Trophic Structure and the Importance of Terrestrial Wetland Producers for Aquatic Food Webs in Tropical Australian Estuaries

Thesis submitted by

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ABSTRACT

Estuaries support a great density and diversity of life and are traditionally considered to be important nursery areas for a variety of species, providing abundant and essential food supply and refuge from predation for juveniles of several fish and invertebrate species. However, to date no study has provided unequivocal evidence supporting this paradigm. In fact, recent studies based on the analysis of stable isotopes have shown that the importance of estuarine terrestrial wetland habitats such as mangroves and salt marsh in supplying energy to animals in adjacent aquatic habitats is not as significant as once thought. The objective of the present thesis is use stable isotopic analysis to clarify the importance of terrestrial wetland productivity as a source of energy for estuarine communities in the Australian Wet and Dry Tropics and to study the processes of energy flow taking place in these systems. Overall, material of terrestrial wetland origin was found to be incorporated into estuarine food webs in Tropical Australia. However, this importance is dependent on several physical and ecological factors including productivity of the different habitats, type and extension of wetland vegetation and connectivity.

In a first study, stable isotope analysis of carbon and nitrogen were used to analyse processes of energy flow and assess the extend to which carbon fixed by terrestrial plants is incorporated into adjacent aquatic food webs in two intermittently connected estuarine pools in the Ross River floodplain in North Queensland, Australia. The two pools differed in surrounding vegetation as one was surrounded by mangroves and the other by the salt couch *Sporobolus virginicus.* Since $\delta^{13}C$ values of C3 mangroves (low $\delta^{13}C$) are very different from those of the C4 salt couch (high $\delta^{13}C$), it was possible to determine the importance of terrestrial wetland producers by comparing isotope values of consumers between sites. The IsoSource model was also used to clarify the importance of the different potential sources to consumers. An incorporation mangrove and *S. virginicus* material was detected for several fish and invertebrate species at both sites, indicating that carbon of terrestrial origin is incorporated in the estuarine food

web. A linear negative relationship between $\delta^{13}C$ and $\delta^{15}N$ was also detected for primary producers, primary consumers and secondary consumers at the *Sporobolus* pool. This relationship was similar for the different trophic levels and was found to be useful to calculate trophic positions. A food web of ~3.5 trophic levels was found at both pools.

In a more detailed study, $\delta^{13}C$ and $\delta^{15}N$ analysis was used to determine the extent to which carbon of terrestrial origin is important for nutrition of juveniles of four penaeid prawn species, and to detect and describe ontogenetic variations in diet. These species were selected because penaeids are known to depend on estuarine wetland habitats such as mangroves and salt marsh at their juvenile stage. Although an incorporation of mangrove and salt marsh carbon was detected, it was not of a major importance for any species, and autochthonous sources seemed more important. Ontogenetic shifts in diet were detected for *Penaeus* (*Fenneropenaeus*) *merguiensis*, *Metapenaeus bennetae* and *Penaeus esculentus*, and corresponded to an increase in mean trophic level as well as to changes in the ultimate sources of energy.

In a broader scale study, the incorporation of terrestrial wetland productivity in estuarine food webs was studied in four open estuarine systems in Tropical Australia. These included a near-pristine system in the Wet Tropics (Deluge Inlet), two impacted systems in the Wet Tropics (Victoria and Half Moon Creeks), and a near pristine system in the Dry Tropics (Blacksoil Creek). Incorporation of mangrove derived carbon was detected for Deluge Inlet and Victoria Creek and incorporation of carbon of sugarcane origin was also detected for fish from Victoria Creek. The degree of incorporation of mangrove carbon into estuarine food webs seemed to relate directly to the type and extent of mangrove vegetation adjacent to the estuary. Trophic structure differed between estuaries, but in all areas a constant trophic length with about four trophic levels was detected. Stable isotope results also suggest a high level of omnivory and diet overlap between fish species at Deluge Inlet, Half Moon Creek and Blacksoil Creek, but not for the agriculture impacted system of Victoria Creek, which can be a reflection of the great level of anthropogenic impact in this area.

In a final study, the seasonality in importance of autochthonous and allochthonous carbon for aquatic communities in six intermittently connected estuarine areas of the Australian Dry Tropics was investigated. Results varied between sites, depending of site-specific ecological conditions. The hydrology regime was a major factor controlling the sources of energy in these areas, controlling the amount of terrestrial material available to aquatic animals throughout the year and allowing the presence of an energetic connectivity between the terrestrial and aquatic environments. An important seasonal variation in the main sources of energy was detected in two systems, where a greater incorporation of carbon of terrestrial origin was present after the wet season. Hence, aquatic food webs may rely alternatively on autochthonous and allochthonous sources of energy, depending on the season. Trophic organization, including level of omnivory, diet overlap and trophic length, was also found to differ between systems and seasons due to differences in species composition, resource availability, connectivity, and type and level of environmental disturbances. While trophic length seems to be similar between open estuarine areas, with food webs having ~4 trophic levels, in intermittently connected areas trophic length was more variable between systems, with between 3.2 and 4 trophic levels.

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All research procedures reported here received the approval from the Animal Ethics Committee, James Cook University.

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(Kátya Abrantes)

Chapter 1

General Introduction

Estuaries are conspicuous features along the edges of every continent, occurring at the interface between freshwater and marine environments (Bucher & Saenger 1991). These systems support a great density and diversity of life, and are among the most economically valuable ecosystems on earth (Costanza et al. 1997). However, they are also subjected to enormous human pressure since throughout history their locations at the mouths of rivers and streams have made them ideal for the settlement of human civilizations, providing a range of basic goods and services such as food and transportation. This pressure has been intensified over the last century (Junk 2002), and on-going destructive activities are still being implemented throughout the world, as short-term economical benefits usually take precedence over environmental issues. Nowhere are these pressures greater than in tropical areas, where massive and increasing population numbers place incredible pressures on estuarine environments (Thanh et al. 1996, Stobutzki et al. 2006).

Worldwide, human induced changes in environmental conditions have resulted in a range of ecological alterations to natural estuarine communities, including lengthening of dry seasons, altering ground water levels, and decreasing connectivity and habitat heterogeneity (Brock et al. 1999, Bunn & Arthington 2002). As a result, vast expanses of wetland areas have vanished, and those remaining are very vulnerable to

anthropogenic impacts, including urban development and farming (Junk 2002). It is therefore crucial to understand the role of the different wetland habitats to the overall functioning of estuarine ecosystems. Only then it will be possible to provide useful advice to wetland management, assess conservation priorities, assist in habitat rehabilitation projects and predict and mitigate the effects of Climate Change on estuarine communities.

At the most basic level, the stability of a community depends on the availability of food for its different components, and on the stability of trophic interactions among the different species within the food web (Polis & Strong 1996). Information on energy sources and trophic structure is therefore vital for the understanding of the dynamics and persistence of ecological systems through time (Polis 1994, Polis & Strong 1996, Polis et al. 1997). Hence, it is crucial to develop a detailed evaluation of the contributions of different primary producers to food webs across the great diversity of biotic and abiotic conditions encountered in estuarine systems (Sheaves et al. in press).

Estuarine productivity and the nursery paradigm. Estuarine areas and their component habitats are highly productive (Schelske & Odum 1961, Teal 1962, Odum 1968, Nixon 1980, Qasim & Wafar 1990), and are traditionally considered to provide abundant and essential food supply and refuge from predation for juveniles of several fish and invertebrates (e.g. Boesch & Turner 1984, Robertson & Blaber 1992, Paterson & Whitfield 2000). Consequently, estuaries are considered to be important nursery areas for a variety of species, many of which are of economical, recreational or cultural importance (Boesch & Turner 1984, Robertson & Duke 1987, Beck et al. 2001,

Laegdsgaard & Johnson 2001). This nursery role is particularly important in tropical and subtropical regions of the world, where dense mangrove forests and extensive salt marsh meadows occur (Lugo & Snedaker 1974, Twilley 1998).

A range of methodologies have been applied to the study of the importance of mangroves and salt marsh for estuarine food webs, including ecosystem mass balance calculations (e.g. Teal 1962), correlations between wetland area and fishery productivity (e.g. Turner 1977, Loneragan et al. 2005), and diet studies based on gut contents (e.g. Odum & Heald 1972) or stable isotope analysis (e.g. Bouillon et al. 2002a). However, and despite that the role of tropical estuaries as nursery grounds is frequent used as the main argument for their conservation (Twilley 1998), to date no study has provided unequivocal evidence supporting this paradigm. In fact, recent studies based on stable isotopic analysis have shown that the importance of estuarine terrestrial wetland habitats such as mangroves and salt marsh in supplying energy to animals in adjacent aquatic habitats may not be as significant as once thought (e.g. Lee 1995, Loneragan et al. 1997, Bouillon et al. 2004b).

Stable isotope analysis has been used to study the relative importance of material from different origin in permanent lakes (e.g. France & Steedman 1996, Grey et al. 2001), streams and rivers (e.g. Rounick et al. 1982, Hamilton et al. 1992), estuaries and bays (e.g. Newell et al. 1995, Bouillon et al. 2002a) and seas (e.g. Grebmeier et al. 1988, Achituv et al. 1997). This methodology has also been used to describe trophic relationships between animals in a variety of terrestrial (e.g. Ambrose & DeNiro 1986, Ponsard & Arditi 2000), freshwater (e.g. Gu et al. 1996, Xu et al. 2005) and marine (e.g. Sheaves & Molony 2000, Alfaro et al. 2006) environments. However, the great majority of this research has been conducted in temperate systems, and information on

the sources of energy and food web structure in tropical estuaries in general and in Australian estuaries in particular is still lacking.

***Idiosyncrasy of Australian estuaries*.** Australian rivers and estuaries are variable in hydrology when compared to systems from the rest of the world (Eyre 1998, Puckridge et al. 1998). Australian estuaries can be classified into five groups according to their hydrology and meteorology: Mediterranean, Temperate, Transitional, Arid Tropical and/or Subtropical, and Wet and Dry Tropical and/or Subtropical (Eyre 1998). The present thesis focuses on energetic processes taking place in estuarine systems of the latter category.

Wet and Dry Tropical and Subtropical estuaries are found in the east coast of Australia from northern New South Wales to Queensland, in the Northern Territory and in northern Western Australia, and account for ~68% of Australia's estuaries (Bucher & Saenger 1991, Bucher & Saenger 1994). These systems are characterized by large freshwater inputs during the short wet season (summer) and, particularly in dry tropics systems, very little or no flow during the dry season (winter). Hence, estuaries in Tropical Australia have a distinctly seasonal regime of freshwater inflow. Additionally, although adjacent areas are often interconnected by the flood waters during the wet season, for most of the year the most upstream parts of these estuaries are reduced to a series of disconnected units (Finlayson & McMahon 1988). It is therefore important to characterise the energetic processes taking place both in the open areas of estuaries and in these intermittently connected pools to accurately describe the food web functioning in these areas.

Because of the large size and relative environmental constancy of open estuarine areas, it is likely that sources of energy and food web structures are more or less consistent between similar systems, and between seasons in the same system. In contrast, the small size and relative isolation of intermittently connected estuarine pools, coupled with the seasonality in hydrologic conditions, is likely to lead to a cyclical variation in sources of energy for aquatic animal communities. For instance, during the wet season there is likely to be a greater incorporation of terrestrial organic material transported from the catchment and from upstream reaches into the aquatic environment. This seasonality should also translate to differences in food and habitat availability, which in turn affect the dynamics of the whole community (Wantzen et al. 2002, Douglas et al. 2005). Hence, for these areas, it is important to understand the sources of carbon and pathways of energy flow occurring during both connection and disconnection periods, i.e. both during the wet and dry seasons.

Despite the prevalence of estuarine systems in Tropical Australia (Erskine et al. 2005), there is still a paucity of basic food web studies for these areas. Most rivers and estuaries of Tropical Australia are still in near pristine condition (Hamilton & Gehrke 2005), and are subjected to fewer impacts than systems in other regions of the Indo-Pacific (Valiela et al. 2001). However, there is still an ongoing tendency of increasing human activities in these coastal areas (Yapp 1986, Junk 2002). It is therefore imperative to determine the food sources and understand the structure and dynamics of biotic communities in these systems while they are still in almost pristine condition, so that baseline knowledge is available for future comparison with impacted systems. This information can further be translated for use as a baseline for the remediation of estuaries in other tropical countries, where no pristine systems remain.

Aims and structure of the thesis

The objective of the present study is to determine the importance of terrestrial wetland productivity as a source of energy for estuarine communities in the Australian Wet and Dry Tropics, and to study the processes of energy transfer taking place in these systems. Hence, four studies were designed and implemented, corresponding to the four data chapters of this thesis.

Chapters 2 and 3 focus on trophic processes taking place in two floodplain pools in the Ross River floodplain, in Townsville, Queensland. The two floodplain pools were selected for being relatively isolated and having contrasting types of surrounding wetland vegetation (mangrove forest vs. salt marsh), hence providing a natural situation with almost experimental conditions. In **Chapter 2**, the isotope composition of a wide range of producers and animal species from the two pools is analysed (i) to determine if trophic levels of consumers can be calculated based on a baseline $\delta^{13}C$-$\delta^{15}N$ relationship, and (ii) to assess the extend to which carbon fixed by terrestrial plants (mangroves and salt marsh grasses) is incorporated into these relatively isolated aquatic food webs. In **Chapter 3**, the same wetland pools are studied but this time in a species-specific approach, where stable isotopic analysis is used to investigate the sources of energy for four species of commercially important penaeid prawns. In particular, (i) the species-specific importance of terrestrial and aquatic productivity for penaeid prawn nutrition is analysed, and (ii) ontogenetic variations in sources of carbon are investigated.

The first two chapters combined not only provided important information on the main energetic processes taking place in these areas, but also served as a baseline for the development and design of the ecological questions introduced in Chapters 4 and 5,

providing an indication of the type of questions that could be answered using stable isotope analysis, and a foundation for the more appropriate approaches to be used in the analysis of the stable isotope data.

Therefore, in **Chapter 4,** stable isotope analysis is used to determine the extent to which carbon from terrestrial wetland origin is incorporated into aquatic food webs in four open estuarine systems. The specific aims were: (i) to develop a detailed understanding of the sources of energy and food web structure in a near-pristine estuary in the Australian Wet Tropics, and (ii) compare that to systems impacted by agriculture, urban development, and to a near-pristine system in the Dry Tropics.

In **Chapter 5**, seasonal variations in the importance of autochthonous and allochthonous sources of energy for aquatic communities in intermittently connected estuarine areas in the Australian Dry Tropics are analysed. Here, stable isotopic analysis is used to (i) identify differences in sources of carbon for aquatic animal communities between locations, (ii) identify seasonal changes in sources of carbon for the different locations, and (iii) investigate the sources of energy and trophic pathways in both near pristine systems and systems subjected to various anthropogenic impacts. **Chapter 6** corresponds the General Discussion, where the main findings of this study are summarised and placed into a broader ecologic context.

Chapter 2

Trophic Structure and Importance of Terrestrial Wetland Producers for Aquatic Animal Communities in the Ross River Estuarine Floodplain

2.1. INTRODUCTION

Stable isotope analysis can be useful in defining trophic relationships between the wide range of organisms that take part in estuarine food webs, including autotrophs and heterotrophs, terrestrial and aquatic fauna, invertebrates and vertebrates (e.g. Persic et al. 2004, Alfaro et al. 2006). To capture the structure and complexity of these food webs, it is important to consider as many of their components as possible, including both primary producers and consumers, and use the highest taxonomic resolution possible (Martinez 1991, 1993). However, the high cost of stable isotopic analysis means that in most cases only a limited number of species is considered. Although such an approach can be satisfactory to answer particular ecological questions, a more comprehensive representation of the different food web components is needed to address broader scale questions.

Stable isotope analysis has been widely used in an attempt to determine the importance of mangrove or salt marsh productivity in supporting adjacent aquatic food webs (e.g. Riera et al. 1999, Bouillon et al. 2002a, Bouillon et al. 2002b, Connolly et al.

2005b). Traditionally, these terrestrial components of estuarine wetland habitats have been considered as important sources of carbon for aquatic invertebrates and fish (Odum & Heald 1975). However, recent studies based on stable isotope analysis suggest that carbon of terrestrial wetland origin only makes a limited contribution, and is often incorporated by a limited number of species (Riera et al. 1999, Bouillon et al. 2002b). These studies have generally been based on stable isotope analysis of producers and consumers collected in rivers and creeks that run through mangrove forests (Bouillon et al. 2002b), or on the comparison of carbon isotopic composition of animals found in mangrove areas with those from adjacent open water (Newell et al. 1995, Chong et al. 2001, Bouillon et al. 2004a) or seagrass (Loneragan et al. 1997) habitats. However, these studies have been conducted in large estuarine areas, where the tidal movement can lead to a rapid dissipation of mangrove or salt marsh carbon throughout a large area, making it difficult to detect inputs from these sources. In contrast, the study of relatively isolated areas with limited water exchange has the potential to provide a different perspective on inputs of energy of terrestrial wetland origin into the aquatic food webs.

Stable isotope analysis has also been used in the study of food web parameters such as trophic levels and food chain length (e.g. Kwak & Zedler 1997, Kaehler et al. 2000). Initially, trophic length and trophic position of consumers were calculated based only on $\delta^{15}N$ values (e.g. Vander Zanden et al. 1997, Jepsen & Winemiller 2002). However, this method can lead to erroneous results since different producers in the same area can have different $\delta^{15}N$, and because $\delta^{13}C$ and $\delta^{15}N$ values of producers may not be independent (Vander Zanden & Rasmussen 1999). The effectiveness of these studies relies on predictable changes in $\delta^{15}N$ through the trophic links, meaning that initial

differences in $\delta^{15}N$ values of primary producers will be maintained as the energy passes through the trophic chain. Hence, differences in $\delta^{15}N$ can only be used to unambiguously assign and compare trophic positions when comparing organisms deriving nutrition from the same primary producers, or from primary producers with similar $\delta^{13}C$ and $\delta^{15}N$. Establishing a consistent link between $\delta^{13}C$ and $\delta^{15}N$ should therefore be of a great importance, potentially providing a reliable baseline to compare animals' $\delta^{15}N$ values against when estimating trophic positions. Although several studies have used stable isotope analysis to analyse the food sources and trophic relationships in estuarine organisms (e.g. Loneragan et al. 1997, Connolly et al. 2005a), to date no study has documented the existence of a $\delta^{13}C$ vs. $\delta^{15}N$ relationship for estuarine producers.

In this Chapter, stable isotope composition of a wide array of aquatic organisms (including primary producers and consumers) collected from two relatively isolated floodplain pools in the Ross River estuary was analysed to (i) determine if trophic level of consumers can be calculated based on a baseline $\delta^{13}C$-$\delta^{15}N$ relationship, and (ii) to assess the extent to which carbon fixed by terrestrial wetland producers is incorporated into adjacent aquatic food webs in these areas. The two floodplain pools considered were selected for being small and relatively isolated and for differing in type of surrounding wetland vegetation (mangrove vs. salt mash).

2.2. METHODS

2.2.1. Study Area

The study was conducted in the Annandale Wetland on the Ross River floodplain in North Queensland, Australia (19.19'S; 146.44'E) (Figure 2.1). Although most of the river's margins are impacted by urban development, the Annandale Wetland, a vegetated tidal estuarine floodplain of about 0.5 km^2 persists, about 9.3 km upstream from the river mouth and just downstream of Aplin's Weir, an impoundment that separates the Ross River estuary from its freshwater reaches. The wetland includes about 20 unvegetated pools, which are periodically isolated from each other and from the main river.

To assess the extent of incorporation of terrestrial wetland carbon into aquatic food webs, stable isotope composition of organisms collected in two pools differing in surrounding riparian vegetation was analysed: one pool is bordered by a thicket of the mangrove *Aegiceras corniculatum* (Mangrove site), and the other by a grass meadow mainly composed by the C_4 salt couch *Sporobolus virginicus* (*Sporobolus* site) (Fig. 2.1). The Mangrove site has a maximum depth of 0.4 m at low tide, an area of about 700 m^2, and is surrounded by a ~3 m wide band of *A. corniculatum* mangrove. A few *Avicennia marina*, *Rhizophora stylosa* and *Excoecaria agallocha* mangrove trees are also present. Beyond the mangrove band lies a dense meadow of the salt couch *S. virginicus*. The *Sporobolus* site is located about 400 m upstream of the Mangrove site, has a maximum depth of 1.3 m, and an area of about 1250 m^2 at low tide. It is surrounded by a *S. virginicus* and *Sesuvium portulacastrum* salt marsh, the latter in very low densities (<0.01% ground cover). The only mangroves occurring in this area

are a few small *A. corniculatum* trees present along less than 1% of the pool margin. Both pools have muddy unvegetated substrates and in both cases extensive areas of terrestrial wetland vegetation (i.e. mangroves and salt marsh) are submerged at high tides, becoming then accessible to fish and aquatic invertebrates.

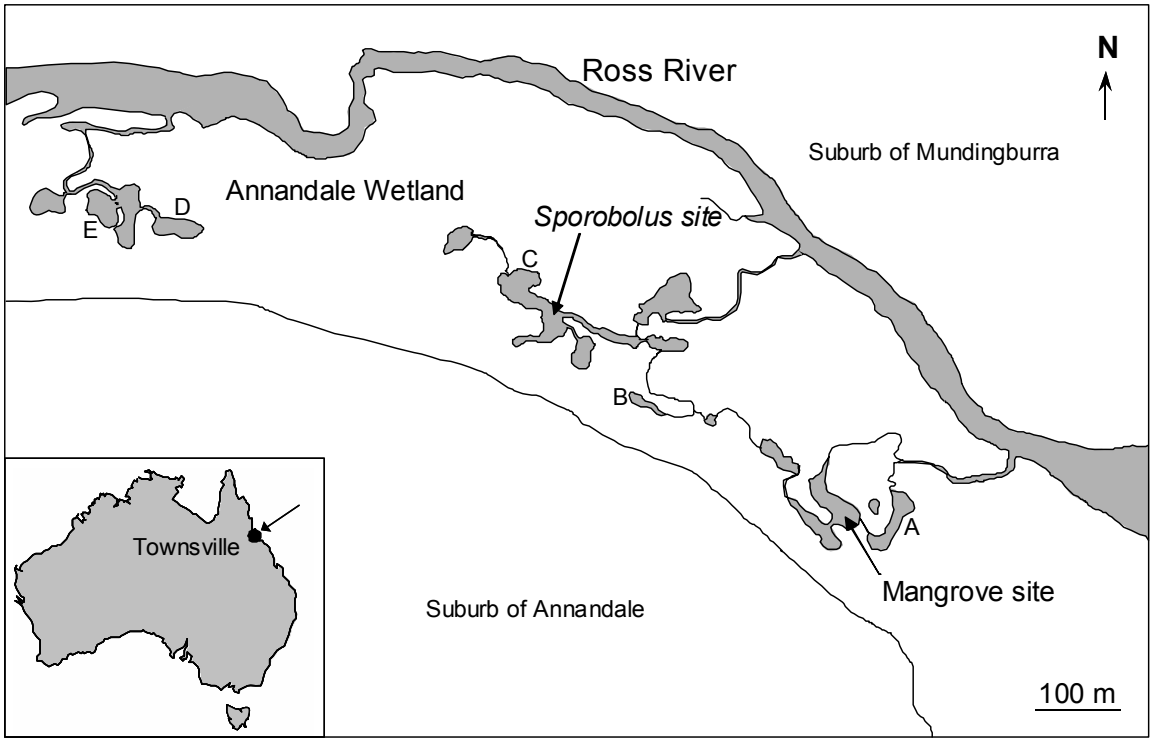

Fig. 2.1. Geographic location and sketch map of the two sampling locations in the Ross River estuarine floodplain. Pools marked with letters (A-E) correspond to locations sampled for the validation of the comparison of $\delta^{13}C$ and $\delta^{15}N$ values of animals between sites (see text).

Both pools are tidal and connected to the main river by narrow (maximum width ~2 m) channels (~270 and ~300 m long) at high tides over 2.4 m. Hence, connections occur daily at most high tides, with the exception of neap tide periods when disconnection periods can last up to five days. However, because the tidal connection level is well

above mean sea level in Townsville (1.9 m), most connection events are brief and connection depths are shallow. Consequently, only the highest tides lead to substantial connection, and currents within the pools are very slow. Thus, these pools correspond to discrete and relatively isolated habitat units that provide limited opportunities of emigration or immigration of organisms. As a result, any variability in carbon or nitrogen isotope composition arising from the movement of animals between habitats is likely to be minimised.

Since carbon isotope composition of C_3 mangroves (low $\delta^{13}C$) is very different from that of the C_4 salt couch *S. virginicus* (high $\delta^{13}C$), if mangrove or salt marsh productivity has a significant contribution to aquatic food webs, it should be reflected in the carbon isotope composition of consumers present at the two locations, which should then exhibit values at the opposite ends of the $\delta^{13}C$ spectrum. On the other hand, if animals rely mostly on aquatic producers, their $\delta^{13}C$ values should be more similar between sites, as estuarine aquatic producers have less variable $\delta^{13}C$ (France 1995b).

2.2.2. Sample Collection

Sampling was conducted in October 2003 (*Sporobolus* site) and October 2004 (Mangrove site). The fact that sampling of the two pools was not contemporaneous does not affect this study since comparisons between pools are confined to the relative relationships between isotope composition of consumers and producers within each pool, and so not affected by temporal factors.

Primary Producers. At each site, fresh leaves from salt marsh plants and mangrove trees located at the edge of the pools were collected. Decomposing mangrove leaves were also picked from the bottoms of the pools and combined for the analysis. Epiphytes were removed from mangrove roots with a pair of forceps at the Mangrove site, and scrapped with a scalpel from *S. virginicus* leaves at the *Sporobolus* site. This material was collected from different locations within each pool and combined for the analysis. In the laboratory, epiphytes were carefully washed with distilled water, and all possible debris and other contaminants removed under a dissecting microscope. These epiphytes mainly comprised filamentous green and red algae and diatoms. Suspended green filamentous algae, only found at the *Sporobolus* site and in very low biomass, were also hand picked for analysis.

Epilithic microalgae were collected from several locations at each site by carefully scrapping greenish pebbles with a scalpel. The scrapped material was then passed through a 125 μm sieve, washed, and collected in a 5 μm GF/F Whatman filter. Inspection under the microscope revealed that it was mainly composed by filamentous green algae, diatoms and cyanobacteria. The material colleted from different locations within each pool was combined for analysis. Two fractions of seston, which included living plankton and suspended particulate organic matter, were collected by pumping water with a bilge pump sequentially through 250 μm and 53 μm plankton nets. Results from these two fractions were considered as indicative of values of plankton.

Microphytobenthos was collected from different locations at each site. At the Mangrove site, where obvious mats of microphytobenthos were present, these were collected by carefully removing the conspicuous layer above the substrate with a spatula. This layer was then washed with distilled water through a 5 μm filter and all sediment particles

removed under a dissecting microscope. At the *Sporobolus* site, microphytobenthos was collected by scrapping the surface sediments with a spatula and filtering the material through a 53 µm sieve into a glass bottle. Colloidal silica (LUDOX^{TM}) was added to a density of 1.2 and about two hours later the surfacing material was collected, washed and collected into a 5 µm GF/F Whatman filter. Contaminants were carefully removed with a pair of fine forceps or a needle under a dissecting microscope. The final fraction was mainly composed of diatoms, other microalgae and some detritus.

Animals. Fish, prawns and shrimps were captured during low tides with a 12 mm mesh seine net, a 18 mm mesh size cast net and a 6 mm mesh strait-bottom dip net. Gastropods and crabs were collected by hand from a range of locations within each pool. Only animals present in the subtidal or intertidal area, i.e. from areas more accessible to fish were collected. Peracarid crustaceans were collected from the substrate by sieving the surface sediment through a 500 µm sieve, and sorting the animals under a dissecting microscope in the laboratory.

