seasonal variation at both habitats is acting as an important factor in shaping the associated patterns. In this particular study, the total variability accounting for the first two axes of correspondence ordination is relatively low, approximately 33%. This fact suggests that much variance remains unexplained, and serves to highlight the complexity of biological systems in intertidal habitats.

The persistence of intertidal fish in sandy shore surf zones and estuary mouths is consistent with trends found in studies of tropical rocky shore habitats, such as those by Grossman (1982) in California, Collette (1986) in Miami, and Mahon and Mahon (1994) in Barbados. In this study, assemblage structure was considered to be persistent over the winter season of each year, despite strong seasonal changes of distribution in response to flux of recruitment in the summer season.

Rahel (1990) has pointed out that the perception of assemblage persistence and stability depends on the chosen level of taxonomic and numerical resolution. When numerical resolution is coarse, such as presence/absence or rank abundance indices, assemblages may seem not to change significantly even when individual species undergo wide random fluctuation (Ebeling *et al.*, 1990; Rahel, 1990). Detection of assemblage change is also more difficult when taxonomic resolution is coarse (relative abundance of higher taxa or foraging guilds) than when it is fine (species relative abundance) (Rahel, 1990). Recently, Sale and Guy (1992) have demonstrated that shifting the taxonomical resolution of coral reef fish to larger taxonomic scales does not reveal more persistence assemblage than smaller levels. In the present study, similarity in assemblage structure and stability of assemblage abundance were recognised at the species level, which is a relatively precise taxonomic resolution for juvenile and adult fishes.

CHAPTER 5

COMPARATIVE DIETARY STUDIES OF SELECTED JUVENILE FISHES FROM TROPICAL INTERTIDAL ZONES

INTRODUCTION

It is believed that the dynamics of marine fish populations are dependent on mortality during the egg and larval stages (Cushing, 1975), spawner abundance (Myers and Barrowman, 1996), and subsequent patterns of larval recruitment to a certain habitat (Lasker, 1981; Doherty and Williams, 1988; Tyler, 1992). Failure of larvae to obtain adequate food may be a major factor influencing growth rates, mortality and recruitment success (Leggett, 1986). According to studies on habitat preference, habitat selection in fishes is strongly affected by two major factors, foraging profitability (Werner and Hall, 1976; Werner *et al*, 1983) and predation risk (Schmitt and Holbrook, 1985; Mittlebach, 1986). Often a trade-off between food accessibility and predation risk results in the occupation of habitats which, although safer, provide diminished foraging returns. There is a significant positive relationship between growth rate and food consumption in both fish (Elliot, 1979) and other aquatic organisms (Condrey, 1982). In addition, rapid growth rates favour the survival of young fish because mortality decreases with increasing size (Werner and Gilliam, 1984).

Shallow coastal areas are recognised as important habitats for the early life history stages of fishes (Weinstein, 1979; Boesch and Turner, 1984; Orth *et al.*, 1984), because they provide abundant food, and predation is low (Boesch and Turner, 1984). Dietary studies can provide valuable information about the feeding activity and feeding success in a particular habitat. However, little is known about the diet of juveniles associated with intertidal areas of sandy shore surf zones and estuary mouths in the tropics. Most previous publications have claimed that juveniles move into intertidal areas for feeding

(Joseph, 1973; Boesch and Turner, 1984; Orth *et al.*, 1984; Ruple, 1984; Lasiak, 1986; Robertson and Duke, 1987; Bennett, 1989; Brown and McLachlan, 1990). Thus diet and feeding success are important factors in assessing the nursery function of these habitats. The aims of this study are: 1) to compare the diet of juvenile fishes in sandy shore surf zones and estuary mouth habitats; and 2) to quantify the extent of ontogenetic variation in the diet of selected juvenile fishes from sandy shore surf zones and estuary mouth habitats.

MATERIALS AND METHODS

Collection of Material

To quantify ontogenetic shifts in diet and compare the diets of juvenile fishes between habitats, specimens of four selected juvenile species, *Leiognathus splendens*, *Sillago analis*, *Stolephorus nelsoni* and *Valamugil seheli* were taken from bi-monthly beach seine samples (see Chapter 2 for methods). These four species were chosen because they were present in nearly all the catches throughout the year in both habitats. Specimens were immediately preserved in 10 % neutral formalin-seawater after collection. The body walls of fish larger than 10 cm standard length were incised in order to facilitate fixation of stomach contents.

Specimens obtained in 1992 and 1993 were pooled because of the extreme variability in numbers among locations and between seasons. Hence these samples provide a preliminary observation of the spectrum of diets found at different habitats. Fish were grouped into length classes which varied across species. The standard length of *S. analis* and *V. seheli* ranged from 15 mm to 200+ mm, so the standard length interval used for these species was 30 mm. The standard length for *S. nelsoni* and *L. splendens* ranged from 25 to 60+ mm and 7 to 50+ mm respectively so 10 mm classes were used for these species. Where possible at least 10 specimens per size class were examined within each habitat.

The stomach of each fish was removed and examined under a low power microscope. Undigested and semi-digested food items were sorted and identified to the lowest taxonomic level.

In *V. seheli*, which lacks a formal stomach (Harrison and Howes, 1991), the contents of the anterior half of the intestines were examined. Initial investigations of *V. seheli* indicated that for almost all specimens examined, both the gizzard and the anterior half of the intestine were empty. A similar situation has been found in other mullets from southern Queensland (Morton *et al.,* 1987). This species was subsequently omitted from the analyses.

Determination of Food and Feeding Habits

Qualitative Analysis

Qualitative analysis involved the identification of all food items found in the stomach contents. The majority of food items were identified (following Barnes, 1980) and placed in broad categories, such as gastropods, bivalves, polychaetes, amphipods, isopods, copepods, crabs, insects and fishes. Vacuity, the relative percentage of empty stomachs to the total number of stomachs examined, was also estimated.

Quantitative Analysis

Index of Relative Importance: The relative abundance of prey items in fish diets can be estimated in a variety of ways (Hyslop, 1980). The three major methods most commonly used for quantitatively analysing fish diets are number, occurrence, and volume.

In the numerical method, the numbers of each prey item in each non-empty stomach in a sample were counted and expressed as the percentage of the total number of food items. This value was then averaged over the total number of non-empty stomachs examined (**%N**), thus yielding a percentage composition of each prey item.

The occurrence of prey was quantified by recording the frequency of occurrence of each food item in the stomach, and expressing this value as a percentage of the total number of non-empty stomachs examined (**%F**).

Volumetric analysis of prey items are usually achieved by either (1) displacement, or (2) by recording three dimensional measurements and calculating the volume from appropriate formula. However, it is very difficult to measure the volume of a digested item accurately. In this study, a modified version of the weight points method (Hynes, 1950) was used to obtain volumetric measurements. The volume of each food type was visually estimated on a petri dish and expressed as a proportion of the total area covered by combined food items. In order to equalise the contribution of each food item for each stomach, the proportions for each food type were multiplied by a percentage stomach fullness index assigned by Ball's criteria (1961) for giving percentage volume importance (**%V**).

Data Analyses

Analysis of Food and Feeding Habits

Assessment of food and feeding habits has previously been concerned mainly with identifying the most important food items present in the stomach. In this study, the index of relative importance (**IRI**) was calculated in order to estimate the contributions of each prey type to the diet (Pinkas *et al.*, 1971; Hyslop, 1980). This index is calculated as follows:

$$\mathbf{IRI} = (\mathbf{\%N} + \mathbf{\%V}) \times \mathbf{\%F},$$

where %N is the percentage of prey items contributing to total diet, %V is the percentage of volume importance, and %F is the frequency of occurrence of prey categories. In this procedure, a mean for each prey item belonging to each size class was calculated, thus providing an estimate of the relative proportion of dietary categories ingested by each individual in each size class.

The term "importance" is considered to be somewhat ambiguous (Berg, 1979). In the present study, this term was used in the sense of the "dominant food item" consumed.

Influence of Season, Habitat and Ontogeny on Diets

Many quantitative methods have been developed in order to describe the degree of difference between the diets of two fish species or the same species at different habitats (Krebs, 1989). In the present study a multivariate analysis of variance (MANOVA) was employed. Multivariate methods have an advantage over other methods in that they estimate variations and covariations of prey species abundances within each predator species (Macdonald and Green, 1986). Hypothesis testing concerning diet differences can then be followed.

Data relating to ontogenetic shifts, and the influence of season and habitat on the diets of all three selected species were added to the 1994 study program. This three-dimensional multivariate design included the different size classes of each selected species collected from each location of sandy shore surf zone and estuary mouth habitats in both summer and winter seasons. Approximately 10 randomly selected individuals of the total specimens available (if less than 10), of each species for each size class from each location were used for the diet study. The dependent variables were IRI values of total prey species identified from stomach contents.

A three-factor MANOVA was used to test overall differences among mean prey IRI for all habitats, seasons and size classes within the data matrix of each fish species. As the data matrix contains many dependent variables, Green (1979) and Macdonald and

Green (1986) have suggested that a great deal of information is redundant. In order to retain all information, some prey species (i.e. those that occurred in less than 5 % of total observations) were added to the most closely related group. In an initial examination of the data, unequal numbers of individuals were apparent for each size class at each location of sandy shore surf zone and estuary, and some size classes were absent from these locations. In order to overcome this logistical problem, a mean IRI for prey from each size class at each location in each habitat and season was calculated and only a subset of the variables available were used for the MANOVA. These variables were selected through the use of a Principal Component Analysis (PCA, see also Appendix 4 for analysis result). In this analysis, the covariance matrix ranked the variables according to the additional information each one added to the entire data matrix. Variables in which the IRI contributed more than 1 % of total variance were identified and selected as dependent variables in the MANOVA model. Prior to PCA, a log (X+1) transformation was applied to each dependent variable in order to normalise the data and eliminate outliers for MANOVA.

The three-factor MANOVA could only be applied to the diet data of *S. analis* because it occurs in intertidal areas year-round. It was not possible to test the seasonal effects on diet for *Stolephorus nelsoni* and *Leiognathus splendens*, because these species are often absent or in low numbers in winter. Subsequently, only the effects of habitat and ontogeny were tested with MANOVA (i.e. two-factor MANOVA design including 2 habitats x 4 size classes).

RESULTS

The following results come from two main data sources: the 1992-1993 collection and the 1994 collection (Table 5.1). The 1992-1993 data were used for determining gut

Table 5.1. The number of total stomachs examined and, in parenthesis, the number of stomachs containing food items, for each size class of species examined. (SSSZ= sandy shore surf zone samples; EM= Estuary mouths; SL= standard length)

TAXA (size in mm)	1992-1993		1994					
	SSSZ	EM	Saunders Bh. (SS 2)	Toolakea Bh. (SS 3)	Pallarenda Bh. (SS 1)	Deep Ck. (EM 3)	Bohle River Mth. (EM 2)	Ross River Mth. (EM 1)
Stolephorus nelsoni								
SL < 20	1 (0)	5 (1)	7(2)	10(7)	11(6)		10(10)	
20 < SL<30	43(5)	32(24)	6(2)	11(4)	20(20)		20(12)	10(10)
30< SL <40	34(3)	23(13)	10(3)	10(10)	22(15)	4(2)	17(11)	13(9)
40< SL <50	45(18)	34(29)	10(1)	10(10)	14(6)		3(2)	10(4)
50< SL <60	48(18)	12(8)	11(1)	11(11)		1(0)	1(1)	5(2)
TOTAL	171 (44)	102 (75)	44(9)	52 (42)	67 (47)	5 (2)	51 (36)	38 (25)
Sillago analis								
SL<30	46(22)	58(48)	2(2)	8(3)	3(1)		5(1)	40(38)
30 < SL <60	42(26)	89(74)	9(3)	9(3)	16(13)	10(8)	15(15)	26(25)
60 < SL <90	31(15)	64(50)	13(7)	3(2)	3(3)	8(6)	14(1)	26(23)
90 < SL <120	14(4)	48(37)	6(3)	2(2)	2(1)	1(1)	10(1)	20(16)
120 < SL <150	12(8)	1(1)						
TOTAL	145 (75)	260 (210)	30 (15)	22 (10)	24 (18)	19 (15)	44 (18)	112 (102)
Leiognathus splendens								
SL <10	28(0)	24(21)	10(0)					
10 < SL <20	33(5)	60(46)	20(5)	20(2)	20(6)	21(13)	1(0)	10(6)
20 < SL <30	43(15)	48(20)	23(7)	10(7)	21(10)		12(12)	
30 < SL <40	28(7)	27(18)	10(1)		13(2)		7(7)	
40 < SL <50	26(6)	14(6)	1(0)		10(2)			
TOTAL	158 (33)	173 (111)	64 (13)	30 (9)	64 (20)	21 (13)	20 (19)	10 (6)

fullness and vacuity indices, feeding intensity and diet compositions while the 1994 data were used for statistical inferences of temporal, spatial and ontogenetic dietary shifts.

Vacuity

The percentage of fish with empty stomachs was 2-3 times lower for estuary mouth habitats than sandy shore surf zones. Of the 177 *Stolephorus nelsoni*, 145 *Sillago analis* and 158 *Leiognathus splendens* taken from sandy shore surf zone samples, 127 (71%), 75 (52%) and 125 (79%) respectively had empty stomachs (Table 5.1). On the other hand, examination of 102, 260 and 173 stomachs belonging to the same sequence of species from estuary mouth habitats, showed that only 27 (26%), 50 (19%) and 62 (36%) stomachs, respectively, were empty (Table 5.1).

In both *S. nelsoni* and *L. splendens*, chi-square tests revealed that the proportion of stomachs containing foods in estuary mouths were significantly higher than in those from sandy shore surf zones ($\chi^2_4 = 35.44$ and $\chi^2_4 = 45.26$ respectively with $p < 0.001$). There was no significant difference between habitats for *S. analis*.

Feeding Intensity

The average stomach fullness across all size classes was also indicative of a greater volume of food being present in the stomachs of estuary mouth samples (Figures 5.1 A, C and E).The feeding intensity of *Stolephorus nelsoni, Sillago analis* and *Leiognathus splendens* was generally high in estuary mouths as revealed from the percentage stomach fullness values (Figs. 5.1 A, C and E). The maximum values (~80 %) occurred in the stomach of small *S. analis* taken from estuary mouths. Stomach fullness tended to decrease with increasing size. This trend was also apparent for this species in sandy shore surf zones, although at a relatively lower order of magnitude. A consistent level of stomach fullness (approximately 20%) is evident across all size classes of *S. nelsoni* taken from estuary mouths, whereas a gradual increase in fullness with increasing size is

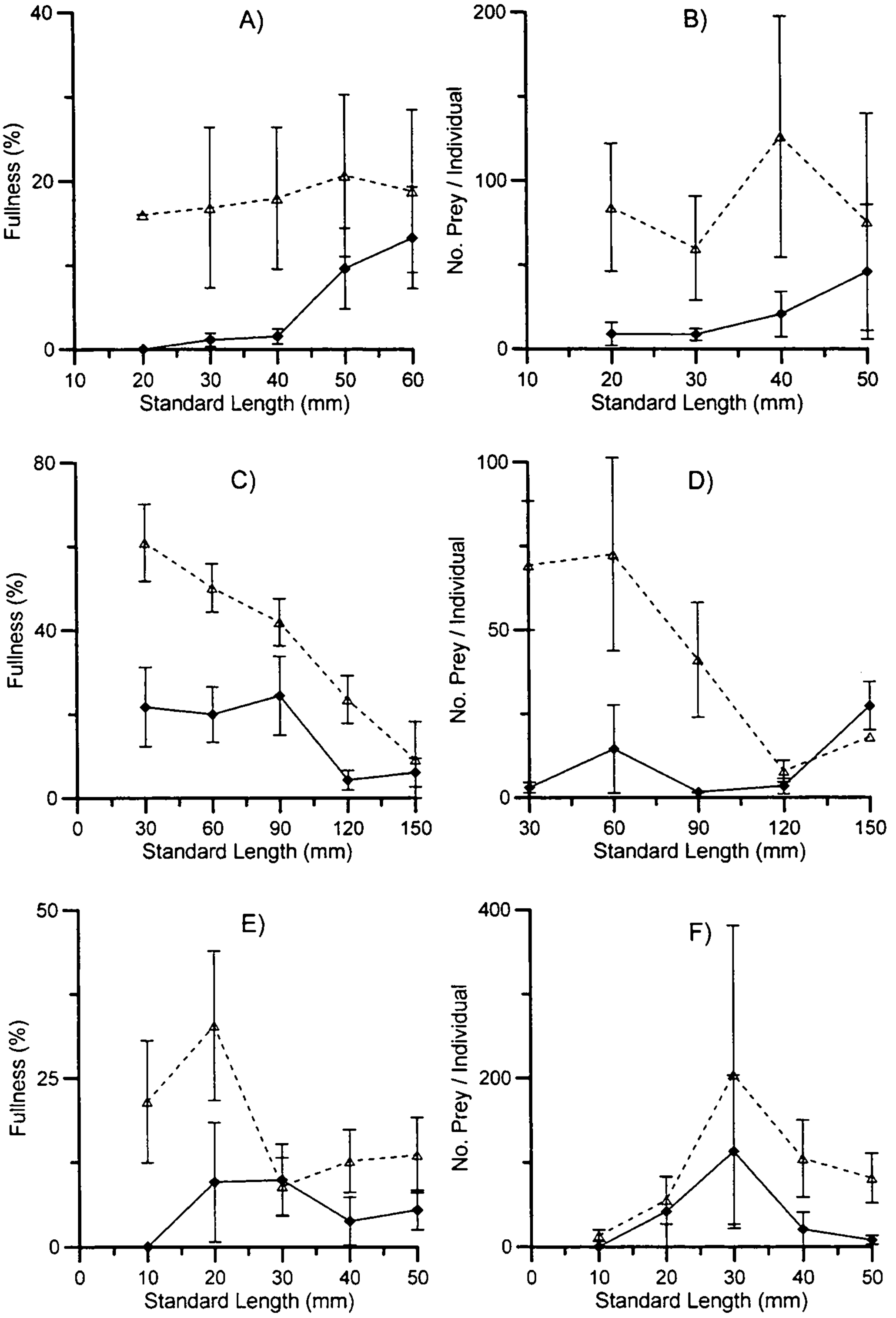


Figure 5.1. Habitat differences and ontogenetic changes in stomach fullness and number of prey items per individual (± 1SE)
A and B. *Stolephorus nelsoni*
C and D. *Sillago analis*
E and F. *Leiognathus splendens*
(♦: sandy shore surf zone samples; Δ: estuary mouths samples)

observed for samples taken from sandy shore surf zones (Fig. 5.1 A). *Leiognathus splendens* showed a similar trend to that found for *S. analis*, where stomach fullness declined with increasing fish length for samples collected at both estuary mouth and sandy shore surf zone habitats.

Intraspecific Variation in Diets

Stolephorus nelsoni

Analyses were preliminarily conducted on the stomach contents of 273 juvenile *Stolephorus nelsoni* across 5 size classes < 60 mm SL from the 1992-1993 collections (Tables 5.1 and 5.2; Figs 5.2 A and B). Preliminary investigations provided an initial overview of ontogenetic changes in the diet based on a comparison between sandy shore surf zones and estuary mouths habitats. Although the diets were varied, several distinctive trends were apparent. The representation of food items within each size class was noticeably different. In addition, the number of prey items per individual fish was clearly higher in estuary mouths than in sandy shore surf zones.

Harpacticoid and cyclopoid copepods, ostracods, amphipods, snails, bivalves and *Acetes sibogae* made a major contribution to the volume of the gut contents *of S. nelsoni* from both habitats (Table 5.2). Cyclopoid copepods, snails and bivalves were generally present in greater amounts in the gut contents of fish from estuary mouths than fish caught over sandy shore surf zones.

Ontogenenetic changes in diet were detected for *Stolephorus nelsoni*. Initially, fish smaller than 20 mm SL consumed plankton, while the diets of larger fish consisted of both small and large benthic invertebrates. During the planktivorous stage, cyclopoid copepods accounted for the majority (approximately 85 % of total IRI) of ingested materials. The number of cyclopoid copepods present decreased with increasing fish size and was paralleled by an increasing consumption of small benthic invertebrates

Table 5.2. Composition of stomach contents of *Stolephorus nelsoni*: pooled data from all sampling periods for fish obtained in 1992-1993 (%N= percentage of the total number of food items; %F= percentage of frequency of occurrence; %V= percentage volume importance; IRI= Index of relative importance)

A) Estuary mouths

Contents	Size 10<SL<20 (n=5)				Size 20<SL<30 (n=32)				Size 30<SL<40 (n=23)				Size 40<SL<50 (n=34)				Size 50<SL<60 (n=8)			
	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI
Harpacticoid Copepods					6.76	3.36	12.50	1012.50	2.87	0.74	15.00	188.50	2.13	0.95	16.66	256.75				
Cyclopoid Copepods	2.46	0.60	7.50	183.75	16.03	7.26	34.06	2141.00	1.60	0.33	15.00	105.13	10.84	7.40	12.50	1823.75	11.69	6.40	12.50	1808.75
Ostracods					0.63	0.13	9.38	56.25	1.66	0.81	22.50	243.75	5.23	0.66	21.66	687.00	2.43	0.17	7.29	71.25
Amphipods					2.30	2.53	8.75	337.75	6.91	2.50	25.00	941.25	0.42	0.06	4.16	16.13				
Lucifer spp.	0.04	1.40	2.50	28.80																
Acetes sibogae									0.05	0.63	3.75	26.50	8.58	7.00	12.50	1557.50	10.54	8.17	16.66	1683.75
Mictyris platycheles									0.07	0.13	2.50	3.88								
Snails					4.39	2.79	17.50	591.25	11.27	4.50	22.50	1511.00	3.59	1.07	12.91	292.25	0.52	0.09	6.66	16.00
Bivalves					1.77	0.45	16.25	105.25	3.80	1.93	12.50	572.50	6.70	3.22	21.66	874.88	2.98	0.72	14.16	138.63
Polychaete					0.05	0.10	1.25	1.50									0.23	0.67	4.16	29.63
Fishes									0.66	6.00	12.50	666.25					4.16	2.50	4.16	221.88
Unidentified					0.71	0.21	16.56	64.38	7.05	0.41	17.50	701.35	1.43	0.29	6.25	85.75	0.74	0.08	4.16	27.38

B) Sandy shore surf zones

Contents	Size 10<SL<20 (n=1)				Size 20<SL<30 (n=43)				Size 30<SL<40 (n=34)				Size 40<SL<50 (n=45)				Size 50<SL<60 (n=48)			
	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI
Cyclopoid Copepods					4.38	1.08	12.73	411.64	1.74	0.67	4.55	92.82	8.49	1.99	10.91	929.82	7.53	2.82	13.64	973.18
Ostracods									0.10	0.02	9.09	11.82	0.43	0.09	9.09	51.82				
Lucifer spp.																	0.23	0.36	0.91	5.91
Acetes sibogae													5.33	4.15	6.36	663.09	9.10	6.33	19.19	1504.36
Mictyris platycheles													3.83	2.84	7.73	468.82	1.43	0.95	7.27	190.27
Matuta lunaris																	7.37	0.86	9.09	823.09
Polychaetes																	1.01	0.61	1.01	17.91
Polyclad									0.15	0.27	1.14	5.34								
Snails									0.96	0.41	4.55	68.64	0.99	0.14	12.73	85.30	1.95	0.91	9.09	286.36
Bivalves									0.64	0.15	9.09	78.18	0.24	0.03	6.36	18.45	1.06	0.25	12.93	76.18
Fishes													1.82	0.36	1.82	43.64				
Unidentified					0.16	0.01	0.91	1.73	0.18	0.07	0.91	2.55					4.02	0.18	11.31	316.27

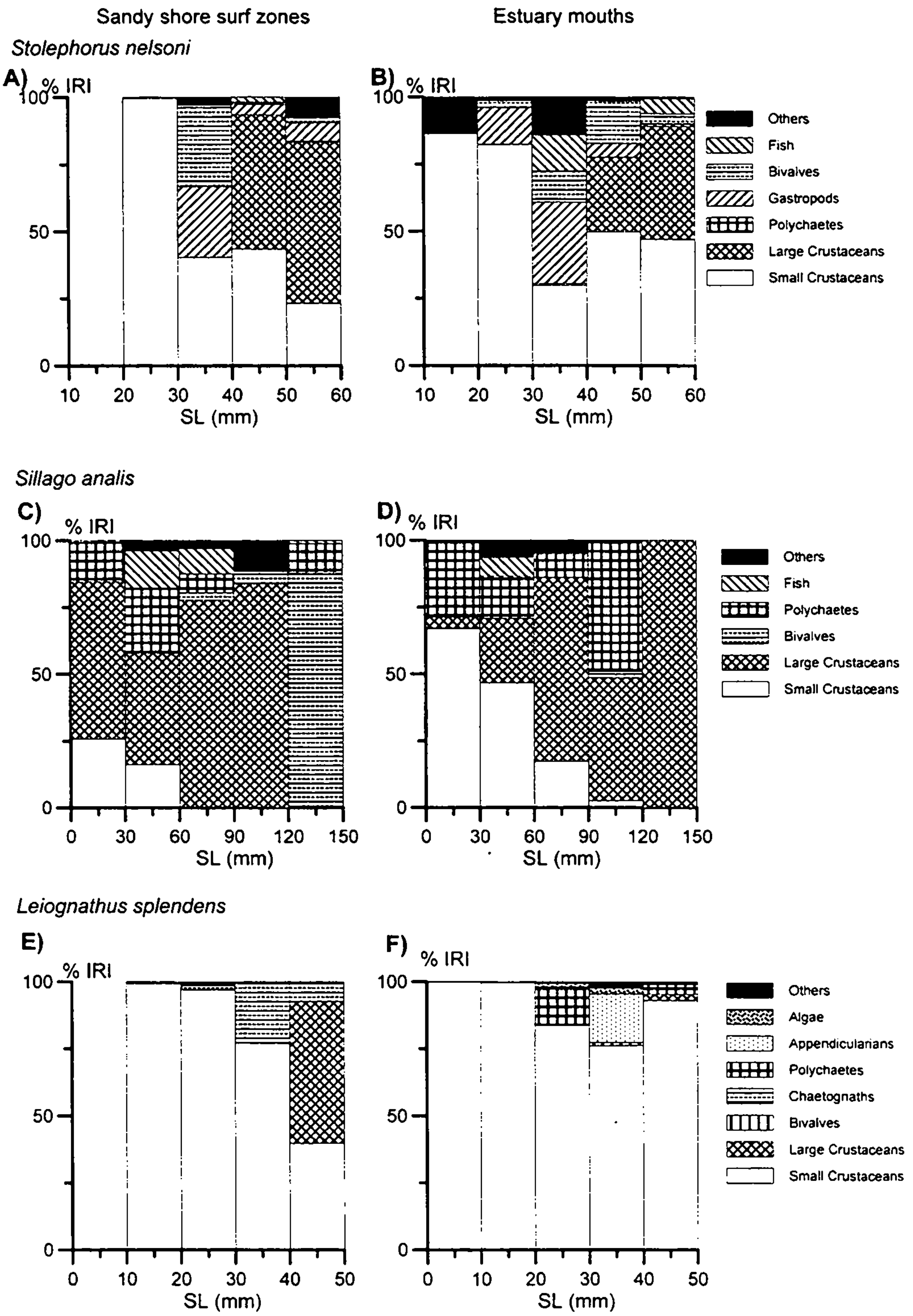


Figure 5.2. Ontogenetic changes in the diet of selected species. The histogram represents relative IRI percentage proportions of major dietary components.