Animals were immediately anaesthetized in ice water and frozen as soon as possible (Ethics Approval A852_03). Total lengths (TL) of fish, prawns and shrimps and carapace widths (CW) of crabs were measured to the nearest 1 mm with Vernier callipers. Prawn and shrimps were measured from the tip of the rostrum to the apex of telson, with the exception of *Penaeus* (*Fenneropenaeus*) *merguiensis,* which were measured from the orbital spine to the apex of telson, as the rostrum in this species is frequently broken in the nets.

2.2.3. Sample Processing and Analysis

All samples were processed within a day or two of collection. For fish, decapod crustaceans and large gastropods, each sample comprised only one individual to allow detection of differences in food preference between individuals. An effort was made to capture at least two individuals per species at each site.

Whenever possible, only white muscle tissue was used for the analysis, since it is less variable in $\delta^{13}C$ and $\delta^{15}N$ than other tissue types (Pinnegar & Polunin 1999, Yokoyama et al. 2005). This was excised from the trunk behind the pectoral fin in fish, from the abdominal muscle in prawns and shrimps, from claws and legs of crabs and from the muscular foot of gastropods. Because of their small size, peracarid crustaceans were processed whole after being held in filtered saltwater for 24 h to allow for food material in their digestive system to clear (Frazer 1996). These samples were not acid washed as Bunn et al. (1995) reported ecologically significant shifts and higher variability in $\delta^{15}N$ among treated samples. For small invertebrates (peracarids and small gastropods), several individuals were combined in each sample in order to obtain enough dry material for analysis. Pooling has the advantage of reducing the intraspecific variability in the isotopic values, but loses information on individual differences.

Samples were dried to a constant weight at 60°C, homogenized with a mortar and pestle into a fine powder, and weighed to the nearest 0.00001 g into pre-weighed 5 x 8 mm tin capsules. Capsules were then sealed and compacted into the form of a ball, and sent to the Faculty of Environmental Sciences at Griffith University in Queensland

(Australia), where the isotopic composition was measured with an Isoprime mass spectrometer coupled with an element analyser. Results are expressed as per mil (‰) deviations from the standards, as defined by the equation:

$$\delta^{13}C, \delta^{15}N = [(R_{sample}/R_{reference})-1] \times 10^3$$

, where $R = {}^{13}C/{}^{12}C$ for carbon and ${}^{15}N/{}^{14}N$ for nitrogen.

PDB limestone and atmospheric dinitrogen served as reference standards for $\delta^{13}C$ and $\delta^{15}N$ respectively. Duplicates were run every 12th sample and two standards were also run after every 12 samples. Results had a precision of ± 0.3‰ (1 SD) for $\delta^{13}C$ and ± 0.1‰ (1 SD) for $\delta^{15}N$, which was maintained with reference samples of calibrated Australia National University (ANU) cane sucrose for $\delta^{13}C$, and atmospheric dinitrogen for $\delta^{15}N$. The nitrogen and carbon content of each sample was also measured.

2.2.4. Data Analysis

Trophic Structure

For each site, stable isotope results of both producers and consumers were plotted in $\delta^{13}C$ versus $\delta^{15}N$ diagrams to analyse differences in diet and trophic position between the different animal groups. To facilitate interpretation, the most important primary producers were grouped into logical categories based on their taxonomic and isotopic similarity: **(1) mangroves**; incorporating *A. corniculatum* and *A. marina* mangrove leaves and decomposing A. *corniculatum* leaves; **(2) *S. virginicus***; the C_4 salt couch; **(3) suspended producers**; incorporating seston and suspended green filamentous

algae; **(4) benthic producers**; including epilithic microalgae and microphytobenthos; and **(5) epiphytes**.

Animals were separated by taxa and fish were placed into seven trophic categories: herbivore, detritivore, omnivore, planktivore, macrobenthic carnivore, minor piscivore and major piscivore. For most fish species, the classification was based on Wilson & Sheaves (2001) and Baker & Sheaves (2005). Combined, these two studies (a) included most fish species analysed in this study, (b) consider ontogenetic variations in diet, and (c) included samples from the Ross River estuary, among other areas in North Queensland. When the diet of a fish species is not reported in either of these studies, other pertinent published diet studies were used (see Annex I).

Relationship Between Consumers' $\delta^{15}N$ and Trophic Position

Nitrogen isotope composition is generally used to determine trophic positions. However, for animals collected at the *Sporobolus* site, a linear negative relationship between $\delta^{13}C$ and $\delta^{15}N$ values was visually obvious for several trophic groups, indicating that it is not valid to calculate trophic levels using $\delta^{15}N$ values without taking into consideration $\delta^{13}C$. Therefore, an ANCOVA was run to test if there was a significant and consistent relationship between $\delta^{13}C$ and $\delta^{15}N$, and to test for differences in $\delta^{15}N$ with trophic levels, in order to determine if the $\delta^{13}C$-$\delta^{15}N$ relationship could be used to assign trophic levels. For the purpose of this study, trophic level is defined as the vertical position of an organism in the food web (Post et al. 2000). The ANCOVA model was run based on the average results for each species. Here, $\delta^{15}N$

was the dependent variable (with individual taxa as replicates), trophic level was the fixed factor, and $\delta^{13}C$ the covariate.

Three broad trophic categories were considered: producers, primary consumers and secondary consumers. Only organisms of these trophic categories were considered because they were of known trophic level, and because these three trophic categories correspond approximately to an integer value of trophic level. Piscivores were also present in this pool, but their nitrogen isotope composition did not differ from secondary consumers, indicating that they occupied a similar trophic level in these pools. For the primary consumer group, both invertebrates and fish were considered. This aggregation was only carried out after verifying that no differences in the $\delta^{13}C$ vs. $\delta^{15}N$ relationship were present between the two groups, using ANCOVA.

It was not possible to conduct a similar analysis for organisms from the Mangrove site due to the limited number of species of the different trophic guilds collected at this site.

Sources of Energy

For each site, the relative importance of the different producers to invertebrate and fish consumers was investigated. In an initial approach, the shifts in $\delta^{13}C$ and $\delta^{15}N$ values of producers and consumers that were collected at both sites were compared graphically, and any similarity in direction of change interpreted as a possible result of a trophic relationship.

Because it could be argued that the changes in isotope composition between sites could be a result of a temporal variation in $\delta^{13}C$ or $\delta^{15}N$ values, and not related to the site of collection, two penaeid prawn species, *Penaeus* (*Fenneropenaeus*) *merguiensis* and *Metapenaeus bennetae* (10 - 30 mm TL; *n* = 1 - 6), were sampled at different times from five pools within the Ross River floodplain (Fig. 2.1) to determine if animal carbon or nitrogen isotope composition within each pool varies with time. Collections were carried out between October 2003 and February 2006. Each individual pool was only sampled in a maximum of three occasions separated by a minimum of five months.

The importance of the different producers for animal nutrition was also determined using the IsoSource model (Phillips & Gregg 2003). The IsoSource model calculates the possible combinations of the different autotrophs that can explain the isotopic values of consumers, by analyzing small increments (1% in this case) of each of the autotrophs' possible contributions, from 0 to 100%. The combinations that correspond to a result within a small distance of that of the consumer are considered feasible solutions, with the final results being a distribution of feasible solutions for each autotroph (Phillips & Gregg 2003). A mass balance tolerance level of 0.1‰ was used, as it is considered to be appropriate for diet studies, incorporating an uncertainty of the same magnitude of the measurement errors and source variability (Phillips & Gregg 2001).

Related producers, when presenting similar isotopic composition, were grouped to minimize the number of sources and hence simplify and narrow the range of possible solutions (Phillips et al. 2005). Therefore, the five producer categories mentioned

above were used for the models. Mangroves were only considered for the analysis of the Mangrove site since very few mangrove trees were present at the *Sporobolus* site, and hence mangrove carbon was not likely to be significantly incorporated by aquatic organisms.

Prior to running the models, isotopic values of consumers were corrected for trophic fractionation. A $\delta^{13}C$ fractionation of 1‰ and a $\delta^{15}N$ fractionation of 3‰ was assumed, as these values have been found to be appropriate estimates when analysis is conducted on non-acid treated white muscle tissue (McCutchan Jr et al. 2003, Vanderklift & Ponsard 2003). IsoSource results are summarised in tables where the median and 1^{st}-99^{th} percentile of putative contribution are indicated. IsoSource results are not presented in the form of the classic histograms of distribution of feasible contributions because the large number of species analysed would require a great volume of graphic output without adding to the interpretation.

The IsoSource model was run for decapod crustaceans and fish, but not for other invertebrate species, as $\delta^{15}N$ fractionation can be very variable in invertebrates of low trophic levels (Vander Zanden & Rasmussen 2001, McCutchan Jr et al. 2003, Vanderklift & Ponsard 2003), depending both on taxa and type of diet (Adams & Sterner 2000, Scheu & Folger 2004, Yokoyama et al. 2005, Goedkoop et al. 2006). This high variability in $\delta^{15}N$ trophic fractionation in primary consumers results from final fractionation depending on both metabolic and assimilative fractionation, which can differ according to the diet (Vander Zanden & Rasmussen 2001). In higher consumers however, trophic fractionation depends principally on metabolic fractionation, and because animal material is biochemically more uniform, results are more consistent (Vander Zanden & Rasmussen 2001). For these animal groups, the IsoSource was not

run based solely on $\delta^{13}C$ values because several producer categories had similar $\delta^{13}C$, and hence the models would lead to inconclusive results.

2.3. RESULTS

2.3.1. Stable Isotope Results

Producers

At both sites, producers differed in both $\delta^{13}C$ (Table 2.1) and $\delta^{15}N$ (Table 2.2). Mangroves had the lowest $\delta^{13}C$ at both sites, and the remaining producers were relatively enriched in ^{13}C (Table 2.1). The dominant salt marsh plant *S. virginicus* was among the producers with the highest $\delta^{13}C$ at both the Mangrove and the *Sporobolus* sites. At the Mangrove site, $\delta^{13}C$ ranged between -29.7‰ for mangroves and -15.8‰ for epilithic microalgae (Table 2.1). A similar range was present at the *Sporobolus* site, where $\delta^{13}C$ ranged from -27.4 to -13.3‰. $\delta^{15}N$ had narrower ranges of distribution, ranging from 0.8 to 7.0‰ at the Mangrove site, and from 0.9 to 5.9‰ at the *Sporobolus* site (Table 2.2).

Consumers

A total of 11 invertebrate and 11 fish species were collected at the Mangrove site, and 20 invertebrate and 31 fish species at the *Sporobolus* site. At each site, animals were well separated in $\delta^{13}C$ and $\delta^{15}N$ (Tables 2.3 and 2.4; Fig. 2.2).

Fish tended to have higher $\delta^{15}N$ values than invertebrates (Fig. 2.2) and among invertebrates, decapod crustaceans had the highest $\delta^{15}N$. Similarly, among fish, species of higher trophic categories (based on diet information from the literature) were in general more enriched in ^{15}N (Tables 2.3 and 2.4). However, at the *Sporobolus* site, major piscivores, which included the barramundi *Lates calcarifer,* the barracuda *Sphyraena barracuda* and the bigeye trevally *Caranx sexfasciatus*, had $\delta^{15}N$ values similar to planktivores and macrobenthic carnivores (Fig. 2.2), indicating similar trophic levels.

Table 2.1. Carbon isotope composition of producers collected at the Mangrove and *Sporobolus* sites. For *n* = 2 range is indicated, and for *n* > 2 mean (± SE) is presented.

Producer	*n*	$\delta^{13}C$ (‰)
Mangrove site		
Decomposing *Aegiceras corniculatum* leaves	2	-29.7 to -28.3
Sesuvium portulacastrum	1	-27.6
Avicennia marina	3	-27.0 ± 0.9
Aegiceras corniculatum	1	-26.5
Epiphytes	1	-22.3
Seston (250 - 500 µm)	1	-19.1
Seston (53 - 150 µm)	1	-19.0
Microphytobenthos	3	-16.5 ± 0.3
Sporobolus virginicus	2	-16.3 to -16.0
Epilithic microalgae	2	-15.9 to -15.8
***Sporobolus* site**		
A. corniculatum	2	-27.4 to -26.3
Decomposing *A. corniculatum* leaves	4	-27.0 ± 0.5
S. portulacastrum	2	-27.0 to -25.2
Seston (250 - 500 µm)	1	-20.6
Seston (53 - 250 µm)	1	-19.3
Epiphytes	1	-19.0
Green filamentous algae	1	-18.8
S. virginicus	2	-15.7 to -15.4
Epilithic microalgae	1	-15.0
Microphytobenthos	2	-14.2 to -13.3

In the Mangrove site, fish $\delta^{15}N$ ranged from 6.0‰ for the phytodetritivore *Valamugil buchanani* to 11.9‰ for the planktivore *Ambassis nalua* (Table 2.3), a difference of 5.9‰. If a $\delta^{15}N$ fractionation value of 3‰ is assumed, this difference corresponds to ~2 trophic steps, suggesting that the food web has ~4 trophic levels. For the *Sporobolus* site, there was a difference of 6.4‰ between the herbivore *Selenotoca multifasciata* and the planktivore *A. nalua* (Table 2.4), suggesting a slightly longer food web with ~4.1 trophic levels. However, for this site a more precise estimate of trophic length based on a $\delta^{13}C$-$\delta^{15}N$ relationship was possible (see Section 2.3.2).

Table 2.2. Nitrogen isotope composition of producers collected at the Mangrove and *Sporobolus* sites. For $n = 2$ range is indicated, and for $n > 2$ mean ± SE is presented.

Producer	*n*	$\delta^{15}N$ (‰)
Mangrove site		
Seston (250 - 500 µm)	1	0.8
Seston (53 - 150 µm)	1	1.9
Microphytobenthos	3	2.9 ± 0.3
Epilithic microalgae	2	3.0 to 3.2
Decomposing *Aegiceras corniculatum* leaves	2	4.1 to 5.1
Epiphytes	1	4.4
Sporobolus virginicus	2	4.6 to 5.1
Sesuvium portulacastrum	1	5.8
Avicennia marina	3	5.9 ± 0.3
Aegiceras corniculatum	1	7.0
***Sporobolus* site**		
Microphytobenthos	2	0.9 to 1.9
Seston (53 - 250 µm)	1	1.1
S. portulacastrum	2	1.3 to 3.6
Epilithic microalgae	1	2.1
Seston (250 - 500 µm)	1	2.4
Green filamentous algae	1	2.8
S. virginicus	2	3.0 to 4.6
A. corniculatum	2	3.3 to 4.0
Decomposing *A. corniculatum* leaves	4	3.8 ± 0.4
Epiphytes	1	5.9

Table 2.3. Size range and carbon and nitrogen isotopic composition (mean ± SE) of organisms collected at the Mangrove site. Sizes indicate total length for fish (in 5 mm size classes), prawns, shrimps and gastropods. *n* = number of samples analysed. When *n* = 2, the range is presented. Numbers between brackets indicate number of individuals included in the samples composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Invertebrates				
Gastropods				
Aplysia dactylomela	2	70-86	-22.6 to -22.2	9.2 to 9.6
Neritina violacea	1(5)	18	-14.7	1.8
Telescopium telescopium	1(3)	70	-19.0	6.3
Terebralia palustris	1(3)	70	-16.1	5.1
Peracarid crustaceans				
Amphipods f. Aoridae	1(~50)	-	-24.0	5.3
Apseudes sp.	1(~50)	-	-20.6	5.3
Tanais sp.	1(~20)	-	-17.6	3.4
Decapod crustaceans				
Metapenaeus bennetae	3	40-45	-17.6 ± 0.6	7.0 ± 0.3
Palaemonetes atrinubes	1	20	-17.4	8.1
Penaeus esculentus	3	25-45	-18.7 ± 0.6	6.2 ± 0.3
Penaeus merguiensis	4	30-40	-15.6 ± 0.2	8.4 ± 0.7
Fish				
Detritivores				
Liza subviridis	2	100-115	-19.0 to -18.6	8.7 to 9.3
Valamugil buchanani	1	65	-15.4	6.0
Omnivores				
Tetractenos hamiltoni	1	35	-18.1	9.6
Planktivores				
Ambassis nalua	1	40	-19.5	12.0
Leiognathus equulus	1	30	-17.2	11.2
Macrobenthic carnivores				
Acanthopagrus australis	1	30	-18.0	10.7
Acanthopagrus berda	2	30-35	-19.6 to -19.1	10.5 to 12.3
Acanthopagrus spp. (juv)	2	20	-19.9 to -18.7	10.4 to 11.0
Gerres filamentosus	1	60	-16.7	10.5
Platycephalus fuscus	1	35	-16.8	10.8
Psammogobius biocellatus	1	30	-20.1	7.1
Unknown feeding guild				
Unidentified Gobiidae	1	25	-13.7	6.5

Table 2.4. Size range and carbon and nitrogen isotopic composition (mean ± SE) of organisms collected at the *Sporobolus* site. Sizes indicate total length for fish (in 5 mm size classes), prawns, shrimps and gastropods, and carapace width for crabs. *n* = number of samples analysed. When *n* = 2, the range is presented. Numbers between brackets indicate number of individuals included in the samples composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Invertebrates				
Gastropods				
Aplysia dactylomela	2	44-48	-17.5 to -17.4	6.9 to 7.5
Nerita polita	1(5)	14	-13.5	5.1
Neritina violacea	1(5)	18	-14.2	5.9
Onchidium daemelii	2	23-30	-12.8 to -11.3	4.3 to 4.4
Telescopium telescopium	1(3)	75	-15.3	5.9
Terebralia palustris	1(3)	65	-15.2	4.2
Peracarid crustaceans				
Tanaids f. Leptocheliidae	2(~50)	-	-17.3 to -16.8	5.8 to 5.9
Decapod crustaceans				
Acetes sibogae	1(4)	13	-19.6	8.5
Clibanarius taeniatus	1	12	-13.2	5.3
Metapenaeus bennetae	3	20-25	-14.7 ± 0.2	7.9 ± 0.1
Metopograpsus frontalis	2	11	-15.5 to -14.9	5.7 to 5.8
Palaemonetes atrinubes	5	10-18	-15.1 ± 0.2	9.0 ± 0.1
Parasesarma erythrodactyla	2	10-25	-14.8 to -13.8	6.4 to 6.7
Penaeus esculentus	3	20-30	-16.4 ± 0.3	7.7 ± 0.4
Penaeus merguiensis	3	35-40	-13.8 ± 0.4	8.2 ± 0.2
Penaeus monodon	3	20-30	-16.7 ± 0.1	8.5 ± 0.1
Portunus pelagicus	1	70	-16.8	8.9
Scylla serrata	2	100-127	-15.3 to -14.1	9.5 to 10.5
Uca coarctata	3	13-15	-12.4 ± 0.2	6.4 ± 0.1
Unidentified alpheid shrimp	2	6-7	-19.1 to -18.2	8.9 to 9.1
Fish				
Herbivores				
Selenotoca multifasciata	5	20-125	-17.1 ± 1.4	5.1 ± 0.5
Siganus lineatus	2	35-50	-19.5 to -19.4	7.3 to 8.6
Detritivores				
Liza subviridis	1	100	-18.9	9.9
Valamugil buchanani	2	35-50	-16.8 to -16.8	7.7 to 8.8
V. buchanani	2	75-80	-15.0 to -13.8	6.4 to 6.6
Omnivores				
Chelonodon patoca	2	55-60	-17.8 to -18.2	8.0 to 8.5
Planktivores				
Ambassis nalua	3	20-40	-18.5 ± 0.5	11.5 ± 0.6
Leiognathus equulus	3	35-40	-14.9 ± 0.1	9.5 ± 0.1
L. equulus	1	80	-16.9	11.1

Table 2.4. (cont.) Size range and carbon and nitrogen isotopic composition (mean ± SE) of organisms collected at the *Sporobolus* site. Sizes indicate total length for fish (in 5 mm size classes), prawns, shrimps and molluscs, and carapace width for crabs. *n* = number of samples analysed. When *n* = 2, the range is presented. Numbers between brackets indicate number of individuals included in the samples composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Fish				
Planktivores				
Leiognathus decorus	1	45	-17.7	10.6
Pseudomugil signifer	2	10-25	-16.9 to -17.8	10.4 to 11.6
Macrobenthic carnivores				
Acanthopagrus australis	6	40-90	-15.1 ± 0.3	10.2 ± 0.1
Acanthopagrus berda	4	35-55	-15.6 ± 0.1	10.5 ± 0.1
Arothron manilensis	5	40-70	-18.2 ± 0.3	9.8 ± 0.3
Acentrogobius viridipunctatus	1	20	-15.3	10.1
Cynoglossus bilineatus	1	35	-13.1	8.3
Gerres filamentosus	5	55-60	-15.9 ± 0.4	10.4 ± 0.1
Glossogobius sp.	1	100	-16.3	9.5
Periophthalmus argentilineatus	1	25	-13.3	10.2
Sillago analis	5	105-	-14.8 ± 0.2	9.5 ± 0.1
Sillago burrus	2	90-95	-13.8 to -12.9	9.9 to 10.7
Sillago sihama	3	45-65	-14.3 ± 0.3	9.0 ± 0.1
Minor piscivores				
Butis butis	2	50	-18.6 to -18.5	9.4 to 9.6
Lutjanus argentimaculatus	1	80	-16.6	11.5
Lutjanus russellii	2	65-80	-17.9 to -17.6	9.3 to 9.7
Platycephalus fuscus	3	100-	-15.5 ± 0.1	10.5 ± 0.2
Platycephalus endrachtensis	3	95-115	-16.2 ± 0.4	9.9 ± 0.4
Psammogobius biocellatus	6	50-60	-15.6 ± 0.7	8.4 ± 0.4
Terapon jarbua	2	75	-16.6 to -13.8	9.7 to 10.9
Major piscivores				
Caranx sexfasciatus	2	45-50	-18.5 to -15.8	8.4 to 9.4
Lates calcarifer	1	390	-17.1	11.1
Sphyraena barracuda	1	100	-16.2	11.4
Unknown feeding guild				
Unidentified Gobiidae	1	25	-14.0	6.8

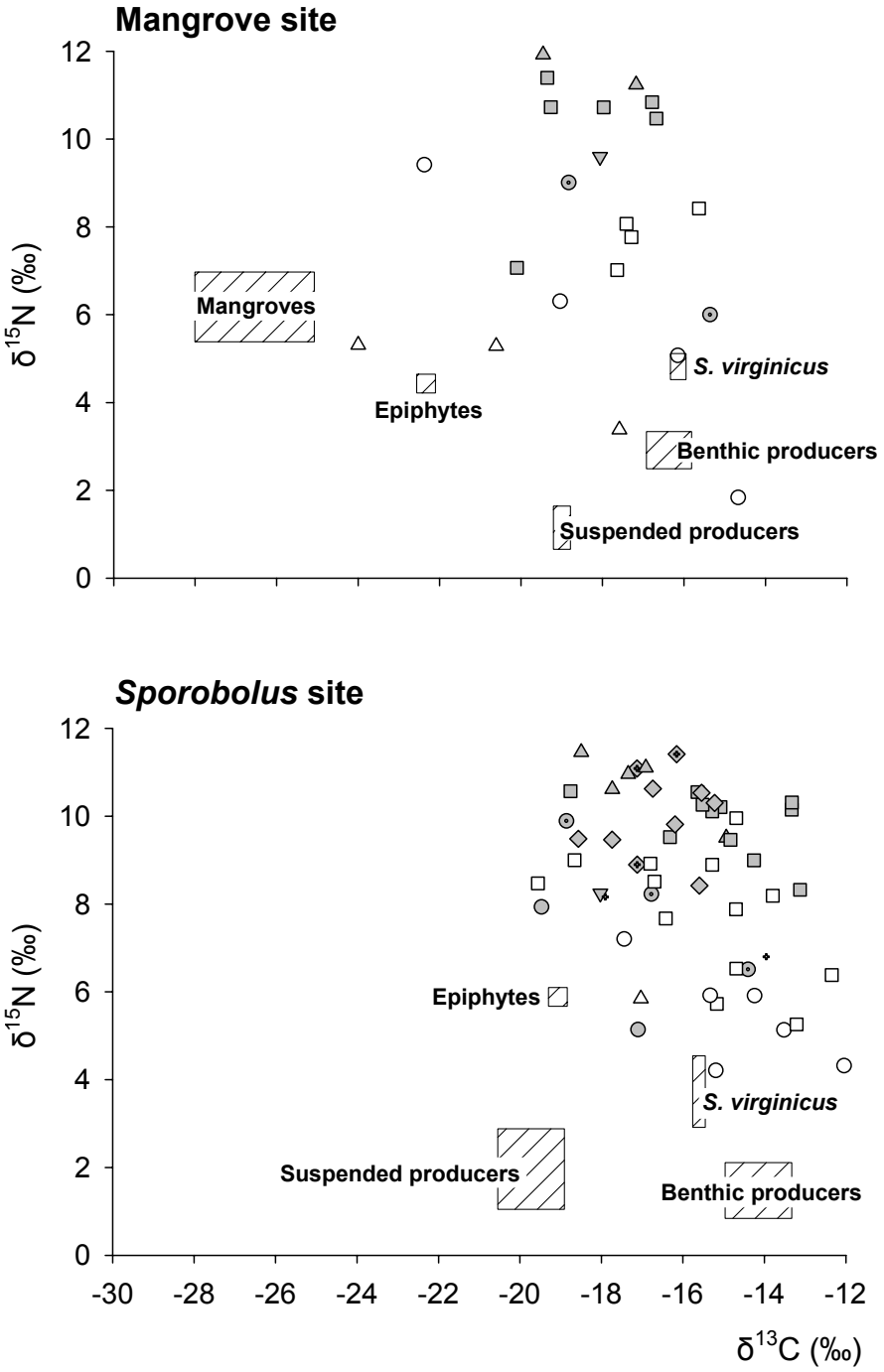

Fig. 2.2. Mean isotopic composition of producers (boxes), invertebrates (white symbols) and fish (grey symbols) from the two Ross River floodplain pools. Source categories (as defined in text) are plotted as boxes delimiting isotopic values of all producers within the category. Invertebrates: ○- molluscs; △- peracarid crustaceans; □ - decapod crustaceans. Fish: ○ - herbivores; ⊙ - detritivores; ▽– omnivores; △ - planktivores; ▣ - macrobenthic carnivores; ◇- minor piscivores; ◈ - major piscivores; ⋆ - unknown diet.

2.3.2. Relationship Between $\delta^{15}N$ and Trophic Position

Since a linear negative relationship between $\delta^{13}C$ and $\delta^{15}N$ was visually detected for several trophic groups at the *Sporobolus* site, the relationship between $\delta^{15}N$ and trophic position was further studied for this site. Producers included *S. virginicus* and all aquatic producers with the exception of suspended producers, since planktonic organisms have rapid carbon and nitrogen turnover and can be temporarily variable in $\delta^{13}C$ and $\delta^{15}N$ (Gearing et al. 1984, Gu et al. 1994, Cabana & Rasmussen 1996). Primary consumers included the herbivorous fish *Siganus lineatus* and the phytodetritivores *V. buchanani* and *Liza subviridis*, as well as all second trophic level invertebrates (all invertebrates with the exception of penaeid prawns and the portunid crabs *Scylla serrata* and *Portunus pelagicus*) (Table 2.5). *S. multifasciata* was not included because individuals of this species were very variable in $\delta^{13}C$, a variability that is present across estuarine systems in tropical Queensland (unpubl. data). Secondary consumers included macrobenthic carnivores and planktivores (Table 2.5). In this category, only fish species were included.

Since primary consumers included both invertebrates and fish, an ANCOVA was used to test for differences in the $\delta^{13}C$-$\delta^{15}N$ relationship between these groups, after the assumptions of homogeneity of variances (p = 0.7932) and parallelism between lines (p = 0.9300) were met. This resulted in a significant model (R = 0.84, $F_{(2, 14)}$ = 16.17, p = 0.0002), with an effect of $\delta^{13}C$ on $\delta^{15}N$ (p = 0.0007), but no effect of taxon (invertebrate vs. fish) (p = 0.1047), indicating that the relationship between $\delta^{13}C$ and $\delta^{15}N$ was similar for fish and for invertebrate primary consumers. Therefore, these two groups were combined into the primary consumers category in the analysis of the entire data set.

Table 2.5. Primary and secondary consumers considered for the analysis of the relationship between consumer's $\delta^{15}N$ and trophic position. Diet type and reference are also indicated. Bact = bacteria eaters; Detr = detritivores; Herb = herbivores; Ins = insectivores; MBC = macrobenthic carnivores; PDetr = phytodetritivores; Plank = planktivores.

Species	Diet type	References
Primary Consumers		
Invertebrates		
Aplysia dactylomela	Herb	Rogers et al. (2003)
Nerita polita	Bact	Salvat & Denizot (1982); Camilleri (1992)
Neritina violacea	Bact	Camilleri (1992)
Onchidium daemelii	Bact	Camilleri (1992); Bouillon et al. (2002a)
Telescopium telescopium	Herb/Bact	Meziane & Tsuchiya (2002)
Terebralia palustris	Herb/Bact	Meziane & Tsuchiya (2002); Fratiniet al.(2004)
Tanaids f. Leptocheliidae	Detr	Holdich & Jones (1983)
Acetes sibogae	Plank	Coman et al. (2006)
Clibanarius taeniatus	Detr	Kunze & Anderson (1979)
Metopograpsus frontalis	Herb	Camilleri (1992)
Parasesarma erythrodactyla	Herb	Camilleri (1992)
Uca coarctata	Herb/Bact	France (1998); Meziane et al. (2002)
Fish		
Siganus lineatus	Herb	Choat & Clements (1998)
Liza subviridis	PDetrit	Sheaves & Johnston (2006a)
Valamugil buchanani	PDetrit	Wilson & Sheaves (2001); Moorthy et al. (2002)
Secondary Consumers		
Acanthopagrus australis	MBC	Baker & Sheaves (2005)
A. berda	MBC	Baker & Sheaves (2005)
Acentrogobius viridipunctatus	MBC	Baker & Sheaves (2005)
Ambassis nalua	Plk	Wilson & Sheaves (2001); Baker & Sheaves (2005)
Arothron manilensis	MBC	Kulbicki et al. (2005)
Cynoglossus bilineatus	MBC	Blaber (1980)
Gerres filamentosus	MBC	Wilson & Sheaves (2001)
Glossogobius sp.	MBC	Geevarghese (1983)
Leiognathus equulus	Plk	Wilson & Sheaves (2001)
L. decorus	Plk	Wright (1989); Hajisamae et al. (2004)
Periophthalmus argentilineatus	MBC	Blaunstein et al. (1996)
Pseudomugil signifer	Plk /Insect	Booth et al. (1985); Morton et al. (1988)
Sillago analis	MBC	Wilson & Sheaves (2001)
S. burrus	MBC	Wilson & Sheaves (2001)
S. sihama	MBC	Wilson & Sheaves (2001)

In the full data set, isotope composition of the three trophic groups (producers, primary consumers, secondary consumers) had homogeneous variances (p = 0.1610) and formed parallel lines (p = 0.4540). Hence, an ANCOVA was computed, resulting in a significant model (R = 0.90, $F_{(3, 35)}$ = 109.932, p = 0.0000) with significant effects of $\delta^{13}C$ on $\delta^{15}N$ (n = 39; df = 1; F = 44.56; p = 0.0000), indicating a strong linear relation between $\delta^{13}C$ and $\delta^{15}N$, and a significant effect of trophic group on $\delta^{15}N$ (n = 39; df = 2; F = 156.70; p = 0.0000). Since the three lines were parallel, trophic group had an effect only on the intercept of the $\delta^{13}C$-$\delta^{15}N$ relationship, i.e. on the height of the regression line, which indicates trophic position. Consequently, for this pool, primary producers or primary consumers could be used as a baseline trophic level to determine a species' trophic position by analysing the difference in $\delta^{15}N$ between this species and the baseline, while considering the relationship with $\delta^{13}C$.

In this case, primary consumers were 3.9‰ higher in $\delta^{15}N$ than primary producers, and secondary consumers were 3.6‰ higher in $\delta^{15}N$ than primary consumers (Fig. 2.3). These values correspond to a distance of 1.3 trophic levels between producers and primary consumer, and 1.2 trophic steps between primary consumers and secondary consumers, if a $\delta^{15}N$ fractionation of 3‰ is assumed. Since piscivores were no more enriched in ^{15}N than secondary consumers (macrobenthic carnivores and planktivores) (Fig. 2.2), these results suggest that food web in this area has only ~3.5 trophic levels, or alternatively that $\delta^{15}N$ trophic fractionation in this system is around 3.7‰, and that the trophic web only has ~3 trophic levels. Both these values of trophic length are however lower than the 4.1 calculated based on the difference in $\delta^{15}N$ between *S. multifasciata* and *A. nalua* (see Section 4.2.1).

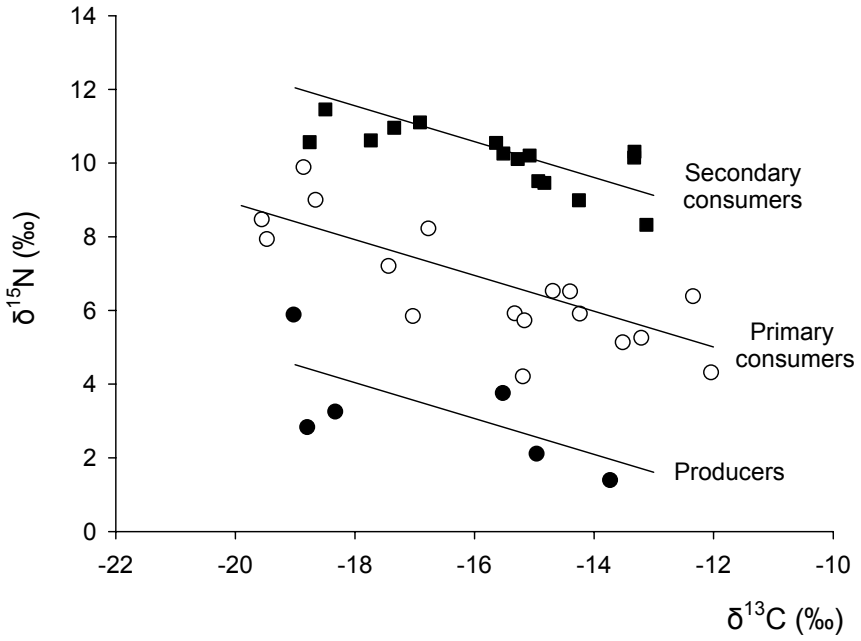

Fig. 2.3. Relationship between $\delta^{13}C$, $\delta^{15}N$ and trophic position for primary producers, primary consumers and secondary consumers found at the *Sporobolus* site. Each symbol represents the mean for a taxonomic group. Lines represent best fit for each trophic group, following results from ANCOVA: primary producers (●): $\delta^{15}N = -0.486 \times \delta^{13}C - 4.72$; primary consumers (○): $\delta^{15}N = -0.486 \times \delta^{13}C - 0.83$; secondary consumers (■): $\delta^{15}N = -0.486 \times \delta^{13}C + 2.84$.

2.3.3. Sources of Energy

At both sites, different species had distinct carbon and nitrogen isotope composition (Tables 2.3 and 2.4), suggesting the dependence on different sources of energy.

2.3.3.1 Variation of $\delta^{13}C$ and $\delta^{15}N$ Values Between Sites

Producers

Among producers, epiphytes and microphytobenthos shifted in $\delta^{13}C$ from lower values at the Mangrove site to higher values at the *Sporobolus* site (Fig. 2.4). This shift was coupled with an increase in $\delta^{15}N$ for epiphytes, and a decrease in $\delta^{15}N$ for microphytobenthos. Epilithic microalgae also shifted towards higher $\delta^{13}C$ values at the *Sporobolus* site, although the shift was not as pronounced as for epiphytes and microphytobenthos (Fig. 2.4). As microphytobenthos, epilithic microalgae also showed a small shift in $\delta^{15}N$ towards lower values. Suspended producers and *S. virginicus* did not show any change in $\delta^{13}C$ or $\delta^{15}N$ between sites (Fig. 2.4). Mangroves were not included in this comparison because these were only present in very low numbers at the *Sporobolus* site, and hence could not be of importance for animals at this site.

Consumers

Validation of the comparison of animals' $\delta^{13}C$ and $\delta^{15}N$ values between sites. To determine if differences in animals' isotope composition between pools were a result of the effect of site or simply a result of a temporal variability in isotope composition, prawns were collected from five floodplain pools at different times, and their $\delta^{13}C$ and $\delta^{15}N$ values compared between times. In most cases, within a pool, carbon and nitrogen isotope composition of prawn juveniles were constant through time (Fig. 2.5), indicating that $\delta^{13}C$ and $\delta^{15}N$ values could be validly compared between the Mangrove and *Sporobolus* pools, even though collections were carried out in different seasons and in different years. In some cases however, isotope composition of animals

collected in the same pool differed between times (Fig. 2.5). This was the case of *P. merguiensis* juveniles collected in pools A and C and *M. bennetae* from pool C. These differences are likely to be a result of seasonal variations in sources of energy, since pools were sampled in different seasons (March and October), or a result of a recent migration of animals into the pools.

Invertebrates. A shift in $\delta^{13}C$ from lower values at the Mangrove site to higher values at the *Sporobolus* site was observed for most invertebrate species (Fig. 2.4). The herbivorous sea hare *Aplysia dactylomela* and the detritus feeder *Telescopium telescopium* showed the strongest shift (Fig. 2.4). The caridean shrimp *Palaemonetes atrinubes* and the penaeid prawns *Penaeus esculentus*, *P. merguiensis* and *M. bennetae* showed a similar shift, although less pronounced. For these species, the shift in isotopic composition seems to track epiphytes, suggesting that these producers may have an important contribution to these invertebrates in this area. Although these changes were also similar to those shown by microphytobenthos, only *P. merguiensis* had $\delta^{13}C$ values that could result from the consumption of these producers. For the remaining species, microphytobenthos were too enriched in ^{13}C to be the main contributors (Fig. 2.4). However, a combination of epiphytes and microphytobenthos could explain the similar shifts between these producers and consumers.

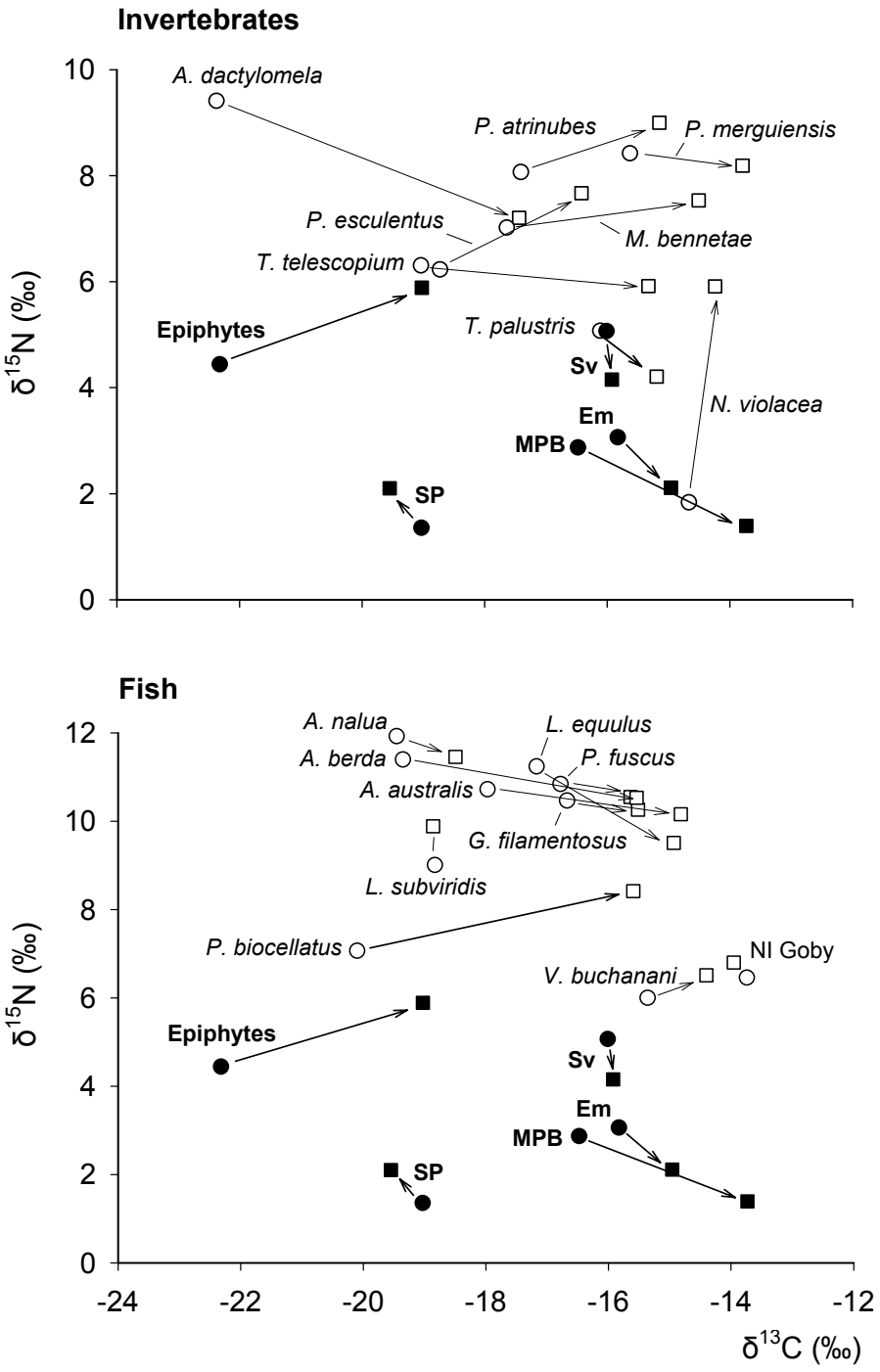

Fig. 2.4. Mean $\delta^{13}C$ and $\delta^{15}N$ values of producer categories (black symbols), and animals (white symbols) collected at the Mangrove (circles) and *Sporobolus* (squares) sites, illustrating the difference between sites. Producers: Em = epilithic microalgae; MPB = microphytobenthos; SP = suspended producers; Sv = *S. virginicus*. Note the difference in the *y* axis.

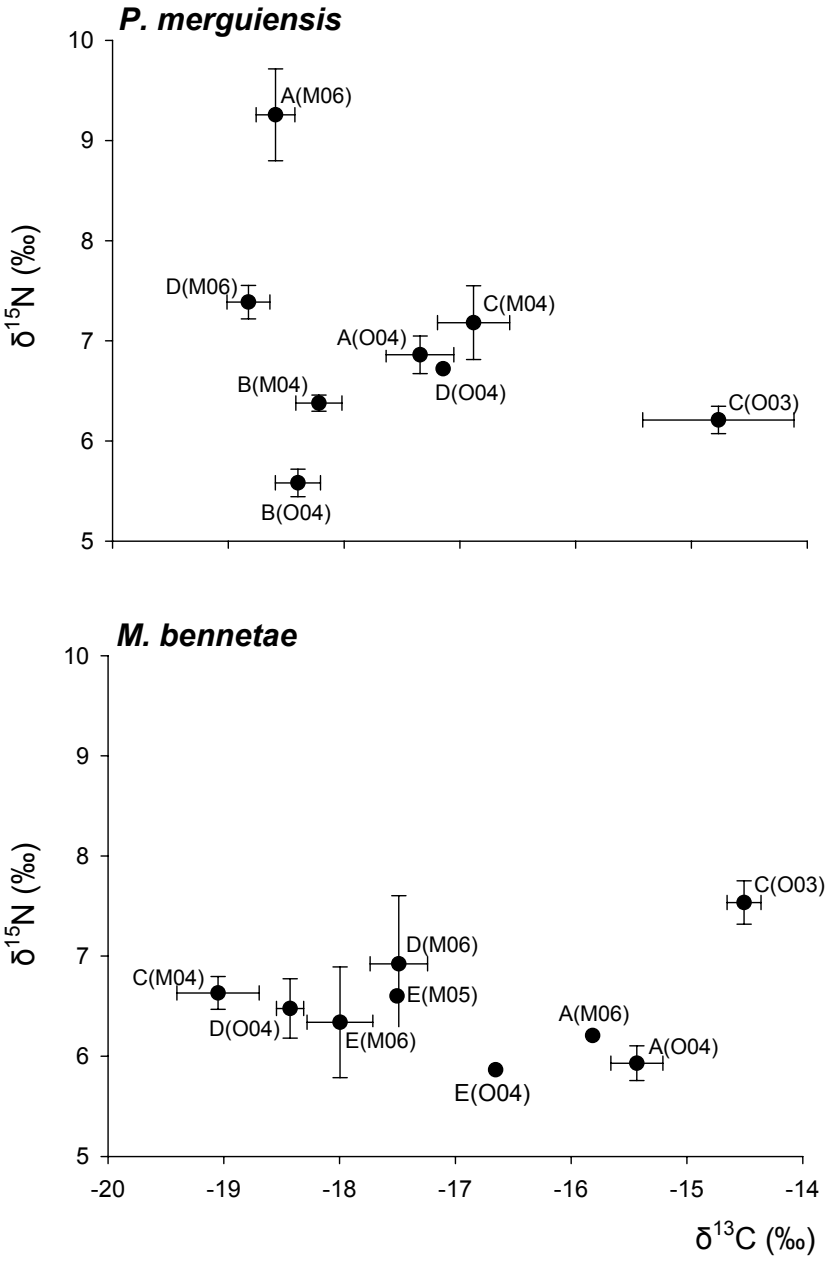

Fig. 2.5. Carbon and nitrogen isotope composition (mean ± SE) of *P. merguiensis* and *M. bennetae* prawns collected from five semi-isolated pools in the Ross River floodplain. Site of collection is indicated by letters (A-E) (refer to the map on Fig. 2.1). Date of collection is in brackets: O03 = October 2003; M04 = March 2004; O04 = October 2004; M06 = March 2006.

Fish. As with invertebrates, most fish species also showed a shift in $\delta^{13}C$ from lower values at the Mangrove site to higher values at the *Sporobolus* site (Fig. 2.4). Differences in $\delta^{13}C$ were larger for *Acanthopagrus berda, Acanthopagrus australis* and *Psammogobius biocellatus* (Fig. 2.4). The first two species had similar $\delta^{15}N$ values between sites, while *P. biocellatus* had $\delta^{15}N$ 1.3‰ higher at the *Sporobolus* site. As with most invertebrates, $\delta^{13}C$ values of these fish species appear to be tracking epiphytes. *Leiognathus equulus*, *Platycephalus fuscus* and *Gerres filamentosus* also shifted towards higher $\delta^{13}C$ at the *Sporobolus* site, although in these cases the differences were less pronounced (Fig. 2.4).

Only for the planktivorous *A. nalua,* the phytodetritivorous *L. subviridis* and *V. buchanani* and the unidentifiable goby were $\delta^{13}C$ and $\delta^{15}N$ values similar between sites (Fig. 2.4). For the first two species this could be a reflection of a diet ultimately based on suspended producers, given the similarity in $\delta^{13}C$ between these species and suspended producers (Fig. 2.4). In addition, these two species, as suspended producers, also showed no change in $\delta^{13}C$ or $\delta^{15}N$ between sites. On the other hand, *V. buchanani* and the unidentifiable goby had higher $\delta^{13}C$ values, closer to *S. virginicus*, microphytobenthos and epilithic microalgae (Fig. 2.4). The goby did not show any change in $\delta^{13}C$ or $\delta^{15}N$ between sites, indicating that *S. virginicus* could be an important component of its diet. In contrast, *V. buchanani* shifted towards slightly higher $\delta^{13}C$ values at the *Sporobolus* site, which could reflect dependence on epilithic microalgae, which changed in a similar way (Fig. 2.4).

2.3.3.2. IsoSource Mixing Model

Mangrove site. Although the IsoSource model was not computed for invertebrate primary consumers due to the high variability in $\delta^{15}N$ fractionation among these species, in certain cases it was possible to determine the importance of the different producers based on the similarity in $\delta^{13}C$ values. For example, Aorid amphipods had the lowest $\delta^{13}C$ among invertebrates (Table 2.3), with values that indicated mangroves as important contributors, since no other producers had similar or lower $\delta^{13}C$ values (Table 2.1). At the other end of the $\delta^{13}C$ spectrum, *Neritina violacea* was the most ^{13}C enriched species (Table 2.3), with $\delta^{13}C$ values close to benthic producers such as microphytobenthos and epilithic microalgae (Table 2.1), suggesting a major dependence on these sources. Other invertebrate species had intermediate values (Table 2.3) and hence it was not possible to determine the contribution of the different producers.

Prawns and shrimps also had distinct $\delta^{13}C$ and $\delta^{15}N$ values (Table 2.3). For these species however, the IsoSource model could be computed and lead to different results for different species (Table 2.6). Mangroves appeared to make a clear contribution (minimum potential contribution >0%) only for *P. esculentus*, while *S. virginicus* appeared as a crucial source of carbon only for *P. merguiensis* (Table 2.6). However, a variety of aquatic producers also appeared as important contributors for all species (Table 2.6).

Table 2.6. IsoSource results for decapods and fish collected at the Mangrove site. Values for each source represent the median followed by the 1st to 99th percentile range of potential contribution. For each animal species, producers with a necessary contribution (minimum potential contribution >0%) are in bold. Trophic level = trophic level considered for the IsoSource model. BP = benthic producers; Epiph = epiphytes; Mangr = mangroves; SP = suspended producers; *S. virg* = *S. virginicus*.

Species	Trophic level	Sources				
		Mangr	*S. virg*	SP	BP	Epiph
Invertebrates						
Decapod crustaceans						
Metapenaeus bennetae	2.5	6; 0-13	9; 0-22	**58; 47-69**	17; 0-36	11; 0-24
Palaemonetes atrinubes	2.5	10; 0-22	20; 0-44	18; 0-38	35; 0-71	18; 0-41
Penaeus esculentus	2.5	**12; 6-15**	1; 0-4	**72; 77-86**	2; 0-7	4; 0-15
Penaeus merguiensis	2.5	3; 0-8	**52; 36-71**	10; 0-26	**29; 1-53**	6; 0-15
Fish						
Detritivores						
Liza subviridis	2.3	**33; 29-35**	**62; 59-65**	0; 0-2	0; 0-5	0; 0-11
Valamugil buchanani	2.0	0; 0-2	5; 0-13	3; 0-8	**91; 79-98**	1; 0-3
Omnivores						
Leiognathus equulus	3.0	**23; 16-28**	**66; 61-72**	1; 0-4	3; 0-10	1; 0-22
Tetractenos hamiltoni	2.5	**29; 26-30**	**68; 66-70**	0; 0-1	0; 0-3	2; 0-7
Planktivores						
Ambassis nalua	3.2	**49; 49-49**	**51; 51-51**	0; 0-0	0; 0-0	0; 0-0
Macrobenthic carnivores						
Acanthopagrus australis	3.0	**25; 7-33**	**49; 41-59**	3; 0-11	6; 0-21	14; 0-48
A. berda	3.1	**43; 34-47**	**46; 41-52**	1; 0-5	4; 0-10	6; 0-22
Acanthopagrus spp. (juv)	2.5	**33; 13-44**	**34; 24-45**	4; 0-13	9; 0-26	20; 0-58
Gerres filamentosus	3.0	12; 0-21	**55; 45-66**	5; 0-14	11; 0-29	17; 0-40
Platycephalus fuscus	3.0	**14; 1-23**	**43; 1-72**	2; 0-6	4; 0-12	37; 0-95
Psammogobius biocellatus	2.5	**29; 28-30**	0; 0-0	**69; 69-71**	0; 0-1	1; 0-3

Fish displayed a small range of $\delta^{13}C$ values, between -19.5 and -16.7‰, and most species were also similar in $\delta^{15}N$ (Fig. 2.2). Hence, IsoSource results were similar for most species, and indicate that most fish depended mainly on terrestrial producers, having mangroves and/or the salt couch *S. virginicus* as the main sources of nutrition (Table 2.6). The importance of the remaining classes of producers seems to be limited in most cases. Only for *V. buchanani* and *P. biocellatus* the IsoSource results show aquatic producers (benthic producers for *V. buchanani* and suspended producers for *P. biocellatus*) as the main contributors (Table 2.6). Note that the two phytodetritivorous mullet, *L. subviridis* and *V. buchanani,* were well separated in both $\delta^{13}C$ (-18.8 vs. -

15.4‰) and $\delta^{15}N$ (9.9 vs. 6.0‰), suggesting that, although both phytodetritivores, these species rely on different nutritional sources, with the IsoSource model indicating that *L. subviridis* depending mostly on terrestrial wetland carbon and *V. buchanani* on aquatic benthic producers (Table 2.6).

Sporobolus site. As in the Mangrove site, different invertebrate species from the *Sporobolus* site had distinct carbon and nitrogen isotope compositions (Table 2.4), suggesting the dependence on different sources of carbon. Among gastropods, the two nerites, *Nerita polita* and *N. violacea*, and the pulmonate *Onchidium daemelli* were the most enriched in ^{13}C, with $\delta^{13}C$ values close to benthic producers (Table 2.4). Most species however had $\delta^{13}C$ values that could result from an assimilation of different combinations of producers (Fig. 2.2), and hence it was not possible to identify the main contributors unambiguously.

Crustaceans also differed in $\delta^{13}C$ and $\delta^{15}N$. The planktivore *Acetes sibogae* had the lowest $\delta^{13}C$ values (Table 2.4). Although the IsoSource model could not be run for this species as corrected isotope values fell outside the limits of available producers, it was possible to detect a trophic relationship based on the comparison of isotopic composition of *A. sibogae* and suspended producers. *A. sibogae* was similar in $\delta^{13}C$ to suspended producers (-19.6 vs. -20.0‰), and had $\delta^{15}N$ values 6.7‰ higher than these producers, a distance that corresponds to ~2 trophic steps, agreeing with the possibility that this species feeds on zooplankton, which is in turn dependent on suspended producers. Similarly, for alpheid shrimps and the fiddler crab *Uca coarctata* no IsoSource solution was possible. However, if $\delta^{13}C$ and $\delta^{15}N$ values of alpheid shrimps are corrected for fractionation for 1 trophic level they fall very close to epiphytes, while

if isotope values of *U. coarctata* are corrected for 1.5 trophic levels they fall close to microphytobenthos, indicating a likely dependence on these producers.

For the remaining decapods, the IsoSource model lead to a variety of taxon-specific solutions (Table 2.7). As for the Mangrove site, the salt couch *S. virginicus* appeared as a main contributor to *P. merguiensis* nutrition (Table 2.7), although in this case with greater values of putative contribution than at the Mangrove site. *S. virginicus* also appeared as important for *M. bennetae, P. atrinubes, S. serrata, Parasesarma erythrodactyla* and *Clibanarius taeniatus.* However, aquatic producers were the main contributors to nutrition for a number of species, although the relative contribution of the different types of producers varied between species (Table 2.7).

As with invertebrates, fish were also well separated in $\delta^{13}C$ and $\delta^{15}N$ and, as a result, the IsoSource model suggested the dependence on different sources by the different species. The model was not computed for *S. multifasciata* since the five individuals analysed had very variable $\delta^{13}C$ values. For seven other species, corrected isotopic values fell outside the polygon of autotrophs, and hence no IsoSource solution was possible. These were the phytodetritivorous *L. subviridis*, the herbivorous *S. lineatus,* the planktivorous *A. nalua,* the carnivorous *Arothron manilensis* and *Lutjanus russellii*, and the piscivorous *Butis butis* and *C. sexfasciatus.* However, corrected $\delta^{13}C$ and $\delta^{15}N$ values of most of these species fell close to epiphytes and suspended producers, suggesting that these may be at the basis of the food chains of these species. For the planktivore *A. nalua*, however, a fractionation for one trophic level resulted in values close to *A. sibogae* ($\delta^{13}C$ = -19.5 and -19.6‰ respectively, and $\delta^{15}N$ = 8.5 in both cases), indicating than these shrimps or other plankton feeding invertebrates may be important dietary components.