A. *Stolephorus nelsoni* from sandy shore surf zones. B. *S. nelsoni* from estuary mouths.
C. *Sillago analis* from sandy shore surf zones. D. *S. analis* from estuary mouths.
E. *Leiognathus splendens* from sandy shore surf zones. F. *L. splendens* from estuary mouths.

Small Crustaceans: the combined percentage points of Ostracods, Copepods, Amphipods, and *Lucifer* (see Table 5.2 for details);

Large Crustaceans: the combined percentage points of *Acetes, Callinassa*, Hermit crabs, *Uca* spp., *Portunus* sp., *Mictyris platycheles*, Grapsid Crabs, *Matuta lunaris* and *Matuta* sp., other crabs (see Table 5.2 for details).

such as harpacticoid copepods and amphipods. The transition from planktonic to benthic feeding began gradually once the fish reached a length of approximately 20 mm SL. Initially, the diet of fish larger than 20 mm SL consisted primarily of snails and bivalves. This food source was gradually replaced by more motile and larger food items such as *Acetes sibogae* (Table 5.2 A; Fig. 5.2 B). At sizes larger than 30 mm, *Acetes sibogae* and small juvenile fish, namely mugilids and leiognathids, were an additional food source found in the stomachs of *S. nelsoni*. Both cyclopoid and harpacticoid copepods were still present in specimens larger than 30 mm SL from estuary mouths, and collectively accounted for ~ 5-45 % of the total IRI. This range was much greater than that from sandy shore surf zones where the contribution of copepods to the diets of fish was ~ 25-45 % of the total IRI.

At the intermediate size class (30-40 mm SL), there was an ontogenetic shift in diet where snails and bivalves replaced small crustaceans as the preferred food source in both habitats (Fig. 5.2B). In specimens 40-50 mm SL (Fig. 5.2B), *Acetes sibogae* and molluscs together were the numerically dominant prey in estuary mouths while *A. sibogae* and *Mictyris platycheles* were dominant from sandy shore surf zones. Foods similar to those for other size classes were found in fish 50-60 mm SL, with copepods and *A. sibogae* being the dominant taxa in the diet of fish from estuary mouths and *A. sibogae* and *Matuta lunaris* being dominant in the diet of fish from sandy shore surf zones.

In 1994, nine taxa were identified as the major contributors to the diets of *S. nelsoni*: cyclopoid and harpacticoid copepods, ostracods, isopods, *Lucifer* sp., penaeid shrimp juveniles, crab megalopa, snails and bivalves (see PCA results, Appendix 4.1). The composition of the diet of *S. nelsoni* varied significantly between habitats and among size class (MANOVA, $F_{9,8}$= 4.141 and $F_{27,30}$= 1.944 respectively, $p < 0.05$; Table

5.3). There was a two-fold difference in the consumption of harpacticoid copepods by *S. nelsoni* between habitats; IRI = 286.98 ± 98.36 and 124.05 ± 83.14 for sandy shore surf zones and estuary mouth habitats respectively (Two-way ANOVA, $F_{1,16}= 4.76$, $p < 0.05$; Fig. 5.3A). The consumption of harpacticoid copepods by *S. nelsoni* also changed with fish size (Two-way ANOVA, $F_{3,16}= 3.39$, $p < 0.05$; Fig. 5.3B). The consumption of harpacticoid copepods in specimens smaller than 50 mm was high (444.59 ± 204.10 at 40 mm SL) and declined to nearly nil in specimens larger than 50 mm SL.

Table 5.3. MANOVA of dietary data obtained from 1994 data by habitat (H) and size for *Stolephorus nelsoni*.

Source of Variation	Value	*F*	Num-*df*	Den-*df*	*p*-value
H	0.823277	4.141	9	8	0.0289*
Size	1.910769	1.9492	27	30	0.0388*
H x Size	1.727499	1.5084	27	30	0.1372

Sillago analis

A total of 405 *Sillago analis* juveniles from the 1992-1993 collections were examined (Tables 5.1, 5.4 and 5.5; Figs. 5.2 C and D). Preliminary qualitative studies on the food habits of *S. analis* indicate that this species feeds primarily on benthic invertebrates. Amphipods, isopods, *Acetes sibogae*, penaid shrimps, *Callinassa, Mictyris platycheles, Matuta* crabs, *Mesodesma eltanae* and polychaete worms were common preys items and contributed substantially to the volume of gut contents of *Sillago analis* in each habitat type (Tables 5.4 and 5.5). However, this contribution was smaller for fish caught from sandy shore surf zones.

The major prey items for size classes smaller than 30 mm SL taken from estuary mouth habitats were harpacticoid and calanoid copepods. These items accounted for ~65 % of the total IRI, while the remaining items were predominantly polychaetes (~30%). In contrast, both types of copepods were missing from the diets of fish taken

Table 5.4. Composition of stomach contents of *Sillago analis*: pooled data from all sampling periods of estuary mouths for fish obtained in 1992-1993 (%N= percentage of the total number of food items; %F= percentage of frequency of occurrence; %V= percentage volume importance; IRI= Index of relative importance)

Contents	Size SL<30 (n = 58)				Size 30<SL<60 (n = 90)				Size 60<SL<90 (n = 64)				Size 90<SL<120 (n = 52)				Size 120<SL<150 (n = 1)			
	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI
Total Crustaceans	19.51	10.81	39.33	2206.00	47.91	29.87	93.85	5025.23	50.49	23.50	73.69	5776.60	16.99	12.42	28.05	1211.09	6.00	6.67	6.67	1266.67
Harpacticoid Copepod	12.41	4.55	19.33	1523.87	19.43	8.97	27.67	2432.07												
Calanoids Copepods	4.01	2.54	7.33	465.73	2.91	1.38	8.00	265.60												
Amphipods	1.52	1.22	4.00	82.13	7.33	3.84	17.21	525.40	9.26	3.82	14.44	1135.00	1.47	0.40	2.22	62.16				
Isopods					2.04	1.44	2.77	83.00	0.83	0.20	1.67	25.87								
Acetes sibogae	0.42	1.07	4.00	89.60	2.25	1.35	5.77	234.33	12.17	8.07	16.00	1865.00	3.39	2.75	4.17	383.73	6.00	6.67	6.67	1266.67
Penaeids	0.67	0.32	1.33	19.73	0.67	0.78	1.11	24.00	1.11	0.71	2.22	60.40								
Callinassa spp.	0.14	0.91	2.00	13.87	4.18	4.55	13.44	538.47	4.49	3.53	14.25	403.87	3.61	2.69	6.11	164.73				
Crabs:*Mictyris platycheles*	0.35	0.20	1.33	11.07	6.11	5.31	11.11	816.00	7.89	2.69	8.89	508.73	6.03	5.08	9.72	479.33				
Crabs: *Uca*									0.67	0.13	0.67	8.00	0.42	0.23	0.83	8.13				
Crab: Grapsids									6.67	1.33	6.67	800.00								
Crabs: *Matuta lunaris*					1.71	0.73	3.33	61.17	0.74	0.35	2.22	36.40	1.25	0.93	1.67	54.67				
Crabs:*Portunus* spp.					1.29	1.51	3.44	45.20	6.67	2.67	6.67	933.33	0.83	0.33	3.33	58.33				
Insect:	0.05	0.11	0.67	1.58	3.34	1.63	8.33	434.43												
Mesodesma eltanae					0.03	0.40	0.67	4.27					1.39	0.27	4.17	54.40				
Total Polychaetes	6.88	6.47	12.00	876.67	10.26	6.43	19.44	1102.60	6.48	3.95	16.11	582.33	10.17	3.95	16.67	1221.00				
Polychaetes:Maldanidae									6.48	3.95	16.11	582.33	3.50	1.29	10.00	287.67				
Polychaete:Nereidae	6.88	6.47	12.00	876.67	10.26	6.43	19.44	1102.60					6.67	2.67	6.67	933.33				
Nematode	0.21	0.19	1.33	8.00	0.08	0.03	0.67	1.07												
Sipunculids					0.42	0.33	1.67	18.73	0.83	0.47	1.67	32.47								
Anemone									2.37	0.98	8.89	211.47								
Medusa									1.66	0.91	3.89	79.40								
Total Fish					4.44	1.72	11.11	500.00	0.56	0.13	2.22	22.93	0.06	0.13	0.83	2.33				

Table 5.5. Composition of stomach contents of *Sillago analis*: pooled data from all sampling periods of sandy shore surf zones for fish obtained in 1992-1993 (%N= percentage of the total number of food items; %F= percentage of frequency of occurrence; %V= percentage volume importance; IRI= Index of relative importance)

Contents	Size SL<30 (n = 46)				Size 30<SL<60 (n = 42)				Size. 60<SL<90 (n = 31)				Size 90<SL<120 (n = 14)				Size 120<SL<150 (n = 12)			
	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI
Total Crustaceans	16.99	11.41	17.19	1989.38	24.78	14.49	33.49	2341.31	12.82	8.22	14.84	2037.66	14.41	7.81	18.75	2111.13	0.03	0.15	1.25	3.50
Amphipods					2.32	1.50	4.86	121.94												
Isopods	4.49	3.59	4.69	606.56	4.78	3.49	6.24	500.94	0.16	0.19	0.78	4.30								
Acetes sibogae	4.69	3.44	4.69	328.13	4.16	3.75	6.25	791.25	6.25	5.00	6.25	1125.00	6.60	6.38	9.38	1273.63				
Penaeids	1.56	0.63	1.56	54.69																
Callinassa spp.					1.56	1.25	1.56	70.31												
Hermit Crab: *Dardanus* spp					2.08	1.25	2.08	110.94												
Crabs:*Mictyris platycheles*	6.25	3.75	6.25	1000.00	0.51	1.50	4.16	133.69					1.56	0.19	3.13	87.50				
Crab: Grapsids									6.03	2.94	6.25	896.25								
Crabs: *Matuta lunaris*					9.38	1.75	8.33	612.25	0.39	0.09	1.56	12.11	6.25	1.25	6.25	750.00	0.03	0.15	1.25	3.50
Snails													1.56	0.44	3.13	100.00				
Mesodesma eltanae									1.18	0.19	3.13	68.44	2.43	0.19	5.21	113.19	7.36	3.44	8.13	632.50
Total Polychaetes	3.23	3.84	4.69	348.59	9.92	4.85	18.39	933.63	2.44	1.28	9.38	186.25					1.32	0.29	5.63	76.53
Polychaete:Maldanidae					2.33	0.73	3.64	86.38	0.51	0.63	3.13	56.56								
Polychaete:Nereidae	3.23	3.84	4.69	348.59	7.59	4.12	14.75	847.25												
Polyclad									0.42	0.22	3.13	31.88								
Nemertean					0.47	0.47	0.69	10.44					1.04	1.19	2.08	74.06				
Sipunculids									0.09	0.38	3.13	23.13								
Anemone					0.89	0.13	1.56	27.00	0.53	0.19	4.69	22.29	1.39	1.00	3.13	119.38				
Total Fishes	0.10	0.38	1.56	11.88	4.22	3.11	8.33	536.94	3.83	1.66	4.69	246.56					0.05	0.13	3.13	8.59
Gobiidae					0.35	0.21	0.69	6.19												
Stolephorus					0.69	0.69	0.69	15.38												
Mugilidae					0.05	0.21	0.69	2.88	3.13	1.25	3.13	218.75								
Leiognathidae					3.13	2.00	6.25	512.50												

from sandy shore surf zones in these size classes. The major prey items in this habitat were crustaceans, making up 85% of the total IRI. The dominant taxa in the crustacean group were *Mictyrus platycheles* and isopods, representing 25% and 45% of total IRI respectively. Polychaetes were also present and made up ~15% of the total IRI.

The diets of fish in the 30-60 mm and 60-90 mm SL size classes from estuary mouth habitats consisted of crustaceans, fish and polychaetes. Crustaceans, particularly copepods, were the dominant food items. However, the samples showed an increased consumption of larger crustaceans such as soldier crabs *Mictyrus platycheles*, ghost shrimps *Callinassa* sp. and amphipods. This pattern was also observed in the diets of fish belonging to the same size classes from sandy shore surf zones. The relative dominance of *M. platycheles* in previous size classes was replaced by *Matuta lunaris*, grapsid crabs and *Acetes sibogae*, and the proportion of fish in the diet also increased.

The proportion of crustaceans and polychaetes was approximately equal (~50%) in the diet of fish belonging to the size class of 90-120 mm SL from estuary mouth habitats. *Acetes sibogae* and *M. platycheles* were still the major components of the crustacean group. In contrast, approximately 90% of the diet of fish in the 90-120 mm size class in sandy shore surf zones consisted of crustaceans, particularly *A. sibogae* and *M. lunaris*.

The gut contents of *S. analis* primarily consisted of undigested *Acetes sibogae.* Partly digested *Mesodesma eltanae* and semi digested prey items were difficult to identify, however some fish identifications were possible and gobies, anchovies, mullets and leiognathids were distinguished in the stomach content analyses.

The number of prey items per individual for *S. analis* taken across all size classes is higher in estuary mouth habitats than sandy shore surf zones (Fig. 5.3D). In most of the stomachs examined from sandy shore surf zones, juveniles had either one large prey

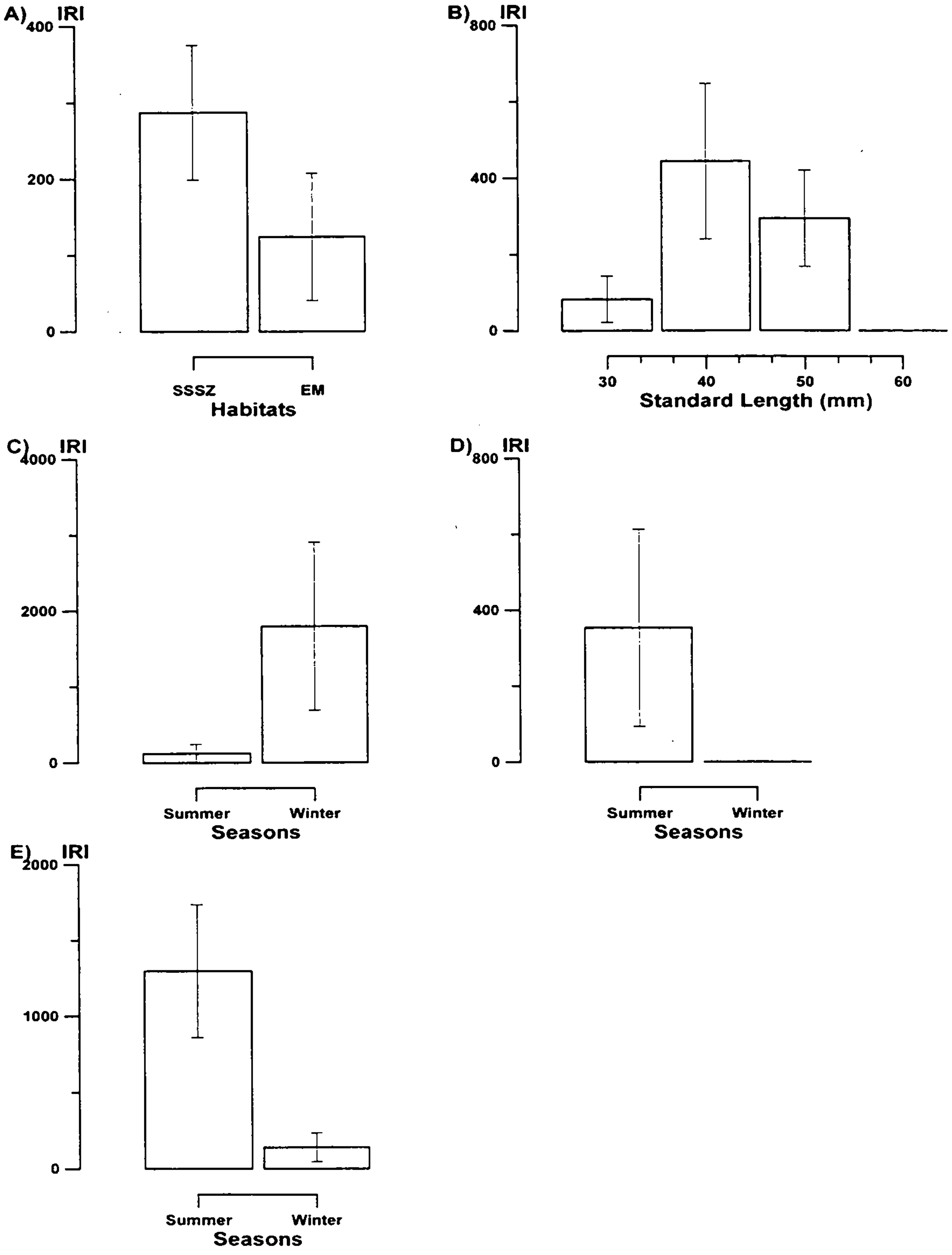


Figure 5.3. Mean ± SE of significant dependent variables from Analysis of Variance after Multivariate Analysis of Variance for IRI

A) Habitat difference in IRI of Harpacticoid Copepod in diet of *Stolephorus nelsoni*

B) Size class variations in IRI of Harpacticoid Copepod in diet of *S. nelsoni*

C) Seasonal difference in IRI of *Acetes sibogae* in diet of *Sillago analis*

D) Seasonal difference in IRI of fish in diet of *Sillago analis*

E) Seasonal difference in IRI of harpacticoid copepod in diet of *Sillago analis* item such as a whole fish or polychaete, or many items belonging to just one taxa. Small food items were an important component of the diet of fish from the estuary mouth habitat and conversely, of little importance as main food items in sandy shore surf zones.

Sixteen food taxa were identified as the major contributors to the diet of *S. analis* and made up 96% of the total variance (PCA results, Appendix 4.2). These included harpacticoid and calanoid copepods, amphipods, isopods, penaeid shrimp, portunid crabs, insects, nereid polychaetes, other polychaetes, nematodes, medusa, fish, *A. sibogae*, *Mictyrus platycheles*, *Callinassa* sp., and *Mesodesma eltanae*. A three-way crossed MANOVA of IRI of these diets revealed that the diet of *S. analis* varies significantly with season, ($F_{16,17}$= 3.7560, $p < 0.01$; Table 5.6). This pattern was due to the consumption of more *Acetes sibogae* and fish in summer (Three-way ANOVA, $F_{1,32}$= 7.25, $p < 0.05$; Fig. 5.3C and $F_{1,32}$= 20.35, $p < 0.05$; Fig. 5.3D respectively), and a higher consumption of harpacticoid copepods in winter (Three-way ANOVA, $F_{1,32}$= 4.27, $p < 0.05$; Fig. 5.3E).

Table 5.6. MANOVA of dietary data obtained from 1994 data by habitat (H) season (S) and size (SZ) for *Sillago analis*.

Source of Variation	Value	*F*	Num *df*	Den *df*	*p*-value
Habitat (H)	0.6827	2.2856	16	17	0.0503
Season(S)	0.7795	3.7560	16	17	**0.0049***
HxS	0.5937	1.5523	16	17	0.1887
Size (SZ)	1.6854	1.5225	48	57	0.0641
H x SZ	1.3184	0.9311	48	57	0.5980
S x SZ	1.7087	1.5714	48	57	0.0510
H x S x SZ	1.3346	0.9516	48	57	0.5675

Leiognathus splendens

A total of 331 juvenile *L. splendens* were examined from the 1992-1993 collections. These fish were divided into five size classes ranging from less than 10 mm to 50 mm in length (Table 5.1). Qualitative analyses of diets indicate that *L. splendens* are omnivores, feeding primarily on bentho-pelagic organisms, especially small crustaceans (Tables 5.7 A and B). The number of prey items per individual fish revealed that although patterns were similar between habitats, a distinctly higher proportion of prey was found in the diet of fish in estuary mouths than in the diet of fish in sandy shore surf zones across all size classes (Fig. 5.1F). Furthermore, several food items such as *Lucifers*, bivalves, polychaetes and nematodes did not occur in the diets of fish collected in sandy shore surf zones.

Young juveniles with SL < 10 mm from estuary mouths fed exclusively on planktonic and benthic copepods, with these food items accounting for 88 % of the total IRI. In contrast, the youngest stage of all *L. splendens* (< 10 mm SL) examined from sandy shore surf zones had empty stomachs. Copepods were a dietary item of larger fish (10 -50 mm SL) in estuary mouths and sandy shore surf zones and consistently accounted for more than 80 % of the total IRI (Figs. 5.2 E and F). Food items in large specimens (30 - 50 mm SL) of *L. splendens* consisted primarily of both harpacticoid and cyclopoid copepods and occasionally included *Lucifer* sp., amphipods, ostracods, polychaetes, chaetognaths, appendicularians and filamentous algae (Table 5.7 A). A decrease in the consumption of copepods was evident in fish 40-50 mm SL from sandy shore surf zones. In this size class copepods were replaced by *Acetes sibogae* and chaetognaths.

Ranking by the primary Principal Components Axis of the 16 prey items demonstrated that the following items accounted for most of the variance in the data: *A. sibogae*, harpacticoid and cyclopoid copepods, ostracods, amphipods, nematodes, polychaetes, snails, appendicularians and algae (see also Appendix 4.3). There was no

Table 5.7. Composition of stomach contents of *Leiognathus splendens*: pooled data from all sampling periods for fish obtained in 1992-1993 (%N= percentage of the total number of food items; %F= percentage of frequency of occurrence; %V= percentage volume importance; IRI= Index of relative importance)

A) Estuary mouths

Contents	Size SL<10				Size 10<SL<20				Size 20<SL<30				Size 30<SL<40				Size 40<SL<50			
	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI
Harpacticoid Copepods	3.14	1.56	11.1	470	1.17	0.98	11.1	214.44	6.9	2.8	13.9	807.5	10.6	2.1	11.1	1266.7	9.09	2.67	11.1	1176
Cyclopoid Copepods	32.7	17.3	41.1	4689.6	40.7	27.4	55.6	6332.4	8.2	2	23.6	762.3	19.7	6.1	41.1	2442.3	27.2	7.59	46.4	3288
Ostracods	4.7	2.44	12.2	698.47	6.16	3.38	13.3	906.22	0.5	0.1	2.78	15.11	1.46	0.4	2.22	37.33	0.33	0.33	11.1	66.67
Amphipods									1.5	0.3	3.89	25.44	0.84	0.2	9.26	44.73	0.2	0.33	11.1	23.33
Lucifer spp.																	0.69	0.11	5.56	40.28
Acetes sibogae					0.02	0.03	1.11	0.49												
Callinassa spp.									0	0	1.39	0.67					1.39	0.89	5.56	113.9
Hermit Crabs									0.3	0.5	1.11	8.11								
Bivalves	0.56	0.13	1.11	6.89	0.03	0.09	1.11	1.2	0	0.3	1.39	4.72	1.54	0.4	3.7	63.56				
Polychaetes					1.11	0.44	1.11	15.56	4.5	2.6	5.83	271					0.24	1.56	22.2	180
Nematodes									0.1	0	3.33	2.33	0.7	0.1	7.4	56				
Appendicularias									0	0	4.44	2.58	6.87	2.3	13.3	903.11				
Chaetognaths																	0.41	0.06	3.18	13.56
Fishes					0.14	0.13	1.11	2.72												
Unidentified eggs					0.63	0.38	1.11	10.11	0.1	0	1.11	1.44	0.94	0.2	6.67	67.33				
Algae									1	0.2	2.22	24	2.54	0.9	3.33	103.67				

B) Sandy Shore Surf Zones

Contents	Size SL<10				Size 10<SL<20				Size 20<SL<30				Size 30<SL<40				Size 40<SL<50			
	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI	%N	%V	%F	IRI
Harpacticoid Copepods					11.1	8.89	11.1	2000	12	5.8	12.2	1383	0.74	0.1	1.11	16.33	3.16	0.63	4.77	162.6
Cyclopoid Copepods					1.11	0.22	1.11	13.33	4.9	2.8	8.51	499.9	4.37	2.6	10	625	8.36	2	8.33	776.7
Ostracods									0.3	0.1	1.11	3.56	0.25	0	1.11	2.77	1.18	0.26	4.77	61.44
Acetes sibogae					1.11	0.44	1.11	15.56									11.1	2.22	11.1	1333
Callinassa spp.													0.05	0.1	1.11	1.58	0.03	0.06	1.59	1.33
Insects									2.2	0.9	2.22	31.11								
Chaetognath									0.6	0.2	3.7	27.67	2.21	1	6.67	191.33	2.28	0.22	8.33	187.6
Appendicularia									0.1	0	1.11	1.51								

significant difference in the IRI values of major prey items between habitats, size classes and on their interactions (Two way crossed MANOVA, $p > 0.05$, Table 5.8 B).