Table 2.7. IsoSource results for decapods and fish collected at the *Sporobolus* site. Values represent the median and the 1st to 99th percentile range of potential contribution. For each animal species, producers with a necessary contribution (minimum potential contribution >0%) are in bold. Trophic level = trophic level considered for the IsoSource model. BP = benthic producers; Epiph = epiphytes; Mangr = mangroves; SP = suspended producers; *S. virg* = *S. virginicus*.

Species	Trophic level	Sources			
		S. virg	SP	BP	Epiph
Decapod crustaceans					
*Clibanarius taeniatus**	2.0	**11; 1-19**	0; 0-2	**88; 81-94**	1; 0-5
Metapenaeus bennetae	2.5	**40; 1-80**	10; 0-19	**30; 2-58**	20; 0-41
Metopograpsus frontalis	2.0	23; 0-49	**21; 14-27**	**44; 26-61**	12; 0-25
Palaemonetes atrinubes	2.5	**64; 57-69**	0; 0-2	2; 0-6	**34; 31-37**
Parasesarma erythrodactyla	2.0	**85; 81-88**	0; 0-0	**15; 12-17**	0; 0-2
Penaeus esculentus	2.5	20; 0-40	**45; 39-52**	13; 0-28	**21; 9-33**
Penaeus merguiensis	2.5	**75; 56-86**	1; 0-4	**20; 12-32**	2; 0-11
Penaeus monodon	3.0	10; 0-22	**75; 70-80**	7; 0-16	7; 0-14
Portunus pelagicus	3.0	9; 0-19	**68; 63-72**	6; 0-13	**18; 11-24**
Scylla serrata	3.0	**42; 7-70**	6; 0-13	18; 0-42	**34; 18-51**
Fish					
Detritivores					
Valamugil buchanani (small)	2.0	**32; 29-35**	0; 0-0	1; 0-3	**66; 65-68**
V. buchanani (large)	2.0	**83; 66-93**	1; 0-3	**5; 7-24**	2; 0-8
Omnivores					
*Chelonodon patoca**	2.3	0; 0-0	**41; 39-43**	0; 0-0	**59; 57-61**
Leiognathus equulus (small)	3.0	32; 0-65	**20; 11-29**	22; 0-45	**26; 7-43**
L. equulus (large)	3.0	0; 0-8	0; 0-2	1; 0-4	**95; 92-97**
*Leiognathus decorus***	2.5	0; 0-2	0; 0-2	0; 0-1	**98; 98-100**
Planktivore					
Pseudomugil signifer	3.0	14; 0-29	**11; 6-16**	10; 0-20	**65; 56-74**
Macrobenthic carnivores					
Acanthopagrus australis	3.0	**31; 1-58**	6; 0-14	19; 0-39	**45; 29-60**
Acanthopagrus berda	3.0	17; 0-34	**9; 3-14**	11; 0-23	**64; 53-74**
Acentrogobius viridipunctatus	3.0	26; 0-53	**12; 4-19**	18; 0-37	**44; 29-59**
Cynoglossus bilineatus	3.0	15; 0-33	**7; 1-12**	**70; 57-81**	8; 0-17
Gerres filamentosus	3.0	24; 0-48	**9; 1-16**	16; 0-33	**51; 37-65**
Psammogobius biocellatus	2.5	29; 0-59	**13; 5-21**	20; 0-41	**38; 21-54**
Periophthalmus sp.	3.2	**82; 62-94**	1; 0-5	**13; 4-25**	4; 0-12
Sillago analis	3.0	33; 0-67	**19; 10-28**	23; 0-46	**24; 5-42**
Sillago burrus	3.2	**92; 75-99**	0; 0-3	6; 0-15	2; 0-8
Sillago sihama	3.0	29; 0-61	**18; 9-25**	**38; 16-58**	15; 0-32
Minor piscivores					
Lutjanus argentimaculatus	3.0	6; 0-14	**25; 21-27**	4; 0-10	**64; 59-70**
Platycephalus endrachtensis	3.0	15; 0-31	**35; 29-40**	10; 0-21	**40; 30-49**
Platycephalus fuscus	3.0	23; 0-45	6; 0-13	15; 0-31	**56; 43-69**
Terapon jarbua	3.0	28; 0-54	6; 0-13	18; 0-37	**48; 33-63**
Major piscivores					
Lates calcarifer ***	3.1	0; 0-1	**65; 58-68**	0; 0-0	**17; 31-42**
Sphyraena barracuda	3.0	5; 0-12	**85; 81-89**	3; 0-8	**6; 1-11**

* - tolerance was increased to 0.2‰ in order to obtain a possible solution
** - tolerance was increased to 0.3‰ in order to obtain a possible solution

For the remaining fish species, IsoSource models indicated that, as for invertebrates, different species relied on a different set of producers (Table 2.7). However, in contrast with the situation at the Mangrove site, at the *Sporobolus* site aquatic producers appeared as the main contributors for most species (Table 2.7). The salt couch *S. virginicus* appeared as a necessary contributor only for *Periophthalmus argentilineatus*, *Sillago burrus, V. buchanani* and *A. australis*. For most fish species however, this producer appeared with a wide range of possible contributions and hence it is not possible to be certain of its contribution for nutrition. Nevertheless, the maximum potential contribution of *S. virginicus* was often substantial to high.

2.4. DISCUSSION

2.4.1. Relationship Between $\delta^{15}N$ and Trophic Position

At the *Sporobolus* site, there was a linear relationship between $\delta^{13}C$ and $\delta^{15}N$ values of organisms of each trophic level. This relationship was also similar for the different trophic levels, differing only in the intercept of the lines (i.e. on $\delta^{15}N$ values), indicating that animal trophic levels can be calculated using primary producers or primary consumers as a baseline. This is the first time such a relationship has been identified for an estuarine system, and the first time such relationship has been found to persist up the food chains, through higher trophic levels.

Regarding invertebrate primary consumers, the relationship was significant event though the species considered included herbivores and bacteria feeders, as well as species that are likely to feed on a mixture of both, suggesting that trophic fractionation in animals that feed on bacteria and herbivores is similar. The relationship between $\delta^{13}C$ and $\delta^{15}N$ values was also similar for primary consumers regardless of broad taxonomic category (invertebrates or fish), again suggesting similar values of trophic fractionation for both groups. This is at odds with a review by Vanderklift & Ponsard (2003), who concluded that $\delta^{15}N$ fractionation of invertebrates of low trophic level is lower than that of fish. However, only one of the fish species considered by those authors was a primary consumer, namely the herbivorous Nile tilapia *Oreochromis niloticus*, and this species has a low $\delta^{15}N$ fractionation of 1‰ (Focken 2001), a value similar to that found for low trophic level invertebrates in that review (Vanderklift & Ponsard 2003). To my knowledge, to date no study has analysed trophic fractionation in any other herbivorous or detritivorous fish species, or compared $\delta^{15}N$ values of these groups to those of low trophic level invertebrates. Given the results of the present study, it is possible that, as with invertebrates, fish primary consumers have low values of $\delta^{15}N$ fractionation compared to fish species of higher trophic levels.

Since the relationship between $\delta^{13}C$ and $\delta^{15}N$ was similar for invertebrate and fish primary consumers, it seems reasonable that trophic levels of other organisms can be calculated based on either of these taxa. This fact has important implications for the planning and design of food web studies based on stable isotope analysis since it implies that it may not be necessary to collect a wide range of producers and/or invertebrate primary consumers to calculate trophic length and trophic positions. In fact, carbon and nitrogen isotope composition of fish primary consumers appears to be

an appropriate proxy for invertebrate primary consumers and hence fish may also serve as a suitable baseline for analyses of trophic length and trophic positions. This has real logistic benefits for food web studies since it can be difficult to collect a range of invertebrate primary consumers in estuarine areas, as many such species are inconspicuous, of small size, reside in burrows or other difficult to sample habitats, and can be hard to identify. Perhaps even more crucially, the diets of many, or even most, groups of invertebrates are poorly known, especially for tropical systems. In contrast, fish primary consumers, in particular detritivores, are very abundant in tropical estuaries (Sheaves 2006) and are easily collected and identified.

Results suggest that $\delta^{15}N$ values are good indicators of animals' trophic levels, but only when used in conjunction with $\delta^{13}C$. The concept of using $\delta^{13}C$-$\delta^{15}N$ relationships of primary producers to assign trophic levels was first introduced by Vander Zanden & Rasmussen (1999), and was found to be useful for the determination of animals' trophic levels in temperate lake systems in Canada. Long lived primary consumers such as gastropods are generally used to determine the isotope composition of the base of the food web they represent, since these species accurately integrate temporal and spatial variations in producers' isotopic composition (Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 1999, Post 2002b). This is an important approach because $\delta^{15}N$ fractionation of primary consumer invertebrates such as gastropods can be variable (Kurata et al. 2001, Vander Zanden & Rasmussen 2001), and is generally lower than that of fish (Vanderklift & Ponsard 2003), and hence trophic position of fish could be underestimated if based only on $\delta^{15}N$ values of producers.

However, in the present study, primary consumers were found to be 3.9‰ higher in $\delta^{15}N$ than primary producers, a value higher than the 3‰ considered as average for $\delta^{15}N$ fractionation for muscle tissue (McCutchan Jr et al. 2003). From primary consumers to secondary consumers, a 3.7‰ increase in $\delta^{15}N$ was detected, again higher than 3‰. The fact that in both cases (from primary producers to primary consumers and from primary consumers to secondary consumers) the differences in $\delta^{15}N$ between trophic categories were larger than 3‰ seems to indicate that a certain level of omnivory is present both among primary consumers and secondary consumers, with different species feeding on more than one trophic level. This could be a result of opportunistic omnivory and scavenging and/or predatory behaviour present in many estuarine invertebrates (e.g. Dahdouh-Guebas et al. 1999) and fish (e.g. Livingston 1982, Wilson & Sheaves 2001, Baker & Sheaves 2005) species. On the other hand, the differences in $\delta^{15}N$ between trophic categories were consistent for the entire $\delta^{13}C$ spectrum, indicating that omnivory is widespread in the animal community. This is further suggested by the similarity in isotope composition of macrobenthic carnivores and piscivores, which indicates that these species, although having ostensibly different diets, occupy similar trophic levels.

Alternatively, there is also the possibility that mean $\delta^{15}N$ fractionation in this area is higher than the assumed 3‰, since fractionation values close to 4‰ have been documented in other situations (Hobson & Welch 1992, Hesslein et al. 1993, Vander Zanden & Rasmussen 2001). In fact, if $\delta^{15}N$ fractionation is around 3.8‰, results would suggest the presence of exactly one trophic step between the primary producer and primary consumer categories, and again exactly one trophic step between the primary

consumer and secondary consumer categories, making a food web with only three trophic levels.

For this site (*Sporobolus* site), the difference in $\delta^{15}N$ between the herbivorous *S. multifasciata* and the planktivorous *A. nalua* suggested a food web with 4.1 trophic levels. However, when the relationship between in $\delta^{15}N$ and $\delta^{13}C$ is taken into account, it is clear that the food web was actually shorter, with only about 3.5 trophic levels. This clearly illustrates that trophic length should not be calculated based on differences in $\delta^{15}N$ between animals from different trophic chains, since these can be ultimately relying on sources with different $\delta^{15}N$, and an effort must be made to consider organisms with similar sources in the base of their food chain, as for example detritivores and macrobenthic carnivores (as long as they have similar $\delta^{13}C$).

Following this recommendation, for the Mangrove site trophic length should not be calculated based on *V. buchanani* and *A. nalua*, since these two species are in different food chains (detritus and planktonic food chains respectively). A comparison between *V. buchanani* and a macrobenthic carnivore of close $\delta^{13}C$ such as the flathead *P. fuscus* for example would be more appropriate. This would result in a difference in $\delta^{15}N$ of 4.8‰, which would indicate a trophic length of 3.6 trophic levels, a value shorter than 4, and similar to that found for the *Sporobolus* site when based on a $\delta^{15}N$ fractionation of 3‰ (3.5 trophic levels). Therefore, although 31 species were collected at the *Sporobolus* site and a smaller number (11 species) at Mangrove site, it seems that trophic length was similar for both sites, with around 3.5 trophic levels.

2.4.2. Sources of Energy

At both sites, different animal species rely differently on the available sources of carbon. Both the analysis of the shift in animals' $\delta^{13}C$ and $\delta^{15}N$ values and the IsoSource model indicate that there is an incorporation of carbon of terrestrial origin into the aquatic food web in these areas, although the source differs between sites (mangrove vs. salt marsh).

Variation of $\delta^{13}C$ and $\delta^{15}N$ Values Between Sites

Producers. Among aquatic producers, although suspended producers had similar values at both sites, epiphytes, microphytobenthos and epilithic microalgae were more depleted in ^{13}C at the Mangrove site, suggesting an incorporation of carbon of mangrove origin by these producers. Mangroves fix carbon through the C_3 pathway, forming tissues with relatively low $\delta^{13}C$, which gradually respire and release ^{13}C depleted dissolved organic carbon into the water (Zieman et al. 1984). The decomposition of leaves and other mangrove debris also leads to great quantities of ^{13}C depleted organic carbon to be released into the water. This carbon is further decomposed into dissolved inorganic carbon and into dissolved CO_2, which will be utilized by aquatic producers as a substrate. Therefore, the initial pool of carbon available for aquatic producers in mangrove areas includes not only bicarbonate and dissolved CO_2, but also respiratory ^{13}C depleted CO_2 from mangrove origin, and hence $\delta^{13}C$ of these producers will be more negative in locals with significant mangrove input. Consequently, even if the carbon of mangrove origin is not directly incorporated by the aquatic animals, there is this indirect pathway through aquatic producers. This effect

has been previously documented for other aquatic systems (Lin et al. 1991, Bouillon et al. 2000, Dehairs et al. 2000, Bouillon et al. 2004a).

Consumers. The similarity in isotope shifts of consumers between pools indicates that animals were present at each area for long enough for their tissues to reflect the isotope composition of the available producers, suggesting that the results of the analysis reflect the processes occurring within the pools, and were not confounded by the movement of animals between habitats.

Both spatial (Fry 1984, Kitting et al. 1984, Melville & Connolly 2003) and temporal (McCutchan Jr & William Jr 2002) tracking of stable isotope composition of producers by consumers have been found to be useful to determine trophic relationships. In this study, most invertebrates and fish showed a shift in $\delta^{13}C$ from lower values at the Mangrove site to higher values at the *Sporobolus* site. This isotopic shift is consistent with the presence of ^{13}C depleted mangrove derived carbon at the Mangrove site. However, the shift in $\delta^{13}C$ was also similar in direction and magnitude to that of epiphytes and microphytobenthos, suggesting that these two types of algae may be important contributors to aquatic animals in these pools. It is therefore difficult to determine if mangrove carbon is being incorporated directly by aquatic animals, or if the animals' low $\delta^{13}C$ values found at the Mangrove site are simply a result of an incorporation of carbon from aquatic producers such as epiphytes and microphytobenthos, which happens to be depleted in ^{13}C due to the presence of ^{13}C depleted CO_2 of mangrove origin in the water. This situation clearly illustrates how difficult it can be to accurately describe food webs in aquatic systems, even when using

modern approaches such as the spatial analysis of stable isotope data. Nevertheless, tesults of the IsoSource model, discussed below, were useful to clarify this question.

IsoSource Mixing Model

Results of the IsoSource model suggest that carbon of terrestrial wetland origin was incorporated by aquatic animals at both sites, and that the lowest $\delta^{13}C$ values of animals collected in the Mangrove site were a result of a direct incorporation of mangrove carbon, rather than an indirect affect caused by the depleted dissolved inorganic carbon pool resulting from the presence of respired mangrove CO_2 in the area. Although at the Mangrove site most invertebrate species seem to rely mostly on aquatic producers, an important incorporation of mangrove derived carbon was detected for most fish species. These may be feeding on small invertebrates such as Aorid amphipods, which seem to rely significantly on mangrove carbon, or on other organisms not collected in this study. Therefore, it may be necessary to analyse a large number of species, including both invertebrates and fish, in order to detect an incorporation of mangrove carbon into aquatic food webs.

A number of studies conducted in tropical mangrove systems have reported a limited input of mangrove carbon into estuarine organisms (e.g. Loneragan et al. 1997, Chong et al. 2001, Bouillon et al. 2004a, Bouillon et al. 2004b, Guest & Connolly 2004). This has been attributed to the low nutritional value of mangrove leaves (Russell-Hunter 1970, Skov & Hartnoll 2002), and to the retainment of nutrients by mangrove trees during the process of leaf senescence, a process previously described for mangrove

trees (Kao et al. 2002), salt marsh plants (Shaver & Melillo 1984) and seagrass (Stapel & Hemminga 1997). However, most of these studies considered solely relatively conspicuous invertebrate species and hence the level of incorporation of mangrove carbon could have been underestimated.

At the *Sporobolus* site, in addition to the major contribution from aquatic producers, the energy fixed by salt marsh vegetation appeared to make an important contribution to several species, including both invertebrates and fish, a result that has been documented by previous authors (e.g. Deegan & Garritt 1997, Kwak & Zedler 1997, Guest et al. 2004).

The IsoSource model was found to be useful in providing important information on trophic processes within the two areas analysed, especially when used in conjunction with the similarity in changes in isotope composition of producers and consumers between sites. For example, *P. merguiensis* prawns showed relatively high $\delta^{13}C$ values and an isotopic shift similar to microphytobenthos, and the IsoSource model also suggested benthic producers as well as *S. virginicus* as the main contributors at both sites (Tables 2.6 and 2.7), clarifying the importance of these producers.

For *P. atrinubes* shrimps on the other hand, the IsoSource model did not lead to conclusive results regarding the main sources of nutrition at the Mangrove site, as all sources appeared with relatively wide ranges of distribution of potential contribution (Table 2.6). At the *Sporobolus* site however, *S. virginicus* and epiphytes showed a substantial contribution with high certainty. Since epiphytes were important contributors at the *Sporobolus* site, it is likely that these producers are also important for animals at

the Mangrove site, a result that is also suggested by the similarity in isotopic shift between *P. atrinubes* and epiphytes. Also, for *V. buchanani*, the shift in isotope composition suggests a dependence on epilithic microalgae, which is in accordance with IsoSource results, that indicate that both at the Mangrove and the *Sporobolus* sites benthic producers were important contributors to this species' nutrition (Tables 2.6 and 2.7).

In some cases however, results from the two analyses were not in agreement. For example, for *P. biocellatus*, the isotopic shift between sites suggests that epiphytes were important contributors. However, IsoSource results only show epiphytes as potentially important contributors at the *Sporobolus* site (Tables 2.6 and 2.7). This could be an indication that the shift in carbon isotope composition of *P. biocellatus* is a result of dependence on terrestrial wetland carbon, i.e. on mangrove carbon at the Mangrove site and on salt marsh carbon at the *Sporobolus* site*,* and that epiphytes are actually not important to *P. biocellatus* nutrition. On the other hand, the phytodetritivorous *L. subviridis* and the planktivorous *A. nalua* showed isotopic shifts similar to those of suspended producers. However, while at the *Sporobolus* site corrected isotope values of these two species indicate that suspended producers are probably important contributors, for the Mangrove site the IsoSource model suggests mangroves and *S. virginicus* as the main contributors (Table 2.6).

Hence, when interpreting results from the IsoSource model, it is very important to take into account some of its limitations. Firstly, results do not correspond to an exact solution for the diet of a species, but to a distribution of possible solutions, given a set of possible contributors. Moreover, uncertainties regarding the exact fractionation of $\delta^{13}C$ and $\delta^{15}N$ through a trophic link can lead to erroneous estimates of trophic levels

and of the relative contribution of the different food sources. On the other hand, the use of carbon and nitrogen trophic fractionation values over multiple trophic steps can also be inappropriate due to potential isotopic differences between tissues on a same prey organism (Lorrain et al. 2002), coupled with the isotopic routing phenomena (Schwarcz 1991, Gannes et al. 1998, Vanderklift & Ponsard 2003). Moreover, factors such as type of diet and the nutritional status of the animals can also affect trophic fractionation (Focken 2001, Gaye-Siessegger et al. 2003, Gaye-Siessegger et al. 2004). These uncertainties occur at each trophic step, compounding at each trophic link and leading to a higher final variability in isotopic fractionation and, consequently, to a higher probability of leading to incorrect IsoSource results.

Differences in digestibility and in concentration of carbon and nitrogen in the different diet sources also limit the effectiveness of linear models such as the IsoSource in determining the contributions of different sources to a species' diet (Phillips & Koch 2002). Although concentration dependent models have been developed for cases were the elemental concentrations of the different sources vary significantly (Phillips & Koch 2002), the applicability of these models is still very limited as it is necessary to have a good baseline knowledge of the nutritional, physiological, and ecological characteristics of each species (Robbins et al. 2002), and this is lacking for the great majority of aquatic species.

Despite its limitations, the IsoSource model was found to be useful in providing information on trophic processes in the two areas analysed, especially when used in conjunction with the similarity in changes of isotope composition of producers and consumers between sites, with both approaches suggesting that an incorporation of carbon of terrestrial origin into aquatic food webs is present in these areas.

2.4.3. Conclusions

Stable isotopic analysis is a valuable technique to describe the trophic structure and sources of energy fuelling food webs in estuarine systems. However, it is important to have a basic knowledge on the ways this methodology can be used in these systems, including its limitations.

This is the first study to detect a baseline $\delta^{13}C$-$\delta^{15}N$ relationship for different trophic categories, and to use it to calculate trophic length in an estuarine system. This is also the first study to report similar levels of trophic fractionation for fish primary consumers and for invertebrate primary consumers. This finding has important practical implications since it implies that trophic positions and trophic length do not necessarily need to be calculated based on primary producers or on invertebrate primary consumers, and that fish primary consumers can be equally used for this purpose. Given the frequent occurrence and high densities of detritivorous mullet species in Australian tropical estuaries (Sheaves 2006), I suggest that whenever possible the mullet species of lowest $\delta^{15}N$ is used as a baseline to calculate trophic levels of other fish species. In this manner, it will be possible to compare trophic length as well as trophic positions of different species between systems. Nevertheless, $\delta^{15}N$ values should always be used in conjunction with $\delta^{13}C$, i.e. taking into account the possibility of correlated variability between $\delta^{15}N$ and $\delta^{13}C$ for the primary producer baseline.

Evidence of an input of terrestrial wetland energy into aquatic food webs was present at both locations, and the comparison of carbon and nitrogen isotope composition of animals between the two sites helped clarify important aspects of energy sources for several species. The IsoSource model was also found to be useful to determine food

sources and trophic relationships, but its output must be carefully interpreted, and was more valuable if used in combination with the method of spatial analysis of isotope data. However, results of these two methodologies should not be blindly applied, as attention must be given to the ecologic characteristics of each particular species and the environment, and unreasonable results must never be considered as representing the reality.

Chapter 3

Diet and Sources of Energy Supporting Juvenile Penaeid Prawns in an Australian Dry Tropics Estuary

3.1. INTRODUCTION

Prawn fisheries are among the main sources of income in several tropical countries (Dann et al. 1994, Anon 2000), with the most important species usually belonging to the family Penaeidae. Throughout the tropical and subtropical regions of the world, juveniles of many commercial penaeids inhabit intertidal estuarine wetlands, including salt marshes and mangrove swamps (e.g. Young & Carpenter 1977, Rogers et al. 1993, Wenner & Beatty 1993, Adnan et al. 2002, Loneragan et al. 2005). These wetland communities are highly productive (Schelske & Odum 1961), and are widely considered to provide an abundant and essential food supply for juvenile prawns. Although this importance is frequently used as an argument for conservation of these habitats, a relationship between the extent of wetland areas and fisheries production is yet to be confirmed (Lee 2004, Loneragan et al. 2005). Moreover, recent studies based on stable isotope analysis show that the importance of mangrove and salt marsh productivity in supplying energy to penaeid prawns in adjacent aquatic habitats may not be as significant as once thought (e.g. Loneragan et al. 1997, Chong et al. 2001).

It is however imperative to conclusively resolve this contention, in order to provide a basis for the development of rational wetland conservation and management priorities. In doing this, it is particularly important to develop a detailed understanding of the importance of different habitats to penaeid prawns, and to identify the exact sources of energy supporting these species at the different stages of their life-cycles, since penaeids are known to display a diversity of ontogenetic variations in diet and feeding strategies (Dall et al. 1990, Chong et al. 2001).

Most stable isotope studies of penaeid diets have been conducted in large tidal estuarine areas (e.g. Primavera 1996, Loneragan et al. 1997, Chong et al. 2001, Macia 2004), where carbon from terrestrial origin is rapidly diluted and redistributed by water movement, limiting the ability of detecting its incorporation by aquatic animals. However, the analysis of small and relatively isolated areas should provide a different and perhaps more useful perspective on the "real" importance of the assimilation of mangrove or salt marsh carbon by the different species, as under these conditions the mixing and outwelling of energy of terrestrial origin is likely to be less significant.

Therefore, in this part of the study, stable isotope analysis of carbon and nitrogen will be used (i) to determine the extent to which carbon of terrestrial origin is important for nutrition of juveniles of four commercially important penaeid prawn species inhabiting semi-isolated wetland pools, and (ii) to detect and describe the extent of ontogenetic variation in diet for these penaeids.

3.2. METHODS

3.2.1. Study Area

This part of the study was conducted in the same relatively isolated areas of the Ross River estuarine floodplain described in Chapter 2 (see Section 2.2.1). Due to the relative isolation of these pools, it is likely that most animals arrive as post larvae and undergo their growth within the pools, reflecting the isotopic composition of the available food sources in their tissues.

3.2.2. Sample Collection and Processing

Primary Producers. For this Chapter, the same set of primary producers used for Chapter 2 was considered. Collection and processing protocols are therefore described in Section 2.2.2.

Animals. Animal collections were carried out at the same time as producers. Prawns within the available size ranges were captured during low tides with a 6 mm mesh strait-bottomed dip net and 18 mm mesh size cast nets (Ethics Approval A854_03). Animals were immediately anesthetized in ice water and frozen as soon as possible. In the laboratory, animals were measured to the nearest 1 mm from the tip of the rostrum to the apex of telson with Vernier calipers. However, *Penaeus* (*Fenneropenaeus*) *merguiensis* were measured from the orbital spine to the apex of telson, as the rostrum in this species is very long and fragile, and so frequently broken during capture.

3.2.3. Sample Processing and Analysis

All samples were processed and analysed as described in Chapter 2, Section 2.2.3.

3.2.4. Data Analysis

Verification of the assumption of low movement of animals between pools

The assumption of low movement of animals between pools was tested by the analysis of the variability of carbon and nitrogen isotope composition of animals between pools. Hence, *Penaeus* (*Fenneropenaeus*) *merguiensis* and *Metapenaeus merguiensis* juveniles (TL < 30 mm) were collected from eleven separate pools on the Ross River floodplain (Figure 3.1) in March 2006. If animal carbon and nitrogen isotope composition has a low variability within a pool, but clear differences between pools, then it would be reasonable to assume that animals have been in pools long enough to develop distinct isotope compositions. If on the other hand animals show a high within-pool, or low within- and between-pool variability, this would indicate a possibility of extensive movement between pools.

Variation of animal $\delta^{13}C$ and $\delta^{15}N$ values with site, species and size class

At each site, between three and nine juveniles of each species were analysed. When a range of sizes was present, animals were also divided into size classes. To explain the extent to which animals' $\delta^{13}C$ and $\delta^{15}N$ values depend on site of collection, species and size class, classification and regression trees (CARTs) were constructed (De'ath &

Fabricius 2000) using the TREES package on S-PLUS 2000®. CART models were run for each element separately because each element gives information on different features of the food web: $\delta^{13}C$ is analysed to detect differences in diet, and $\delta^{15}N$ gives information on the animals' trophic position.