Table 5.8. MANOVA results of the 1994 dietary data by habitat (H) and size (SZ) for *Leiognathus splendens*.

Source of Variation	Value	*F*	Num *df*	Den *df*	*p*-value
Habitat (H)	0.6161	2.1401	9	12	0.1096
Size (SZ)	1.6351	1.1524	36	60	0.3083
H x SZ	1.6167	1.1306	36	60	0.3313

DISCUSSION

While several studies have determined the diets of fish from one habitat (Lasiak, 1986, Morton *et al.,* 1987; Robertson, 1988; Gibson and Robb, 1996), few have compared the composition of diets and the amount of food ingested between habitats. In a temperate example, Thorman (1982) showed that the composition of the diets of fish was influenced by habitat. The present investigation is one of the few studies that compares the composition of the diets of fish between two intertidal habitats, sandy shore surf zones and estuary mouths, in the tropics.

This investigation has shown that *Stolephorus nelsoni* and *Sillago analis* juveniles in both sandy shore surf zones and estuary mouths are primarily benthic carnivores, feeding primarily on molluscs and crustaceans. The structure of their mouth parts reflect the feeding strategies of these fish (Hoedt, 1984; Gunn and Milward, 1985). Specialisation of gill rakers of *Stolephorus* spp. for predation has been demonstrated by Hoedt (1984). The powerful pharyngeal teeth and body shape of *S. analis* suggest these fish are capable of searching and crushing hard bodied prey such as gastropods and bivalves (Gunn and Milward, 1985; McKay, 1992). Analysis of the diet of *Leiognathus splendens* suggests that this species is an omnivore since both plant and animal items were found in the stomach contents. Equipped with incisor teeth on a protractile mouth, *L. splendens* is well adapted for sucking in mobile prey items such as harpacticoid copepods, polychaetes and nematodes, and for scraping off attached algae (Jones, 1985; Jayabalan, 1991).

Spatial and Temporal Differences in Diets

Food is one of the most important factors which regulates or affects the abundance, growth, survival, and probably migration, of fish (Cushing, 1975). The stomach contents of fish represent the best quality of foods available in habitats within their foraging range. Consequently, differences in gut contents for a given species reflects differences in feeding habits, food accessibility, and by inference, habitat quality (McIvor and Odum, 1988).

The occurrence of a higher proportion of stomachs which contained food in combination with a relatively higher proportion of food in each stomach (Figs. 5.1 A, C, and E)for *Stolephorus nelsoni*, *Sillago analis* and *Leiognathus splendens* from estuary mouths as compared with sandy shore surf zones suggests that the accessibility of food sources and habitat quality may be greater for estuaries. The gut fullness index of fish from estuary mouth habitats indicates that these fish are active foragers and that they have more food available to them than fish from sandy shore surf zones. Thus, differences in the fullness index between the two habitats may reflect habitat quality.

Brown and McLachlan (1990) suggested that a surf zone, in general, is much richer in zooplankton than deeper water. A recent study on the recruitment of *Chanos chanos* in the Philippines by Taki *et al.* (1990) and Morioka *et al.* (1993), found that the feeding rate of *Chanos chanos* larvae in surf zone conditions was low (5.3% and 7.3% respectively). Low feeding intensity of the three selected juveniles species was also evident in this study. On the basis of this evidence for both larvae and juveniles, the feeding conditions of sandy shore surf zones in the tropics seems to be limited. The mechanisms associated with this phenomenon are yet to be studied.

A detailed description of the diet of *Stolephorus nelsoni* has been provided by Hoedt (1984) for inshore areas around Townsville. He found that the diet of *S. nelsoni* included microphagous and macrophagous components, from single prey items, such as *Acetes sibigae*, to hundreds of minute prey items. Similar prey items falling in the same range as Hoedt (1984) were also found in the present study. However, the comparison of the diet of *S. nelsoni* in sandy shore surf zones was significantly different from estuary mouth samples (MANOVA, Table 5.3). This result highlights the spatial variation among inshore habitats and suggests that there is a difference in habitat quality between sandy shore surf zones and estuary mouths.

The diet of *Sillago analis* has previously been investigated by Lenanton (1969), Gunn and Milward (1985), and Brewer and Warburton (1988 and 1992). They reported that *S. analis* consumed different groups of prey at different locations in Australia. Ghost shrimps *Callinassa* spp., amphipods and harpacticoid copepods were the dominant components of estuary mouth samples (present study, Tables 5.4 and 5.5; Brewer and Warburton, 1992). *Mesodesma eltanae,* recognised as dominant food items for *S. analis* by Gunn and Milward (1985), were also found in this study but to a lesser extent than crustaceans. The stomach contents of these fish also indicated that this species showed a preference for larger prey items in sandy shore surf zones and smaller prey species in estuary mouths. Variations in the current findings and those of other studies are most likely a reflection of the fact that diet differences are determined by site-specific features and prey availability. Erftemeijer and Allen (1990) studied intertidal macrobenthic fauna in Irian Jaya (Indonesia) and found that sand-dominated flats had a lower biomass than silt and clay dominated flats (2.6 and 10.4 g AFDW m^{-2} respectively). The optimal foraging theory proposes that predators choose prey items that will offer an alternative of maximising the energy gained per unit time spent foraging (Krebs, 1985). The scarcity of prey items in sandy shore surf zones may force *S. analis* to select large prey items in order to maximise energy intake, while in estuary mouth habitats energy is maximised by consuming large numbers of small prey items. Thus, *S. analis* appears capable of switching its feeding methods in different habitats to maximise energy intake. This may indicate a degree of opportunistic behaviour especially in *S. analis* of the present study. The ability to switch from one feeding method to another is particularly common among herring (Clupeidae; Crowder and Binkowski, 1983; Crowder, 1985; Gibson and Ezzi, 1990) and has also been recorded in mackerel (F. Scombridae; Pepin *et al.*, 1988).

Randall (1967) suggested that tropical marine fishes would not be expected to show significant differences in their diet with season, although some variation might be expected from local fluctuations in the abundance of prey organisms. In this study, I found a marked seasonal difference in the diet of *S. analis*. This pattern is most likely a result of prey availability, which is linked to high recruitment episodes of juvenile fishes in summer, (Fig. 5.3D) and along shore migration of *Acetes sibogae* in winter (Xiao and Greenwood, 1992).

Leiognathus splendens was the only species where there was no indication of ontogenetic, temporal and spatial changes in diet for the 1994 samples (Table 5.8). Copepods were the main source of food in all studied size classes, probably due to the fact that only the smaller size classes were sampled in this study. Smaller *L. splendens* spend more time feeding in the water column than larger ones which prefer benthic feeding (Jayabalan, 1991). The proportion of prey items per individual in both sandy shore surf zones and estuary mouths were very similar (Fig. 5.1F). There is a minor difference in feeding habits between habitats for 40-50 mm SL specimens, in that the diets of fish from estuary mouths were made up of ~ 80-85 % copepods while the diets of fish from sandy shore surf zones were made up of ~ 50 % copepods, and an increasing number of other benthic organisms. This pattern suggests that the switch from planktonic to benthic feeding may occur earlier in fish from sandy shore surf zones as compared to fish from estuary mouth habitats.

The comparison of the diet of *S. nelsoni, S. analis* and *L. spendens* between sandy shore surf zones and estuary mouth habitats showed that all studied species exploited the same food categories, although to different degrees. The main differences between diets from both habitats were most likely caused by varying degrees of utilisation within each habitat, and resource availability.

If an animal chooses a particular habitat on the basis of a greater availability of food in that habitat, it has been hypothesised that the dietary breadth should be narrower (Crowder and Cooper, 1982) and the guts fuller. This was not the case, however, in the present study, where no consistent differences were found between dietary breadth and the amount of food found in the guts of fish collected from their associated habitats. Thus, in the shallow habitats of the present study, fish are apparently not associated with a particular habitat because it provides more food.

Ontogenetic Dietary Change

The results of this study indicate that dietary shifts occur with development (Figs. 5.2A-F). Such changes in diet have been described in the literature for numerous fish species (Helfman, 1978 and Werner and Gilliam, 1984). However, the nature of these changes may differ.

For example, there is a dramatic change in the consumption of harpacticiod copepods for *Stolephorus nelsoni* individuals belonging to the 50-60 mm size class (Fig. 5.3B) whilst *Sillago analis* changes to larger prey as fish sizes increases (Tables 5.4 and 5.5). In contrast, there are very few differences in the diets across the size classes of *Leiognathus splendens* examined (10-50 mm SL), which consistently consume approximately the same type of prey. The diet of fish belonging to the small size classes of *Stolephorus nelsoni, Sillago analis* and *Leiognathus splendens* are probably limited to relatively slow moving prey because of their size and capability to catch prey items. As their jaws and bodies develop, it may become increasingly easy to capture more motile species and crush hard bodied prey items such as gastropods and bivalves. Werner and Gallium (1984) and Osenberg *et al.* (1988) suggested that the ontogenetic changes with increasing size, as well as development of anatomical structure, were evolutionary strategies to allow for adult and juveniles of the same species to co-exist.

Crustaceans and molluscs are the dominant macrobenthic fauna in sandy shore surf zones and estuarine habitats (Brown and McLachlan, 1990; Kennish, 1990; Robertson and Blaber, 1992). In the present study, crustaceans were the most common dietary items found in *S. nelsoni*, *S. analis* and *L. splendens* from both habitats, with fewer molluscs.

Considerable resource overlap within the same habitats was evident for the three species investigated (Tables 5.2, 5.4, 5.5 and 5.7). Food categories such as harpacticoid copepods, amphipods and polychaetes represented a large proportion of the diet of small juveniles of *S. nelsoni* and *S. analis*, and were also recorded in lower numbers in the diet of larger fish. The presence of small prey items in the diet of larger fish may be a result of their incidental consumption with larger prey. In many circumstances the maximum prey size is limited by the mouth gape of the predator, while minimum size is not (Werner and Gallium, 1984; Hickley *et al.*, 1994). Predators capable of feeding on larger prey can choose food from a wider variety of prey categories, as found in diet of *S. nelsoni* and *L. splendens* in the present study(Tables 5.2 and 5.7).

Modde and Ross (1983) have hypothesised that temporal partitioning of resource use by sandy shore surf zone fishes prevents competition, since wave action and long shore currents replenish zooplankton. There was no clear dietary shifts in the planktivore *Leiognathus splendens*, resulting in a potentially large intra-specific dietary overlap among size classes for this species (Tables 5.7A and B). While the

Modde and Ross hypothesis may be true for planktivorous species, the findings of the present study suggest that benthic invertebrates also play an important role in the diet of fish from intertidal zones. With the exception of fish belonging to the small size classes for *L. splendens*, benthic invertebrates were the most common food items in stomach contents of *S. nelsoni, S. analis* and *L. splendens*.

Suboptimal Feeding in Sandy Shore Surf Zones

In conclusion, it is not possible to make strong generalisations about the feeding habits of particular species in intertidal zones based only on stomach content analyses. Substantial variation in gut fullness and IRI could not be explained solely by the variables examined in this study. Feeding success is the result of a complex interaction of several intrinsic factors such as size, anatomical development, and prey avoidance, and extrinsic factors including prey availability, vulnerability, competition with other predators and environmental conditions. However, fish from the sandy shore surf zone habitat displayed a relatively low gut fullness when compared with fish from the estuary mouth habitat. This result may reflect sub-optimal feeding conditions in sandy shore surf zones, which may not have been caused solely by a shortage of available food but also by environmental conditions and the distribution of food resources.

CHAPTER 6

RECRUITMENT AND GROWTH VARIABILITY IN JUVENILE FISHES FROM SANDY SHORE SURF ZONES AND ESTUARY MOUTHS

INTRODUCTION

An understanding of the role of recruitment, age and growth variability is crucial for understanding population dynamics in ecosystems. Most scientists (eg. Houde, 1987; Jenkins *et al.*, 1991; Lasker, 1975 and 1981; Iles and Sinclair, 1982; Cushing, 1980, 1988 and 1990; Miller *et al.*, 1988) have focused their studies on the early life stages of fish and have attempted to account for growth variability as a reflection of a concomitant variability in survival.

Growth is thought to be related to predation vulnerability (Bailey and Houde, 1989; Cushing, 1974 and 1988; Houde, 1987), and starvation processes (Lasker, 1981). If larvae are sufficiently abundant, food may be depleted to the point where they grow more slowly. Slow growth leads to a prolonged early life stage, high predation mortality, and increased cumulative mortality, even if the mortality rate remains constant (Houde, 1987; Bailey and Houde, 1989). On the other hand, rapid growth facilitates a newly-settled juvenile in leaving the most vulnerable size classes quickly, thus conferring a selective advantage over the slow growing population by enhancing their probability of survival (Shepherd and Cushing, 1980). Smith (1985) has critically analysed survival and growth rates of embryonic, larval, juvenile and adult stages of clupeoids by using a life-table approach and has found that the regulation of year-class strength could originate at any stage during early life history.

In general, the life cycle of many marine fishes contains a stage in which juveniles of the species are concentrated in a specific area or "nursery ground" where adults are uncommon. Many fishes are also considered to be dependent on estuaries or coastal habitats during early life (Lenanton, 1982). At the end of this period, a large size can also have continued benefits for a juvenile individual by increasing the probability of survival and ensure that relative sizes are maintained into adulthood (Houde, 1987).

Estuarine fishes (Blaber, 1987; Kennish, 1990; Robertson and Blaber, 1992), and sandy-shore-surf-zone fishes (Brown and McLachlan, 1990), do not spawn in estuaries or sandy shore surf zones. The most common life history patterns are seawater/offshore spawning followed by immigration of larvae and juveniles to shallow coastal habitats. Subsequently, juveniles remain in estuaries or intertidal habitats for some time before emigration to join the adult stock. In tropical Australia, Robertson and Duke (1990) have studied recruitment in relation to growth and movement of juvenile fishes in mangrove estuaries. Apart from this there is a considerable lack of data on recruitment patterns to common intertidal habitats in this region.

The potential to provide accurate determinations of age and age specific growth rates over short time spans of young fish has come about since Panella recognised "microincrements" in fish otoliths in 1971. Consequently, the term "microincrements" has been replaced by that of "daily increments" due to the fact that the formation of a daily increment is widespread in teleosts. Daily periodicity of increment deposition in otoliths has also been validated for a large number of freshwater and marine species (Brothers *et al.*, 1976; Campana and Neilson, 1985; Schmitt, 1984 and reviewed by Jones, 1986; Gjosaeter *et al.*, 1984: Secor *et al.*, 1991). Age validation was also considered to be an important factor in fisheries biology, as a standard solution for confirming the accuracy of "otolith increment techniques" (Beamish and McFarland, 1983). Counting the number of ring increments also allows length at age relationships to be constructed. This method allows for the direct measurement of length at age for further growth and mortality calculations, and provides information on individual age and growth rates (Methot, 1983).

In the present study, 'growth' refers to an individual-standard-length-increment increase (Buesa, 1987). Intraspecific variations in growth rates have been noted and described as functional responses to several factors including temperature, food supply, light, oxygen, and other environmental factors (Weatherly, 1990). There is very limited information available on growth rates based on length-at-age measurements during the period of juvenile residence in presumed coastal nursery habitats in the tropics. Such growth estimates are particularly important since this period may be critical in determining the probability of their survival. In order to answer an important, constantly recurring question in fisheries research, namely whether a specific habitat type influences growth patterns in early life history, the growth patterns of juveniles in selected species from sandy shore surf zones and estuary mouths were estimated and tested for evidence of any significant relationship with habitat. In this study, observations were designed to: 1) validate the periodicity of increment deposition in otoliths of selected species, 2) provide detail on the patterns of utility of both habitats by the selected species based on size class frequency and period of residence, and 3) compare juvenile growth rates from different habitats, sandy shore surf zones and estuary mouths, by using length at age data obtained from growth ring counts on otoliths. The aim of this study was to use growth during the resident period as a criterion for evaluating habitats for their relative value as nursery areas.

MATERIALS AND METHODS

Study species

The four species used in this study were *Leiognathus splendens*; *Sillago analis*; *Stolephorus nelsoni* and *Valamugil seheli*. These species are widespread in the tropical

Indo-Pacific region (Jones, 1985; McKay, 1992; Wongratana, 1987; Fischer and Whitehead, 1974).

Collection methods and sampling

The fishes used in this study were those collected as described in Chapter 3. All specimens were initially preserved in 10 % seawater formalin buffered with borax. All selected specimens were transferred to 70 % ethanol within 3-5 days to minimise exposure to the formalin solution.

A length-at-age relationship was established for the 4 species in the following manner. The standard length (SL) was measured to the nearest 0.05 mm with a pair of vernier callipers and then the otoliths were extracted. After dissection, otoliths were cleaned in distilled water and transferred to 95 % ethanol for a few minutes. All analyses were carried out on the sagittal (largest pair) otoliths. At least 30 fish for each species from each habitat were collected on each trip. Size-frequency histograms based on pooled data from all locations for each habitat and sampling month were also constructed for each selected species using standard length data.

Preparation and analysis of otoliths

Ageing was accomplished by either using the whole otolith or a thin section of the otolith. Whole mounts of otoliths were used for small juveniles whose otoliths were thin, circular and flat. Large otoliths were analysed based on transverse sections using the procedures described in Secor *et al.* (1991). The use of the whole otolith method was avoided for large fishes due to possible under-estimates of increment (Beamish, 1979 a, b; Campana, 1984: Baillon and Kulbicki, 1988).

Daily ages were directly assessed by counting the number of increments in the otoliths from the primordium to the edge. Three replicate counts, without reference to fish length, were performed 3-4 days apart by one reader using a compound microscope.

If one of the three counts differed by > 10 % from the lowest count, an additional count was performed and the outlier discarded. The three final counts were then averaged.

Validation of period of increment formation

Otolith validation has been employed in this study in order to confirm the rate of ring deposition and eliminate the possibility of misinterpretation of daily bands (Beamish and McFarlane, 1983; Lough *et al.*, 1982; Campana and Neilson, 1985; Jones, 1986). In the present study, increment rings were validated using the fluorochrome marker, oxytetracycline. When fish are exposed to oxytetracycline, the substance is metabolised and deposited in their bony parts for a short time to form a thin mark in calcareous structures, including otoliths. Testing the rate of increment deposition involved matching the number of increments following an oxytetracycline induced fluorescent mark on the otolith with the actual number of days passed.

In the present study *Sillago analis, Leiognathus splendens* and *Valamugil seheli* were collected from the Ross River mouth and from Pallarenda by using small beach seine nets. They were then transported to the laboratory in aerated containers and allowed to acclimate to laboratory conditions in 80 L Nally bins for 2 days. After this, they were immersed for 24 hours in seawater containing oxytetracycline at a concentration of 350 mgL^{-1} (Schmitt, 1984). After exposure, the fish were transferred to a 32 L holding aquarium. During this period, they were fed with minced prawns twice a day, at 8:00 am and 5:30 pm. After approximately 60-70 days, the second oxytetracycline treatment was administrated to the experimental fish by using the same procedure and concentration as the first treatment. The fish were maintained and fed for another 10-days or more. *Stolephorus nelsoni* were also obtained for otolith validation but without success, due to the sensitivity of this species to handling and aquarium conditions.

All fish were then euthanased and preserved in 70 % ethanol. For transverse sections, all otoliths were cleaned and embedded in Spurr's resin (Secor *et al.*, 1991). These sections were examined under a compound microscope and ultra-violet (UV) light in a darkened room. The tetracycline bands fluoresce under UV light to enable the number of increments between the first and second tetracycline bands to be counted. These counts were then compared to the number of days between exposure. A total of *14* *Sillago analis*, 8 *Leiognathus splendens* and 6 *Valamugil seheli* were examined. Recently, Hoedt (1994) attemped to validate otolith increment rates for *Stolephorus nelsoni*, however, the study was limited by low survival. Hoedt (1994) examined the otoliths of the few surviving fish by using marginal increments and suggested there was a daily increment.

Data Analysis: Spatial variability in growth

Length-at-age plots were used to provide an estimate of the growth patterns of fish in the two habitats. The age of each fish at the time of capture was measured and the date of birth was back calculated. Since the principal aims of the present study were to evaluate the nursery function in both sandy shore surf zones and estuary mouth habitats, only otoliths of juveniles represented the size classes of the new recruitment to the habitats, which mainly occurred in late September, November and January. To ensure precise allocation of juveniles within a similar recruitment peak or year groups, juveniles were assigned to similar year classes if birth dates were within 60 days before or after the 1st January of each year. In this analysis, otoliths for fishes older than 120 days were also omitted as length frequency plots in the present study, and Robertson and Duke (1990) suggested that most temporary residents commonly spent 3-4 months in these presumed nursery habitats. These criteria were introduced in order to eliminate between-year variation in growth conditions and restrict the analyses to juvenile phases only.

The regression of length-at-age of these selected species was clearly linear for the given size ranges. To determine if there were differences in length-at-age between sandy shore surf zones and estuary mouths within the same year, the slopes were compared using procedures described in Zar (1996). In order to compensate for the accuracy of standard length measurement and increase the likelihood of minimising significant differences due to Type I error, these analyses were interpreted by the use of conservative $\alpha = 0.01$ significance levels, instead of the more prevalent level of $\alpha = 0.05$.

RESULTS

Otolith Validation: *Frequency of Ring Deposition*

In the present study, otolith validation for *Sillago analis, Leiognathus splendens* and *Valamugil seheli*, the number of rings between the first and second tetracycline-HCl marking and the number of days between the first and second markings, had an almost 1:1 correspondence (Table 6.1). This suggests that otolith increments for these species were deposited daily.

Table 6.1. Validation results by using the tetracycline marking technique for selected species under laboratory condition

Species	Batch	Standard Length (mm)	1st OTC Marking	2nd OTC Marking	Total day marking	Range total increment rings	N
Sillago analis	1	20.00-60.00	7-Jul-92	18-Sep-92	72	72-73	7
Sillago analis	2	20.00-60.00	7-Feb-94	14-Apr-94	66	64-67	7
Leiognathus splendens	1	15.00-30.00	3-Feb-94	7-Apr-94	63	61-62	8
Valamugil seheli	1	15.00-60.00	12-Jul-92	17-Sep-92	68	66-67	6

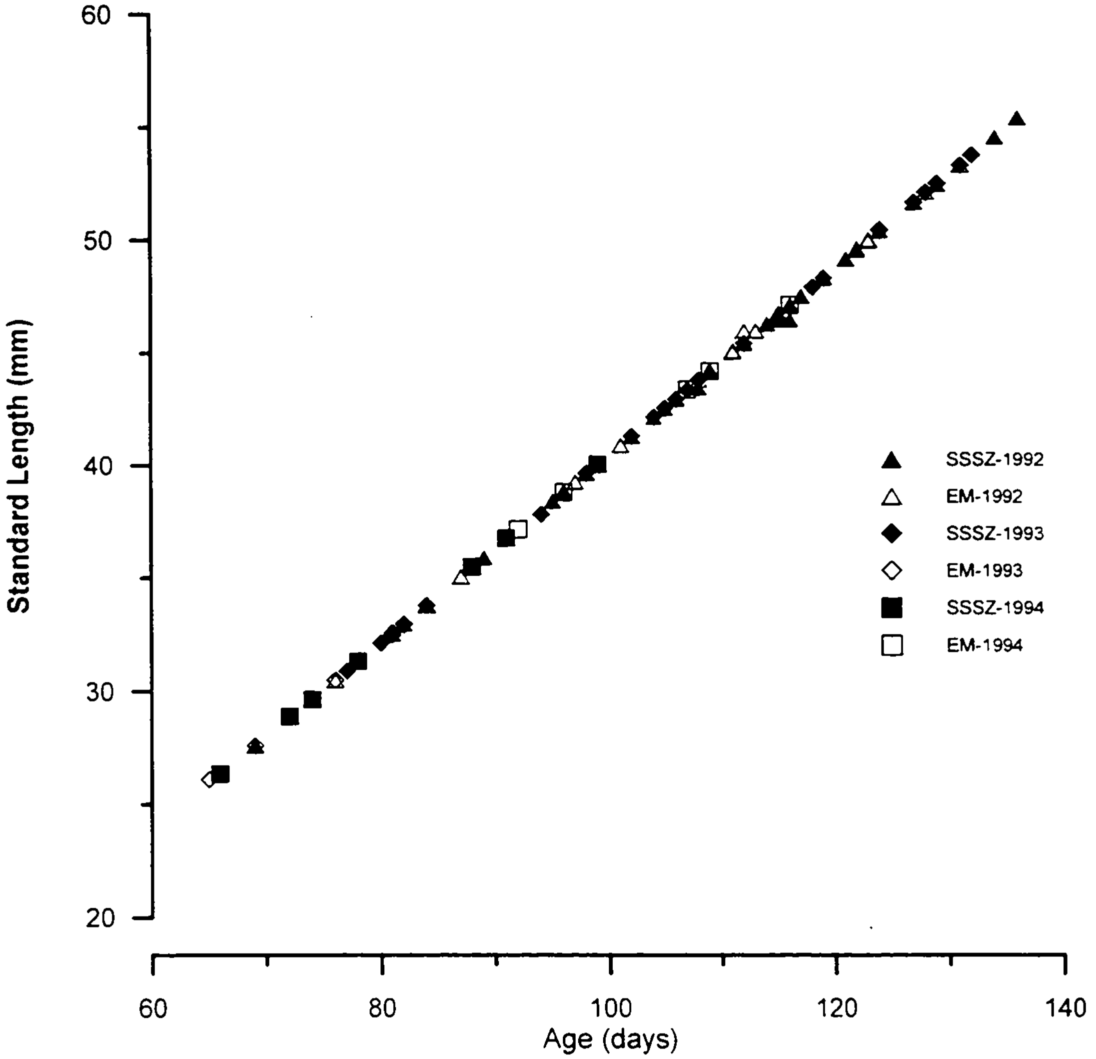
Recruitment Growth and Residence Time: Habitat variability

Stolephorus nelsoni

Examination of size-frequency plots for *S. nelsoni* (Fig. 6.1) revealed that *S. nelsoni* were short term residents in both sandy shore surf zones and estuary mouths. They were

Figure 6.1 Size-frequency plots of *Stolephorus nelsoni* between January 1992 and September 1994.

A) Estuary mouth samples
B) Sandy shore surf zone samples


60
50
40
30
20
Standard Length (mm)
60
80
100
120
140
Age (days)
▲ SSSZ-1992
△ EM-1992
◆ SSSZ-1993
◇ EM-1993
■ SSSZ-1994
□ EM-1994

not often captured but were occasionally present in large numbers. For example, peak abundance occurred in January and March 1992 and in March 1994, after which the abundance declined. The timing of recruitment and the magnitude of abundance varied widely from year to year, and in some months there were no distinct recruits present in the catches from either habitats (eg. November 1993).

A cohort of similar sized fish of *S. nelsoni* was caught in both sandy shore surf zones and estuary mouths, but they occurred most frequently in sandy shore surf zones. Distinct recruitment periods were recorded in July and September 1992 due to the presence of a small number of very small juveniles. Some new recruits were also present in November 1992, January and March 1993. The cohort of 0+ of *S. nelsoni* were present in both habitats for approximately 4-6 months, after which time they were absent from catches. The 1992 - 1994 size frequency plots (Fig. 6.1) also suggest that, by the time individuals have reached a length of 60 - 70 mm, they are mainly found in sandy shore surf zones (in 10 out of 17 occasions) while there was only one occasion when they were recorded in estuarine catches.

Length-at-age of both habitat samples using a similar age range within the same year class, fitted the general linear regression model so that regression coefficients could be compared. In this study, length-at-age since recruitment to sandy shore surf zones and estuary mouths in early 1992 (Fig. 6.1A), and early 1993 (Fig. 6.1B) were used for the analysis. Length-at-age relationships from sandy shore surf zones and estuary mouths for both years showed a similar increase in length with an increase in fish age ($F_{5,110} = 3.20$; $P > 0.01$; Table 6.2 and Fig. 6.2).

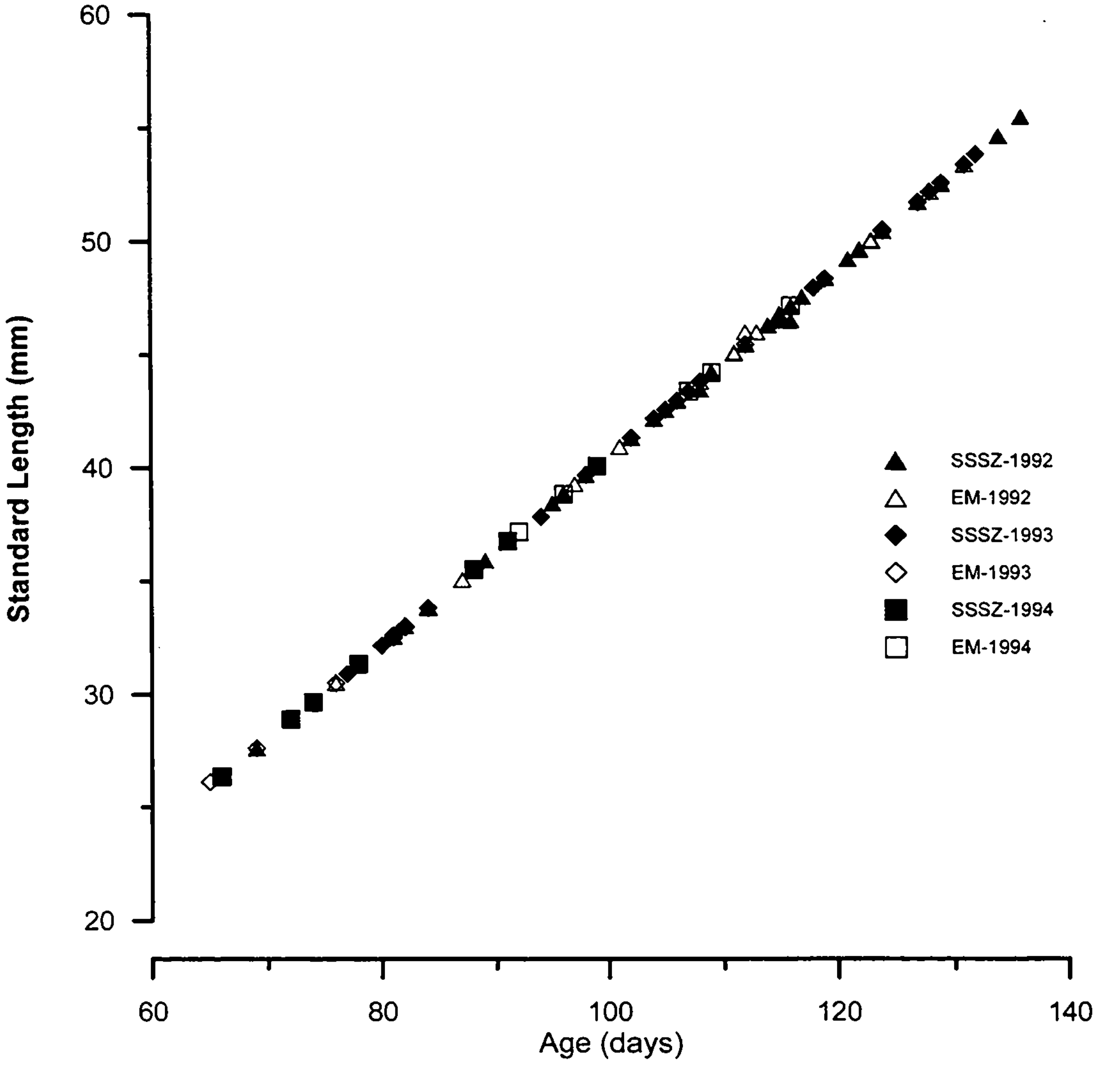


Figure 6.2. Length at age relationship of *Stolephorus nelsoni* taken from sandy shore surf zones (SSSZ) and estuary mouths (EM), between January 1992 and September 1994.

Table 6.2. Calculations for testing for significant differences among slopes of length at age regression line for *Stolephorus nelsoni* taken from sandy shore surf zones and estuary mouths.

Habitat-Year	$\Sigma(\text{Age})^2$	Σ(Age x Length)	$\Sigma(\text{Length})^2$	Residual SS	Residual DF
SSSZ-1992	64576	26114.40	10561.00	0.39	3
EM-1992	126958	51618.60	20987.40	0.30	8
SSSZ-1993	211095	85316.40	34482.40	0.82	22
EM-1993	67007	27154.80	11005.10	0.53	5
SSSZ-1994	327085	132544.00	53712.10	1.56	38
EM-1994	553368	224581.00	91146.00	1.18	43
Pooled Regression				4.78	110
Common Regression	1350089	547329.20	221894.00	5.48	115
				$F_{5,110} = 3.20$	

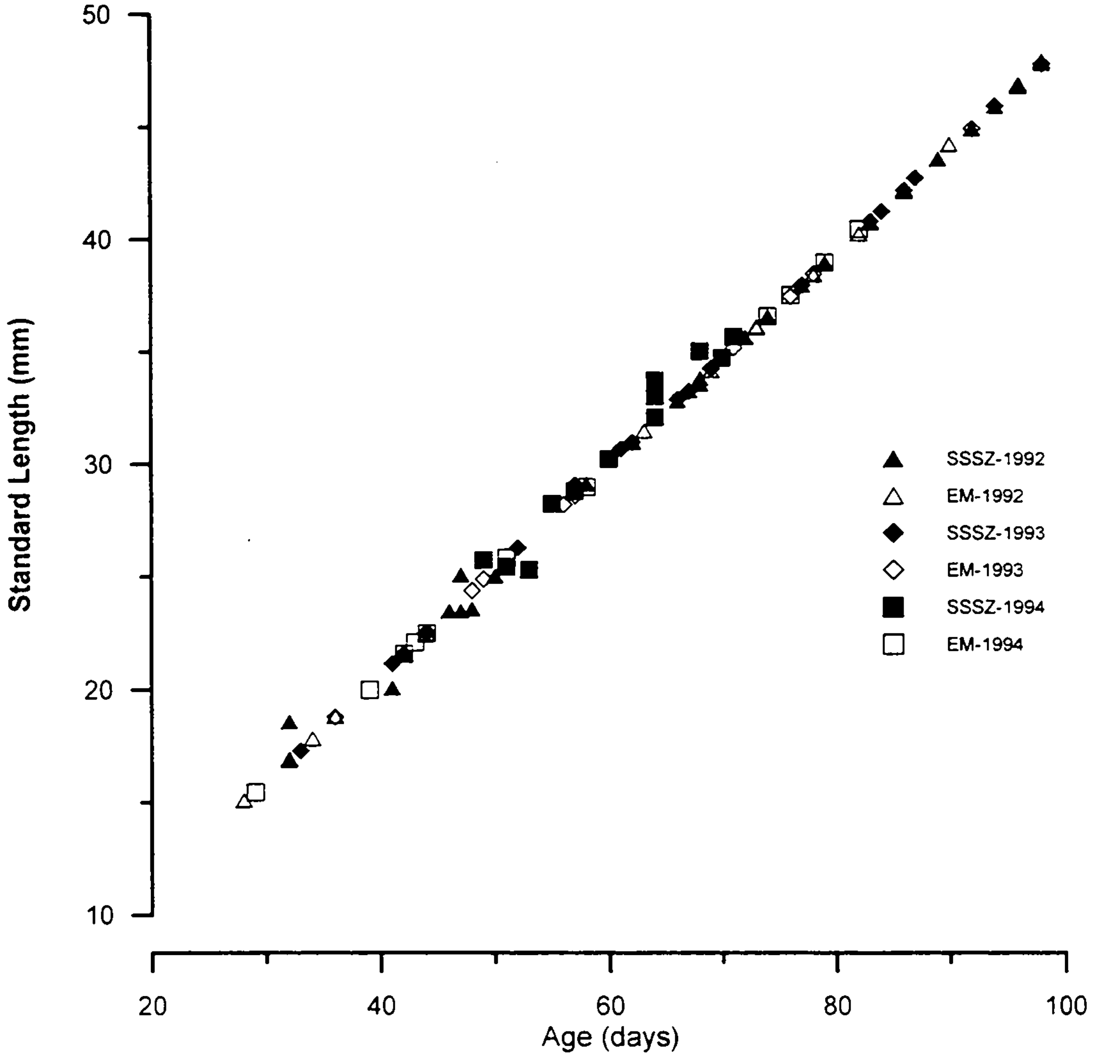
Sillago analis

In most cases, individuals of *S. analis* with a standard length of around 180 mm and larger were observed to have mature gonads. Recruitment appeared to occur all year round, most probably due to continuous spawning events. Juveniles with SL less than 15 mm were very common in most occasional catches throughout the entire study period but larger fish were relatively rare . It is not surprising therefore that this present study was unable to separate the existing cohorts in the size frequency plots for this species from both habitats (Figs. 6.3 A and B).

The relative consistency of all year round recruitment events resulted in abundance trends in sandy shore surf zones and estuary mouths that were almost identical over the 3-year survey (Figs. 6.3 A and B). Consequently, the duration of recruitment and residence times in shallow areas are more difficult to identify because multiple cohorts were probably separated by two weeks to a month apart and thus could not be distinguished when using normal size frequency distribution techniques. Generally, *S. analis* first appeared in sandy shore surf zones and estuary mouths at 12 - 15 mm SL. As they grow bigger, fish 60 - 90 mm in size rapidly decline in abundance (Fig. 6.3).

Figure 6.3. Size-frequency plots of *Sillago analis* between January 1992 and September 1994.

A) Estuary mouth samples
B) Sandy shore surf zone samples


50
40
30
20
10
Standard Length (mm)
20
40
60
80
100
Age (days)
▲ SSSZ-1992
△ EM-1992
◆ SSSZ-1993
◇ EM-1993
■ SSSZ-1994
□ EM-1994

Length at age of samples from both habitats, taken from early 1992, 1993 and 1994 respectively (Figs. 6.4), fitted very well with the general linear regression model. The standard length of fish at the same age which were collected from estuary mouths and sandy shore surf zones were similar in all three sampling years ($F_{5, 98} = 3.09$; $p > 0.01$; Table 6.3 and Fig. 6.4).

Table 6.3. Calculations for testing for significant differences among slopes of length at age regression line for *Sillago analis* taken from sandy shore surf zones and estuary mouths.

Habitat-Year	$\Sigma(\text{Age})^2$	$\Sigma(\text{Age x Length})$	$\Sigma(\text{Length})^2$	Residual SS	Residual DF
SSSZ-1992	36808	18491.30	9300.11	10.59	10
EM-1992	125874	61937.10	30478.10	1.56	17
SSSZ-1993	61690	30553.80	15134.00	1.32	10
EM-1993	107969	53703.50	26720.60	8.62	24
SSSZ-1994	52597	26343.20	13195.30	1.31	13
EM-1994	109007	54163.30	26921.10	8.49	24
Pooled Regression				31.89	98
Common Regression	493945	245192.20	121749.21	36.84	103
				$F_{5, 98} = 3.09$	

Leiognathus splendens

The summer season (November - April) was the main recruitment period of *L. splendens,* with a minor pulse possibly in the late wet and early dry season (May - June). The size frequency plots indicate that the early 0+ age, 7 - 10 mm SL, appeared in the sample in September and probably continued until March of each year (Figs. 6.5A and B). There were virtually no new recruits anywhere in the intertidal zones during the dry season of the year (July – September).

Leiognathus splendens recruitment in sandy shore surf zones and estuary mouths showed similar seasonal utilisation patterns, with the exception of September 1993. While a distinct successive mode from the length frequency distribution was not perceived, new recruits were observed during every sampling month of the wet season, thus indicating that there was continuous spawning during the wet season, and protracted

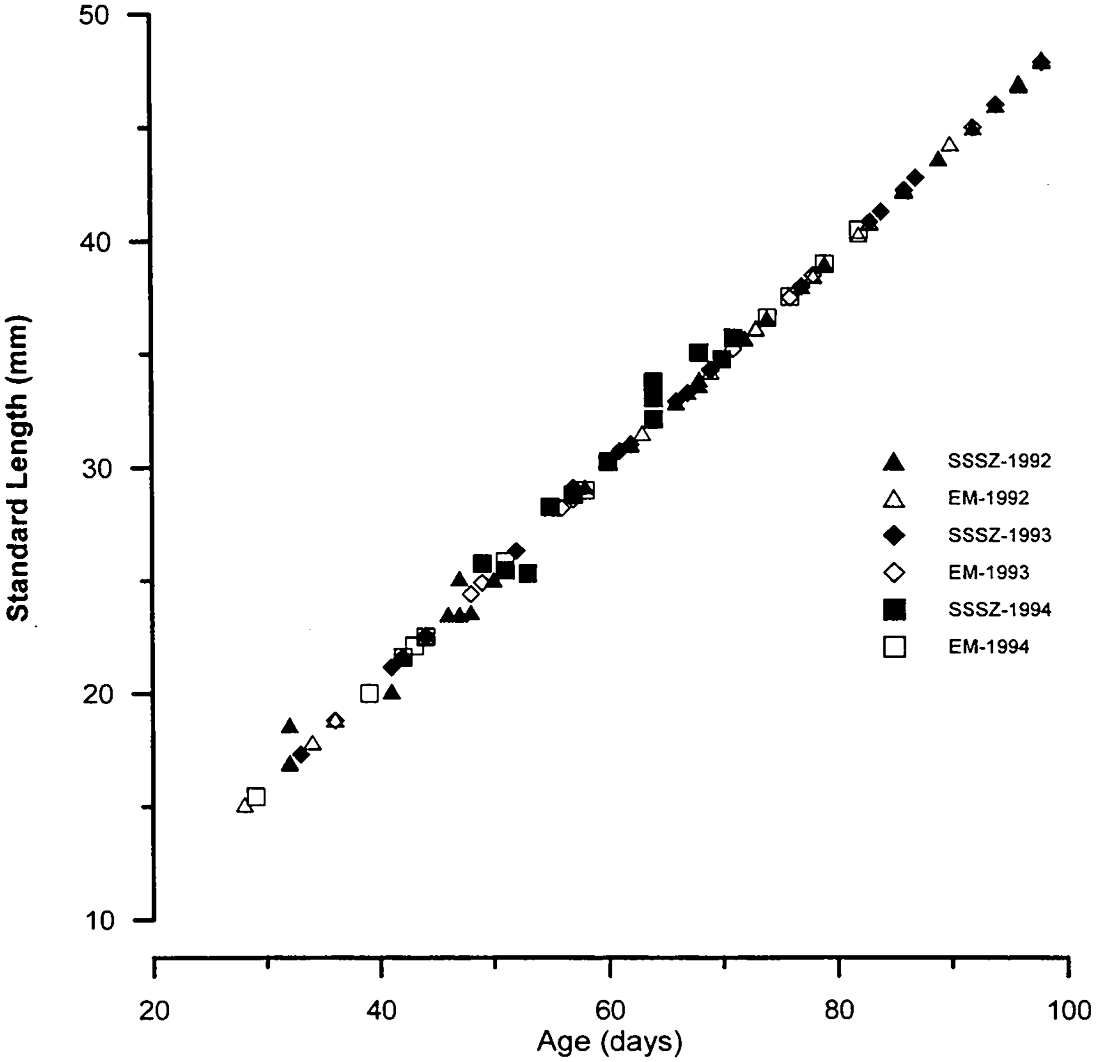
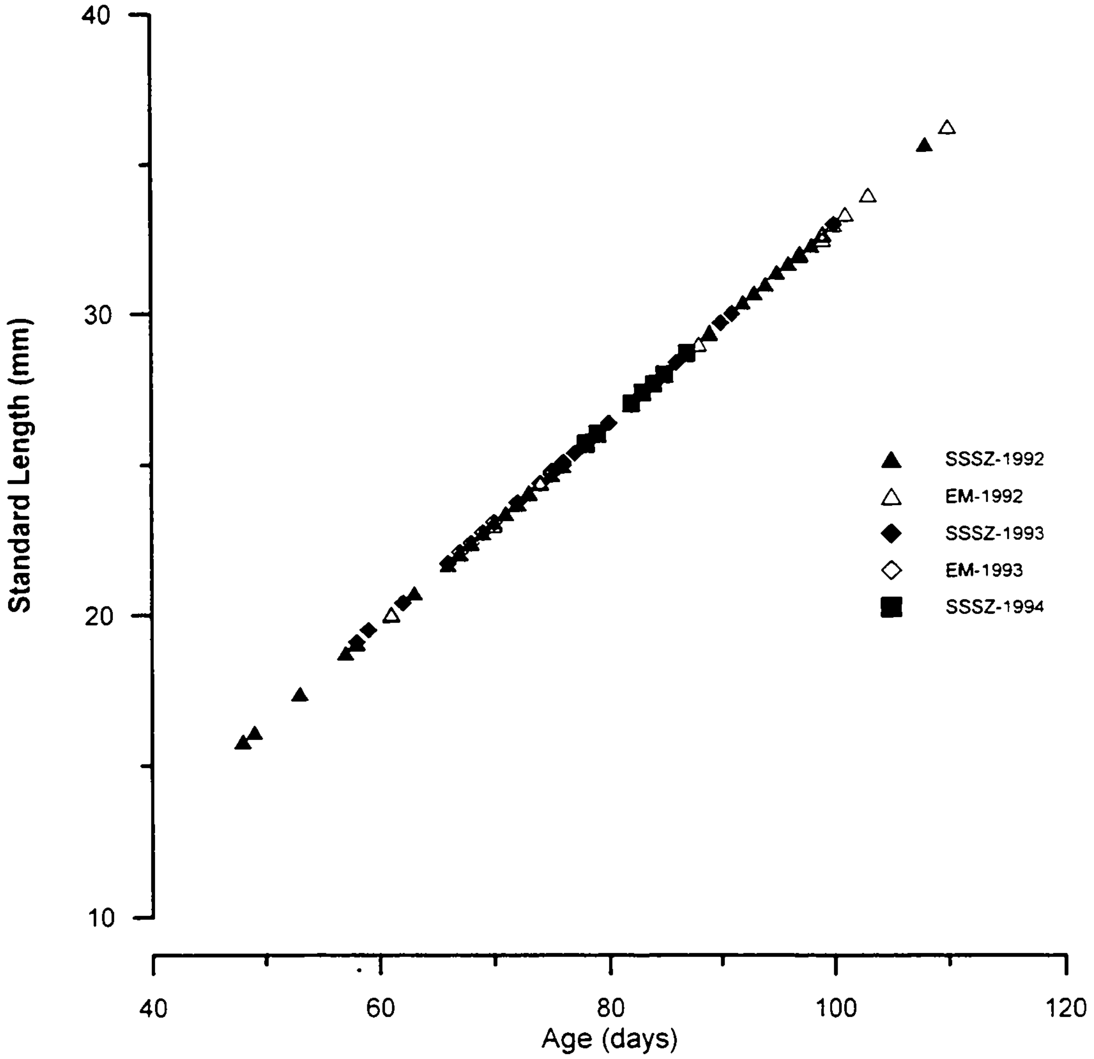


Figure 6.4. Length at age relationship of *Sillago analis* taken from sandy shore surf zones (SSSZ) and estuary mouths (EM),between January 1992 and September 1994.

Figure 6.5. Size-frequency plots of *Leiognathus splendens* January 1992 and September 1994.

A) Estuary mouth samples
B) Sandy shore surf zone samples


40
30
20
10
Standard Length (mm)
40
60
80
100
120
Age (days)
▲ SSSZ-1992
△ EM-1992
◆ SSSZ-1993
◇ EM-1993
■ SSSZ-1994

recruitment in the dry season which resulted in a wide spread in the size of 0+ fish in the population in summer.

Individuals larger than 60 mm SL were rare in most samples, although an unusual catch with specimens larger than 60 mm was obtained from sandy shore surf zones samples in September 1993 before peak recruitment. Preliminary dissection of these fish from this early summer catch revealed that specimens larger than 70 mm SL were female with fully matured eggs. The overwhelming excess of larger mature females in seine samples from sandy shore surf zones in the late dry season provides a very strong indication that *L. splendens* spawn in the vicinity of shallow waters.

A higher degree of loss from intertidal zones is revealed from Figure 6.5, which shows a relatively rapid decline in individual numbers in the following sampling months after the peaks. The residence time of *L. splendens* was roughly estimated to be 4-6 months in both habitats.

Length-at-age plots for both habitat samples in the summers of 1992, 1993 and 1994 revealed linear relationships (Fig. 6.6). The length–at-age relationship for *Leiognathus splendens* were similar for both habitats ($F_{4,\ 107} = 1.67$; $p > 0.01$; Table 6.4 and Fig. 6.6).

Table 6.4. Calculations for testing for significant differences among slopes of length at age regression line for *Leiognathus splendens* taken from sandy shore surf zones and estuary mouths.