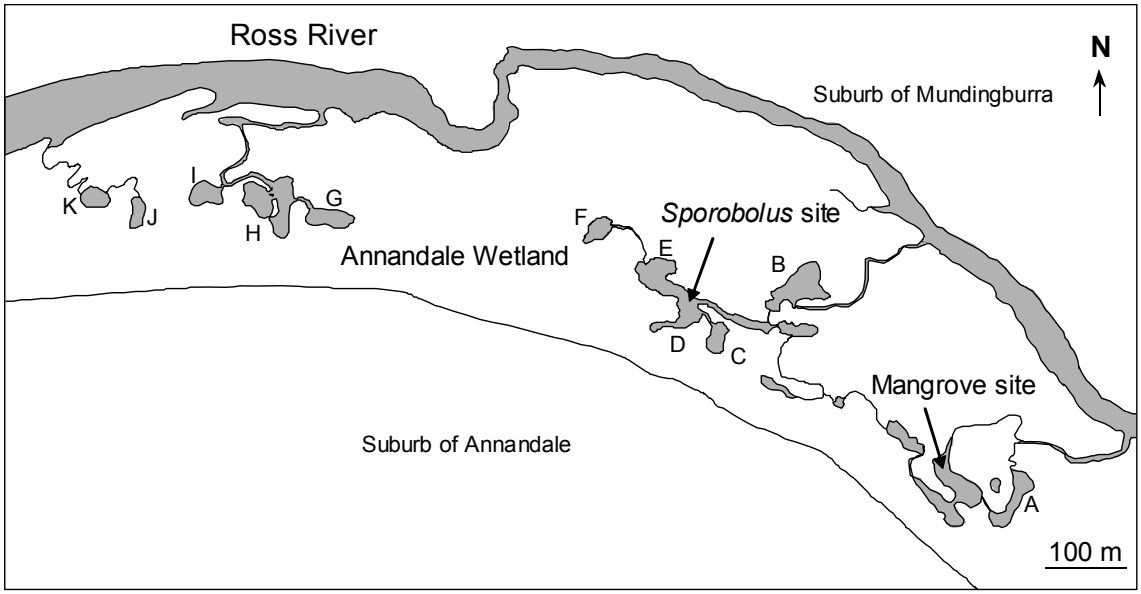

Fig. 3.1. Sketch map of the Ross River estuarine floodplain showing the eleven pools (A-K) where collections of *P. merguiensis* and *M. bennetae* juveniles were carried out for the validation of the assumption of low movement of animals between pools. The two main sites of collection (Mangrove and *Sporobolus* site) are also indicated.

Classification and regression trees are constructed by successively splitting the data into two relatively homogeneous and mutually exclusive groups, based on a single explanatory variable. Splitting is based on minimising the sum of squares about group means. Trees are represented in a graphical way, with the root node on top, representing the initial assemblage of data, from which the branches and leaves emerge. The proportion of the total sum of squares explained by each split is indicated

by the relative lengths of the vertical lines associated with each split. The size of the tree (or number of leaves) is selected by cross-validation and corresponds to the number of final groups. The tree with the lowest cross-validation error (minimum CV error) is logically the one with the best fit. However, the smallest tree for which its estimated error is within one standard deviation from the tree with the lowest CV error (1-SE tree) is more often used, since it is statistically indistinguishable from the minimum CV error tree, explaining only slightly less of the variability, but representing a simpler model. Since cross validation involves a randomization procedure, a different size tree can result from each randomization. Consequently, the procedure was repeated 100 times and the tree size that occurred more frequently was selected.

Sources of energy

As in Chapter 2, the shifts in carbon and nitrogen isotope composition of primary producers and juvenile prawns that were collected at both sites were compared graphically in order to identify similar patterns in isotopic changes between prawns and producers, likely to be related to a major trophic dependence on the respective producer. Since in some cases animals' isotopic shifts could be a result of either a direct incorporation of mangrove carbon, or of a major dependence on aquatic producers such as epiphytes and microphytobenthos (see Chapter 2), the IsoSource mixing model of Phillips and Gregg (2003) was also used to clarify the relative importance of the different producers to juvenile prawns at each site. For the model, taxonomically similar producers were combined into five groups as described in Chapter 2: (1) mangroves, (2) *S. virginicus*, (3) suspended aquatic producers, (4) benthic producers and (5) epiphytes.

For each species and for each size class, the range of possible trophic levels was determined based on the range of values for which an IsoSource solution was possible. Differences in carbon and nitrogen isotope composition of producers and prawns present at each site led to differences in the range of possible trophic levels between species and sites. For prawn species that occur at both sites, the two resulting ranges of trophic levels were used to refine the effective limits of possible trophic level, helping to account for the variability in isotopic fractionation (Vander Zanden & Rasmussen 2001, Post 2002b, McCutchan Jr et al. 2003).

Moreover, because uncertainties in $\delta^{13}C$ and $\delta^{15}N$ trophic fractionation can lead to invalid solutions, for each species the IsoSource model was run for the maximum and minimum possible trophic levels, as well as for the value mid way between. Results are presented in a form of box plots, with the 1st and 99th percentile range and the median value of feasible contributions indicated. For each species, results were compared graphically between sizes, locations and assumed trophic levels. Box plots are presented instead of the usual distributions of feasible solutions because it is easier to visually compare one-dimensional bar graphs.

3.3. RESULTS

3.3.1. Producers

Detailed results of carbon and nitrogen isotope composition of producers are described in Chapter 2, Section 2.3.1.

3.3.2. Consumers

Animal movement between pools

Carbon and nitrogen isotope composition of prawns collected from eleven individual pools showed a low variability within a pool, coupled with clear differences between pools (Fig. 3.2). This validates the assumption of low movement of animals between pools and that penaeids remain in pools for extended periods, long enough to develop distinct isotope compositions that reflect trophic processes occurring within the pool.

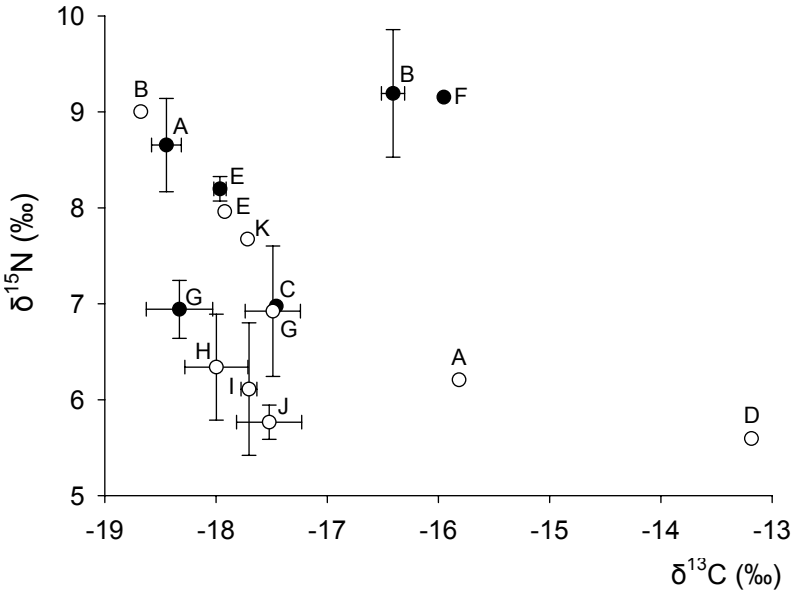

Fig. 3.2. Carbon and nitrogen isotope composition (mean ± SE; *n* = 2-6) of *P. merguiensis* (black symbols) and *M. bennetae* (white symbols) juveniles collected in March 2006, showing the differences between pools. Letters (A-K) represent the pools of collection, as indicated in Fig. 3.1.

Carbon and nitrogen isotope composition of prawn juveniles

M. bennetae, *Penaeus esculentus* and *P. merguiensis* occurred at both sites, while *Penaeus monodon* were only collected from the *Sporobolus* site. Two distinct size classes were present at both sites for *P. merguiensis* juveniles (small: 10-20 and large: 30-40 mm TL), and at the Mangrove site for *M. bennetae* (small: 10-20 and large: 35-45 mm TL). However, at the *Sporobolus* site all *M. bennetae* were of similar size. No easily distinguishable size classes were present for *P. esculentus*, and hence data for the *Sporobolus* site were divided arbitrarily into 10-20 mm (small) and >20 mm TL (large) size classes, while for Mangrove site only individuals between 25 and 45 mm TL were collected and hence no division into size classes was made.

Carbon and nitrogen stable isotope composition of penaeid prawns varied between species, sizes and sites (Table 3.1).

Table 3.1. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of prawn juveniles collected at each site. *n* = number of samples.

Species	Location	Size Class (mm)	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Metapenaeus bennetae	Mangrove site	10 - 20	6	-15.4 ± 0.2	5.93 ± 0.2
		40 - 45	3	-17.6 ± 0.6	7.02 ± 0.3
	Sporobolus site	20 - 25	5	-14.5 ± 0.2	7.54 ± 0.2
Penaeus esculentus	Mangrove site	25 - 45	3	-18.7 ± 0.6	6.23 ± 0.3
	Sporobolus site	10 - 20	5	-15.5 ± 0.5	6.71 ± 0.4
		25 - 60	3	-17.3 ± 1.0	7.76 ± 0.4
Penaeus merguiensis	Mangrove site	10 - 20	4	-17.3 ± 0.3	6.86 ± 0.2
		30 - 40	4	-15.6 ± 0.2	8.42 ± 0.7
	Sporobolus site	10 - 20	3	-14.8 ± 0.7	6.21 ± 0.1
		30 - 40	3	-13.8 ± 0.4	8.19 ± 0.2
Penaeus monodon	*Sporobolus* site	20 - 30	3	-16.7 ± 0.1	8.51 ± 0.1

Isotopic differences between sites, species and sizes classes

Classification and regression trees were used to relate animals' $\delta^{13}C$ and $\delta^{15}N$ values to site of collection, species and size class. According to the 1-SE rule an eight-leaf tree (explaining 76% of total variability) was selected 85% of the time for $\delta^{13}C$, and for $\delta^{15}N$ a three-leaf model (explaining 55% of total variability) was selected 52% of the time.

Prawn $\delta^{13}C$ values depended primarily on site of collection, with animals collected from the Mangrove site showing lower $\delta^{13}C$ than animals collected at the *Sporobolus* site (Fig. 3.3). For the Mangrove site, a secondary split indicates differences between species, as *P. esculentus* had lower $\delta^{13}C$ than *M. bennetae* and *P. merguiensis*. For the two latter species, an additional split suggests clear differences between species, and within each species $\delta^{13}C$ values also differed between size classes, with small *P. merguiensis* having lower $\delta^{13}C$ than large *P. merguiensis*, while small *M. bennetae* juveniles had higher $\delta^{13}C$ than large juveniles (Fig. 3.3).

For the *Sporobolus* site, as in the Mangrove site, there were clear differences in $\delta^{13}C$ between species, as *P. esculentus* and *P. monodon* had lower $\delta^{13}C$ than *M. bennetae* and *P. merguiensis* (Fig. 3.3). A further split was present for *P. esculentus* and *P. monodon*, indicating differences between sizes, with larger juveniles having lower $\delta^{13}C$ than smaller juveniles (Fig. 3.3).

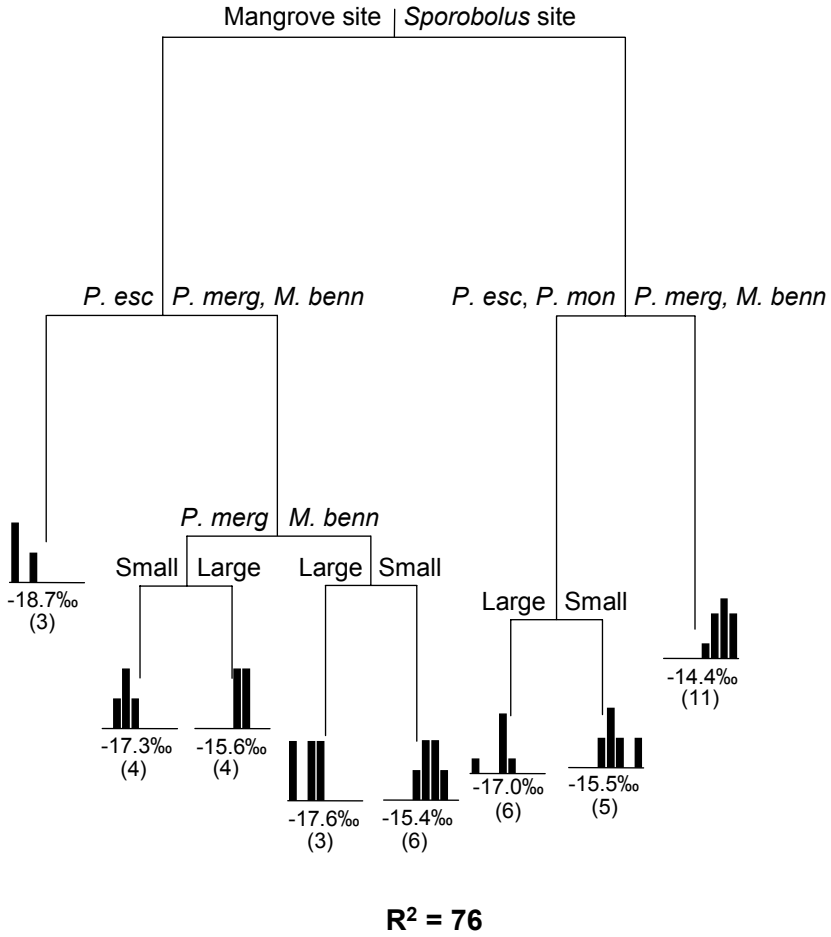

Fig. 3.3. Eight-leaf classification and regression tree explaining prawn' $\delta^{13}C$ values based on site of collection, prawn species and prawn size. Histograms of distribution of $\delta^{13}C$ are presented below terminal nodes, and mean $\delta^{13}C$ and sample size (in brackets) for each group are also indicated. *M. benn = M. bennetae; P. esc = P. esculentus; P. merg = P. merguiensis; P. mon = P. monodon.* Small and Large = smaller and larger size classes respectively.

For $\delta^{15}N$, the CART model indicates that prawn $\delta^{15}N$ values were primarily dependent on juvenile size, as smaller juveniles had lower $\delta^{15}N$ than larger juveniles (Fig. 3.4). At the Mangrove site, a difference in mean $\delta^{15}N$ of 1.3‰ was detected between smaller and larger *M. bennetae* (Table 3.1), corresponding to an increase of approximately 45% of a trophic level (assuming a $\delta^{15}N$ fractionation of +3‰ per trophic level). For *P.*

merguiensis juveniles there was an increase of approximately ~1.7‰ with size, corresponding to 0.6 trophic steps. Similarly, for the *Sporobolus* site, a difference in $\delta^{15}N$ of ~1.5‰ between smaller and larger juveniles was found for *P. esculentus* (Table 3.1), again corresponding to about half a trophic step, while for *P. merguiensis* a larger difference of 2‰ suggested an increase of about 67% of a trophic level with growth.

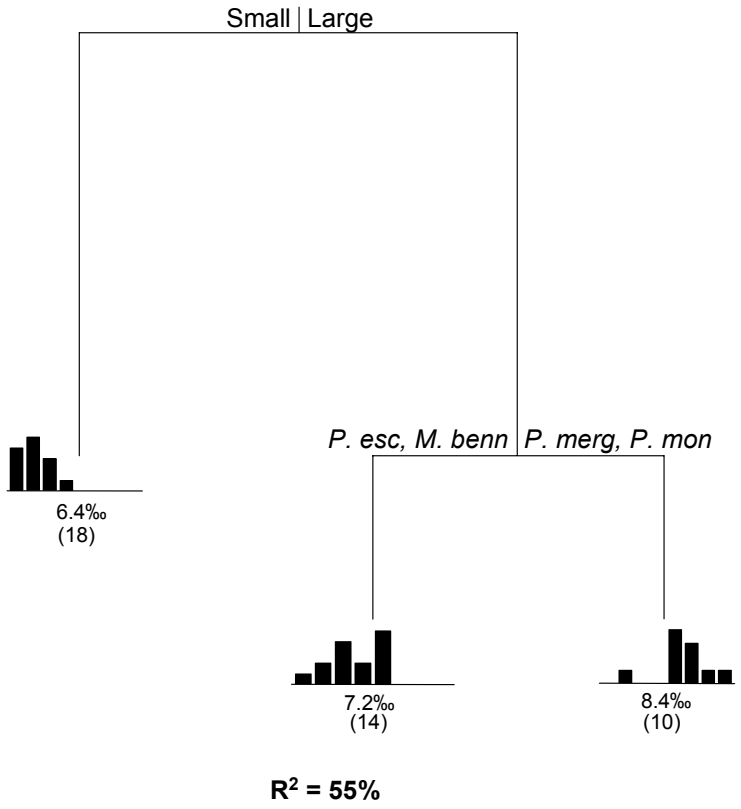

Fig. 3.4. Four-leaf classification and regression tree explaining prawn $\delta^{15}N$ values based on site of collection, prawn species and prawn size. Histograms of distribution of $\delta^{15}N$ are presented below terminal nodes, and mean $\delta^{15}N$ and sample size (in brackets) for each group are also indicated. *M. benn = M. bennetae; P. esc = P. esculentus; P. merg = P. merguiensis; P. mon = P. monodon.* Small and Large = smaller and larger size classes respectively.

No further differences were detected among smaller juveniles, as $\delta^{15}N$ values were similar between species and sites (Fig. 3.4). However, among larger juveniles an

additional split divided *P. esculentus* and *M. bennetae* from *P. merguiensis* and *P. monodon*, with the two first species having lower $\delta^{15}N$ values than the latter two. There was no effect of site on $\delta^{15}N$ values.

3.3.3. Sources of Energy

Variation of isotope composition between sites. Mangroves, *S. virginicus* and suspended producers had similar $\delta^{13}C$ values at both sites, while microphytobenthos, epiphytes and decomposing mangrove leaves shifted in $\delta^{13}C$ from lower values at the Mangrove site to higher values at the *Sporobolus* site (Fig. 3.5). Epilithic microalgae also showed higher values at the *Sporobolus* site, although this shift was not very pronounced. For five out of the seven producer types that occurred at both sites $\delta^{15}N$ values were higher at the Mangrove site (Fig. 3.5). Only epiphytes showed the opposite trend, and suspended producers showed little change.

For large *M. bennetae,* large *P. esculentus* and small and large *P. merguiensis*, the four groups that occurred at both sites, juveniles had lower $\delta^{13}C$ values at the Mangrove site and relatively ^{13}C enriched values at the *Sporobolus* site (Fig. 3.5). The shift in $\delta^{13}C$ between sites was similar to that of epiphytes and microphytobenthos (Fig. 3.5), suggesting a dependence on these autotrophs. The only substantial change in $\delta^{15}N$ between sites was an increase in $\delta^{15}N$ for large *P. esculentus* from the Mangrove site to the *Sporobolus* site, while small *M. bennetae* showed a slight increase and small *P. merguiensis* a slight decrease (Fig. 3.5). Taken together, the shift in $\delta^{13}C$ and $\delta^{15}N$ values of *P. esculentus* juveniles seems to follow the shift in $\delta^{13}C$ and $\delta^{15}N$ of epiphytes

(Fig. 3.5), suggesting that epiphytes may be important producers in the food chains leading to *P. esculentus*.

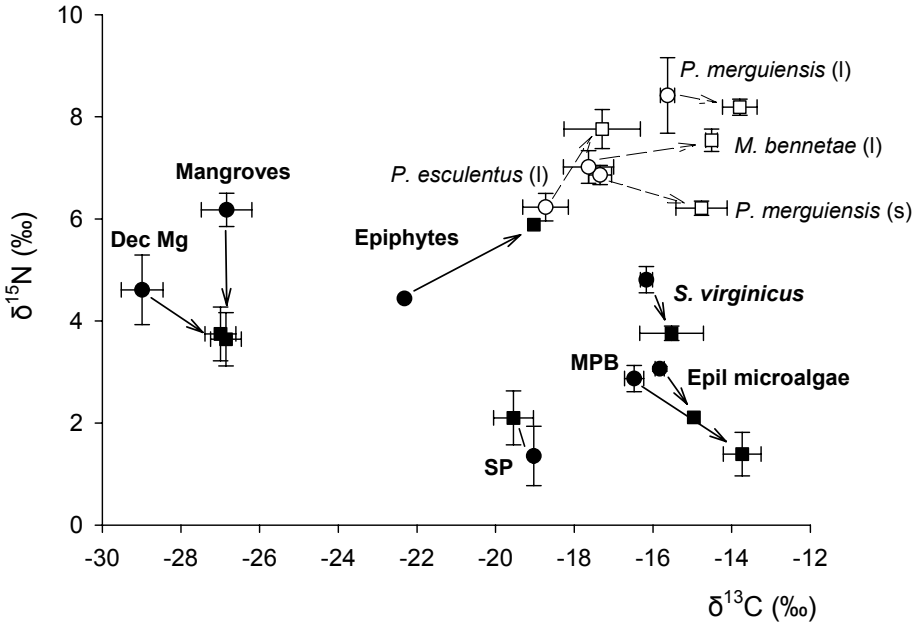

Fig. 3.5. Mean (± SE) $\delta^{13}C$ and $\delta^{15}N$ values of producers (black symbols) and prawns (white symbols) collected at the Mangrove site (circles) and at the *Sporobolus* site (squares), illustrating the difference in isotope composition between sites. Dec Mg = decomposing mangrove leaves; SP = suspended producers. Mangroves include *A. marina* and *A. corniculatum*. l/s - larger/smaller size class respectively. Arrows indicate the direction of change between the mangrove and *Sporobolus* site.

Range of possible trophic levels. Given the isotope composition of producers at each site, the range of possible trophic levels varied between species and sites (Table 3.2). For prawn juveniles that occurred at both sites, the combination of the ranges from both sites was used to narrow the overall range of possible trophic levels (Table 3.2).

Table 3.2. Range of possible trophic levels calculated for each species based on $\delta^{13}C$ and $\delta^{15}N$ values of producers from each site, and final range of possible trophic levels based on the combination of these values.

Species	Trophic level	Mangrove site	*Sporobolus* site	Range of possible trophic levels
Metapenaeus bennetae (small)	Minimum	1.9	-	2.0 - 2.1
	Maximum	2.1	-	
M. bennetae (large)	Minimum	1.6	2.3	2.3 - 2.8
	Maximum	2.8	2.9	
Penaeus esculentus (small)	Minimum	-	1.8	2.0 - 2.6
	Maximum	-	2.6	
P. esculentus (large)	Minimum	1.3	1.8	2.0 - 2.5
	Maximum	2.5	2.9	
P. merguiensis (small)	Minimum	1.5	1.8	2.0 - 2.5
	Maximum	2.8	2.5	
P. merguiensis (large)	Minimum	2.1	2.5	2.5 - 3.2
	Maximum	3.2	3.2	
P. monodon	Minimum	-	2.1	2.1 - 3.2
	Maximum	-	3.2	

Note: the minimum possible trophic level is 2.0, i.e. exactly one trophic level above autotrophs.

Feasible contributions of producers to prawns' diet. Based on the final range of possible trophic levels, the IsoSource model was run for the maximum, minimum and median possible trophic levels. In most cases, the three models led to different results.

For *P. merguiensis*, the only species for which juveniles of both size classes were collected at both sites, mangroves did not appear as important contributors, appearing with low maximum values of feasible contribution for all models at the Mangrove site, with a median contribution always lower than 10% (Fig. 3.6a, b). On the other hand, *S. virginicus* and benthic producers seemed to be important contributors, having moderate to high maximum feasible contributions in most cases (Fig. 3.6). At the *Sporobolus* site, minimum feasible contributions of benthic producers were always non-zero, and

usually greater than 10% (Fig 3.6c, d), providing strong evidence of the importance of benthic producers to *P. merguiensis* juveniles of both sizes.

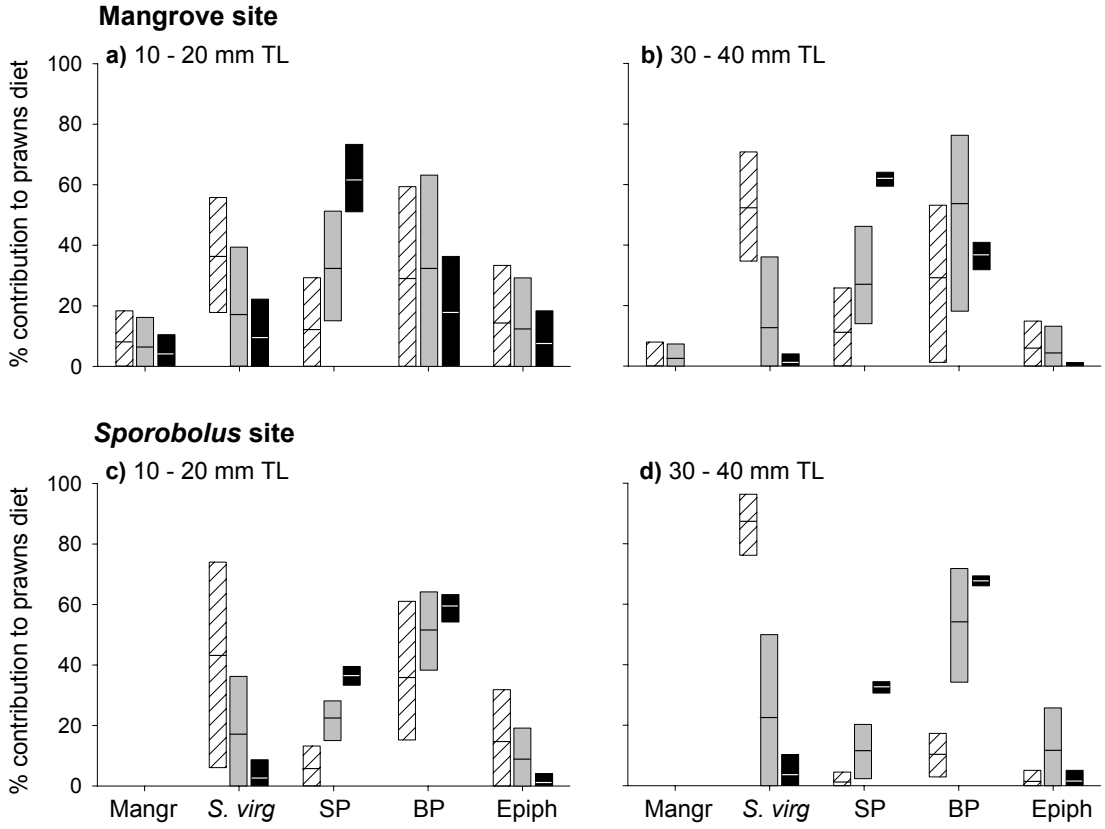

Fig. 3.6. IsoSource results for the minimum (white boxes), intermediate (grey boxes) and maximum (black boxes) possible trophic levels for *P. merguiensis* juveniles collected at the Mangrove and at the *Sporobolus* pools. Boxes represent the 1st to 99th percentile range of feasible contributions of the different autotroph categories. Lines within boxes represent the median value of feasible contributions. Cross-hatched boxes correspond to results for the trophic level suggested by the literature. BP = benthic producers; Epiph = epiphytes; Mangr = mangroves; SP = suspended producers; *S. virg* = *S. virginicus*.

For the smaller size class, the range of possible trophic levels was estimated to be between 2.0 and 2.5 (Table 3.2). According to studies based on gut content analysis,

P. merguiensis juveniles of this size occupy a low trophic level, around 1 step from primary producers or perhaps a little more, but considerably less that 1.5 levels above autotrophs (Chong & Sasekumar 1981, Robertson 1988). For this minimum trophic level of 2.0 (cross-hatched boxes in Fig. 3.6a, c), *S. virginicus* and benthic producers were the most important contributors at both sites, although at the Mangrove site the range of potential contributions included 0% for benthic producers. Other classes of producers had low to moderate maximum feasible contributions at both Mangrove and the *Sporobolus* sites (Fig. 3.6a, c).

The literature suggests a trophic level around 2.5 or slightly higher for larger *P. merguiensis* (Chong & Sasekumar 1981, Robertson 1988), corresponding to the minimum possible trophic level of 2.5, estimated for this size juveniles (Table 3.2). As for the smaller *P. merguiensis* juveniles, *S. virginicus* and benthic producers were the main contributors for large juveniles at both sites for this trophic level (cross-hatched boxes in Fig. 3.6b, d). Suspended producers appear to have some importance, while mangroves and epiphytes do not seem to be important contributors at either site (Fig. 3.6b, d).

As with *P. merguiensis*, mangroves showed reduced putative contributions to nutrition of *M. bennetae* for all models computed for the Mangrove site (Fig. 3.7). For the smaller size class, IsoSource models were only feasible when trophic levels between 2.0 and 2.1 were considered. These models indicated that benthic producers contribute to almost 100% of nutrition of these juveniles (Fig. 3.7a).

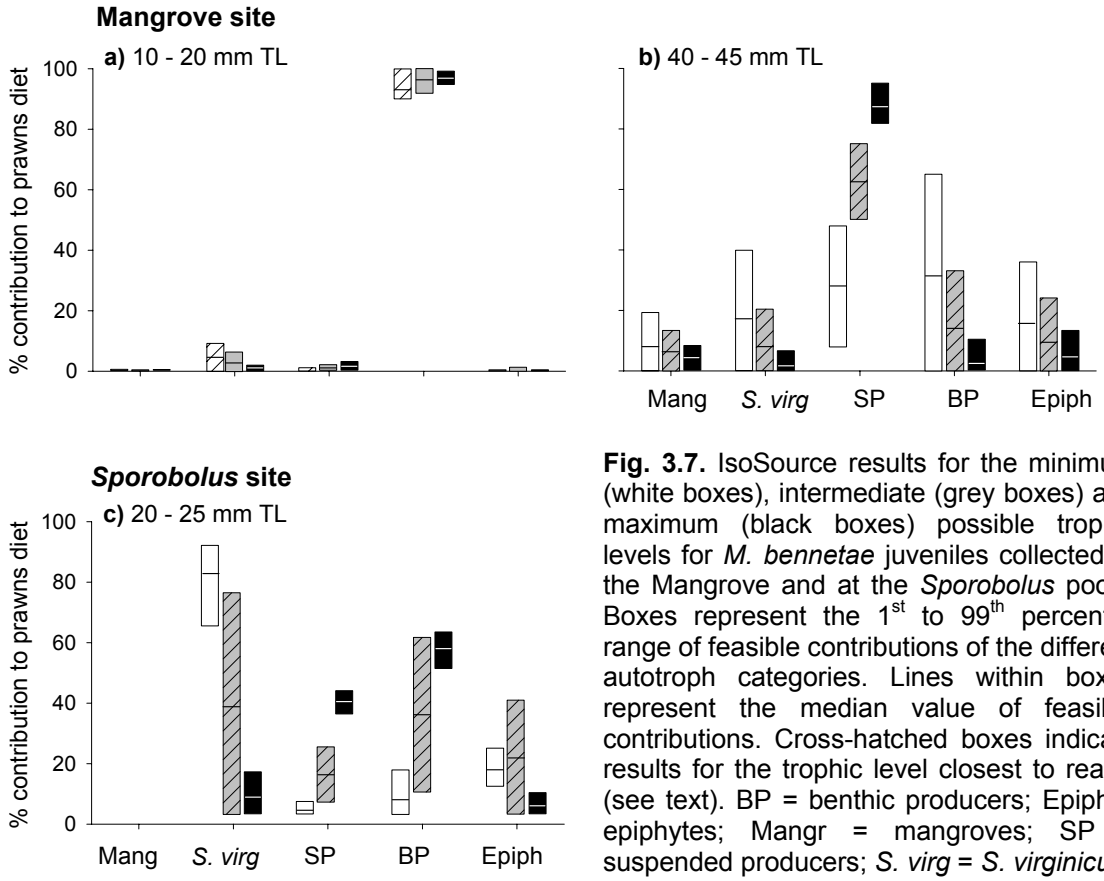

Fig. 3.7. IsoSource results for the minimum (white boxes), intermediate (grey boxes) and maximum (black boxes) possible trophic levels for *M. bennetae* juveniles collected at the Mangrove and at the *Sporobolus* pools. Boxes represent the 1st to 99th percentile range of feasible contributions of the different autotroph categories. Lines within boxes represent the median value of feasible contributions. Cross-hatched boxes indicate results for the trophic level closest to reality (see text). BP = benthic producers; Epiph = epiphytes; Mangr = mangroves; SP = suspended producers; *S. virg* = *S. virginicus*.

For larger *M. bennetae* juveniles, suspended producers appeared as important contributors in all models computed for the Mangrove site, with high values of minimum and maximum potential contributions (Fig. 3.7b). For these large juveniles, trophic levels between 2.3 and 2.8 were possible (Table 3.2). Although no diet studies are available for juveniles of this species, their position in the stable isotope space (Fig. 3.5) suggests that it must have a trophic level similar to that of penaeid species like *P. merguiensis*, of ~2.5 (Wassenberg & Hill 1987, Robertson 1988, O'Brien 1994). Moreover, a difference in $\delta^{15}N$ corresponding to ~0.5 trophic levels was detected between small and large juveniles and hence if small juveniles are of trophic level 2.0

(see above), then larger juveniles must be of trophic level ~2.5. As the intermediate trophic level considered for the IsoSource model was exactly 2.5, results for this model are likely to be closest to the actual trophic level. For this trophic level, suspended producers appeared as the main contributors, with the remaining sources having small to moderate maximum potential contributions (Fig. 3.7b).

For the *Sporobolus* site, there were substantial differences in IsoSource solutions for *M. bennetae* juveniles, depending on the trophic level considered (Fig. 3.7c). For the intermediate trophic level, which is probably the closest to reality (see above), all four classes of producers had a 1st percentile of putative contribution higher than 0% (Fig. 3.7c), indicating that all sources contributed to the model, and were therefore important for nutrition. However, *S. virginicus* and benthic producers had the greatest maximum potential contributions, followed by epiphytes while, in contrast to the Mangrove site, suspended producers had low maximum feasible contributions (Fig. 3.7c).

For *P. esculentus* juveniles, suspended producers appeared as the main contributors to nutrition for all models computed for the Mangrove site (Fig. 3.8a). *P. esculentus* juveniles this size (25-45 mm TL) are around 1.5 steps above autotrophs (Wassenberg & Hill 1987, O'Brien 1994), only slightly higher than the maximum trophic level analysed (2.4). At this maximum trophic level, suspended producers appeared as the main contributors, with a 1st to 99th percentile of potential contribution of 73-86% (Fig. 3.8a). As with *P. merguiensis* and *M. bennetae*, mangroves had a small importance, with a 1st-99th percentile of 4-16%. However, the minimum value of 4% indicates that, although with a small contribution, mangroves are a necessary component of these models. Other producers had lower potential contributions (Fig. 3.8a).

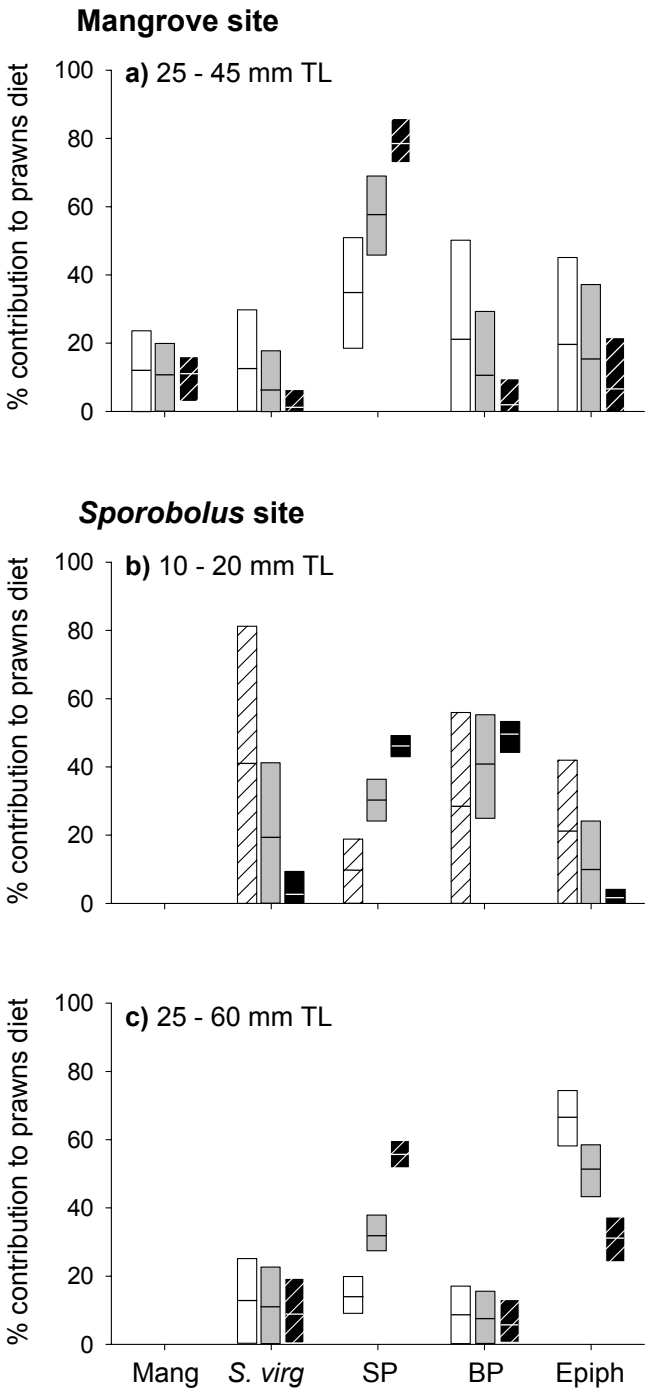

Fig. 3.8. IsoSource results for the minimum (white boxes), intermediate (grey boxes) and maximum (black boxes) possible trophic levels for *P. esculentus* juveniles collected at the *Sporobolus* pool. Boxes represent the 1st to 99th percentile range of feasible contributions of the different autotroph categories. Lines within boxes represent the median value of feasible contributions. Cross-hatched boxes correspond to results for the trophic level closest to that suggested by the literature. BP = benthic producers; Epiph = epiphytes; Mangr = mangroves; SP = suspended producers; *S. virg* = *S. virginicus*.

For the *Sporobolus* site, IsoSource results lead to very different solutions depending on the trophic level considered (Fig. 3.8b, c). According to gut content studies, small *P. esculentus* juveniles are about one trophic level above autotrophs (Wassenberg & Hill 1987, O'Brien 1994), corresponding to the minimum trophic level considered in this study. For this trophic level, the IsoSource model did not lead to a conclusive result, with *S. virginicus,* benthic producers and epiphytes all displaying moderate to high maximum potential contributions coupled with wide ranges of distribution of feasible contributions, which also included 0% (cross-hatched boxes in Fig. 3.8b). Suspended producers had the lowest maximum putative contribution (Fig. 3.8b).

For larger *P. esculentus* juveniles, suspended producers and epiphytes appeared as the main contributors for all trophic levels considered, and *S. virginicus* and benthic producers had low maximums of putative contribution coupled with distributions of putative contribution that included 0%, indicating a small importance (Fig. 3.8c). As mentioned above, the maximum trophic level considered (2.4) is probably closest to reality for this species (Wassenberg & Hill 1987, O'Brien 1994).

As for *P. esculentus,* suspended producers and epiphytes appeared as the main contributors in all models computed for *P. monodon* (Fig. 3.9). This species is considered to be of trophic level ~3 (Luna-Marte 1982, El Hag 1984), and hence results from the maximum considered trophic level (3.2) are probably the most realistic. At this trophic level, suspended producers ranked first in importance followed by epiphytes, both with high medians and narrow ranges of possible contribution, while *S. virginicus*

and benthic producers had low maximum contributions and a range of possible contribution that included 0% (cross-hatched boxes in Fig. 3.9).

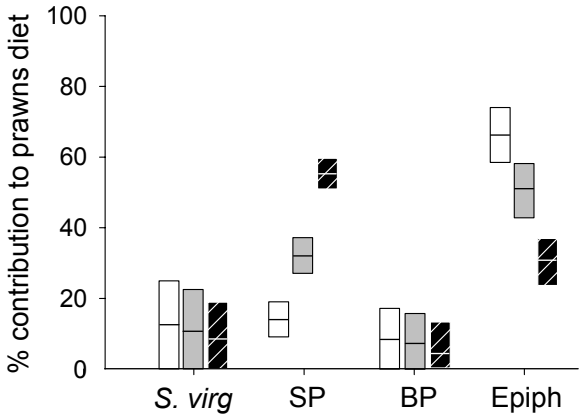

Fig. 3.9. IsoSource results for the minimum (white boxes), intermediate (grey boxes) and maximum (black boxes) possible trophic levels for *P. monodon* juveniles collected at the Mangrove and at the *Sporobolus* pools. Boxes represent the 1st to 99th percentile range of feasible contributions of the different autotroph categories. Lines within boxes represent the median value of feasible contributions. Cross-hatched boxes correspond to results for the trophic level closest to that suggested by the literature. BP = benthic producers; Epiph = epiphytes; SP = suspended producers; *S. virg* = *S. virginicus*.

3.4. DISCUSSION

Although previous studies have reported that the diet of penaeid prawns depends on the availability of food, and that individuals are indiscriminate feeders, consuming whatever is available and assimilating everything they consume (Newell et al. 1995, Chong et al. 2001), results from this study indicate that, under similar conditions of food availability, co-occurring penaeid species can have different diets and even ultimately rely on different sources of carbon. Additionally, prawn diets change substantially with

ontogeny, and between sites dominated by different types of wetland vegetation. Moreover, results strongly suggest that mangrove carbon makes only a limited contribution to penaeid prawn nutrition.

3.4.1. Differences in Diet Between Sites, Species and Size Classes

The fact that juvenile prawns collected at the different pools showed a low within-pool variability in $\delta^{13}C$ and $\delta^{15}N$, coupled with the fact that juveniles collected from a series of pools in March 2006 had different $\delta^{13}C$ and $\delta^{15}N$ values between sites suggests that animals arrived and remained within the areas for long enough to incorporate the isotope composition of the available food sources into their tissues. In fact, juveniles that spend long periods feeding and growing in a particular location are expected to have uniform isotope composition, while more variable values would imply a certain degree of movement between areas or habitats, or diet selectivity at the individual level. This argument of low movement of animals between sites is reinforced by the changes in carbon and nitrogen isotope composition from smaller to larger *P. merguiensis* juveniles, which were almost identical for both sites (see Fig. 3.5). These correlated changes are most parsimoniously explained as a result of sharing the same feeding area, even though the food items consumed were different.

Ontogenetic variation in diet. Stable isotope analysis shows clear ontogenetic shifts in diet for *M. bennetae, P. merguiensis* and *P. esculentus*. These shifts not only

correspond to an increase in mean trophic level, but also to changes in the ultimate sources of energy. These changes, coupled with differences in diet between species, may be important in reducing competition for food both between species and between life stages. In this study, large *P. merguiensis* and *P. monodon* were the species with the highest $\delta^{15}N$, suggesting higher trophic levels than *M. bennetae* and *P. esculentus*.

The observed increases in $\delta^{15}N$ with growth are in accordance with increases in trophic level previously suggested for *P. merguiensis* (Robertson 1988) and *P. esculentus* (Wassenberg & Hill 1987, O'Brien 1994). The current data suggests an increase of around 0.7 trophic levels between sizes for *P. merguiensis* and of around 0.5 for *P. esculentus*. This shift could be even larger for *P. merguiensis* given the high variability in $\delta^{15}N$ values found for the largest size class, which ranged from a value similar to that of smaller juveniles (6.6‰) to the high value of 10.0‰. When compared with the average $\delta^{15}N$ found for the smallest size class, this high value suggests the potential for a difference of more than a trophic level between size classes.

In penaeids, changes in diet and trophic position with growth are explained by an increased ability to capture and handle prey, and a decreased capability for manipulating small food types with the increase in size of the feeding apparatus (O'Brien 1994). Consequently, smaller animals feed mainly on detritus, flocculent detrital material and on small organisms such as copepods and diatoms, while these food sources become more difficult to handle for larger animals. In contrast, greater success in prey capturing and handling makes animals such as polychaetes, bivalves, crustaceans and ophiuroids more available as prey for larger individuals (Dall et al. 1990, O'Brien 1994), leading to an increase in effective trophic level.

No previous study has focused on the diet of *M. bennetae*. This work suggests a trophic level of 1 for 10-20 mm TL juveniles, and an increase of around 1/2 of a trophic level from 10-20 mm to 40-45 mm juveniles. In fact, for small *M. bennetae* juveniles collected from the Mangrove site, IsoSource solutions were only possible if a trophic level of 2 was assumed. The need to assume a trophic level of 2 for these juveniles indicates that the trophic fractionation values of 1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ are realistic since these exact values of trophic fractionation were needed for a feasible IsoSource solution. Moreover, for *P. esculentus* and *P. merguiensis* juveniles, when assuming a $\delta^{15}N$ fractionation value of 3‰, the shifts in $\delta^{15}N$ between size classes corresponded to increases in trophic level that agree with those suggested in previous dietary studies based on gut contents (Wassenberg & Hill 1987, Robertson 1988, O'Brien 1994).

3.4.2. Sources of Energy

Feasible contributions of producers to prawns' diet. Overall, IsoSource results suggest that carbon of mangrove origin is of limited importance for penaeid prawn nutrition in the Ross River estuarine floodplain. In fact, penaeids showed little evidence of incorporation of material of mangrove origin even within the pool surrounded by a mangrove thicket periodically inundated by the tides. Similar results were reported by Newell et al. (1995), Primavera (1996), Loneragan et al. (1997) and Macia (2004) for areas as diverse as Australia, Southeast Asia and East Africa. In contrast, although only sporadically inundated by tides (Edgar 2001), the salt couch *S. virginicus* seemed

to contribute significant amounts of energy to prawn nutrition, representing a substantial subsidy of productivity of terrestrial origin.

Even *P. merguiensis,* a species strongly associated with mangrove areas (Rönnbäck et al. 1999, Vance et al. 2002, Meager et al. 2005), showed a small reliance on mangrove carbon, with a median putative contribution smaller than 10%. This result is in agreement with previous stable isotope (Newell et al. 1995, Loneragan et al. 1997) and gut contents (Robertson 1988) studies, and suggests that the availability of mangrove carbon is not the main factor determining the association of *P. merguiensis* with mangrove areas. In fact, a broad array of producers had substantial contributions to *P. merguiensis* diet, indicating that this species probably consumes material from a range of sources, with its final isotopic composition resulting from the mix of sources consumed.

Loneragan et al. (1997) also suggested that, given their close relationship to mangroves, mangrove carbon is likely to be more important for *P. merguiensis* than for species like *Metapenaeus* spp. and *P. esculentus*, that lack that close association. However, this is not supported by results from this study. Although mangroves had higher potential contribution for *P. merguiensis* than for *M. bennetae* juveniles at the Mangrove site, median putative contributions for *P. merguiensis* were low for all models. Moreover, mangroves also appeared with a slightly lower importance for larger *P. merguiensis* juveniles than for *P. esculentus*.

Variation of $\delta^{13}C$ and $\delta^{15}N$ values between sites. For the three penaeid groups that occurred in both sampling locations (both size classes of *P. merguiensis,* larger *M. bennetae* and larger *P. esculentus*), the shift in $\delta^{13}C$ from lower values at the Mangrove site to relatively higher values at the *Sporobolus* site could be a result of a assimilation of ^{13}C depleted carbon from mangrove origin at the Mangrove site, even though IsoSource results indicate relatively low contributions of these producers. However, those differences were not comparable to the extent of dissimilarity of carbon isotope composition of mangroves and salt marsh, suggesting that although there might be some level of incorporation of carbon from terrestrial origin, it must be associated with a high level of consumption and assimilation of other aquatic producers.

The shifts in animals' $\delta^{13}C$ were similar to that of epiphytes and benthic producers, indicating that these aquatic producers may be important contributors to penaeid diets. However, no exclusive incorporation of carbon from any producer analysed can explain the shift in $\delta^{13}C$ values for any species. For *P. merguiensis* juveniles of both size classes, the shift in $\delta^{13}C$ was closer to that of benthic producers, and given their ^{13}C enriched $\delta^{13}C$ values, benthic producers could be the main contributors to *P. merguiensis* diet. This result is in agreement with results from the IsoSource model, where benthic producers appeared as necessary contributors in three of the four models computed for this species. For large *P. esculentus* juveniles on the other hand, the isotopic shift between sites was more similar to that of epiphytes, suggesting a major dependence on this source. This is again in accordance with IsoSource results, where epiphytes appeared to be the most important contributors at the *Sporobolus* site, and also showed a moderate maximum potential contribution at the Mangrove site.

3.4.3. Conclusion

Stable isotope data indicates that co-occurring species of penaeid prawns can rely on different sources of carbon, and differ in terms of level of omnivory and trophic levels. Moreover, results also suggest a high level of diet plasticity, as well as significant ontogenetic variations in diet for these species. Despite clear differences in carbon sources, the four penaeid species seemed to rely mainly on autochthonous sources of energy, although carbon from the salt couch *S. virginicus* also seemed important in several cases. Despite that some incorporation of mangrove carbon was detected, it did not seem to be of major importance for any of the species considered.

Chapter 4

Sources of Energy and Trophic Structure in Open Estuarine Systems of Tropical Australia

4.1. INTRODUCTION

Stable isotope analysis has frequently been used in the study of estuarine food webs to detail the sources of energy supporting aquatic communities (e.g. Bouillon et al. 2004b, Connolly et al. 2005a), analyse the impacts of sewage inputs (e.g. Fry 1999, Waldron et al. 2001, Hadwen & Arthington 2007), document the effects of species invasions (e.g. Mitchell et al. 1996, Vander Zanden et al. 1999a), among other questions. However, most studies have focused mainly on the invertebrate fauna, and hence trophic pathways to higher trophic levels, as well as linkages among higher-level components are still not well understood. While a number of relatively detailed food web studies have been published for lacustrine (e.g. Gu et al. 1996, Vander Zanden et al. 1999b) and riverine (e.g. Jepsen & Winemiller 2002) systems, a similar level of understanding is not available for estuarine or marine areas. In fact, most published studies from estuarine areas have aimed at identifying the sources of energy for a species or a group of species, generally in relation to the importance of mangroves, salt marsh or seagrass habitats as a source of carbon (e.g. Loneragan et al. 1997, Bouillon et al. 2004b, Nagelkerken & van der Velde 2004, Melville & Connolly 2005), rather than detailing relationships between species and among the estuarine community as a whole.

Complex ecological interactions between species are common in most ecosystems, and are ultimately reflected in the trophic structure and dynamics, and in the persistence of communities through time. Although fish are often at the top of food chains in aquatic systems, they are a trophically diverse group, encompassing species of different sizes and diverse feeding strategies. Despite the importance of understanding the trophic relationships between fish species, no study has investigated this subject in detail using stable isotopes. Past studies have generally considered only a few species (e.g. Sherwood & Rose 2005, Alfaro et al. 2006, Lugendo et al. 2006), frequently of economic importance. Although more detail was probably not necessary for the purpose of those studies, the inclusion of the greatest possible number of species while using the highest taxonomic level possible can elucidate important aspects of interactions between species, which might not be noticeable at coarser levels of taxonomic resolution (Polis 1994). Moreover, the lack of a broad understanding of trophic organisation hinders further studies that rely on the availability of comprehensive food web detail as background knowledge.

A combination of factors makes stable isotope analysis of estuarine organisms complex and difficult to interpret. Firstly, interpretation is complicated by the inherent mobility of animals, and the common occurrence of tidal migrations (Guillard 1998, Krumme & Saint-Paul 2003, Jelbart et al. 2007). Additionally, estuaries often feature a range of primary producers that can have different isotopic compositions and often occur in close proximity to each other. Isotope composition of these primary producers can also vary in space and time (e.g. seagrass (France 1995a, Anderson & Fourqurean 2003), seston (Cifuentes et al. 1996), plankton (Sato et al. 2006) and benthic microalgae (Currin et al. 1995)). Consequently, consumers are likely to feed on a

variety of food types with different isotopic values, and their final isotopic composition will reflect the weighted average of that of the food sources they have consumed.

Despite these difficulties, it is imperative to evaluate the sources of energy supporting animals in these highly dynamic systems, and to identify trophic relationships between species. Although it can be difficult to control for the many factors that influence stable isotope composition of estuarine animals, the analysis of a number of estuaries receiving terrestrial inputs with different $\delta^{13}C$ and/or $\delta^{15}N$ signatures can be used to clarify the importance of terrestrial and aquatic productivity to estuarine food webs.

In Chapter 2, an incorporation of carbon of terrestrial wetland origin into aquatic animals was detected for two relatively isolated estuarine pools in the Ross River floodplain. The two areas considered were small and relatively isolated, and hence the incorporation of energy of terrestrial origin was easily identified. However, the situation is more complex in large open estuarine areas, where currents and tides greatly contribute to the dilution of the material of terrestrial origin through the area. Nevertheless, the comparison of the stable isotopic composition of animals from systems with different ecological conditions, in a similar approach to that applied to the two Ross River floodplain pools in Chapters 2 and 3, should provide important information on the energy sources in these systems.

In the present study, stable isotope analysis is used to determine the extent to which carbon from terrestrial wetland origin is incorporated into aquatic food webs in open estuarine systems and to analyse the trophic structure in these areas. The specific aims were: (i) to develop a detailed understanding of the sources of energy and food

web structure in a near-pristine estuary in the Australian Wet Tropics, and (ii) compare that to systems impacted by agriculture, urban development, and to a near-pristine system in the Dry Tropics.

4.2. METHODS

4.2.1. Study Sites

Four estuarine systems in North Queensland, Australia, were studied: Deluge Inlet, Half Moon Creek and Victoria Creek in the Wet Tropics, and Blacksoil Creek in the Dry Tropics (Figure 4.1). A special attention was given to the near-pristine system of Deluge Inlet, where a wide range of producers and consumers were analysed to provide a comprehensive picture of the trophic processes occurring in an unaltered Australian Wet Tropics estuarine system. Logistic and financial constraints prevented an equivalent level of sampling in the remaining estuaries. Hence, sampling in these systems and subsequent comparisons were mainly centred on the fish community. Victoria Creek and Half Moon Creek were selected because they are subjected to a range of human disturbances: sugarcane plantations at Victoria Creek, and sugarcane and urban development at Half Moon Creek. Blacksoil Creek was used to allow comparison with a pristine system in the Dry Tropics.

Australia's Wet Tropics receives high rainfall through most of the year, supporting a diversity of mangrove species and allowing the development of dense mangrove forests along the margins of estuaries. Deluge Inlet, draining the western side of Hinchinbrook Island and flowing into the Hinchinbrook Channel, is in a pristine area

surrounded by extensive, dense mangrove forests, with scattered areas of seagrass both intertidally and subtidally. Victoria Creek, about 30 km south of Hinchinbrook Channel, is also surrounded by extensive mangrove forests, but a large area of the catchment is highly impacted by sugarcane (*Saccharum* sp.) farming.