Habitat-Year	$\Sigma(\text{Age})^2$	Σ(Age x Length)	$\Sigma(\text{Length})^2$	Residual SS	Residual DF
SSSZ-1992	40423	13317.60	4387.56	0	7
EM-1992	179097	59094.40	19498.70	0.06	17
SSSZ-1993	119025	39232.10	12931.40	0.02	17
EM-1993	159085	52457.50	17297.60	0	26
SSSZ-1994	256694	84643.45	27910.80	0.08	40
Pooled Regression				0.16	107
Common Regression	754324	248745.05	82026.06	0.17	111
				$F_{4,\ 107}=1.67$	

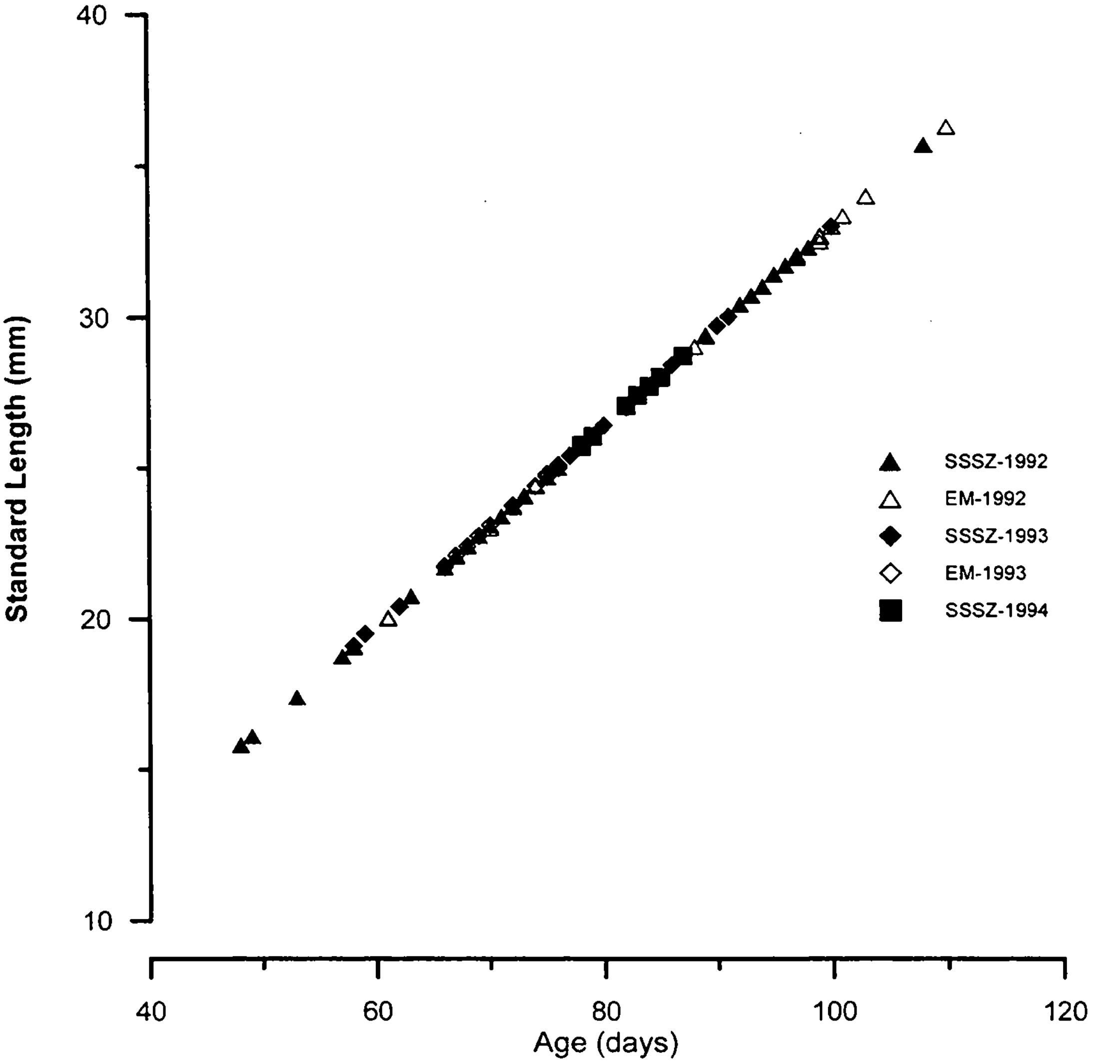


Figure 6.6. Length at age relationship of *Leiognathus splendens* taken from sandy shore surf zones (SSSZ) and estuary mouths (EM),between January 1992 and September 1994.

Valamugil seheli

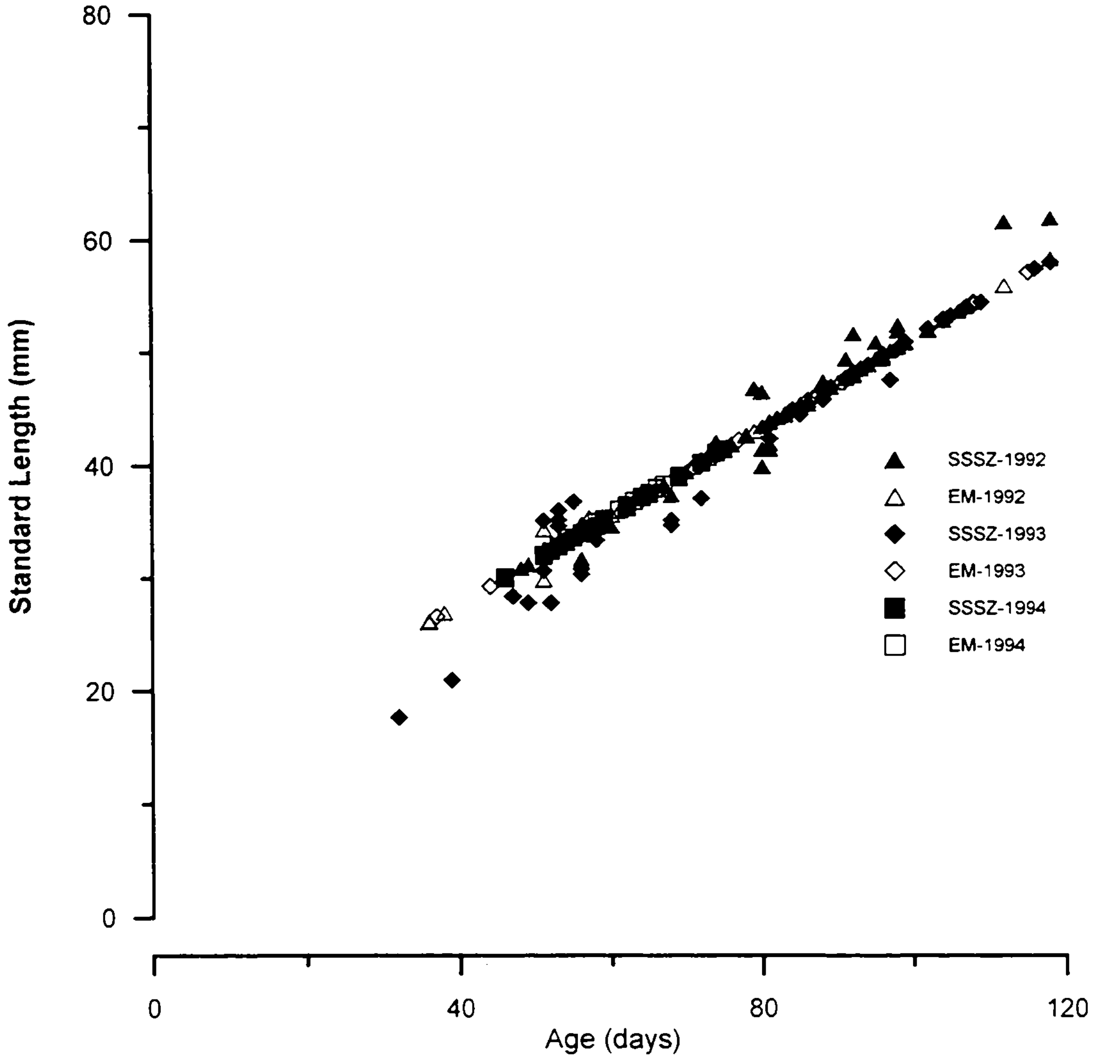
New recruits of *V. seheli* in sandy shore surf zones and estuaries were very similar in SL ranging from 10 - 15 mm (Fig. 6.7). The size frequency distribution of *V. seheli* is very difficult to follow due to the almost continuous recruitment into the area, as new recruits were obtained on almost every sampling occasion. Most size classes in sandy shore surf zones and estuaries were broadly or completely overlapping. Fish ranging in size from 30 - 60 mm from both habitats declined very rapidly in abundance. The distribution of *V. seheli* was also bimodal and wide-spread in the size of 0+ which occurred in February 1992 (Fig. 6.7).

Total abundance of *V. seheli* fell from 100 - 600 individuals in the early dry season (May- June) to 5 - 50 individuals immediately before rising rapidly to 500 and 300 individuals in the late dry (September 1992) and the early wet (November 1994) seasons for sandy shore surf zones and estuary mouths respectively. The absence of *V. seheli* in sandy shore surf zones in September 1994 presumably reflects an extremely low recruitment of this species to sandy shore surf zones, originating from March - July 1994. Trends ascertained by means of sequential successive modes of bimonthly length frequency distributions demonstrate that the interpretation of size class groups for *V. seheli* was extremely difficult. Examination of size-frequency plots for *V. seheli* in estuary mouths and sandy shore surf zones revealed that they may remain in both habitats for at least 4 to 6 months.

Length-at-age for the samples taken from the same progression cohorts in estuary mouths and sandy shore surf zones for November 1993 to March 1993 and November 1994 to March 1994 were plotted and fitted with the general linear model for both time periods. Standard length of *V. seheli* at the same age from estuary mouths were similar

Figure 6.7. Size-frequency plots of *Valamugil seheli* between January 1992 and September 1994.

A) Estuary mouth samples
B) Sandy shore surf zone samples


80
60
40
20
0
Standard Length (mm)
0
40
80
120
Age (days)
▲ SSSZ-1992
△ EM-1992
◆ SSSZ-1993
◇ EM-1993
■ SSSZ-1994
□ EM-1994

to those from sandy shore surf zones on both occasions ($F_{5,232} = 1.20$; $p > 0.01$; Table 6.5 and Fig. 6.8).

Table 6.5. Calculations for testing for significant differences among slopes of length at age regression line for *Valamugil seheli* taken from sandy shore surf zones and estuary mouths.

Habitat-Year	$\Sigma(\text{Age})^2$	Σ(Age x Length)	$\Sigma(\text{Length})^2$	Residual SS	Residual DF
SSSZ-1992	169574	91401.30	49350.32	84.53	20
EM-1992	294287	158397.50	85417.20	161.07	42
SSSZ-1993	109735	61016.25	34354.80	427.76	25
EM-1993	542643	291144.80	156999.86	791.64	81
SSSZ-1994	3364	2006.80	1197.16	0	19
EM-1994	292465	158390.95	86138.79	358.64	45
Pooled Regression				1823.65	232
Common Regression	1412068	413458.12	762357.60	1870.93	237
				$F_{5,232} = 1.20$	

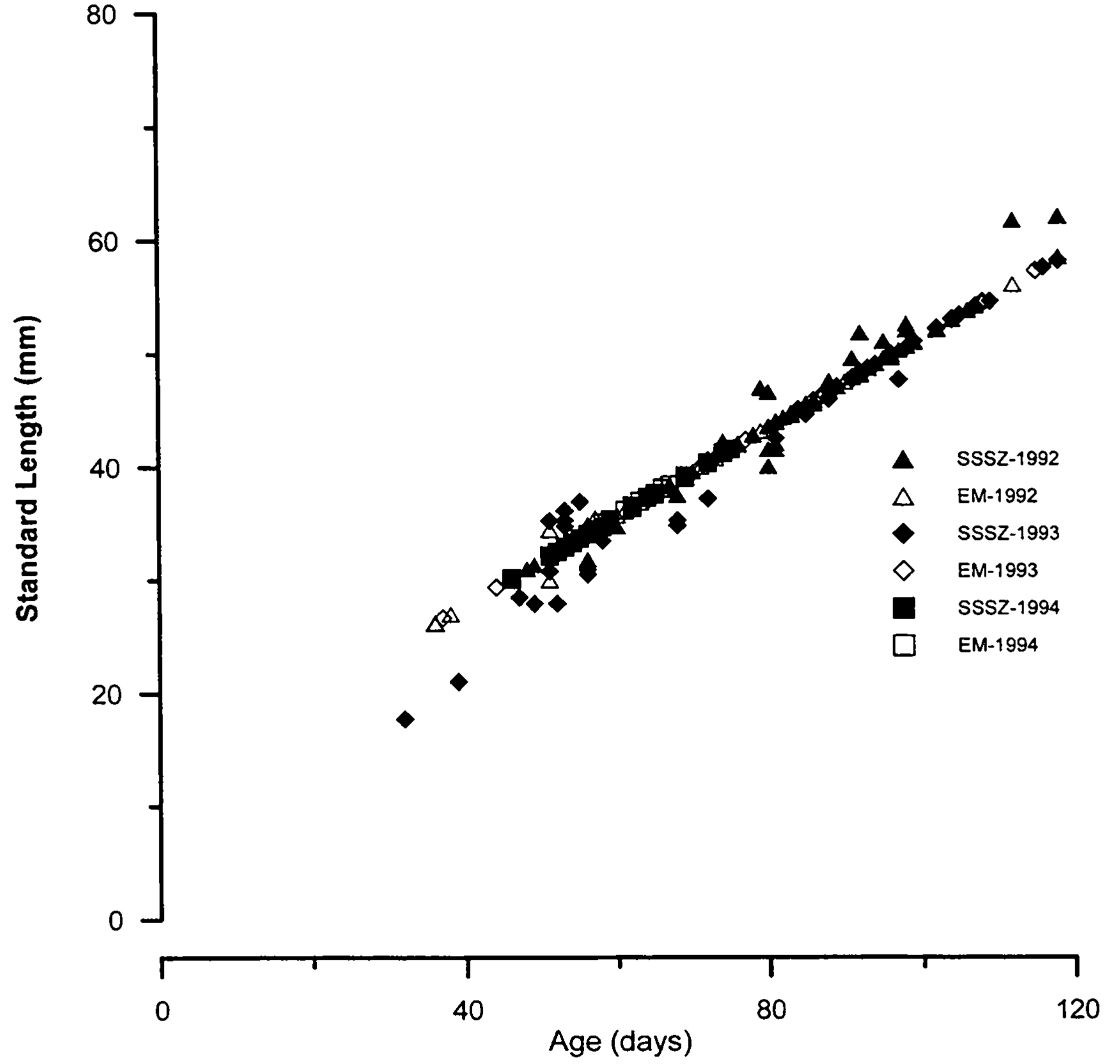


Figure 6.8. Length at age relationship of *Valamugil seheli* taken from sandy shore surf zones (SSSZ) and estuary mouths (EM),between January 1992 and September 1994.

DISCUSSION

Otolith Increment Determination

The otolith validation experiments with OTC marked otoliths conducted during this study confirms that dailyincrements are laid down in *Sillago analis, Leiognathus splendens* and *Valamugil seheli* (Table 6.1). This suggests that the number of otolith increments provide a close estimate of age and a reference point for the interpretation of natural growth events for these selected species. Since age validation for otolith increments in *Stolephorus nelsoni* have been unsuccessful, this study assumes that the increments in the otoliths of this species are laid down daily. This assumption is based on the fact that juvenile stages of the other three selected species showed this pattern and other studies in the tropical region, such as Thorrold (1989) and Thorrold and Williams (1989) have validated daily growth increments in *Herklotsichthys castelnaui*, Molony and Choat (1990) for *Ambassis vachelli*, and Milton *et al.* (1993) for *Herklotsichthys quadrimaculatus* and *Spratelloides delicatulus*.

Otolith increment counts were linearly correlated to somatic growth in terms of standard length for all four selected species. There was no intention to relate growth rates to otolith increment widths in this present study because recent experimental reports have indicated that such relationships are complex (Campana, 1990; Bradford and Geen, 1992).

Recruitment/ Size classes between sandy shore surf zones and estuary mouths

Seasonal patterns of juvenile fish recruitment to sandy shore surf zones and estuary mouths were very regular, even though precise size structures were not ascertained. While large numbers of small size classes were found at different times during the year, the largest peak occurred in the late dry season and extended to the wet season. A multi-peak distribution in the size structure profiles of juveniles collected in intertidal zones can reflect several seasonal abundance groups of immigrating juveniles within a spawning season. Consequently, identical juvenile numbers and size structure profiles between habitats in most cases probably does not result from differences in distance from spawning sites of immigrants but rather from differences in survival and settlement in habitats (Allen and Baker, 1990). Similar numbers of recruits occurring in both habitats indicate that there was no habitat preference for these selected species.

In the present study, juveniles of *S. analis* and *V. seheli* (Figs. 6.3 and 6.7 respectively) are characterised by prolonged recruitment to intertidal habitats. The presence of small juveniles throughout the study periods indicated continuous production and arrival. The continuous recruitment of *S. analis* and *V. seheli* may be an adaptive strategy for reducing competition for resources among associated taxa, thus increasing the likelihood of survival for all constituents (de LaFontaine et. al., 1984). Extension of recruitment periods from weeks to months or year-round events as shown for these two selected species is likely to be common phenomenon in the tropics. Continuous recruitment into a particular habitat by more than one species produces considerable overlap among species (Houde and Lovdal, 1984; Johannes, 1978). This strategy may be described as an adaptive trait for ensuring recruitment survival in situations where prey availability is unpredictable (Lambert and Ware, 1984). This implies that survival of *S. analis* and *V. seheli* is reliant on foraging ability in shallow coastal habitats (Weng, 1986; Blaber, 1987). The simultaneous occurrence of many taxa may not be an advantage to the recruitment success of an intertidal taxon. Density-dependent survival could explain some of the high variability in abundance among observed dates, as was found in plaice nursery grounds in the North Sea (Bergman *et al.*, 1988). If short term interspecific or intraspecific competition for food or refugia is high, one would expect continuous recruitment over longer periods to be a compensatory mechanism which would increase the likelihood of survival. More research on trophic requirements and competition among these juveniles is necessary to address this hypothesis.

In this study, most juveniles that recruit to intertidal zones and shallow areas are expected to originate from parent stocks endemic to the near-shore coast of North Queensland, as adult females with mature eggs of *S. analis*, *L. splendens* and *V. seheli* are occasionally caught by seine nets. Unfortunately, there is no available data on eggs and larvae density to support this claim. Similar sizes of fish recruiting into sandy shore surf zones and estuaries at the same time probably results from the same degree of active or passive transport towards the vicinity of intertidal zones, and may be another reason for supporting the above claim. Although various physical processes that could affect larval and juvenile transport have been discussed by Miller (1988) and Boehlert and Mundy (1988), precise transport mechanisms still remain unknown. The relatively higher abundance of *S. nelsoni* and *L. splendens* in sandy shore surf zones (Figs. 6.1 and 6.5), *V. seheli* in estuaries (Fig. 6.7) and almost the same magnitude of abundance of *S. analis* in both habitats (Fig. 6.3) may be a function of spawning location, means of larval and juvenile transport, and subsequent habitat choice selection.

Length-frequency distributions of selected species indicate that the first recruitment of small juveniles in both habitats are comprised of distinctive modes that theoretically could be followed for a considerable period of time (See Figs. 6.1, 6.3, 6.5 and 6.7). In the tropical environments of this particular study, prolonged recruitment and probable continuous spawning periods of *S. analis* and *V. seheli* cause inaccurate identification and discrimination between distinct cohorts (Fréon, 1984). In fact, the same habitats may be utilised by juveniles of different cohorts where migration alterations mask size structure profiles by means of mixed cohorts (Robertson and Duke, 1990).

Growth Variability

The aim of the present study was to evaluate the variability of growth of selected species between sandy shore surf zones and estuary mouths. Few studies have directly assessed the growth response of larvae or juveniles that stay in "presumably" coastal nursery habitats along appropriate temporal and spatial scales. The present study expected that the growth rate of selected species would be determined primarily by the characteristics of the habitat with estuary mouths producing better growth rates in juvenile fish because conditions there may be more favourable for growth than sandy shore surf zones. However, growth rates did not differ between habitats.

Results from the International Symposium on Age and Growth of Fish held in Iowa, USA, in June 1985 (Summerfelt and Hall, 1987) and the National Workshop on 'The Management of Age and Growth in Fish and Shell Fish' organised by the Australian Society for Fish Biology held in Australia (Smith, 1992) have indicated that growth rates are influenced by maturation and spawning, crowded conditions and population density, productivity of the ecosystem, water chemistry, temperature fluctuations, amount of food and food quality, as well as environmental biotic qualities. The two factors most likely to account for similar growth in this particular study are population density and predation or physical pressure. The main reason for supporting such a claim is that comparable environmental conditions in both habitats were obvious.

During the resident time in the intertidal habitats the length-at-age relationship was linear. The relationships were similar between habitats for a given species. This is reflected in the present findings that individual growth parameters were not biologically significantly different, that the two growth curves appeared similar (Figs. 6.2, 6.4, 6.6 and 6.8), and that the maximum sizes attained by fish in both habitats were similar. Observed length-at-age for estuary mouths were marginally larger than those derived from sandy shore surf zones in all surveys, probably due to the fact that the number of samples from the estuary mouths were larger than those from sandy shore surf zones. However, this finding is probably confounded by the significantly older median age of fish from estuary mouths which would also have contributed to the observed differences in the length frequency distribution. There is no readily apparent biological explanation for the marginally bigger length-at-age relationship in estuary mouths as compared with sandy shore surf zones. Variable growth rates and stunted growth of some recruits is a possible explanation, however the advantage of higher food accessibility in estuary mouths than sandy shore surf zones can not be eliminated, especially in terms of energy uptake and assimilation. Additional studies are needed to resolved this issue.

Bailey and Houde (1989) suggested that under a constant rate of mortality, a small change in growth rate as observed in the present study may lead to large differences in size-frequency distribution patterns, because it changes the time needed to reach a certain stage. Detailed knowledge about growth is therefore essential for a better understanding of the generation of year-class strength. Recently, Francis (1996) has suggested that in terms of comparing the mean growth of the two species or populations, either a comparison of relative growth rates at each age or at each length should yield a better result than a comparison of the usual length-at-age as present in this study. These two methods may be more sensible for future studies.

In this study, no assessment was undertaken for the utilisation of other abundant fish species in both areas, therefore it is not possible to make any suggestions about inter- or intra-specific competition effects. Similarly, the available food resource was not analysed and therefore resource limitation could not be assessed either. Results from temperate studies have indicated that the changes between years in growth rate and length can not be solely ascribed to variations in the abundance of total juveniles in the area. If density was to be a major factor in regulating growth rate with respect to length then a negative interaction between population density and growth rate should be evident. This is an area of research which could be examined in much more detail.

Growth of individuals and populations of fish are directly or indirectly affected by environmental conditions such as availability of food, potential for predation and intensity of competitionr for foods. Similar growth rates of fish between sandy shore surf zones and estuary mouths observed in the present study may be attributed to several factors, including carrying capacity of the habitats, and juvenile abundance, which provide similar growth conditions among habitats. There is little data in the literature for comparisons between habitats, and it is outside the scope of this study to relate this to population effects or food availability. Rosenberg (1981) found size-at-age data was much higher for fish sampled in estuaries as compared with the open coastal area, but the mean growth rates for fish from the two areas were similar. He suggested that physical factors in both habitats may affect growth variability. In the present study, the reasons for this are unclear and there are several possible explanations including: 1) high variability between individuals, 2) individual movement between habitats, and 3) broad diet overlap.

To undertake a study on the growth of individuals within or between populations, it would be necessary to tag individual fish. It is accepted that the tagging process may have an effect on growth rate. The extent of the effect of tags on growth has not been quantified for early juveniles. However, an appropriately small tag may need to be designed for small juveniles to reduce the potential problem of drag or increased fish visibility.

A hypothesis arising from this study is that survival, not growth, is enhanced in both "presumed" nursery habitats. Testing of these hypothesis will be an important step in understanding the role that nurseries play in the life history of many fish. Cushing (1974) and Houde (1987) agreed that mortality rates during the juvenile stage are typically very high, particularly because of heavy predation. An estimation of predation pressure on juvenile fish in the field is difficult, but laboratory results have shown that size and condition are important to successfully escaping predation (Bailey and Houde, 1989).

Chambers and Leggett (1987) have suggested that the generalisation of length-at-age is conditionally limited. The estimate of juvenile growth in the present study only provides an average rate of growth over their life span, so that its use in comparative studies is limited by the subjective nature of connecting corresponding length modes. With the development of accurate growth models and growth histories, a detailed chronological record of events in individual fish and populations can be compared by region and season along with various environmental factors that may affect growth and hence survival in the early larval stages (Campana, 1984; Jones, 1986).

The major findings of the present study indicate that growth rates of tropical intertidal fishes are not influenced in predictable ways by environmental conditions and resources used during their residence in sandy shore surf zones or estuary mouths. Habitat differences may account for the somewhat lower growth rates in sandy shore surf zones and may be the result of less food intake and relatively higher environmental turbulence. The growth analysis based on length-at-age failed to yield convincing evidence for a habitat effect. The hypothesis that the growth of juveniles is especially promoted in estuary mouths was not unconditionally supported in the present study because similar growth rates were detected in both habitats. In order to gain a greater understanding of tropical intertidal fishes, more attention must be paid to the effects of natural variation in growth, and possibly survivorship. This requires an increased emphasis on natural experimentation which can measure such variations.

CHAPTER 7

GENERAL DISCUSSION

Both sandy shore surf zones and estuary mouths in North Queensland form a continuum of areas they are generally characterised by particular physical conditions such as relatively large median grain size, high proportions of sand, relatively low silt and clay levels, and low amounts of organic matter in sandy shore surf zones and vice versa for estuary mouths (Chapter 2). Sandy shore surf zones are rather exposed habitats and experience more extreme physical disturbance of the bottom sediment through tidal and wind-induced waves and currents, than experienced by estuary mouths. Although, tidal and wind-induced waves and currents may strongly influence both habitats at various times. In estuary mouths, salinity levels may be slightly lower than sandy shore surf zones in the wet season but they are more stable in sandy shore surf zones. Conversely, wind may have a greater effect on physical conditions in sandy shore surf zones than in estuary mouths, with increasing turbulence and wave action and swell during the summer season. These differences justify a discussion of the relationships between habitat structure and early life history biology of living organisms in terms of processes occurring within these presumed nursery habitats.

The idea of a 'nursery area' for juvenile fish is one of the most persistent in the fisheries literature. Numerous research reports have focussed on 'juvenile nursery areas' (Harden-Jones, 1968; Boehlert and Mundy, 1988; Miller, 1988; Cushing, 1990; Lafontaine, 1992). It is claimed that such areas provide optimal conditions, in terms of food and shelter, for the growth of juveniles. These areas are mainly located in nearshore waters (Bennett, 1989). North Sea estuarine habitats and tidal flats, and their roles as juvenile nursery areas for plaice *Pleuronectes platessa* L., have been well-documented (Zijlstra, 1988; Nash *et al.*, 1994). In tropical zones, nursery areas have included seagrass beds (Bell *et al.*, 1988), mangroves (Robertson and Duke, 1987) and sandy shore surf zones (Ross *et al.*, 1987). In most cases, researchers have suggested that sites classified as nursery areas may combine the functions of providing food and/or refuge from strong predation. Whether the environment in such habitats is advantageous for juveniles or whether it differs in respect to other nearby habitats, however, remains largely unknown. Furthermore, in order to understand the "nursery function" better, it is necessary to understand the underlying biological processes first.

This study represents the first attempt to make direct comparisons between two presumed nursery areas in the tropics, namely sandy shore surf zones and estuary mouths. Both areas are unvegetated intertidal habitats. The study also examines the criteria used to determine relative nursery value.