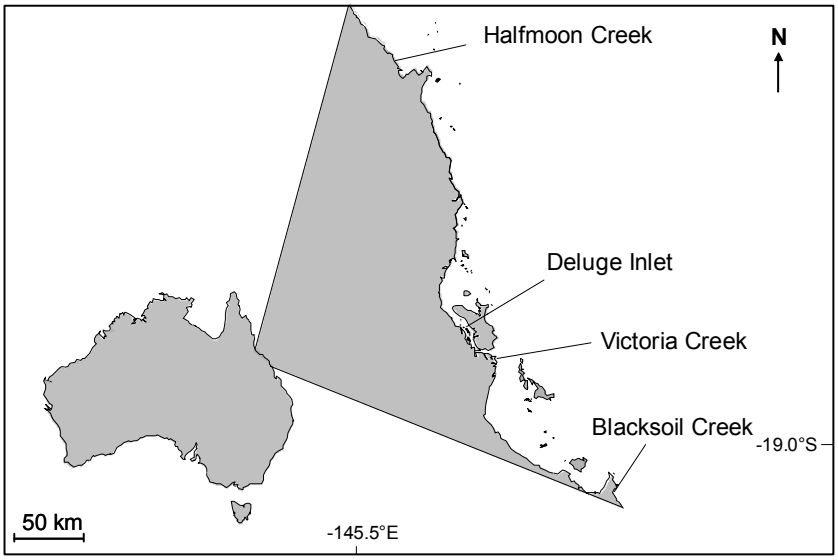

Fig. 4.1. Map showing the location of the four estuarine systems considered in this study. Scale and coordinates are for the inset map.

Half Moon Creek, located 15 km north of the City of Cairns, is surrounded by a fringing mangrove forest with a maximum width of 0.5 km. The original freshwater wetland has been reduced by extensive sugarcane plantations, and an area of the tidal wetland has been lost to urban development, which includes a marina, a golf course, a canal estate and a tourist complex (Sheaves & Johnston 2005). A wastewater treatment plant is also present, discharging its effluents into the creek. Blacksoil Creek, the southernmost location about 110 km south of Victoria Creek, is an almost pristine estuary in the Dry Tropics, surrounded by large areas of heterotrophic, nutrient poor sandflats and saltpan (Alongi 1988, Alongi 1994, Bruinsma 2001). Due to the hypersaline conditions,

mangrove trees are limited to a narrow fringing zone adjacent to the waterway, in the most downstream part of the creek. These thin mangrove borders are interspersed with sand dune vegetation and stands of terrestrial vegetation.

Little seagrass is present in Victoria, Half Moon or Blacksoil Creeks, although it occurs in adjacent coastal areas (Lee Long et al. 1996). Similarly, little or no macroalgae occur in these estuaries (Danaher 1995) given to the absence of a substrate suitable for attachment. Information on ecological and conservation conditions of each estuary can be found in Table 4.1.

Table 4.1. Physical, ecological and conservation conditions of the four estuarine areas considered in this study. Information based on Ozestuaries (www.ozestuaries.org) and Bruinsma (2001), with the exception of Blacksoil Creek, for which information is based on personal observations.

Estuary Conditions	Half Moon Creek	Deluge Inlet	Victoria Creek	Blacksoil Creek
Physical conditions				
Catchment area (km^2)	25	NI	78	NI
Extreme tidal range (m)	3.1	3.5	3.5	3.5
Mean annual rainfall (mm)	2250	2100	2100	950
Intertidal flats (km^2)	0.15	13.35*	8.14	NI
Intertidal proportion	0.90	0.40*	0.84	NI
Intertidal range category	High	Medium*	High	High
Runoff coefficient	0.21	0.34*	0.21	NI
Classification	Tide dominated	Tide dominated	River dominated	Tide dominated
Ecological conditions				
Area of mangrove (km^2)	3.67	97.44*	12.72	Low
Mangrove cover	Extensive	Extensive	Extensive	Scattered
Area of seagrass (km^2)	0	0.65*	0.3	0
Seagrass cover	-	Scattered	Patchy	-
Area of salt marsh (km^2)	0	0	1.15	NI
Salt marsh cover	-	-	Patchy	Scattered
Area of saltpan	0	0	0	Large
Conservation condition				
Ecological condition	Highly modified	Near pristine	Moderately modified	Near pristine
Condition modifiers	Urbanization; agriculture	-	Agriculture	-

NI - no information available
* – data for Hinchinbrook Channel

4.2.2. Sample Collection, Processing and Analysis

Deluge Inlet was sampled between April and June 2005, Victoria Creek in June 2005, Half Moon Creek in December 2004, and Blacksoil Creek in November 2004. Deluge Inlet was sampled intensively to collect both primary producers and as great range of invertebrates and fish as possible. This broad-spectrum trophic collection aimed to represent the estuarine community as completely as possible, in order to describe the energy sources and trophic pathways from lower trophic levels through to fish with as much detail as possible. At the remaining estuaries, sampling was primarily focused on fish, with decapod crustaceans also retained when captured, although no additional effort was made to collect these species.

Fish were collected with 18 mm mesh cast nets, hooks and lines, and block nets (Ethics Approval A852_03). Block nets were deployed at high tide, blocking small tidal inlets (ca. 30 m wide mouths) and trapping fish as the tide receded. Penaeid prawns and decapod crabs were also collected along with the fish. At each estuary, fish sampling was comprehensive, as samples were collected concurrently with two intensive studies on species composition and small scale habitat distribution of fish fauna in the areas (Johnston & Sheaves in press, Baker & Sheaves, unpubl data). All animals retained were immediately euthanized in ice-water slurry, and frozen as soon as possible. Other organisms were collected as described in Chapter 2.

At Deluge Inlet, green leaves of the mangroves *Rhizophora stylosa* and *Sonneratia* sp., as well as the seagrass *Halophila ovalis* were hand picked from individual plants (n = 2-4). Epiphytes were not removed from seagrass blades before analysis and hence seagrass isotopic values reflect those of both seagrass and respective epiphyte

assemblage. Microphytobenthos was also sampled from six different locations by collecting the surface sediments with a spatula and separating the microalgae fraction based on its vertical migration properties (Couch 1989, as modified by Riera & Richard 1996). For this process, sediment was taken to the laboratory as soon as possible after collection, spread finely on flat trays, and covered with a 63 μm mesh nylon screen. It was kept wet and in the dark overnight, and the next day a green matt of algae cells that migrated through the mesh was collected in the nylon screen. The screen and attached algae were dried at 60°C for 24 h. The dry algal material was subsequently removed with a spatula and collected into a glass vial.

Stable isotope samples were processed and analysed as described in Chapter 2.

4.2.3. Data Analysis

Whenever possible, between two and five individuals of fish, decapod crustaceans and large gastropods were analysed per species and per site. When individuals of different sizes were present, these were considered as separate groups. In many cases however, it was only possible to collect one specimen per species. For small benthic invertebrates either one or two samples were analysed, each composed of several organisms in order to obtain enough material for analysis.

Sources of Energy

Since results of the IsoSource model can vary considerably with trophic level considered and with variations in $\delta^{13}C$ and $\delta^{15}N$ trophic fractionation (see Chapter 3), in this study the importance of terrestrial wetland carbon for aquatic organisms was analysed only by graphic comparison of carbon isotope composition of animals with that of the different classes of producers, and by comparing isotope values of fish between sites.

$\delta^{13}C$ values of producers considered for comparisons were taken either from a number of studies along the Queensland coast, or from appropriate published reviews. Hence, each primary producer category was represented by a range of $\delta^{13}C$ values: for mangroves, a range of -29.8 to -25.2‰ was used, corresponding to the range of isotopic values found for 19 individual plants of four species collected in five estuaries along the Central and North Queensland coast (Table 4.2; Fig. 4.2) (unpubl. data). For C_4 terrestrial producers, a range in $\delta^{13}C$ of -16.7 to -13.3‰ was calculated, from the analysis of 24 plants of six species collected from five estuarine areas in Tropical Australia (Table 4.2; Fig. 4.2) (unpubl. data). For aquatic producers, the ranges of $\delta^{13}C$ values were based on relevant published reviews. $\delta^{13}C$ of benthic and planktonic producers were based on France (1995b), where values of -17 ± 4‰ (mean ± SD) for benthic and of -22 ± 3‰ for planktonic marine algae were reported. Similarly, seagrass carbon isotope composition of -11.5 ± 3.2‰ were taken from a review by Hemminga & Mateo (1996) on the variability in seagrass $\delta^{13}C$.

Table 4.2. Mangrove and C_4 wetland producers used to calculate the range in $\delta^{13}C$ characteristic of these producers in Central and North Queensland, with an indication of sites of collection. *n* indicates number of samples analysed.

Wetland producers	*n*	Sites of Collection
Mangroves		
Aegiceras corniculatum	6	Ross River, Munduran Ck, Gonong Ck
Avicennia marina	6	Ross River, Ross Ck, Gonong Ck
Rhizophora stylosa	5	Deluge Inlet, Gonong Ck
Sonneratia sp.	2	Deluge Inlet
C_4 plants		
Atriplex muelleri	3	Twelve Mile Ck, Munduran Ck
Isolepis nodosa	1	Ross Ck
Portulaca oleracea	1	Twelve Mile Ck
Sporobolus virginicus	14	Ross River, Ross Ck, Twelve Mile Ck, Gonong Ck
Suaeda australis	2	Ross Ck
Urochloa mutica	3	Ross Ck, Gonong Ck

Fish $\delta^{13}C$ values were also compared between estuaries with a one-way analysis of variance (ANOVA) followed by the Unequal N HSD multiple comparison test. Fish from Victoria Creek could not be included in the ANOVA since variance was larger than in the other estuaries, and no transformation could overcome this problem. Fish $\delta^{15}N$ values were also compared between sites with a one-way ANOVA to detect any differences that could indicate the incorporation of ^{15}N enriched nitrogen of anthropogenic origin, as some of the study sites were impacted by anthropogenic development.

Trophic Structure

For the study of trophic structure, animals were separated by taxa and fish were classified into seven trophic guilds according to relevant published studies (see Annex I). For each site, the approximate trophic position of each species was estimated

graphically. No relationship between $\delta^{13}C$ and $\delta^{15}N$ was detected for fish primary consumers in Deluge Inlet (p = 0.1027) or Blacksoil Creek (p = 0.2003). Data from the other two estuaries was unsuitable for ANCOVA or correlation analysis as only two primary consumer species were collected in Half Moon Creek, while in Victoria Creek primary consumers formed two well separated groups. Nevertheless, visual analysis of the $\delta^{13}C$-$\delta^{15}N$ plots did not suggest the presence of a $\delta^{13}C$-$\delta^{15}N$ relationship for any trophic guild. Therefore, trophic levels were estimated based only on $\delta^{15}N$ values at all locations, considering a $\delta^{15}N$ trophic fractionation of 3‰ (McCutchan Jr et al. 2003, Vanderklift & Ponsard 2003).

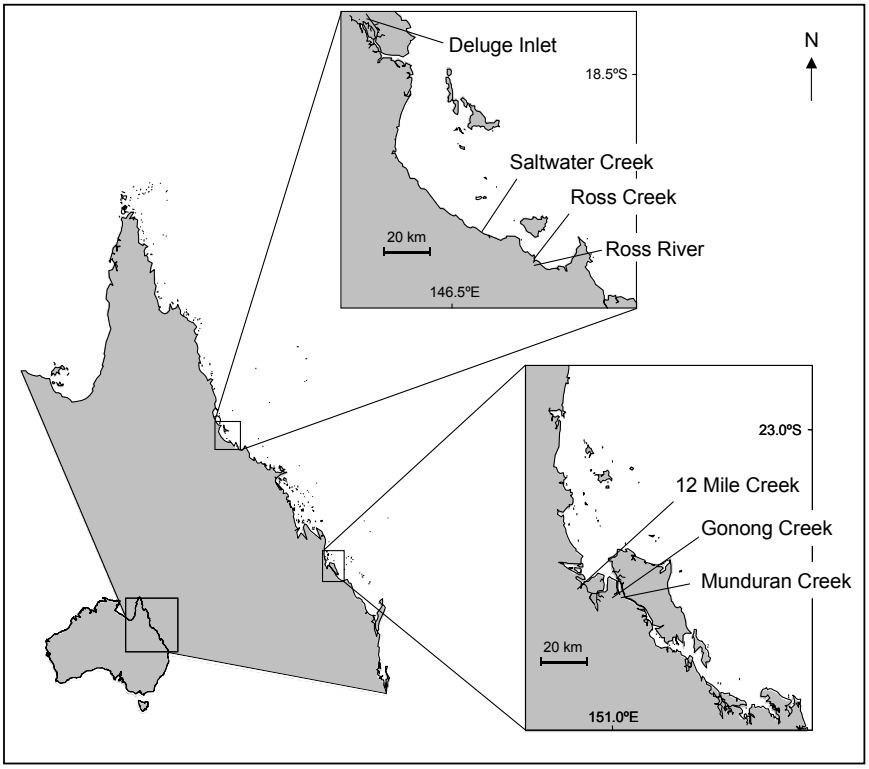

Fig. 4.2. Map showing the geographic locations of collection of mangroves and C_4 plants used for the calculation of the ranges in $\delta^{13}C$ characteristic of these producers used in this study.

Since detritivorous mullet *Valamugil* spp. were found at all sites, these were used as a baseline to estimate trophic positions. A detritivorous fish species was used as a baseline instead of invertebrates because they are easily captured and highly abundant in Tropical Australian estuaries (Sheaves 2006). Moreover, $\delta^{15}N$ values were found not to differ between invertebrate primary consumers and fish of the same trophic level (see Chapter 2). Herbivorous fish species were not used as baseline species because they were not present in all systems.

Food chain length, or the number of transfers of energy from primary producers to the top of the food chain (Post 2002a), was also estimated by calculating the number of trophic steps between the detritivorous mullet of lowest $\delta^{15}N$ and the species of highest $\delta^{15}N$.

Detailed Analysis of the Deluge Inlet Food Web. A detailed investigation of energy sources and trophic pathways was conducted for the near-pristine system of Deluge Inlet. For this study, the isotopic composition of locally collected primary producers was used. Since fish species seemed to form different groups, a similarity profile routine (SIMPROF) based on Euclidian similarities was used to test for evidence of structure at $p = 0.001$, using PRIMER® v.7.

Moreover, for fish species known to feed on particular sources (based on the literature), the importance of each potential source was evaluated. Mangroves, microphytobenthos and seagrass were considered as the potential sources for phytodetritivorous fish. Since $\delta^{13}C$ values of these primary producers were well

separated in $\delta^{13}C$, the IsoSource model was used to identify the main contributors to these species' diets (see Chapter 2 for a description of IsoSource). However, due to the similarity in $\delta^{15}N$ for the three potential contributors, the model was run based only on $\delta^{13}C$ values. As in Chapters 2 and 3, a $\delta^{13}C$ fractionation value of 1‰ was used.

The IsoSource model could not be computed for fish species of higher trophic levels because in some cases similar potential food sources had variable isotope composition. Therefore, the importance of the different potential contributors was qualitatively determined by superimposing the adjusted isotopic values of consumers (corrected for fractionation for one trophic level), onto the isotopic values of the potential food sources. Fractionation values of 1‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ were used. The similarity between corrected isotope values of consumers and the isotopic composition of the potential food sources was considered as indicative of the importance of the respective source to the consumers' diet.

For planktivores and small invertebrate feeders, potential prey included zooplankton, small planktonic shrimps (*Acetes sibogae* and caridean postlarvae) and peracarid crustaceans (Wilson & Sheaves 2001, Nyunja et al. 2002, Baker & Sheaves 2005). For macrobenthic carnivores, potential prey included benthic penaeid prawns (*Penaeus* (*Fenneropenaeus*) *merguiensis*, *Penaeus semisulcatus* and *Penaeus esculentus*), planktonic shrimps (*A. sibogae* and caridean postlarvae), small crabs (Hymenosomatidae, Majidae and Ocypodidae juveniles, *Metopograpsus frontalis*, *Diogenes avarus* and *Uca vomeris*) and other small benthic organisms such molluscs, polychaetes and peracarid crustaceans (Wilson & Sheaves 2001, Baker & Sheaves 2005). In cases where similar sources had similar isotope composition, these were combined into broader categories (e.g. different crab taxa combined into a single crab

category). For major piscivores, potential prey species included ponyfish (*Leiognathus* spp.), silverbiddies (*Gerres* spp.), whiting (*Sillago sihama*) and clupeiods (*Anodontostoma chacunda, Encrasicholina devisi, Herklothichtys* spp., *Nematolosa come* and *Sardinella gibbosa*) (Salini et al. 1990, Baker & Sheaves 2005).

4.3. RESULTS

4.3.1. Sources of Energy

Comparison of Fish $\delta^{13}C$ and $\delta^{15}N$ Values Between Estuaries

Fish $\delta^{13}C$ and $\delta^{15}N$ values differed between estuaries (Fig. 4.3a, b). For $\delta^{13}C$, the range of fish $\delta^{13}C$ was greater at Victoria Creek (14.2‰) than at the remaining systems (7.3 to 9.1‰), varying from values within the range of mangroves to values similar to benthic aquatic producers and C_4 terrestrial producers (Fig. 4.3a). Note that Victoria Creek is the only system where both ^{13}C depleted C_3 mangroves and ^{13}C enriched C_4 sugarcane plantations occur in significant densities. At the remaining sites, the ranges in fish $\delta^{13}C$ were narrower (Fig. 4.3a). Because of the greater variability in fish $\delta^{13}C$ found at Victoria Creek, this estuary could not be included in the ANOVA comparisons. Nevertheless, it was clear that fish from Victoria Creek had generally lower $\delta^{13}C$ values than fish from Half Moon or Blacksoil Creeks (Fig. 4.3a), and that samples from Victoria Creek had a median $\delta^{13}C$ similar to that from Deluge Inlet.

A significant effect of estuary on fish $\delta^{13}C$ was detected for Deluge Inlet, Half Moon Creek and Blacksoil Creek ($F_{(2,75)}$ = 64.592, p = 0.0000). Fish from Blacksoil Creek

were significantly more enriched in ^{13}C than fish from Deluge Inlet (HSD, p = 0.0001) and from Half Moon Creek (HSD, p = 0.0260), and fish from Half Moon Creek were in turn more enriched in ^{13}C than those from Deluge Inlet (HSD, p = 0.0001). The low $\delta^{13}C$ of fish from Deluge Inlet when compared to fish from Half Moon and Blacksoil Creeks suggests that mangrove derived carbon is likely to be more important to aquatic food webs in Deluge Inlet. In Half Moon and Blacksoil Creeks, animals had $\delta^{13}C$ values similar to aquatic benthic producers and C_4 terrestrial producers. Since densities of C_4 producers were very low in these areas, animals' high $\delta^{13}C$ are likely to be a result of a dependence on benthic algae. Some species had however very high $\delta^{13}C$ values, within the range of seagrass $\delta^{13}C$ (Fig. 4.3a), suggesting that seagrass beds in adjacent waters may have an important input into these food webs. Note however that $\delta^{13}C$ values of primary producers considered in this overview figure correspond to values taken from a range of locations (mangroves and C_4 producers) or from the literature (aquatic producers), and not to the actual carbon isotope composition of producers collected in this study.

There was also a significant effect of location on fish $\delta^{15}N$ ($F_{(3,91)}$ = 74.696, p = 0.0000), as fish from the urbanised Half Moon Creek were substantially more enriched in ^{15}N than fish from the remaining estuaries (p = 0.0001 in all cases; Fig. 4.3b). Mean $\delta^{15}N$ values of fish from Deluge Inlet and Victoria Creek did not differ (p = 0.8987), and animals from those two estuaries had significantly higher $\delta^{15}N$ than animals from Blacksoil Creek (p = 0.0002 and p = 0.0005 respectively; Fig. 4.3b).

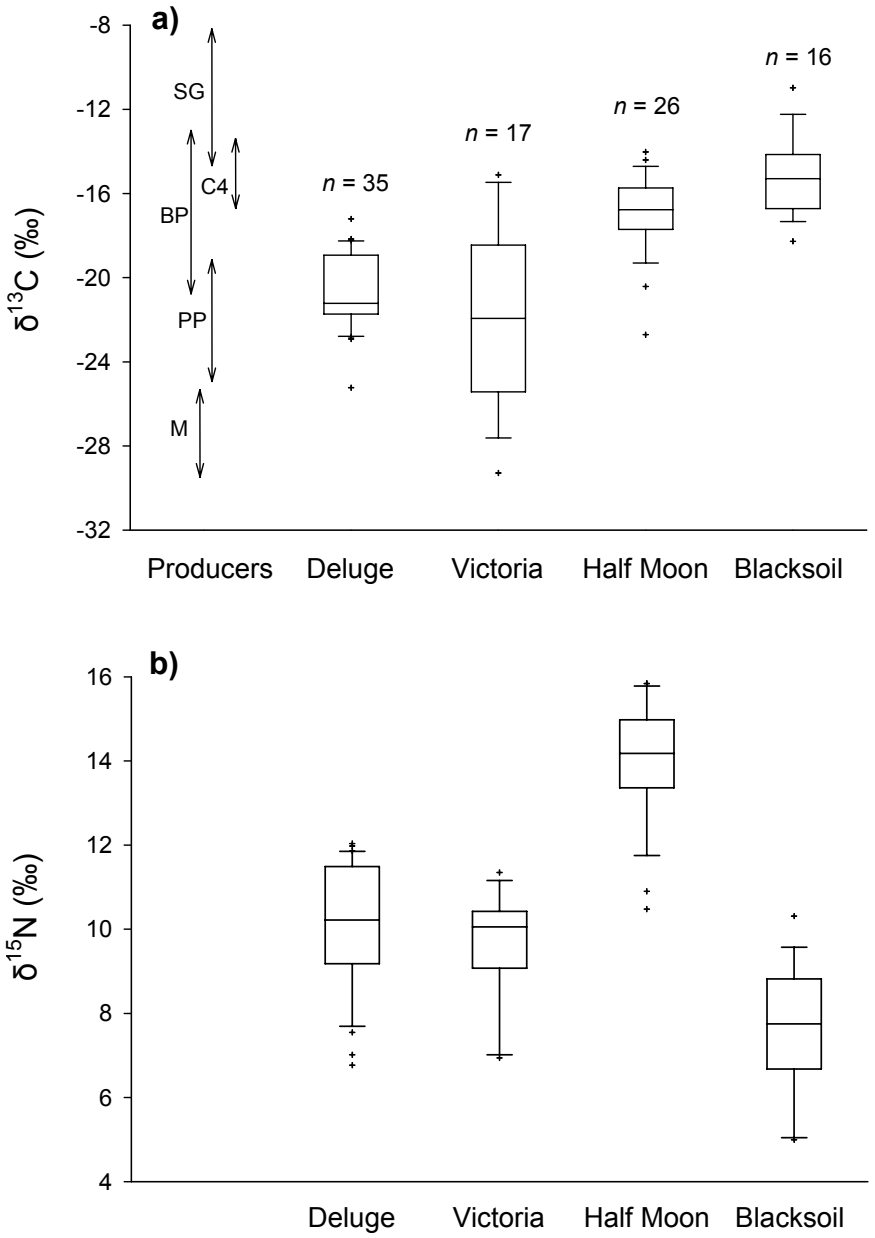

Fig. 4.3. Box plots showing the median (line within the boxes), interquartile ranges (indicated by boxes), 10th and 90th percentiles (whiskers) and outliers (✦) of **a)** $\delta^{13}C$ and **b)** $\delta^{15}N$ values of fish from Deluge Inlet and Victoria, Half Moon, and Blacksoil Creeks. Results calculated based on the average values of each fish species. Arrows indicate range in $\delta^{13}C$ of the different classes of producers (see text). BP = benthic producers; C4 = C_4 producers; M = mangroves; PP = planktonic producers; SG = seagrass. *n* = number of species included.

4.3.2. Trophic Structure

4.3.2.1. Deluge Inlet Food Web

In Deluge Inlet, primary producers including seagrass, microphytobenthos and mangroves were analysed in addition to animals. Zooplankton was also collected and its isotopic composition considered as a proxy for values of phytoplankton. Primary producers had contrasting $\delta^{13}C$, ranging from -28.4 to -18.4‰ (Table 4.3; Fig. 4.4). Mangroves had very low $\delta^{13}C$ (-29.5 to -28.0‰), with values in the lower part of the range found for mangroves in Tropical Queensland (-29.8 to 25.2‰). On the other hand, microphytobenthos and seagrass had $\delta^{13}C$ values lower than the range suggested by the literature for these marine producers (France 1995b, Hemminga & Mateo 1996 respectively). For $\delta^{15}N$, microphytobenthos, the mangrove *R. stylosa* and the seagrass *H. ovalis* had similar and relatively low $\delta^{15}N$ values. Zooplankton, mainly calanoid copepods, had $\delta^{15}N$ values higher than aquatic producers, even after adjustment for trophic fractionation (for a proxy for isotopic composition of phytoplankton), and also higher than most invertebrate species (Table 4.3; Fig. 4.4).

A total of 32 invertebrate and 35 fish species were collected from Deluge Inlet. Animals were well separated in $\delta^{13}C$, ranging from -25.4 to -16.3‰, suggesting considerable differences in ultimate sources of carbon, from a substantial reliance on mangrove carbon to an almost exclusive reliance on seagrass. Among invertebrates, most molluscs had relatively low $\delta^{13}C$ (Table 4.3), suggesting an important incorporation of mangrove carbon (Fig. 4.4). Decapods and peracarids had higher $\delta^{13}C$, ranging from intermediate values that could result from dependence on a combination of sources, to higher values that indicate an almost exclusive incorporation of seagrass (Fig. 4.4).