Abundance and Fish Assemblages

A considerable number of publications have used abundance of juvenile fish as an indicator of nursery habitat (see also Chapter 1). As might be expected from the habitat structure of sandy shore surf zones and estuary mouths and available literature, greater juvenile fish densities should be found in estuary mouths than in sandy shore surf zones. In the present investigation, however, similar total abundance and biomass of fish in sandy shore surf zones and estuary mouths were evident (Table 3.3, Figs. 3.2b and 3.2c). Similar results were evident at both habitats, with no significant differences in abundance or biomass for the species *Stolephorus nelsoni*, *Silllago analis, Leiognathus splendens* in both habitats. A major exception to this trend was *Valamugil seheli*, which showed a significantly higher biomass in estuary mouths than in sandy shore surf zones. In the present study, investigations have also shown that suboptimal feeding conditions existed in sandy shore surf zones. This factor may be important in determining feeding capacity/ accessibility , and the level of abundance in these two habitats. Similar juvenile fish densities between sandy shore surf zones and estuary mouths are not likely to be due to fish activity in searching for food during high tide in the coastal shallow habitats, except for *Valamugil seheli.* Blaber (1987) has suggested that migrations to coastal habitats and a change in feeding ecology are the dominant factors in the life history of *Valamugil seheli.* Several researchers have suggested that the energy value of benthos and bottom detritus in estuaries is higher than zooplankton (Kennish, 1990). It is probable that the large biomass of juvenile *V. seheli* collected in estuary mouths (Table 3.3, Figs. 3.3 and 3.4) is permitted only by the large energy resource contained in the substratum. In this case, it is evident that a higher biomass of mullet in estuary mouths depends upon sequential changes in diet from plankton to benthos and bottom detritus.

Taken alone, fish abundances over time and space were not found to be a good predictor of habitat quality in this study because they only provide an opportunity to identify production limiting periods and some mechanism of population regulation. The presence or absence of juveniles in a particular habitat is not necessarily evidence of preference or suitability because it also depends on the availability of preceding stages. In fact, absolute abundance of juveniles is a function of the size of oceanographic features associated with the spawning event and the early larval distribution areas. There were several processes affecting abundance during this relatively short period of occupation in the presumed nursery ground. Larval supply and mortality pressure both relate to exposure and habitat structure and are significant factors controlling juvenile fish density (Doherty, 1981). The mechanisms of regulation of juveniles in coastal habitats, like those examined in the present study, are still not known in any great detail. Van Horne (1983) has suggested that without a knowledge of local population demography and biology, the assumption that abundance is directly related with habitat suitability is unwarranted. Hobbs and Hanley (1990) have also stated that the presence of organisms quoted in numbers alone are not always a good indicator of habitat quality. They proposed that habitat quality evaluation should be based on underlying relationships between individuals in addition to resource utilisation and population dynamics. The present study suggests that experimental work is still needed to evaluate the importance of physical and biological factors influencing survival and absolute recruitment abundance during the juvenile period in these two presumed nursery habitats. At this stage, laboratory and field research may be useful in determining preferences and the range extension of juveniles in both habitats. A relative abundance index should be developed, as opposed to an absolute measure of population abundance, which is a function of appropriate sampling and of the extent of knowledge of life history of the target species in the whole suspected geographical range of the presumed nursery habitats.

Seasonal Patterns

Recruitment timing, size distribution, and relative abundance of selected species appears to be similar between sandy shore surf zones and estuary mouths. New recruits peaked in summer, from September till March each year. Nevertheless, the temporal patterns of utilisation of these two coastal habitats seem to vary little among years (Figs. 3.4a, b, c and d). These similarities possibly indicate that factors influencing these fluctuations in abundance operated over larger spatial scales. Recruitment patterns like this in temperate zones might be triggered by such physical factors as temperature and photoperiod, current, salinity, turbidity (Boehlert and Mundy, 1988; Miller, 1988), or seasonal production cycles of zooplankton and phytoplankton (Cushing, 1975 and 1990). Even though the regularity with which certain larval fishes arrive at shallow coastal habitats in the tropics is widely recognised, few studies have examined the exact cause.

Seasonal fluctuations in abundance of recruitment among years have been linked to spawner stocks (Myers and Barrowman, 1996) and hydrographic events (Lasker, 1981). Although patterns of coastal water-mass changes outside of estuaries may have affected recruitment patterns elsewhere, this process is probably not useful in explaining the variability observed in estuary mouths in the present study. Estuaries in the present study had no regular input from freshwater runoff, due to drought and weir construction in the main river, which led to low water mass changes. High variability in mortality which is typical of early life history stages of fish could also contribute to the highly irregular abundance patterns in the present study.

Fish Assemblages

Sandy shore surf zones and estuary mouths have more than half of their species assemblages in common (Chapters 3 & 4). The number of species caught in sandy shore surf zones was considerably higher than estuary mouths in summer, while a similar number of species occurred in winter. This pattern is similar to other studies (Warburton, 1978; Quinn, 1980). Blaber *et al.* (1995) suggested that shallow inshore areas, including sandy shore surf zones, were not primarily or solely a transition zone between offshore and estuaries, But these inshore areas do support some fish that move between offshore, inshore and estuarine communities. Differences in the number of species in the present study can probably be accounted for by recruitment events, abundance cycles, inshore-offshore movement and mortality of individual species in both sandy shore surf zones and estuary mouths. This suggests that assemblage patterns in sandy shore surf zones and estuary mouths are very complex, dynamic and variable, and as a consequence of seasonal pattern, are not clearly defined (Figs. 4.2 and 4.3). In the current study, the differences between sandy shore surf zone and estuary mouth habitats are clearly influenced by the population dynamics of the numerically abundant species (Tables 4.1 and 4.2). In particular, the seasonal occurrence of waves and storms in summer and relative calm in winter is a general phenomenon found in tropical North Queensland, may be an important factor in determining seasonal changes in juvenile species-associated patterns in the environment.

Feeding and Growth

Many environmental factors are assumed to be responsible for the distribution of fish populations (Blaber and Blaber, 1980; Horne and Campana, 1989). These often include shallow inshore areas possessing an invertebrate faunal assemblage which provides suitable food items. Within these areas, depth has been identified as one of several important factors which determine the distribution of inshore fishes such as *Sillago analis* (Weng, 1986), and mullets, including *Valamugil* spp. (Blaber, 1987). Substratum type and availability of prey are also important. Harpacticoid and cyclopoid copepods, crabs, *Acetes sibogae*, polychaetes, bivalves and nematodes appear to be the most common prey items consumed by the selected species in the present study (Fig. 5.2, 5.3, 5.4). These organisms exist in the benthic faunas of the soft substrata of sandy shore surf zones and estuary mouths. However, there is currently no quantitative data available on this benthic fauna in either habitat in North Queensland.

Feeding

Relative food availability for juvenile fishes in both habitats may be difficult to determine by simple assessment of prey abundance. In some instances, prey standing crop tends to be a misleading indicator of food abundance. The presence of prey in large numbers does not necessarily indicate high food value for such habitats because sometimes these foods are not appropriate or available for predators as far as size and selective feeding behaviours are concerned. Sometimes, physical factors can be important in determining abundance and distribution patterns of prey.

Juvenile fishes generally spend most of their time in inshore habitats where they are not highly vulnerable to visual aquatic predators (Helfman, 1993). These refuges usually offer few or no feeding opportunities. In the case of the intertidal habitats which were examined in this study, juveniles only came out from their usual refuges to feed for short periods at extra available spaces in intertidal areas during high tide (Gibson, 1993).

Comparative food selection analyses on naturally occurring sympatric species of *Stolephorus nelsoni, Sillago analis* and *Leiognathus splendens* in this present study can not directly infer the presence or absence of interspecific competition over food resources. To test quantitatively for the presence of interspecific competition between these three species, it would be necessary to experimentally manipulate the density of their food resources. However, comparative feeding habits can provide information on potential conflicts over food resources. The results in Chapter 5 indicate that these species share some food resources to a large extent. This overlap may be of no consequence to their obtaining food when the shared resources are abundant (Krebs, 1985). However, if the shared resources become unavailable or limited, these three studied species would either have to shift their feeding habits and search for new food resources, or compete for the limited resources to satisfy their dietary requirements.

Starvation is considered to be a major source of mortality in the early life history stages of fishes, acting either directly, or mediated by reducing growth rates and therefore increasing exposure to size-selective predation (Shepherd and Cushing, 1980). Thus feeding conditions and feeding success in the early life history stages of fishes is considered to be important for recruitment into their own populations. During my dietary study in 1993 and 1994, *S. nelsoni, S. analis* and *L. splendens* from estuary mouths were generally found to be more successful feeders than those caught from sandy shore surf zones (Table 5.1 and Figs. 5.1 A, C and E). There are at least 5 possibilities for this: spatial and temporal resource availability, food selection, competition, predation pressure and physical constraints. Due to limited information on tropical juvenile fish biology, however, sub-optimal feeding in sandy shore surf zones in the present study is possibly related to the above alternatives and habitat, as found in other studies (Taki *et al.*, 1990; Morioka *et al*, 1993). The question is, what is the factor likely to determine sub-optimal feeding in sandy shore surf zones? This is probably one of the interesting questions for further study, particularly with all of the above possibilities being readily testable.

The use of refuge areas in intertidal habitats or elsewhere in 'presumed nursery grounds' implies very little about food availability to juveniles in such potential feeding habitats (Van Horne, 1983; Hobbs and Hanley, 1990; Walters and Juanes, 1993). By moving further, searching for new habitats or spending more time moving, predation risk is probably increased. These pressures lead to feeding patterns which minimise the risk of handling and hunting times (Lima and Dill, 1990). Several researchers have claimed that predators are relatively rare in the presumed nursery habitats of sandy shore surf zones and estuarine systems. This is probably due to relatively few studies having quantitatively examined the extent of predation in different habitats, with most reports of differences between areas being only qualitative. Why are there low numbers of predators in both habitats? Blaber and Blaber (1980) and Cyrus and Blaber (1987) have suggested that turbid conditions reduce the effectiveness of large predators, thereby reducing predation on juvenile fishes in estuaries. But, this does not mean that predators are absent. Qualitative evidence for fish predation on juveniles exists, but the impact of these interactions on recruitment variability remains speculative and not adequately estimated (Bailey and Houde, 1989). Robertson and Blaber (1992) reported several potential predators in mangrove estuaries, such as *Lates calcarifer, Lutjanus* *argentimaculatus, Caranx sexfasciatus,* and *Eleuteronema tetradactylum.* It has also been assumed, without a great deal of firm evidence, that predation is greater on open coasts like sandy shore surf zones, as opposed to shallow bays and estuaries, because open coasts are more likely to have a greater range in the size and species of predators (Toole, 1980). A recent study by Gibson and Robb (1996) on sandy beach habitats of Scotland, found several known and potential predators of juvenile fishes. In addition, in the early stage of my diet study, I examined approximately 10 specimens of *Caranx bucculentus* caught from sandy shore surf zones and found several juveniles of *Stolephorus* spp. in their stomachs.

Overall, there is no clear answer about predation on juveniles of the selected species in both sandy shore surf zones and estuary mouths. It is possible that many potential predators may be not caught during certain times and that major predators of juvenile fishes may vary spatially and temporally. The need for further study to confirm predatory risk in sandy shore surf zones and estuary mouths in the tropics is evident, and could be accomplished by using a simple stomach content analysis to determine predators and potential predators. There is, however, a major problem in predator investigation in that the recognition and identification of partly digested prey is often difficult.

Most literature suggests that shallow coastal habitats are utilised by juvenile fishes because of an abundance of food supply. In fact, enhanced food abundance does not necessary lead to increased fish growth and survival. Abundance and food quality, as well as time available for foraging, determines the actual yield of fish from a particular habitat. Therefore, food rations for a fish in intertidal habitats could in fact be associated with food availability and quality, space utilisation and access time to prey in potential feeding areas within the different habitats (Walters and Juanes, 1993). Foraging efficiency could decrease in these habitats because abundant conspecifics may interfere with foraging. Encounters with a predator in these habitats can cause fishes to run away from rich feeding patches for less profitable ones, thus accepting a lower rate of food intake in the interests of reduced predation risk. Clearly, this needs to be considered along with the response of fish to heterogeneity in food distribution in their habitats. The hypothesis that juveniles inhabit these presumed coastal nursery habitats to receive a trophic advantage and grow faster needs to be further tested.

The present study postulates that intertidal turbulence results in a physically stressful environment in sandy shore surf zones and acts as a major structuring force influencing feeding habits of fishes in the habitat. For example, the findings indicate a lower number of prey items eaten by *Sillago analis*, but of relatively large size. These larger prey items were apparently consumed while ignoring opportunities to feed on small benthic crustaceans or polychaetes. The availability of these latter invertebrates is indicated to some extent by the dietary composition of other the species present in such habitats. These results suggest that *S. analis* may balance foraging profitability with turbulence risk and select the most profitable prey items. Mittlebach (1981) has suggested that size-specific trade-offs between foraging profitability and predation risk is likely to be a common phenomenon among many groups of organisms. Thus, this rule may be applicable in sandy shore surf zones where turbulence may influence foraging patterns along with predation pressure.

In most fishes, changes in diet can have effects on growth (Wootton, 1992). In general, there was an ontogenetic increase in the diversity of prey items consumed and prey size, and probably a change in biochemical characteristics for fishes, in the present study. At least two possibilities are used to explain these changes: progressive anatomical development with age and reducing intraspecific competition between juveniles and adults. In these selected species, Gunn and Milward (1985) demonstrated changes in anatomical structure, especially pharyngeal teeth, with standard length for *Sillago analis* and Hoedt (1984) also showed development and specialisation of gill rakers which are a part of feeding apparatus in *Stolephorus nelsoni*, while there was no study available for *Leiognathus splendens*. It is difficult to verify if competition may act as a mechanism for ontogenetic shifts in food selection. Controlled field experiments are probably the only way to examine the impact of competition. Several researchers (as reviewed in Krebs, 1989) have suggested niche widths and overlap values can also be used to assess competition or indicate the potential competition relating to habitats and the diversity of prey.

Growth Rate

De Lafontaine (1992) has reviewed fisheries research over the past two decades and has demonstrated a shift in the concept of recruitment studies in marine species from precision in estimating mortality rate, to precision in estimating growth rate. This shift has occurred because: 1) growth rate is more feasible to measure and variations easier to detect than mortality rate (Houde, 1987), and 2) growth rate is unique to each individual and does not covary with serial growth rate in each developmental stage. The growth-dependent mortality rate hypothesis "bigger is better" (Shepherd and Cushing, 1980) has indicated that growth rates probably influence survival and they may also affect other life history traits which contribute to reproductive success.

De Lafontaine (1992) also suggested that climatic changes, ecological dynamics of marine systems, survival rates, and physiological conditions may be examined by measuring juvenile fish growth. Moreover, growth and mortality during the juvenile phase are modulated by habitat, food availability, genetics, predation and competition as well as by the carrying capacity of habitats and length of growing season (Conover, 1990).

Growth-related changes in diet have been reported for many species of fish (Gibson and Ezzi, 1987). Karakiri *et al.* (1989) have suggested that the main factors which appear to support significant differences in the growth rate of plaice *Pleuronectes platessa* from the Wadden Sea were food availability, by means of density-dependent growth (Zijlstra *et al.*, 1982), and competition with shore crabs (Berghahn, 1987). Karakiri *et al.* (1989) also found that plaice of the same age caught outside the area presumed to be a nursery in the Wadden Sea were smaller than those inside the nursery. This finding indicates a tendency to use growth information as an indicator of nursery ground quality. High initial growth rates for juveniles in the habitat indicates that such habitats were satisfactory. Food limitations and possible physiological stress associated with habitats may all be important sources of information when explaining growth variability.

The results from age-length studies therefore represent an approximate estimate of growth. However, it still provides a good measurement of habitat quality. Directly assessing a parameter of key importance in early life history may reflect many important factors eg. food availability, predation and indirect mortality. The present study suggests there were similar growth rates for juveniles of selected species between sandy shore surf zones and estuary mouths. However, the exact nature of the similar growth rate between sandy shore surf zones and estuary mouths remains unknown. Exploring the mechanisms and measuring growth rates of individual juveniles over time in each habitat would lead to definitive conclusion with regard to habitat-dependent growth rates, and an unequivocal distinction between the effects of growth versus differential survival of different size classes in sandy shore surf zones and estuary mouth habitats. The results of this present study are quite similar to Nash *et al.* (1994) in that both use length-at-age to evaluate growth between habitats. Nash *et al.* (1994) also used tags to follow the growth of individual juvenile plaice *Pleuronectes platessa* in the nursery ground of the Irish sea, and they found that at the individual level, growth rate tended to be highest when conditions in the nursery ground were optimal whereas at the population level it did not appear to be a simple relationship. The reasons for this are unclear. Population structure and density may be major factors in determining this. It seems likely that prolonged immigration of juveniles to the habitat and emigration of larger fish from the habitat may increase variation in growth estimation. Movement of fishes from one habitat to another may also be present in some species and can create a considerable amount of variation in the analysis. In the present study, sandy shore surf zones and estuaries were virtually continuos habitats, interchanging of juveniles between habitats may have occurred but there is no published data to support such movement of juveniles of the study species in this region. Tagging studies for these selected species may resolve the question about movement patterns and interchange between the two habitats but there were no tagging studies available for these juveniles smaller than 5 cm, possibly due to weakness and relatively small size of the juveniles. Morton (1985) used tags to assess movement patterns for one species congeneric to one within the present study, summer whiting *Sillago ciliata*, over a size range of 14-28 cm FL in Moreton Bay. He found that the average movement of summer whiting was only 3.5 km, which is less than the distance between sandy shore surf zones and estuary mouth habitats in the present study.

The assumption of "bigger is better" may not be universally applicable and will depend on the size structure of the studied fish and all potential predators. In the present study, this hypothesis could not be applied, as there were no significantly different growth rates between populations in both sandy shore surf zones and estuary mouths. No clear answer was found as to why this was the case. One possibility is that the "bigger is better" hypothesis should have some size limitation for early life history stages of fish. Recently, the general acceptance of the "bigger is better" hypothesis for early life history of flatfish has been questioned (Leggett and Deblois, 1994). They found that the smaller individuals of a cohort may not always be the most vulnerable to certain predators. Larger individuals may have a higher probability of encounter due to a larger size and greater movement, and may be selectively pursued, which could result in size selection. In general, the size of predators and size of prey are positively correlated. The smaller fish would be vulnerable to a wider variety and greater size range of fish predators (Chambers and Leggett, 1992). Since Gibson and Robb (1996) demonstrated there were alot of predators in sandy shore surf zones in Scotland, the question about predation pressures in both presumed nursery grounds, sandy shore surf zones and estuary mouths, should be re-examined, especially in the relatively higher diversity community of the tropics. This may give a clear answer about the availability of predators and predation pressures in nursery ground.

What is the carrying capacity of the habitat?

There is an ecological truth that a given habitat will have a certain carrying capacity for a particular species (Krebs, 1985). Some juveniles may be unable to establish feeding territories and colonisation because conspecifics have already occupied all available space, therefore late arrivals may need to migrate to other habitats, as in the case of the American lobster nursery (Wahle and Steneck, 1991). There is currenlty no information available on carrying capacity and nursery function for juvenile fishes in tropical coastal habitats. Further study on carrying capacity assessment of presumed nursery habitats seems warranted before we can recognise real nursery habitats.

Identifying and characterising the primary needs of juveniles to facilitate growth and avoidance from predation should be a basic inclusion with juvenile abundance surveys. For example, availability of food, shelter from predators, presence and/ or density of conspecifics, depth, light, temperature, habitat accessibility and retention mechanisms should be included. Laboratory experiments examining juvenile preferences and tolerances among the range of conditions found in the juvenile distribution may be useful to support field investigations, to provide a better understanding of what constitutes a good nursery habitat.

Relative nursery values of estuary mouths and sandy shore surf zones

In this study no significant difference was detected in the abundance of juvenile fishes between sandy shore surf zones and estuary mouths. Sandy shore surf zones and estuary mouths tended to function as habitat for similar sizes of selected species, while relatively lower stomach content volumes and similar growth rates were apparent in sandy shore surf zones when compared to estuary mouths. Food accessibility as revealed by gut content analysis may help explain differences, but their utility is limited due to the high variability of diets in sandy shore surf zones and estuary mouths.

Of the four selected species examined, there were no differences detected in the number of individuals between sandy shore surf zones and estuary mouths. Of the two habitats, estuary mouths appear to have a relatively higher nursery value for the selected species examined due to feeding accessibility. However, the relative value of nursery habitats on growth in the tropics is probably both species and age specific. Abundance is a poor predictor of nursery value while growth appears to be the best parameter for accessing nursery value. Abundance may reflect the magnitude of the effect but it can not indicate relative value.

Sale (1978) suggested that if living space on intertidal and shallow areas does become available throughout the year, and is obtained by whichever individuals, these inshore habitats may provide a continuous supply for recruits and play a significant role in structuring fish assemblages in adjacent areas. This present study has demonstrated the potential usefulness of food accessibility and growth for assessing the value of sandy shore surf zones and estuary mouths as nursery habitats; however, this requires certain qualifications. Since mean growth rates of populations in each habitat may be age and cohort specific, following the same cohort for age and length is necessary to eliminate these known sources of variation. Using the information gathered in the present study, it is concluded that utilisation of these two habitats may improve the chances of survival for juvenile fishes.

Implications and Further Research

Quantitative data which describes a nursery ground for tropical inshore fishes is lacking. There is also no information to indicate which of many different environmental factors are the most important in the larval and juvenile periods of these fishes.

The present study differs from most recent studies by breaking down nursery values into four formal empirical components: abundance, persistence, feeding success, and growth rates at the species level. The approach used in this study has been shown to be useful for making comparisons between habitats, which is the ideal method for habitat quality determination (Gibson, 1994). Conclusions reached in a study such as this, however, should not be adopted as general principles, with disregard for experimental designs and geographical limitations. Nevertheless, these findings may serve as a tool for improving knowledge, and provide a greater understanding of juvenile fish biology through techniques for identification of juvenile habitats and quantification of juvenile abundance in order to assess the relative importance of different habitats for juveniles.

Establishing nursery ground criteria in tropical zones is relatively difficult due to restricted knowledge of the life history and basic needs of target species, as compared to equivalent habitats in temperate zones. Several criteria that have been used for fish nursery grounds in the North Sea, especially flatfishes, including optimal food availability and conditions, predation pressure, habitat structure, and environmental factors such as temperature, salinity, oxygen, hydrodynamic factors and water depth, may not be applicable to the tropics. Most conclusions suggest that a combination of food availability and density-dependent effects are the most likely explanation for variations in growth for most flatfishes (Gibson, 1994).

The findings of this study provide valuable insights into the juvenile biology of tropical intertidal fishes. The dependence of fish on habitat quality and functional attributes of intertidal habitats appears to be complex, with far-reaching effects. This study has provided a new perspective for nursery determination in the tropics, in terms of a comparative study of nursery functions. More importantly, the results will provide a way of critically evaluating the relative importance of habitats as nursery areas. Preferred habitats for juveniles must be defined in terms of abiotic or biotic factors so that they can be protected or replaced under management policy. Management decisions may therefore be made on a sound scientific basis rather than the traditional belief that inshore habitats act as nursery grounds. Nevertheless further studies of nursery function in the tropics are necessary . What factors really determine temporal and spatial abundance for most of juveniles in both sandy shore surf zones and estuaries? What is the real benefit for juveniles to stay in both sandy shore surf zones and estuary mouths? Are predators relatively rare in both habitats in the tropics? What are the mechanisms that determine if some part of a population remains in areas that have sub-optimal feeding (e.g. sandy shore surf zones)? What factors control growth for juvenile fishes in sandy shore surf zones and estuary mouths? What is the relationship between growth rate and juvenile densities in each habitat?

Appendix 1: Means square estimates and F-ratios for four factor ANOVA. Degree of freedom and Type III Expected Mean Square were obtained from SAS Institue Inc. (1989).

SOURCE	*df*	Type III Expected Mean Square	*F*-value
YEAR :Y	2	$s^2+ 6s^2_{T(Y\bullet S)}+s^2_Y$	Y / T
SEASON:S	1	$s^2+ 6s^2_{T(Y\bullet S)}+s^2_S$	S / T
Y*S	2	$s^2+ 6s^2_{T(Y\bullet S)}+s^2_{Y\bullet S}$	Y * S / T
HABITATS : H	1	$s^2+ 18s^2_{T\bullet H}+s^2_H$	H / T * H
Y*H	2	$s^2+s^2_{Y\bullet H}$	Y * H / s^2
S*H	1	$s^2+s^2_{S\bullet H}$	S * H / s^2
Y*S*H	2	$s^2 +s^2_{Y\bullet S\bullet H}$	Y * S * H / s^2
TRIPS (Y*S): T	10	$s^2+6s^2_{T(Y\bullet S)}$	
T*H	2	$s^2+ 18s^2_{T\bullet H}$	

Appendix 2. The species composition of intertidal fishes in catches from intertidal sandy shore surf zones and estuary mouths, of North Queensland. Taxonomical arrangement followed Nelson (1994) . (Life history: J= Juveniles, A= Adult)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Elopidae							
Elops hawaiensis Regan, 1909	1	0	1	10.90	0	10.90	J
Family Megalopidae							
Megalops cyprinoides (Broussonet, 1782)	1	1	0	1200.00	1200.00	0	J
Family Ophichthidae							
Pisodonophis boro (Hamilton-Buchanan, 1822)	5	4	1	33.15	24.75	8.40	J
Family Engraulidae							
Encrasicholina devisi (Whitley, 1940)	1766	1766	0	1134.09	1134.09	0	J
Stolephorus carpenteriae (De Vis, 1882)	2319	1498	821	2323.84	1809.72	514.12	J
Stolephorus commersonii Lacépède, 1803	1390	1291	99	3127.15	2713.11	414.04	J
Stolephorus insularis Hardenberg, 1933	2831	2711	120	747.31	690.31	57.00	J
Stolephorus nelsoni Wongratana, 1987	15208	12078	3130	12027.22	10066.57	1960.66	J
Thryssa hamiltoni (Gray, 1835)	1291	1256	35	2988.17	2739.56	248.61	J
Thryssa setirostris (Broussonet, 1782)	381	358	23	156.30	148.80	7.50	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Chirocentridae							
Chirocentrus dorab (Forsskål, 1775)	2	2	0	102.50	102.50	0	J
Family Clupeidae							
Anodontostoma chacunda (Hamilton-Buchanan, 1822)	7	2	5	25.10	13.00	12.10	J
Escualosa thoracata (Valenciennes, 1847)	14909	12926	1983	3200.23	2941.13	259.20	J
Herklotsichthys castelnaui (Ogilby, 1897)	38	12	26	233.49	104.49	129.00	J
Herklotsichthys koningsbergeri (Weber & de Beaufort, 1912)	106	39	67	519.34	296.44	222.9	J
Nematalosa come (Richardson, 1846)	441	34	407	1212.61	865.77	346.84	J
Dussumieria elopsoides Bleeker, 1849	2	2	0	3.50	3.50	0	J
Pellona ditchela (Valenciennes, 1847)	28	27	1	62.45	60.35	2.10	J
Sardinella brachysoma (Bleeker, 1852)	653	594	59	1098.21	630.28	467.93	J
Sardinella gibbosa (Bleeker, 1849)	49560	44086	5474	26287.63	18409.51	7878.12	J
Spratelloides gracilis (Schlegel, 1846)	11	11	0	1.80	1.80	0	J
Family Synodontidae							
Saurida micropectoralis Shindo & Yamada, 1972	2	2	0	5.00	5.00	0	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Mugilidae							
Liza tade (Forsskål, 1775)	14	1	13	99.20	2.50	96.70	J
Liza melinoptera (Valenciennes, 1836)	3	0	3	6.90	0	6.90	J
Liza subviridis (Valenciennes, 1836)	1072	731	341	4478.09	799.02	3679.07	J
Liza vaigensis (Quoy & Gaimard, 1824)	1657	282	1375	7179.61	2330.14	4849.47	J
Mugil cephalus Linnaeus, 1758	2	0	2	9.20	0	9.20	J
Rhinomugil nasutus (De Vis, 1883)	1	1	0	0.90	0.90	0	J
Valamugil buchanani (Bleeker, 1853)	313	4	309	699.70	152.80	546.90	J
Valamugil cunnesius (Valenciennes, 1836)	90	4	86	1308.60	6.90	1301.70	J
Valamugil engeli (Bleeker, 1858)	11	9	2	555.40	112.80	442.60	J
Valamugil seheli (Forsskål, 1775)	12035	4893	7142	16765.07	1641.47	15123.60	J
Valamugil speigleri (Bleeker, 1858)	154	34	120	592.35	200.25	392.10	J, A
Family Pseudomugilidae							
Psedomugil gertrudae Weber, 1911	7	0	7	0.95	0	0.95	J
Family Atherinidae							
Atherinomorus endrachtensis (Quoy & Gaimard, 1824)	5119	75	5044	4488.56	68.08	4420.45	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Belonidae							
Strongylura leiura (Bleeker, 1851)	204	93	111	3273.07	1285.89	1987.18	J
Tylosurus crocodilus (Péron & Le Sueur, 1821)	6	5	1	36.90	32.50	4.40	J
Family Hemirhamphidae							
Arrhamphus sclerolepis Günther, 1866	3090	614	2476	20424.11	8642.76	11781.35	J
Hyporhamphus quoyi (Valenciennes, 1847)	1838	648	1190	7547.34	3059.70	4487.64	J
Rhynchorhamphus georgii (Valenciennes, 1847)	1131	500	811	4810.13	3622.2	1187.93	J
Zenarchopterus buffonis (Valenciennes, 1847)	14	4	10	5.85	1.00	4.85	J
Family Syngnathidae							
?*Hippichthys spicifer* Rüppell, 1838	4	2	2	0.30	0.20	0.10	J
Family Dactylopteridae							
Dactyloptena orientalis (Cuvier, 1829)	23	22	1	1.35	1.30	0.05	J
Family Scorpaenidae							
Minous versicolor Ogilby, 1910	4	1	3	0.22	0.10	0.12	J
Family Platycephalidae							
Platycephalus endrachtensis Quoy & Gaimard, 1825	10	4	6	948.05	739.70	208.35	J
Platycephalus fuscus Cuvier, 1829	84	71	14	4197.89	2305.74	1892.15	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Centropomidae							
Lates calcarifer (Bloch, 1790)	4	4	0	2475.00	2475.00	0	J
Family Chandidae							
Ambassis nalua (Hamilton-Buchanan, 1822)	209	82	127	706.70	364.85	341.85	J, A
Ambassis vachellii Richardson, 1846	6193	1522	4671	6299.39	1923.62	4375.78	J
Family Sillaginidae							
Sillago analis Whitley, 1943	3028	1434	1594	16935.53	9726.17	7209.36	J, A
Sillago ciliata Cuvier, 1829	97	16	81	383.21	31.20	352.01	J
Sillago sihama (Forsskål, 1775)	1708	1299	409	4478.18	3260.73	1217.45	J
Family Lactariidae							
Lactarius lactarius (Bloch & Schneider, 1801)	196	196	0	1555.20	1555.20	0	J
Family Carangidae							
Caranx bucculentus Alleyne & Macleay, 1877	13	13	0	51.10	51.10	0	J
Carangoides hedlandensis (Whitley, 1934)	43	36	7	2676.45	2425.30	251.15	J
Caranx papuensis Alleyne & Macleay, 1877	1	0	1	96.10	0	96.10	J
Caranx para Cuvier, 1833	236	236	0	1169.90	1169.90	0	J
Megalaspis cordyla (Linnaeus, 1758)	1	1	0	31.10	31.10	0	J
Scomberoides commersonnianus Lacépède, 1801	90	30	60	707.16	271.04	436.12	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Carangidae							
Scomberoides lysan (Forsskål, 1775)	2	2	0	17.00	17.00	0	J
Scomberoides tala (Cuvier, 1832)	9	7	2	41.85	29.85	0	J
Scomberoides tol (Cuvier, 1832)	347	213	134	1633.14	1092.78	540.36	J
Trachinotus bailloni (Lacépède, 1801)	11	11	0	342.60	342.60	0	J
Trachinotus blochii (Lacépède, 1801)	5214	5205	9	5609.4	5300.5	308.94	J, A
Trachinotus botla (Shaw, 1803)	3	3	0	10.2	10.2	0	J
Family Leiognathidae							
Gazza minuta (Bloch, 1797)	863	824	39	1380.28	1344.78	35.5	J
Leiognathus bindus (Valenciennes, 1835)	298	298	0	278.60	278.60	0	J
Leiognathus decorus (De Vis, 1884)	2219	2141	178	786.32	652.88	133.44	J
Leiognathus equulus (Forsskål, 1775)	135	6	129	115.73	14.80	100.93	J
Leiognathus moretoniensis Ogilby, 1912	3	2	1	7.40	5.10	2.30	J
Leiognathus splendens (Cuvier, 1829)	20563	15731	4832	5824.28	4978.44	845.84	J, A
Secutor ruconius (Hamilton-Buchanan, 1822)	1237	1164	73	592.74	560.37	32.38	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Lutjanidae							
Lutjanus argentimaculatus (Forsskål, 1775)	10	1	9	242.30	0.40	241.90	J
Lutjanus johni (Bloch, 1792)	2	2	0	1.10	1.10	0	J
Lutjanus russelli (Bleeker, 1849)	33	5	28	93.46	22.46	71.00	J
Family Lobotidae							
Lobotes surinamensis (Bloch, 1790)	1	0	1	5.10	0	5.10	J
Family Gerreidae							
Gerres filamentosus Cuvier, 1829	265	80	185	1128.57	330.68	797.89	J
Gerres oblongus Cuvier, 1830	2501	1745	756	270.00	116.35	153.65	J
Gerres oyena (Forsskål, 1775)	1604	894	710	713.15	280.38	432.77	J
Gerres poeti Cuvier, 1830	17	0	17	167.45	0	167.45	J
Family Haemulidae							
Plectorhinchus gibbosus (Lacépède, 1802)	1	1	0	44.50	44.50	0	J
Pomadasys kaakan (Cuvier, 1830)	4	4	0	2.88	2.88	0	J
Pomadasys maculatum (Bloch, 1797)	45	45	0	115.20	115.20	0	J
Family Sparidae							
Acanthopagrus berda (Forsskål, 1775)	10	0	10	80.40	0	80.40	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Polynemidae							
Eleuteronema tetradactylum (Shaw, 1804)	432	423	9	501.28	499.58	1.70	J
Polydactylus multiradiatus Günther, 1860	259	259	0	1361.80	1361.80	0	J
Family Sciaenidae							
Johnius amblycephalus (Bleeker, 1833)	12	8	4	1.70	0.55	1.15	J
Johnius vogleri (Bleeker, 1877)	1	1	0	6.30	6.30	0	J
Otolithes ruber (Schneider, 1801)	10	9	1	100.60	100.20	0.40	J
Family Mullidae							
Upeneus sulphureus Cuvier, 1829	16	16	0	60.41	60.41	0	J
Upeneus vittatus (Forsskål, 1775)	2	2	0	19.00	19.00	0	J
Family Leptobramidae							
Leptobrama mulleri Steindachner, 1878	374	345	29	4198.43	4143.89	54.54	J
Family Drepanidae							
Drepane punctata (Linnaeus, 1758)	61	58	3	1395.4	1395.1	0.3	J,A
Family Teraponidae							
Terapon puta (Cuvier,)	2174	1597	577	52.08	36.43	15.65	J
Terapon jarbua (Forsskål, 1775)	878	518	360	995.44	523.09	472.36	J
Terapon theraps (Cuvier, 1829)	35	26	9	79.66	73.67	5.99	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Cichlidae							
Orechromis mossambica (Peters, 1852)	1	0	1	0.40	0	0.40	J
Family Blennidae							
Omobranchus punctatus (Valenciennes, 1836)	8	4	4	1.52	0.72	0.80	J
Family Callionymidae							
Callionymus sp.	2	2	0	1.10	1.10	0	J
Family Eleotridae							
Butis butis (Hamilton-Buchanan, 1822)	10	1	9	27.20	3.90	23.30	J
Family Gobiidae							
Acentrogobius caninus (Cuvier & Valenciennes, 1836)	4	0	4	19.20	0	19.20	J
Istigobius nigroocellatus (Günther,1873)	4	0	4	1.40	0	1.40	J
Periopthalmus argentilineatus (Valenciennes, 1837)	1	0	1	1.20	0	1.20	J
Silhouettea evanida Larson & Miller, 1986	601	29	572	76.26	2.72	73.54	J, A
Yongeichthys nebulosus (Forsskål, 1775)	13	0	13	57.27	0	57.27	J
Family Ephippidae							
Platax teira (Forsskål, 1775)	2	0	2	12.74	0	12.74	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Scatophagidae							
Selenotoca multifasciata (Richardson, 1844)	316	274	42	256.80	27.15	229.65	J
Family Siganidae							
Siganus fuscescens (Houttuyn, 1782)	671	302	369	141.46	66.37	75.09	J
Siganus lineatus (Valenciennes, 1835)	8	5	3	14.30	7.00	7.30	J
Family Sphyraenidae							
Sphyraena jello Cuvier, 1829	62	46	16	47.00	24.10	22.90	J
Family Trichiuridae							
Trichiurus lepturus Linnaeus, 1758	6	6	0	37.00	37.00	0	J
Family Scombridae							
Scomberomorus queenslandicus Munro, 1943	299	267	32	2828.92	2796.66	32.26	J
Family Bothidae							
Pseudorhombus elevatus Ogilby, 1912	3	3	0	0.10	0.10	0	J
Family Cynoglossidae							
Paraplagusia bilineata (Bloch, 1784)	85	84	1	1179.75	1174.75	5.00	J
Family Triacanthidae							
Triacanthus biaculeatus (Bloch, 1786)	3	3	0	106.61	106.61	0	J
Trixiphichthys weberi (Chadhuri, 1910)	28	27	1	596.34	596.24	0.10	J

Appendix 2 (cont.)

TAXA	Abundance			Biomass			Life History
	Total	SSSZ	EST	Total	SSSZ	EST	
Family Monacanthidae							
Monacanthus chinensis (Cuvier, 1817)	2	2	0	0.19	0.19	0	J
Family Tetraodontidae							
Arothron manilensis (de Procé, 1822)	10	5	5	36.78	20.05	16.73	J
Arothron stellatus (Bloch & Schneider, 1801)	1	1	0	0.10	0.10	0	J
Chelonodon patoca (Hamilton-Buchanan, 1822)	453	340	113	3984.06	3650.07	333.99	J
Lagocephalus lunaris (Bloch & Schneider, 1801)	103	103	0	323.22	323.22	0	J
Lagocephalus spadiceus (Richardson, 1844)	1	1	0	131.40	131.40	0	J
Marilyna pleurostigra (Günther, 1872)	4	2	2	176.30	131.91	44.40	J
Tetractenos hamiltoni (Gray & Richardson, 1843)	17	2	15	121.06	1.56	119.50	J
Torquigener squadimaculata (Ogilby, 1911)	3	3	0	6.60	6.60	0	J
Tylerius spinosissimus (Regan, 1908)	7	1	6	5.60	0.05	5.55	J

Appendix 3.

Intertidal and Deeper Assemblage Patterns

Materials and Methods

Data Collection

Beam trawl surveys were also added to the 1994 sampling program in order to obtain data from deeper habitats. The samples were collected by using 1.5 m x 0.5 m beam trawl. Offshore sampling using a small boat at 2.0-3.0 m depth at approximately 1.5-2.0 km from the shoreline and intertidal samples hauled by hand in 0.50-0.75 m depth. The body and cod-end of the net had a mesh size of 5 mm. Two locations were samples, Pallarenda Beach and Ross River Mouth. Three random sites were sampled within each location. At each site, 3 non-overlapping five-minute trawls was undertaken. The average distance per tow was approximately 150 m. Beam trawl surveys were taken once one visit for every three months (4 per year). Sample treatments for beam trawl samples were the same as for seine catch, except that did not include biomass and length-frequency measurements (*cf.* Chapter 2).

Data Analyses

The fish assemblages in intertidal and offshore locations were assessed by means of a Correspondence Analysis. Abundance from each replicated trawl within each site was pooled and the mean was calculated, thus resulting in 16 location trip combinations.

Results

INTERTIDAL AND DEEPER ABUNDANCE

Assemblages from deep and shallow habitats

The entire beam trawl sampling program of intertidal and offshore habitats yielded a total of 49 species (Table A3.1). The catches comprise 20 species from intertidal zones with other 20 species from offshore habitats and 9 species obtained in both intertidal and offshore areas. There were significant differences in fish abundance higher total numbers of individuals in intertidal habitats (Fig. A3.1A). There were significantly more fish in intertidal than offshore areas.

Ordination by means of Correspondence Analysis based on the total abundance of all species, revealed three major assemblage groups from the two depths of both areas (Fig. A3.1B). The clearest result to emerge from Correspondence Analysis was that the similarities between intertidal and offshore samples of Pallarenda were minor compared to those from Ross River Mouth. This indicates that the contribution of species from offshore habitats of sandy shore surf zones to intertidal assemblages was minimal compared to species share between the two depths of estuarine habitats. The entire species composition of offshore samples were highly dissimilar to that from intertidal samples. Offshore population were therefore unlikely to have any significant impact on intertidal patterns.

Species	Pallarenda		Ross River Mouth		CODE	Species	Pallarenda		Ross River Mouth		CODE
	Intertidal	offshore	Intertidal	offshore			Intertidal	offshore	Intertidal	offshore	
Escualosa thoracata	5	0	51	0	C	*Lethrinus sp.*	0	1	0	0	2
Encrasicholina devisi	35	0	0	0	C	*Gerres oblongus*	2	0	2	0	C
Stolephorus carpenteriae	252	2	12	2	C	*Gerres oyena*	4	0	1	0	C
Stolephorus commersonii	3	0	1	0	C	*Leptobrama mulleri*	2	0	1	0	C
Stolephorus nelsoni	5	1	0	0	SNE	*Drepane punctata*	0	0	1	0	C
Saurida micropectoralis	0	2	0	0	2	*Neopomacentrus violascens*	0	2	0	0	2
Arrhamphus sclerolepis	39	0	28	0	C	*Liza subviridis*	6	0	72	0	C
Rhynchorhamphus georgi	82	0	8	0	C	*Rhinomugil nasutus*	0	0	1	0	C
Zenarchopterus buffonis	4	0	0	0	C	*Valamugil speigleri*	0	0	1	0	C
Strongylura leiura	4	0	0	0	C	*Sphyraena jello*	0	1	0	0	2
Atherinomorus endrachtensis	3	0	16	0	C	*Chlorodon schoenleinii*	0	1	0	0	2
Centriscus scutatus	0	1	0	0	CSC	*Halichores melanochir*	0	1	0	0	2
Platycephalus fuscus	0	1	0	0	2	*Callionymus sp.*	3	0	0	0	C
Epinephelus sexfasciatus	0	2	0	0	1	*Istigobius sp.*	0	1	0	0	2
Ambassis vachelli	1	0	1	0	C	*Silhouttea evanida*	2	0	6	1	C
Terapon puta	25	4	13	1	TPU	*Siganus fuscescense*	0	2	0	0	2
Sillago analis	2	1	14	0	C	*Paraplagusia bilineata*	3	0	0	1	C
Sillago sihama	34	1	12	0	C	*Trixiphichthys weberi*	0	1	0	0	TWE
Siphamia roseigaster	0	49	0	0	SRO	*Monacanthus chinensis*	0	2	0	0	MCH
Gnathodon speciocus	0	4	0	0	2	*Tylerius spinosissimus*	0	1	0	0	1
Scomberoides tol	1	0	2	0	C	*Arothron manillensis*	0	1	0	0	2
Leiognathus decorus	30	0	2	1	C	*Chelonodon patoca*	2	0	1	0	C
Leiognathus splendens	1	0	0	1	C	*Tetractenos hamiltoni*	0	0	1	0	C
Lutjanus russelli	0	2	0	0	1	*Torquiner piosae*	0	2	2	0	2
Pomadasys maculatum	0	0	0	1	C						

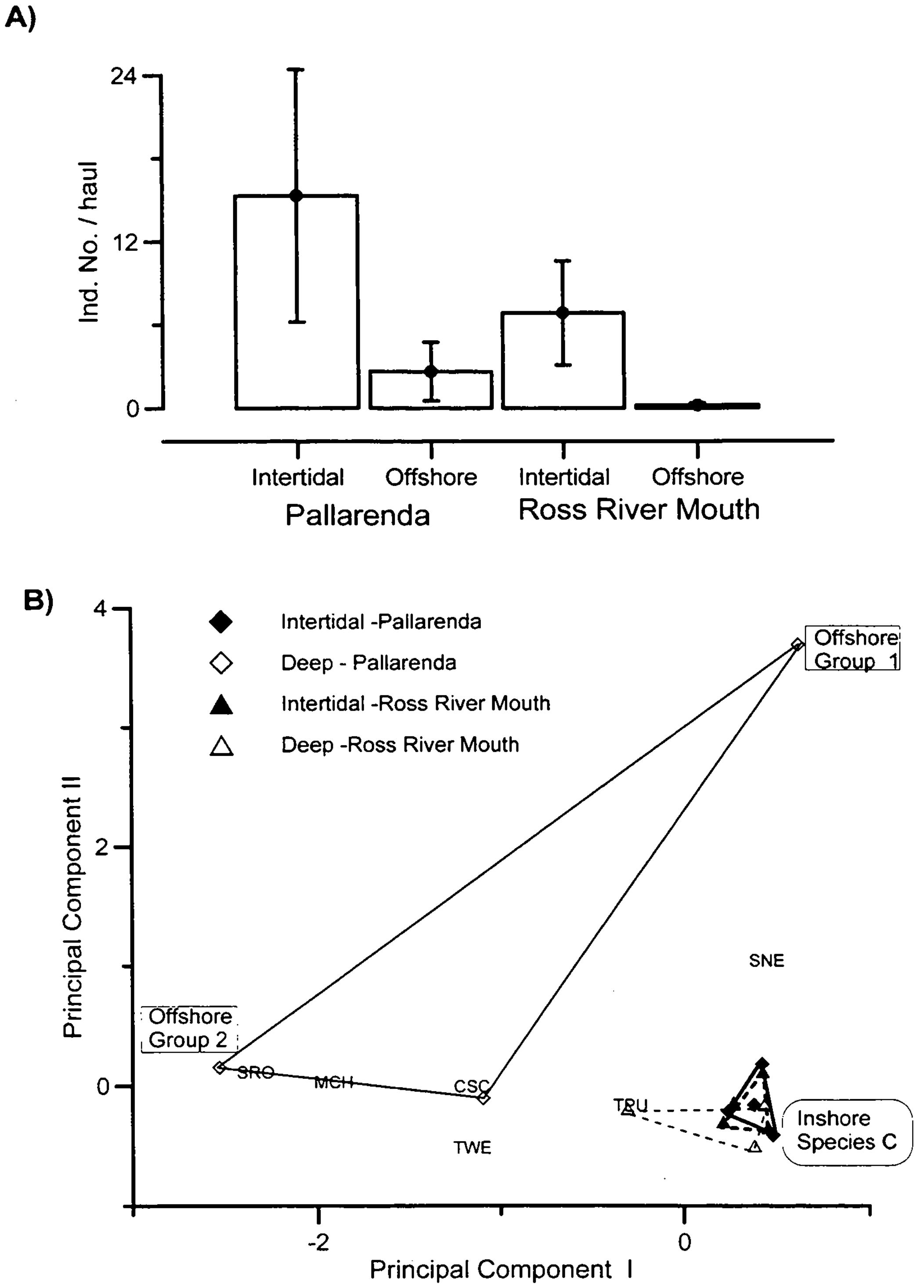


Figure A3.1

A) Mean±95% CI of number of individuals per trawl taken from intertidal and deeper areas at Pallarenda and Ross River Mouth.

B) First and second principal component axes of Correspondence Analysis based on intertidal and deeper samples from Pallarenda and Ross River Mouth. (Offshore Group1, Offshore Group 2 and Inshore species C refers to species in Table A4.1 with code 1, 2 and C respectively.

Appendix 4

The dietary data of *Stolephorus nelsoni, Sillago analis* and *Leiognathus splendens* obtained in 1994 were submitted to Principal Component Analysis by mean of variance-covariance matrix. The results of the analysis are given as following sections: Appendix 4.1 for *Stolephorus nelsoni*, Appendix 4.2 for *Sillago analis* and Appendix 4.3 for *Leiognathus splendens*.

Acronyms for diet prey groups as shown in Appendies 4.1, 4.2 and 4.3 are:

Ace = *Acetes sibogae*
Alg = Algae
Amp = Amphipods
Ane = Anemones
App = Appendicularians
Biv = Bivalves
Bry = Bryozoans
Cal = *Callinassa* sp.
Clu = Clupeid Fish
Cra = Crabs and other crabs
Cte = Ctenophores
Cyc = Cyclopoid Copepod
Fsh = Unidentified Fish
Gas = Gastropods
Gra = Grapsid Crabs
Har = Harpacticoid Copepod
Her = Hermit Crabs
Hym = Hymenosomatid Crabs
Ins = Insects
Iso = Isopods
Luc = *Lucifer* sp.
Mal = Maldanid Polychaetes
Mat = *Matuta lunaris*
Med = Medusa
Meg = Crab Megalopa
Mes = *Mesodesma eltanae*
Mic = *Mictyris platycheles*
Mug = Mugilid Fish
Nea = Nematodes
Nee = Nemerteans
Ner = Nereid Polychaetes
Ost = Ostracods
Pen = Juv. Penaeid Shrimps
Poh = Polychaetes
Pol = Polyclads
Por = Portunid Crabs
Rot = Rotifers
Sip = Sipunculids
Uca = *Uca* spp.
Uni = Unidentified Items

Appendix 4.1 Principal Component Analysis for diet of ***Stolephorus nelsoni***

```
                           Principal Component Analysis

                               Total Variance = 71.579677898

                          Eigenvalues of the Covariance Matrix

                    Eigenvalue        Difference        Proportion        Cumulative

         PRIN1        27.1187           10.2870          0.378860           0.37886
         PRIN2        16.8317            8.2284          0.235146           0.61401
         PRIN3         8.6033            3.0228          0.120192           0.73420
         PRIN4         5.5805            0.5652          0.077963           0.81216
         PRIN5         5.0153            2.2095          0.070066           0.88223
         PRIN6         2.8059            0.4934          0.039199           0.92143
         PRIN7         2.3125            1.0598          0.032307           0.95373
         PRIN8         1.2527            0.5349          0.017501           0.97123
         PRIN9         0.7178            0.1936          0.010029           0.98126
         PRIN10        0.5243            0.1987          0.007324           0.98859
         PRIN11        0.3255            0.0381          0.004548           0.99313
         PRIN12        0.2875            0.1506          0.004016           0.99715
         PRIN13        0.1369            0.0720          0.001912           0.99906
         PRIN14        0.0648            0.0625          0.000906           0.99997
         PRIN15        0.0023            0.0023          0.000032           1.00000
         PRIN16        0.0000             .              0.000000           1.00000

                               Principal Component Analysis

                                       Eigenvectors

                   PRIN1       PRIN2       PRIN3       PRIN4       PRIN5       PRIN6

       HARPACT   0.364836    -.074698    0.711792    -.126980    0.375690    -.022789
       CYCLOP    0.068049    -.100647    -.156048    0.036649    -.208765    0.462780
       OSTRACOD  0.302675    0.167976    -.018527    0.176650    -.106748    -.284479
       ISOPODS   0.033737    -.037491    -.038474    0.044107    -.091232    0.142518
       LUCIFER   0.053004    0.063270    -.151663    -.333172    0.349795    0.047299
       ACETES    -.057920    0.895438    0.156306    0.002930    -.256499    -.045233
       PENAEID   0.270835    0.182994    -.236555    -.469297    0.262917    -.292028
       MEGALOPA  0.070211    0.049102    0.008536    0.033583    -.131055    -.037639
       MATUTA    -.031678    0.073355    0.261049    -.049813    0.046650    0.375853
       DOTILLA   -.032127    0.158798    0.154488    0.135342    0.092099    0.280920
       HYMENO    0.020321    0.096432    -.044098    0.208192    0.152691    0.043516
       SNAILS    0.557421    -.176169    0.168653    0.277958    -.388783    -.183711
       BIVALVES  0.608652    0.144463    -.386906    -.023076    0.077507    0.436636
       CLUPEIDS  -.030633    0.070936    0.252437    -.048170    0.045111    0.363454
       MULLETS   -.017221    0.126718    -.154455    0.686489    0.569985    -.060423
       UNIDEN    0.014495    0.008229    -.063526    -.038461    -.055286    0.104254


                   PRIN7       PRIN8       PRIN9      PRIN10      PRIN11      PRIN12

       HARPACT   -.173253    -.225401    -.162872    0.279908    0.011460    0.003958
       CYCLOP    0.236649    -.081706    -.133268    0.507269    0.354294    0.156579
       OSTRACOD  -.365242    0.408822    -.114163    -.083398    0.633463    0.121546
       ISOPODS   0.110644    -.024053    -.066260    0.021062    0.201683    -.289679
       LUCIFER   0.162511    -.431349    0.415863    -.276057    0.503296    0.047430
       ACETES    0.106461    -.233190    -.001777    0.159284    -.019104    -.086537
       PENAEID   0.372262    0.413968    -.051572    0.146951    -.181005    0.131479
       MEGALOPA  -.401508    -.012799    0.606878    -.030018    -.164162    0.003799
       MATUTA    0.101972    0.406219    0.228924    -.080211    0.068630    -.093795
       DOTILLA   0.121664    0.049420    -.181932    -.463341    -.153161    0.410787
       HYMENO    0.013902    -.141266    -.272461    -.307344    0.070826    0.324007
       SNAILS    0.498592    -.102926    0.246661    -.154980    -.074182    0.064659
       BIVALVES  -.302203    -.080709    -.114117    -.087695    -.252782    -.212864
       CLUPEIDS  0.098608    0.392818    0.221372    -.077565    0.066366    -.090701
       MULLETS   0.159038    0.063189    0.209067    0.263747    -.030134    -.093315
       UNIDEN    -.174571    -.003534    0.260891    0.331646    -.105406    0.707666
```

```
                 Principal Component Analysis

                         Eigenvectors

                 PRIN13      PRIN14      PRIN15      PRIN16

    HARPACT    0.055181    0.087447    0.018549    0.000000
    CYCLOP     0.159899    0.274293    -.336439    0.000000
    OSTRACOD   0.103508    -.091624    -.024838    0.000000
    ISOPODS    0.176989    0.296987    0.838823    -.000000
    LUCIFER    0.036303    -.125148    -.020738    0.000000
    ACETES     -.043799    -.041146    0.002802    0.000000
    PENAEID    0.074819    0.268719    0.022326    0.000000
    MEGALOPA   0.201278    0.599815    -.122629    0.000000
    MATUTA     -.216717    -.038292    -.010953    -.695150
    DOTILLA    0.621981    0.008421    -.002253    0.000000
    HYMENO     -.603644    0.505993    0.023129    0.000000
    SNAILS     -.080542    -.085942    -.006000    0.000000
    BIVALVES   -.065546    -.172251    -.007493    0.000000
    CLUPEIDS   -.209568    -.037028    -.010592    0.718865
    MULLETS    0.074983    -.046796    0.001927    0.000000
    UNIDEN     -.146509    -.270173    0.406671    0.000000
```

Appendix 4.2 Principal Component Analysis for diet of *Sillago analis*

```
                        Principal Component Analysis
                        Total Variance = 120.7190084
                    Eigenvalues of the Covariance Matrix
               Eigenvalue       Difference       Proportion       Cumulative
 PRIN1          24.3238          7.86565          0.201491          0.20149
 PRIN2          16.4581          4.41688          0.136334          0.33783
 PRIN3          12.0412          1.78908          0.099746          0.43757
 PRIN4          10.2522          1.64521          0.084926          0.52250
 PRIN5           8.6070          1.39025          0.071297          0.59379
 PRIN6           7.2167          0.93359          0.059781          0.65358
 PRIN7           6.2831          0.40632          0.052047          0.70562
 PRIN8           5.8768          0.89442          0.048682          0.75430
 PRIN9           4.9824          0.84512          0.041272          0.79558
 PRIN10          4.1372          0.36099          0.034272          0.82985
 PRIN11          3.7763          0.63626          0.031281          0.86113
 PRIN12          3.1400          0.88172          0.026011          0.88714
 PRIN13          2.2583          0.27042          0.018707          0.90585
 PRIN14          1.9879          0.32940          0.016467          0.92231
 PRIN15          1.6585          0.04224          0.013738          0.93605
 PRIN16          1.6162          0.41404          0.013388          0.94944
 PRIN17          1.2022          0.12614          0.009959          0.95940
 PRIN18          1.0760          0.08003          0.008914          0.96831
 PRIN19          0.9960          0.20118          0.008251          0.97656
 PRIN20          0.7948          0.17731          0.006584          0.98315
 PRIN21          0.6175          0.10947          0.005115          0.98826
 PRIN22          0.5081          0.14550          0.004209          0.99247
 PRIN23          0.3626          0.14100          0.003003          0.99548
 PRIN24          0.2216          0.09518          0.001835          0.99731
 PRIN25          0.1264          0.03397          0.001047          0.99836
 PRIN26          0.0924          0.04029          0.000765          0.99912
 PRIN27          0.0521          0.01403          0.000432          0.99955
 PRIN28          0.0381          0.02240          0.000315          0.99987
 PRIN29          0.0157          0.01569          0.000130          1.00000
 PRIN30          0.0000          0.00000          0.000000          1.00000
 PRIN31          0.0000           .               0.000000          1.00000

                                Eigenvectors
          PRIN1      PRIN2      PRIN3      PRIN4      PRIN5      PRIN6      PRIN7
HAR    0.246892   -.066960   -.542152   -.256807   0.176656   -.169548   0.152204
CAL    0.152076   -.007389   -.292875   -.198897   0.128540   -.106756   0.072919
AMP    0.444522   0.214419   -.163262   -.025309   -.009764   0.153713   -.286458
ISO    0.256740   -.069215   0.273036   -.083845   0.126398   0.334760   0.179042
ACE    0.364100   0.318035   0.461284   -.349690   -.044324   -.338084   0.145944
PEN    0.118609   0.031228   0.200301   -.079811   0.028928   -.074642   -.300332
CAS    0.379643   0.331520   -.249779   0.147428   0.057005   -.074786   0.082572
HER    0.008679   0.034793   -.040377   -.009869   -.019546   0.039873   -.009499
CRB    0.019328   0.107251   -.036845   0.039861   -.031994   0.163169   -.171245
DOT    0.340519   -.322254   0.022330   0.482090   -.446361   -.190897   0.089884
UCA    0.044909   0.053158   0.044279   0.031447   0.004589   -.150030   -.032421
GRA    0.004830   0.146293   0.109149   0.020128   0.096255   0.157057   0.232444
MAT    0.022984   -.088134   0.000255   0.373114   0.663659   -.215652   0.215334
POR    0.211709   0.143584   -.080269   0.208559   -.092758   0.281113   -.197742
INS    0.124976   -.165389   -.070549   0.108647   -.010799   -.030929   -.001058
SNA    0.008051   0.010353   0.045601   0.059177   -.117422   -.167440   0.094719
MES    0.055177   0.075624   -.034345   0.229758   -.289676   -.116724   0.420842
POL    0.064499   0.299750   0.046752   0.356156   0.179193   0.409518   0.077438
MAL    0.021463   0.023170   0.036126   -.125038   -.083150   0.177940   0.284811
NER    0.373831   -.624269   0.117382   -.149255   0.156217   0.216599   0.014183
PCL    -.009016   0.012248   0.040405   0.074274   0.108317   0.023467   -.011038
NEM    0.065490   -.003665   -.085275   -.074553   0.048222   -.040619   0.034252
NTE    0.003825   -.012447   0.052643   -.083180   -.057590   0.073491   0.154068
SIP    0.002136   0.034531   0.092028   0.007800   0.090807   0.117676   0.299020
ANE    0.041814   0.102720   0.167807   0.146360   0.117387   -.327029   -.053297
MED    0.072891   0.149057   0.114845   -.020470   0.077203   -.069798   -.018782
FSH    0.143011   -.123593   0.288746   0.150595   0.202159   -.116720   -.267260
GOB    0.024419   -.015590   0.054163   -.076709   -.002134   0.065945   0.079063
ANC    0.029213   -.018651   0.064798   -.091771   -.002553   0.078893   0.094587
MUL    -.005642   -.002339   0.047841   -.072949   -.073564   0.108132   0.286531
LIO    -.036900   -.008101   -.014146   0.056351   0.135186   -.057266   0.035789
```

```
                             Eigenvectors
        PRIN8     PRIN9    PRIN10    PRIN11    PRIN12    PRIN13    PRIN14
HAR  -.214271  0.004685  0.198255  0.049770  0.161038  0.049671  -.089416
CAL  -.060227  -.095230  0.242923  0.102550  0.161920  -.091013  0.262556
AMP  0.362232  0.047281  0.178016  -.024220  -.142629  -.127352  0.295167
ISO  -.087304  -.158276  0.435602  -.557600  0.003765  0.040549  -.153932
ACE  -.064610  -.381804  -.220499  0.155157  0.104817  0.107493  0.081804
PEN  0.080598  0.150783  0.129595  -.134135  0.052787  -.376712  -.220532
CAS  -.039148  0.306253  -.399009  -.230999  -.139700  0.139812  -.333473
HER  0.115697  0.138461  -.083828  -.130425  -.121252  0.159976  0.201668
CRB  0.056519  -.158175  -.129504  0.218139  0.067768  0.084252  -.015328
DOT  -.175050  -.144434  -.012648  -.167736  -.081419  -.000941  0.260707
UCA  0.037686  0.079681  -.076878  -.064114  -.018620  0.002754  -.053566
GRA  -.460189  0.149050  -.021922  0.025986  -.217072  -.228175  0.209481
MAT  0.314694  -.288353  -.120909  -.089126  -.060469  -.059039  0.026269
POR  0.145100  -.270544  -.032652  0.183581  0.141299  -.194622  -.083317
INS  -.116964  0.117097  -.088931  -.039833  0.251668  0.283806  0.076355
SNA  0.004084  -.026025  0.186749  0.156988  -.106636  -.002253  0.025210
MES  0.239766  0.070932  0.215121  0.169160  0.207209  -.205669  -.341925
POL  -.263757  -.059954  0.109059  0.312656  0.046358  0.199530  0.016283
MAL  0.381300  0.252636  -.072915  -.061254  -.033831  0.223159  0.327981
NER  0.012011  0.099296  -.201541  0.386073  -.255910  -.086473  -.166393
PCL  -.019174  0.030721  0.188914  0.029566  0.087951  0.270730  0.018696
NEM  -.018126  -.038900  0.031427  0.064028  0.026862  -.021326  0.056116
NTE  0.156472  -.014302  0.074221  0.057061  -.021268  0.200491  -.391986
SIP  -.044930  0.236569  -.150264  0.076929  0.254866  -.396340  0.138725
ANE  0.048358  0.278898  0.434491  0.306878  -.389100  0.109092  0.031750
MED  -.120553  0.248948  -.049113  -.063884  -.107252  -.168723  -.018446
FSH  0.001119  0.333920  0.033958  0.015317  0.572564  0.159842  0.071194
GOB  0.086729  -.024231  0.000334  0.020003  -.073346  0.174248  -.011574
ANC  0.103758  -.028988  0.000400  0.023931  -.087747  0.208461  -.013846
MUL  0.240101  0.151107  0.016524  0.071844  0.171977  -.078227  0.152179
LIO  0.112365  -.143231  -.072885  -.129370  -.059256  -.188198  0.131395
```

```
                             Eigenvectors
       PRIN15    PRIN16    PRIN17    PRIN18    PRIN19    PRIN20    PRIN21
HAR  0.105394  -.067250  0.246558  0.098135  -.090111  0.214814  -.293393
CAL  -.142454  0.062965  -.226776  0.065383  0.130026  0.014856  0.311220
AMP  -.141934  0.160066  -.206766  0.046386  0.011404  -.153799  -.081210
ISO  0.246871  -.112127  -.062753  -.054638  0.074569  -.117651  0.037995
ACE  -.048072  -.036117  0.049363  -.088259  -.020533  -.006681  0.012898
PEN  -.059806  -.026624  0.281304  -.007126  -.185961  0.428135  0.283057
CAS  0.065741  -.134263  0.053950  -.040411  0.098920  -.039938  0.036423
HER  -.064678  -.076820  -.045861  -.336940  0.323532  0.240686  0.057084
CRB  0.691273  -.007405  -.179096  0.349387  0.233816  0.252996  0.224618
DOT  -.069454  -.058533  -.002203  0.280603  -.022232  0.143359  -.053235
UCA  -.059387  -.013602  -.078305  0.271447  -.074340  0.058627  0.099422
GRA  0.052366  0.358345  -.140218  -.134952  -.065418  0.438948  -.060408
MAT  0.006220  -.029497  -.178572  -.033837  -.162081  0.130852  0.013760
POR  0.101879  0.050189  0.086461  -.275958  -.221886  0.044752  -.328818
INS  0.265253  0.458600  0.012305  -.335220  -.338534  -.249532  0.276548
SNA  0.214622  -.063005  0.074026  -.265511  0.264443  -.066434  -.168566
MES  -.055348  0.082237  -.056746  -.143748  0.148843  0.009682  0.214597
POL  -.310105  -.096688  0.241271  0.104169  0.017157  -.035270  0.208890
MAL  0.022375  -.074290  0.152537  -.057751  -.037300  0.240157  0.045643
NER  -.048746  -.072045  0.051932  -.058065  0.105767  -.059837  0.107374
PCL  -.059580  -.164740  0.130757  0.112678  0.111732  -.019853  -.012305
NEM  -.068748  -.005618  -.082381  -.044718  0.114767  -.078543  0.317010
NTE  -.192944  0.478440  -.245935  0.202752  0.119172  0.177663  -.166909
SIP  0.119679  -.161627  -.156836  0.064660  0.136133  -.205642  -.293733
ANE  0.257638  -.015870  0.043560  -.026465  -.110458  -.060617  -.065082
MED  0.018154  0.148035  -.079406  0.298138  -.068404  -.346161  0.034508
FSH  -.069057  0.078207  -.048390  0.020611  0.222832  0.141436  -.212268
GOB  -.026573  0.103330  0.036189  0.135532  -.107347  0.012666  -.159218
ANC  -.031790  0.123618  0.043294  0.162143  -.128425  0.015153  -.190480
MUL  0.129604  -.080631  0.209325  0.235375  -.356382  -.022007  0.117927
LIO  0.073510  0.455923  0.630662  0.129636  0.424073  -.139299  0.004381
```

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                              Eigenvectors
       PRIN22     PRIN23     PRIN24     PRIN25     PRIN26     PRIN27     PRIN28
HAR  0.158184   -.157583   -.171134   -.079225   0.087712   -.027839   -.060109
CAL  -.039986   0.202666   0.240849   0.318725   -.398303   0.136776   0.016052
AMP  0.041109   -.043249   -.224759   -.090815   0.328093   -.145564   0.093199
ISO  -.053308   0.041764   -.082882   -.011359   -.086189   0.070927   -.001031
ACE  -.003755   -.138862   -.076384   -.003505   0.000361   -.041993   0.004871
PEN  0.292433   -.013523   0.252699   0.001910   0.020622   -.123060   0.186045
CAS  -.164700   0.173070   0.132593   -.041380   -.087015   0.017557   0.025972
HER  0.174984   -.264799   -.013783   0.112234   -.147222   0.032915   -.020150
CRB  0.081914   -.031735   -.033225   0.011885   0.023505   -.107496   -.036193
DOT  0.063855   -.080891   0.112268   -.086564   -.081319   -.026709   0.011656
UCA  -.141561   0.181974   -.229932   0.345888   0.172543   0.458143   0.407245
GRA  -.242813   0.079219   -.025473   0.050693   0.223843   -.019814   -.093856
MAT  0.121275   -.026199   0.021800   -.016536   0.084475   -.010536   -.070726
POR  -.203919   -.030318   0.272795   0.151615   -.209024   0.242882   -.123095
INS  0.162283   -.107165   0.032621   0.073589   0.069445   -.047381   0.233284
SNA  0.409930   0.346598   0.199636   0.008255   0.373835   0.382660   0.012576
MES  -.075886   0.023560   -.215140   0.188208   0.089212   -.279590   -.174063
POL  0.286511   0.030964   -.140517   -.086144   -.066935   0.047812   0.092571
MAL  0.089858   -.030570   0.063205   0.034404   -.097738   0.082889   -.101214
NER  -.053252   -.015980   -.069141   0.100736   0.035546   0.035991   -.042205
PCL  -.315648   -.371622   0.432196   0.368101   0.448515   -.117370   0.044685
NEM  -.217404   0.138333   0.401110   -.590996   0.171626   -.009847   -.023035
NTE  0.102504   -.279962   0.174247   -.214169   -.086095   0.272223   0.159235
SIP  0.134689   -.140709   0.167653   -.035651   -.101953   -.159975   0.476957
ANE  -.190020   -.100627   -.022694   -.102622   -.342710   -.043000   0.134882
MED  0.321727   -.184495   0.181559   0.185322   -.006595   0.110417   -.555869
FSH  -.102983   0.217157   -.115592   -.104603   -.035773   0.041235   -.217780
GOB  0.071127   0.340148   0.149145   0.113315   -.023104   -.285568   0.025419
ANC  0.085092   0.406935   0.178429   0.135565   -.027640   -.341639   0.030410
MUL  -.169743   0.005848   -.032804   -.193764   0.085322   0.299087   -.117683
LIO  -.139567   -.002719   -.043184   0.013491   -.086244   0.003622   0.067766
```

```
                    Eigenvectors
                 PRIN29     PRIN30     PRIN31
           HAR  0.208698   0.000000   0.000000
           CAL  -.242409   0.000000   0.000000
           AMP  -.114219   0.000000   0.000000
           ISO  0.059948   0.000000   0.000000
           ACE  -.019330   0.000000   0.000000
           PEN  -.057403   0.000000   0.000000
           CAS  -.251983   0.000000   0.000000
           HER  0.259956   0.128368   0.587404
           CRB  0.011788   0.000000   0.000000
           DOT  -.008969   0.000000   0.000000
           UCA  0.462669   0.000000   0.000000
           GRA  -.051882   0.000000   0.000000
           MAT  -.026133   0.000000   0.000000
           POR  0.224646   0.000000   0.000000
           INS  0.015347   0.000000   0.000000
           SNA  -.167401   0.000000   0.000000
           MES  0.128868   0.000000   0.000000
           POL  0.028480   0.000000   0.000000
           MAL  0.121714   -.123778   -.566399
           NER  -.018525   0.000000   0.000000
           PCL  -.102380   0.000000   0.000000
           NEM  0.475852   0.000000   0.000000
           NTE  -.128809   0.000000   0.000000
           SIP  0.062302   0.000000   0.000000
           ANE  0.055267   0.000000   0.000000
           MED  0.234841   0.000000   0.000000
           FSH  -.010950   0.000000   0.000000
           GOB  0.109002   0.785368   0.000000
           ANC  0.130404   -.583722   0.332893
           MUL  -.269099   0.103275   0.472580
           LIO  0.018174   0.000000   0.000000
```

Appendix 4.3 Principal Companent Analysis for diet of *Leiognathus splendens*

```
                       Principal Component Analysis

                     Total Variance = 41.788799313

                  Eigenvalues of the Covariance Matrix

              Eigenvalue      Difference       Proportion       Cumulative

  PRIN1         16.7359         9.36342         0.400488          0.40049
  PRIN2          7.3725         2.30301         0.176423          0.57691
  PRIN3          5.0695         1.65136         0.121312          0.69822
  PRIN4          3.4181         0.86396         0.081795          0.78002
  PRIN5          2.5542         0.38523         0.061121          0.84114
  PRIN6          2.1689         0.33433         0.051902          0.89304
  PRIN7          1.8346         0.90539         0.043902          0.93694
  PRIN8          0.9292         0.16915         0.022236          0.95918
  PRIN9          0.7601         0.22564         0.018188          0.97737
  PRIN10         0.5344         0.28332         0.012789          0.99016
  PRIN11         0.2511         0.13262         0.006009          0.99616
  PRIN12         0.1185         0.07672         0.002835          0.99900
  PRIN13         0.0418         0.04177         0.001000          1.00000
  PRIN14         0.0000         0.00000         0.000000          1.00000
  PRIN15         0.0000         0.00000         0.000000          1.00000
  PRIN16         0.0000          .              0.000000          1.00000


                       Principal Component Analysis

                               Eigenvectors

               PRIN1      PRIN2      PRIN3      PRIN4      PRIN5      PRIN6
HARPACT     0.692997   -.071870   -.151226   -.221666   -.314320   -.364144
CYCLOP      0.152299   -.073918   0.780628   -.328906   -.105116   0.243285
OSTRACOD    0.366982   -.191559   0.076077   0.573545   0.331331   0.058014
AMPHIPOD    0.052519   0.307571   0.270101   0.286304   -.337016   -.338446
ISOPODS     -.024763   0.001710   -.008288   0.074649   -.148903   0.186240
ACETES      0.059952   0.167770   -.131993   -.291931   0.125362   0.098731
POLYCHAE    0.315585   0.776374   -.104187   0.004491   0.181929   0.137963
SNAILS      0.071944   -.031936   0.100685   -.272945   -.109888   0.190588
BIVALVES    0.039677   0.054225   -.008766   -.196457   -.027129   0.012519
ROTIFER     0.016009   0.049448   0.312417   0.093465   0.154050   -.037016
NEMATODE    0.386794   -.320327   -.078065   0.156733   -.129281   0.139611
BRYOZOA     -.030564   0.249210   0.009179   0.347158   -.515338   0.490354
APPENDIC    0.042914   0.153220   0.364416   0.115158   0.266711   -.354438
CTENOPH     -.001352   0.065316   0.026128   0.010843   0.344764   0.115296
ALGAE       0.307509   -.068672   -.027667   -.078862   0.289556   0.430226
UNIDENT     0.037000   0.153593   -.111434   -.233309   0.056013   -.070923


               PRIN7      PRIN8      PRIN9     PRIN10     PRIN11     PRIN12

HARPACT     -.136426   0.070970   0.071241   -.218774   -.112480   -.224550
CYCLOP      0.162112   -.039888   -.154543   -.033244   -.095109   0.005049
OSTRACOD    0.395656   -.016683   0.205151   0.041368   -.300309   -.107831
AMPHIPOD    -.166954   -.066702   0.214186   0.461844   -.054720   0.456183
ISOPODS     -.004022   0.374236   0.282505   -.638800   -.030254   0.542181
ACETES      0.163183   -.021746   0.617604   0.162975   0.472869   -.095486
POLYCHAE    0.093776   -.244260   -.315675   -.192531   0.020019   0.098320
SNAILS      -.123894   -.137612   0.160235   0.081035   -.081397   -.059151
BIVALVES    0.193264   0.292002   -.064190   0.181202   -.186474   0.044102
ROTIFER     0.230537   -.042158   0.069285   -.146177   0.408254   -.000469
NEMATODE    0.012973   0.116926   -.357908   0.192618   0.604369   0.247029
BRYOZOA     -.049883   0.249311   0.072786   0.061057   0.038998   -.469989
APPENDIC    -.295023   0.335809   0.140297   -.137352   0.176862   -.289297
CTENOPH     -.443416   0.417291   -.244659   0.120501   0.014220   -.016676
ALGAE       -.387713   -.062065   0.269934   0.209173   -.189878   0.196590
UNIDENT     0.439055   0.562048   -.042273   0.292556   -.133468   0.084270
```

```
              Principal Component Analysis

                      Eigenvectors

              PRIN13      PRIN14      PRIN15      PRIN16

HARPACT     0.131999    -.026623    -.125737    0.193865
CYCLOP      0.085104    -.115729    -.253283    -.191898
OSTRACOD    0.216722    0.020263    0.095699    -.147552
AMPHIPOD    0.125372    -.004092    -.019326    0.029797
ISOPODS     0.063024    0.011500    0.054314    -.083743
ACETES      0.252486    0.034188    -.204228    -.256327
POLYCHAE    -.027795    0.015621    0.073777    -.113751
SNAILS      0.176776    0.002370    0.867675    0.000000
BIVALVES    -.079916    0.867897    0.000000    0.000000
ROTIFER     0.016925    0.113630    0.082878    0.773321
NEMATODE    -.119676    0.028331    0.133806    -.206305
BRYOZOA     -.058324    -.011925    -.056320    0.086835
APPENDIC    -.402573    0.039061    0.184484    -.284442
CTENOPH     0.632542    -.014950    -.070606    0.108862
ALGAE       -.442500    -.033074    -.156208    0.240845
UNIDENT     -.174718    -.462574    0.127196    0.135590
```

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