Table 4.3. Size range and $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of organisms collected at Deluge Inlet. Sizes indicate total length for fish (in 5 mm size classes), prawns, shrimps and molluscs, and carapace width for crabs. *n* = number of samples analysed. When *n* = 2, the range is presented. Numbers between brackets indicate number of individuals included in the sample, in cases where samples were composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Halophyla ovalis	2	-	-18.5 to -18.2	2.2 to 2.6
Microphytobenthos	6	-	-22.8 ± 0.3	2.9 ± 1.2
Rhizophora stylosa	4	-	-28.0 ± 0.6	2.4 ± 0.6
Sonneratia sp.	2	-	-29.5 to -28.9	2.4 to 3.1
Zooplankton	1	-	-20.0	7.6
Invertebrates				
Molluscs				
Callista sp.	1(>10)	3	-23.8	5.6
Cerithidea cingulata	1(>10)	3	-20.2	6.9
Gari sp.	1(~10)	5	-22.7	6.8
Litoria scabra	3	10-12	-24.7 ± 0.1	6.0 ± 0.1
Mytilus sp.	1(3)	20	-25.1	6.6
Nassarius sp.	1(>10)	5	-21.1	8.1
Nerita costata	4	16-20	-23.4 ± 0.1	6.9 ± 0.2
Saccostrea equinata	3	80-90	-24.3 ± 0.5	6.6 ± 0.2
Tapes sp.	1(>10)	3	-25.4	6.2
Tellina sp.	1(>10)	3	-25.2	4.8
Polychaetes				
Nereidae	1(~30)	-	-22.7	6.8
Oweniidae	1(~30)	-	-21.2	6.1
Dorvilleidae	1(~30)	-	-22.0	7.7
Peracarid crustaceans				
Amphipod sp.1	2(~10)	-	-19.6 to -18.9	4.2 to 4.5
Amphipod sp.2	1(~10)	-	-22.2	3.2
Cirolanidae	1(~10)	-	-22.9	5.3
Phoxocephalidae	1(~10)	-	-18.3	6.4
Decapod crustaceans				
Acetes sibogae	2 (5)	25	-23.4 to -23.0	8.5 to 8.7
Caridea (postlarvae)	1(5)	4	-22.9	8.0
Diogenes avarus	1(2)	2	-20.7	7.7
Hymenosomatidae (juv)	1(5)	2	-21.3	5.6
Majidae (juv)	1(3)	6	-20.4	7.3
Metopograpsus frontalis	2	23-25	-23.1 to -23.0	7.6 to 7.8
Ocypodidae (juv)	2(5)	2	-19.6	4.1 to 4.5
Penaeus esculentus	1	42	-22.3	6.3
Penaeus merguiensis	3	50-55	-20.6 ± 0.0	8.0 ± 0.5
Penaeus semisulcatus	1	36	-18.3	6.4
Portunus pelagicus	1	22	-18.0	5.4
P. pelagicus	1	114	-22.2	7.1
Scylla serrata	2	47-66	-19.5	8.0
Uca vomeris	1	30	-16.3	5.6

Table 4.3. (cont.) Size range and $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of organisms collected at Deluge Inlet. Sizes indicate total length for fish (in 5 mm size classes), prawns, shrimps and molluscs, and carapace width for crabs. *n* = number of samples analysed. When *n* = 2, the range is presented. Numbers between brackets indicate number of individuals included in the sample, in cases where samples were composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Fish				
Herbivores				
Hyporhamphus quoyi	2	145	-19.3 to -19.2	7.0 to 8.2
Siganus lineatus	3	45-65	-25.2 ± 1.1	8.4 ± 0.2
Zenarchopterus buffonis	2	120	-22.9 to -22.8	8.8 to 9.0
Detritivores				
Anodontostoma chacunda	3	50-85	-20.4 ± 0.6	7.8 ± 0.2
Nematolosa come	3	60-85	-20.6 ± 1.0	6.8 ± 0.3
Valamugil sp.	2	90	-19.3 to -18.9	6.8 to 7.2
Omnivores				
Marilyna pleurosticta	2	75-105	-22.7 to -21.8	8.1 to 8.7
Planktivores				
Ambassis nalua	1	55	-21.6	10.7
Ambassis telkara	5	20-60	-21.2 ± 0.5	10.3 ± 0.3
Encrasicholina devisi	1	75	-21.3	11.1
Herklotsichthys castelnaui	3	60-80	-22.9 ± 0.4	9.8 ± 0.1
Herklotsichthys koningsbergeri	2	105	-17.5 to -16.9	9.3 to 9.8
Leiognathus decorus	3	45-65	-21.7 ± 0.6	10.8 ± 0.1
Leiognathus equulus	4	30-55	-21.5 ± 0.2	10.6 ± 0.3
Sardinella gibbosa	2	75-85	-19.0 to -18.7	8.5 to 8.8
Macrobenthic carnivores				
Acanthopagrus berda	3	55-150	-22.1 ± 0.2	10.1 ± 0.1
Arothron manilensis	1	140	-22.0	9.9
Gerres erythrourus	2	85-95	-21.9 to -21.2	8.9 to 10.0
Gerres filamentosus	3	60-145	-22.8 ± 0.4	9.2 ± 0.6
Pomadasys kaakan	2	75-130	-22.0 to -21.0	10.2 to 11.4
Sillago sihama	2	100	-22.2	9.4 to 9.8
Toxotes chatareus	3	70-210	-21.5 ± 0.2	10.2 ± 0.1
Minor piscivores				
Apogon hyalosoma	2	75-80	-21.5 to -20.4	10.1 to 10.3
Butis butis	1	85	-21.5	10.5
Lethrinus lentjan	2	70	-21.9 to -21.2	9.2 to 9.4
Lutjanus russellii	2	60-120	-21.4 to -20.9	11.1 to 11.4
Major piscivores				
Atule mate	1	265	-18.2	11.8
Caranx ignobilis	4	295-355	-18.5 ± 0.4	11.7 ± 0.3
Caranx sexfasciatus	1	160	-18.2	11.5
Gazza minuta	4	35-65	-18.3 ± 0.2	11.4 ± 0.1
Scomberoides commersonnianus	3	310-560	-18.7 ± 0.5	12.0 ± 0.3
Scomberoides lysan	2	110-195	-19.0 to -18.7	11.7 to12.4
Scomberoides tala	2	315-375	-19.8 to -19.2	11.3 to 12.4
Sphyraena barracuda	2	375-510	-19.6 to -19.0	11.7 to 11.9
Sphyraena putnamae	1	445	-18.9	11.5

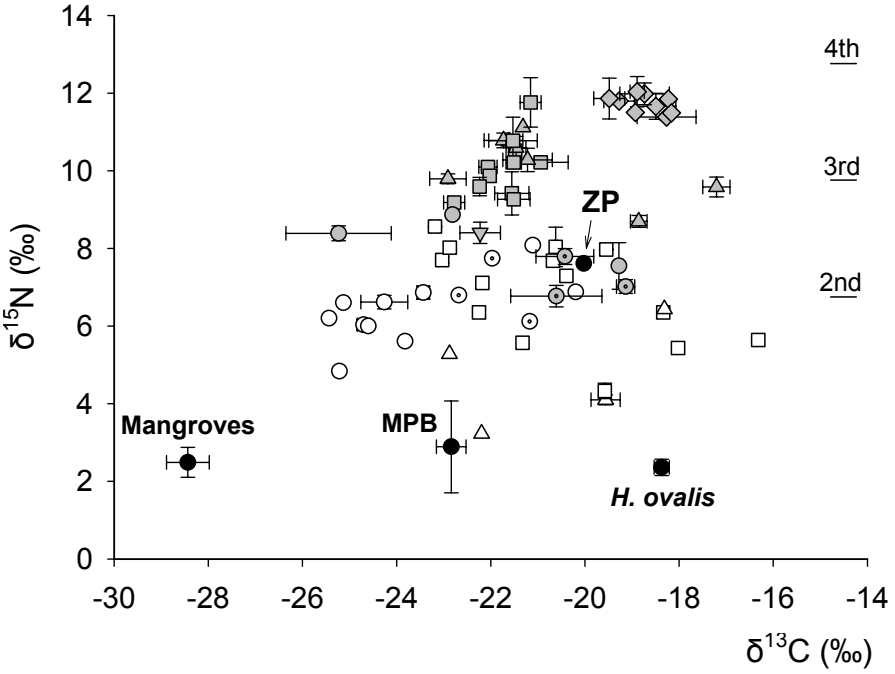

Fig. 4.4. Mean $\delta^{13}C$ and $\delta^{15}N$ (± SE) of producers and zooplankton (black symbols), invertebrates (white symbols) and fish (grey symbols) from Deluge Inlet. $\delta^{15}N$ levels corresponding to the different trophic levels are indicated on the right of the graph (see text). Invertebrates: ○ - molluscs; ⊙ - polychaetes; △ - peracarids; □ - decapods. Fish: ● - herbivores; ◉ - detritivores; ▽ - omnivores; ▲ - planktivores; ■ - carnivores (macrobenthic carnivores and minor piscivores); ◇ - major piscivores. MPB = microphytobenthos; ZP = zooplankton.

In general, fish had higher $\delta^{15}N$ values than invertebrates (Fig. 4.4). $\delta^{15}N$ values reflected the trophic levels assumed from the literature, as species from lower trophic levels had lower $\delta^{15}N$ than species from higher trophic levels (Table 4.3; Fig. 4.4). A difference of 5‰ was found between the detritivore mullet *Valamugil* sp. and the double-spotted queenfish *Scomberoides lysan*, the piscivore of highest $\delta^{15}N$. This difference corresponds to ~1.7 trophic steps, suggesting that the food web in this area comprises at least 3.7 trophic levels (Fig. 4.4).

Fish from different trophic guilds formed relatively distinct groups (Fig. 4.4), with detritivores having the lowest $\delta^{15}N$ and major piscivores the highest $\delta^{15}N$ values. A SIMPROF analysis suggested the presence of three major groups ($p \leq 0.01$), one composed of major piscivores, one mainly of detritivorous species and one of carnivorous (macrobenthic carnivores and minor piscivores) species (Fig. 4.5). Herbivores (*Siganus lineatus*, *Hyporhamphus quoy* and *Zenarchopterus buffonis*) and planktivores (*Herklotsichthys* spp., *Ambassis* spp., *Leiognathus* spp., *E. devisi* and *S. gibbosa*) did not form groups and appeared as outliers (*S. lineatus*) or grouped with species of other trophic groups (Fig. 4.5).

In fact, different species of herbivorous and planktivorous fish species had distinct $\delta^{13}C$ values, indicating clear differences in sources of carbon (Figs. 4.4 and 4.6). For example, *S. lineatus* and *Z. buffonis* had lower $\delta^{13}C$ than *H. quoyi* (Fig. 4.6a), despite the fact that *Z. buffonis* and *H. quoyi* are confamilials. Planktivores also showed differences in $\delta^{13}C$ values, with *Herklotsichthys koningsbergeri* and *S. gibbosa* more enriched in ^{13}C than the remaining species (Table 4.3, Fig. 4.6b,c), suggesting that these planktivores are in two different trophic pathways.

Although herbivorous and planktivorous species had distinct $\delta^{13}C$, macrobenthic carnivores and minor piscivores had similar $\delta^{13}C$ profiles (Figs. 4.4 and 4.6), suggesting cross-linking or amalgamation of the food chains. These higher trophic level species were also more variable in $\delta^{15}N$, being distributed along a continuum in the $\delta^{15}N$ scale (Fig. 4.4a), suggesting a high degree of omnivory and diet overlap between species.

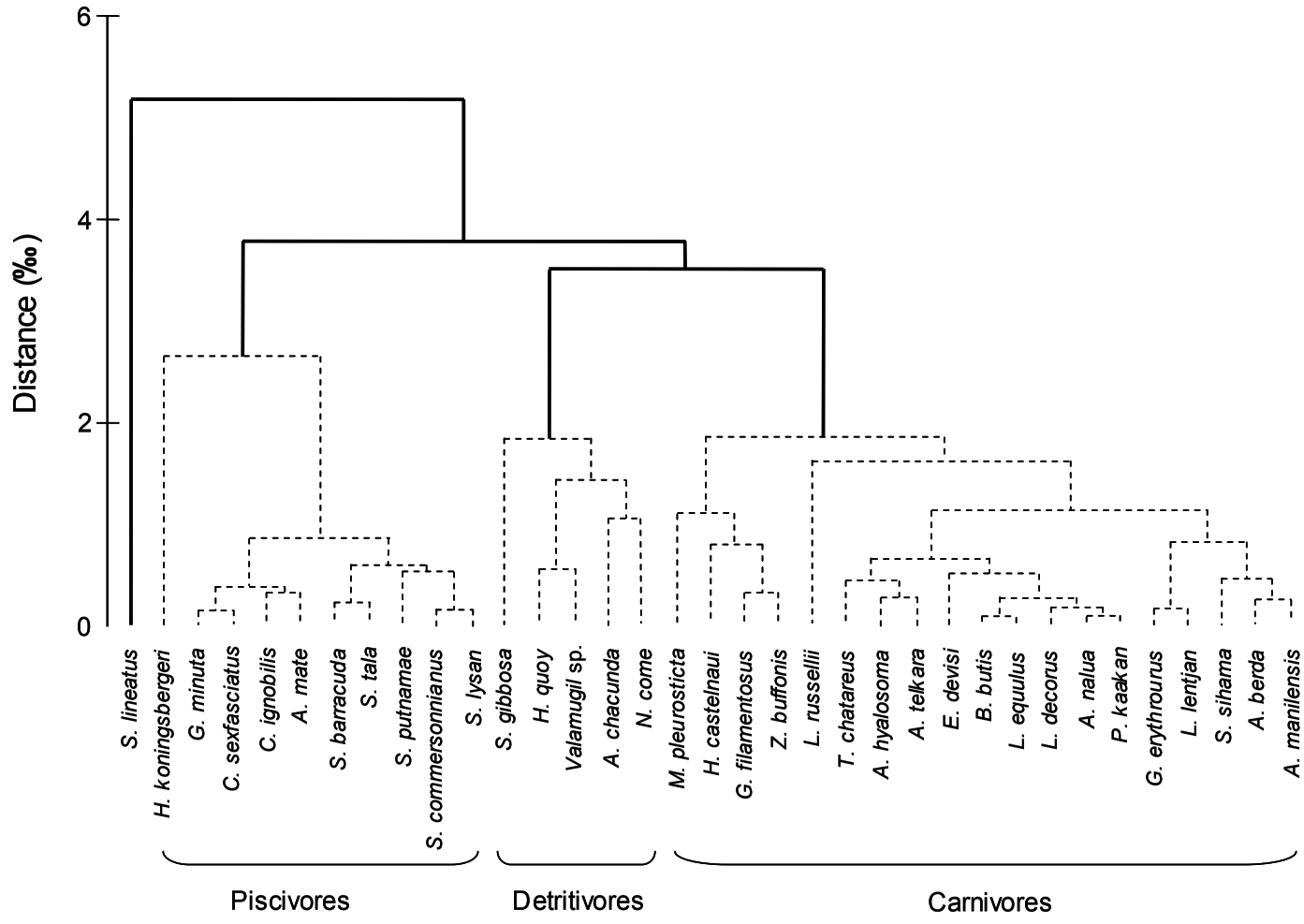

Fig. 4.5. Cluster analysis (group average) based on Euclidian similarities in fish $\delta^{13}C$ and $\delta^{15}N$ values, displaying coherent groups (bold lines) identified by SIMPROF analysis at $p = 0.01$. Species are indicated in the *x* axis, and *y* axis corresponds to Euclidian dissimilarities between groups (‰).

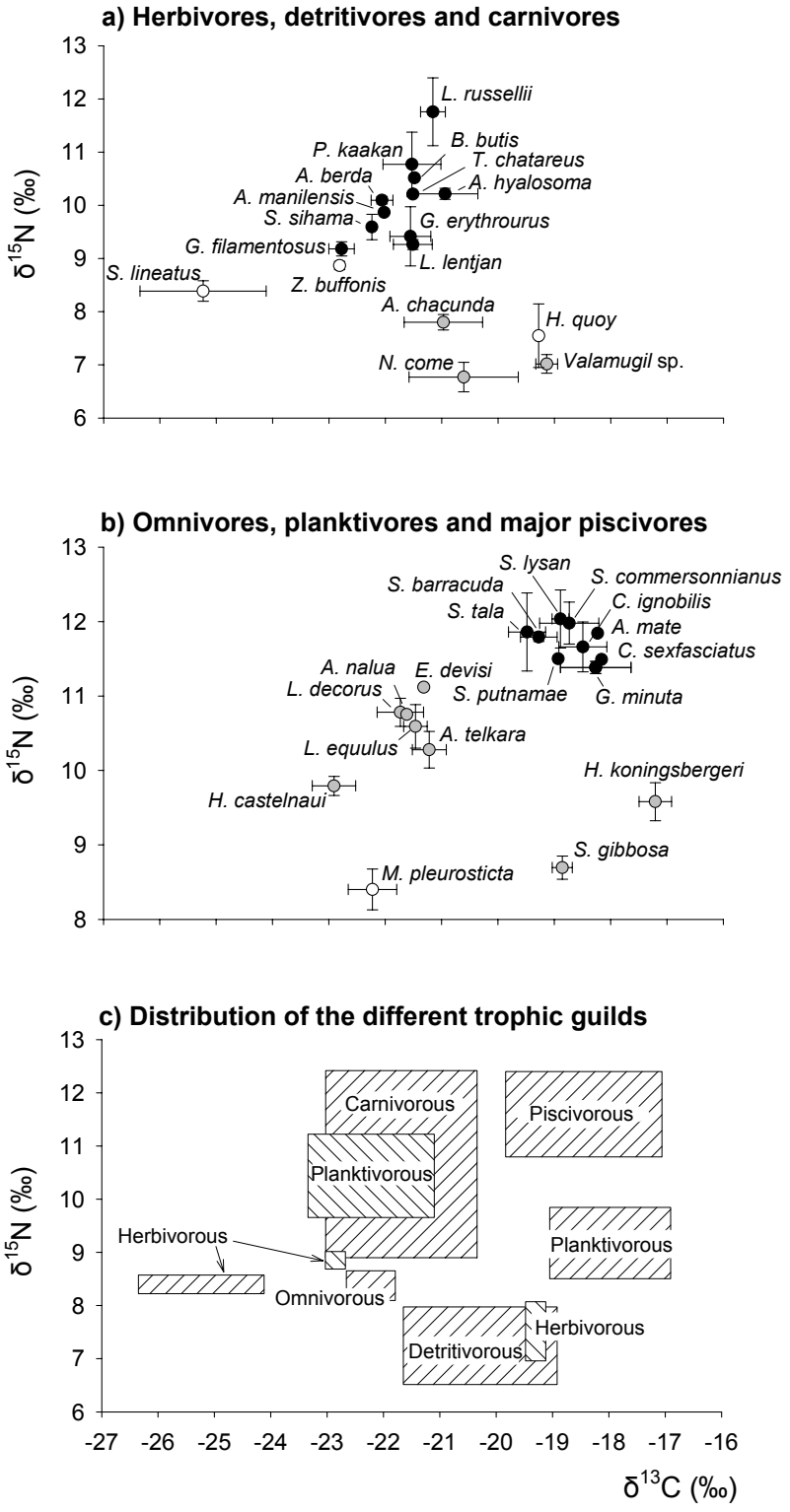

Fig. 4.6. Mean isotopic values (± SE) of fish from Deluge Inlet. **a)** ○ - herbivores; ◍ - detritivores; ● - carnivores (macrobenthic carnivores and minor piscivores). **b)** ○ - omnivores; ◍ - planktivores; ● - major piscivores. **c)** Indication of distribution of the different trophic groups in the $\delta^{13}C$-$\delta^{15}N$ plane. Note the differences in the *y* axis.

Based on the isotopic profiles of organisms, it was possible to identify a number of trophic pathways from primary producers, as well as strong trophic links between species. For example, mangroves, microphytobenthos and seagrass are the producers that can potentially contribute to nutrition of phytodetritivorous fish (*A. chacunda, N. come* and *Valamugil* sp.). After correction for fractionation, $\delta^{13}C$ values of phytodetritivorous fall between microphytobenthos and seagrass (Fig. 4.7). Since carbon and nitrogen isotope composition was similar for the three species, the IsoSource model was run for the average value, providing an indication of the relative contribution of the different carbon sources.

Results indicate that seagrass makes an important contribution to the diet of detritivorous fish at Deluge Inlet, and that microphytobenthos could also have an input as high as 60% (Fig. 4.7). On the other hand, although $\delta^{13}C$ values of phytodetritivorous fish were much higher than mangroves, it is possible that mangroves make an important contribution to these species as in models where the contribution of *H. ovalis* is high and microphytobenthos low, a small contribution from mangroves (maximum of 27% putative contribution) is required to achieve mass balance (Fig. 4.7). $\delta^{15}N$ values of the three phyodetritivorous species also indicate that these species have an effective trophic level higher than 2, as when $\delta^{15}N$ was corrected for fractionation for one trophic level, it was still more enriched than $\delta^{15}N$ of all potential sources (Fig. 4.7). The difference in $\delta^{15}N$ between *Valamugil* sp. (mean $\delta^{15}N$ = 7.0‰) and microphytobenthos (2.9‰) suggests a mean trophic level of 2.3 for this species. This implies that 0.3 trophic levels should be added to the trophic length calculated based only on the difference in $\delta^{15}N$ between *Valamugil* sp. and *S. lysan* (see above), and that food web in this area has ~4.0 trophic levels.

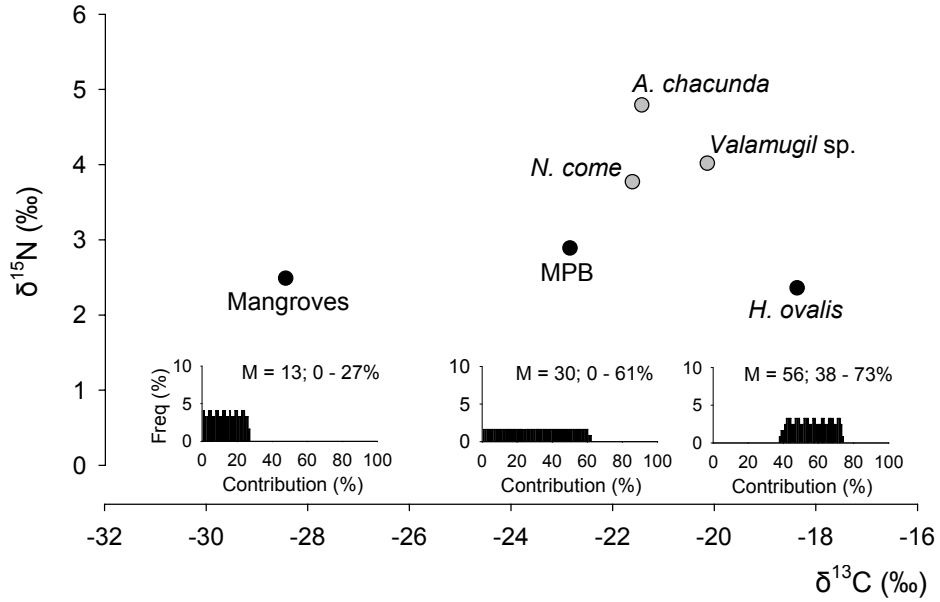

Fig. 4.7. Corrected $\delta^{13}C$ and $\delta^{15}N$ values of phytodetritivorous fish (○) and original $\delta^{13}C$ and $\delta^{15}N$ values of potential contributors (●) for Deluge Inlet. Distributions of feasible contributions of the different producers to phytodetritivores are also indicated, based on the IsoSource model (run on $\delta^{13}C$ values) (M = median; range = 1^{st}-99^{th} percentile). MPB = microphytobenthos.

The IsoSource model could not be computed for planktivores and small invertebrate feeders due to the large differences in $\delta^{13}C$ and $\delta^{15}N$ values among the different peracarid groups. For *A. nalua*, *A. telkara, E. devisi, L. decorus* and *L. equulus*, corrected isotope values fall close to small shrimps such as *A. sibogae* and shrimp postlarvae (Fig. 4.8a), although having slightly lower $\delta^{15}N$ than these groups. *H. castelnaui* had lower $\delta^{13}C$ and $\delta^{15}N$ than these species (Fig. 4.8a). For *S. gibbosa,* corrected values fell in the centre of the polygon formed by the potential food sources, indicating that this species probably feeds on a combination of different sources (Fig. 4.8a). *H. koningsbergeri* was the most ^{13}C enriched planktivore, with corrected isotope

values falling close to phoxocephalid amphipods (Fig. 4.8a), suggesting a benthic rather than a planktonic diet. Note that the planktivorous *A. sibogae* and shrimp post larvae had $\delta^{13}C$ values lower than zooplankton (Fig. 4.8a), suggesting the presence of zooplankton of two different sources in the area, or alternatively a recent migration of these animals from another area.

For macrobenthic carnivores and minor piscivores, correction for fractionation resulted in $\delta^{13}C$ values in the lower part of the $\delta^{13}C$ spectrum (Fig. 4.8b). Since different sources had similar isotope composition, and because members of the peracarid and gastropod groups had variable $\delta^{13}C$ and $\delta^{15}N$ values, no clear trophic links could be drawn for most species. However, it was possible to identify relatively strong trophic relationships for species with the most extreme isotope values. For example, carbon and nitrogen isotope composition of the Moses perch *Lutjanus russellii* was closer to *A. sibogae* shrimps, shrimp post larvae and small crabs, although a contribution of other organisms with higher $\delta^{13}C$ and $\delta^{15}N$ is necessary to lead to *L. russellii*'s high values (Fig. 4.8b). On the other hand, isotope composition of the threadfin silverbiddy *Gerres filamentosus* was closer to more ^{15}N depleted benthic animals such as molluscs and peracarids such as cirolanid isopods (Fig. 4.8b), suggesting an important dependence on these sources.

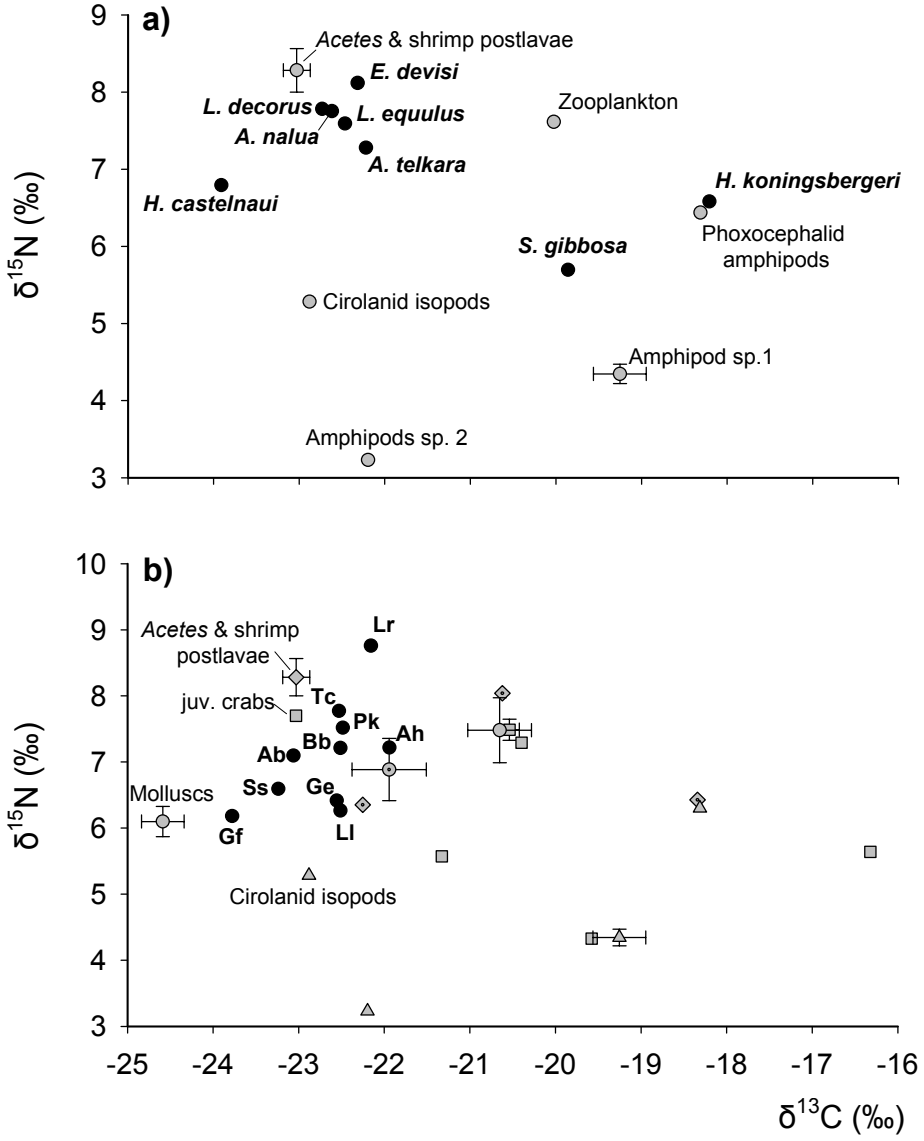

Fig. 4.8. Corrected $\delta^{13}C$ and $\delta^{15}N$ of fish consumers (black symbols, bold) and original values of potential food sources (grey symbols) for Deluge Inlet. **a)** Small invertebrate feeders with zooplankton, benthic peracarids and *Acetes* and shrimp post larvae; **b)** macrobenthic carnivores and minor piscivores with molluscs (○), peracarids (△), polychaetes (⊙), *Acetes* and shrimp postlarvae (◇), prawns (◈), and crabs (□); **c)** major piscivores with clupeoids, ponyfish, silverbiddies and whiting. Ab = *A. berda*; Ah = *A. hyalosoma*; Bb = *B. butis*; Ci = *C. ignobilis;* Cs = *C. sexfasciatus*; Gm = *G. minuta;* Ll = *L. lentjan*; Lr = *L. russellii*; Pk = *P. kaakan*; Sb = *S. barracuda*; Sc = *S. commersonnianus;* Sl = *S. lysan*; Sp = *S. putnamae;* Ss = *S. sihama*; St = *S. tala*; Tc = *T. chatareus.* Error bars correspond to standard errors, where organisms of same taxonomic group that had similar $\delta^{13}C$ and $\delta^{15}N$ values were grouped (**a** and **b**), or standard errors for a species (**c**). Species or groups of species mentioned in text are indicated. Note the differences in the *y* axis.

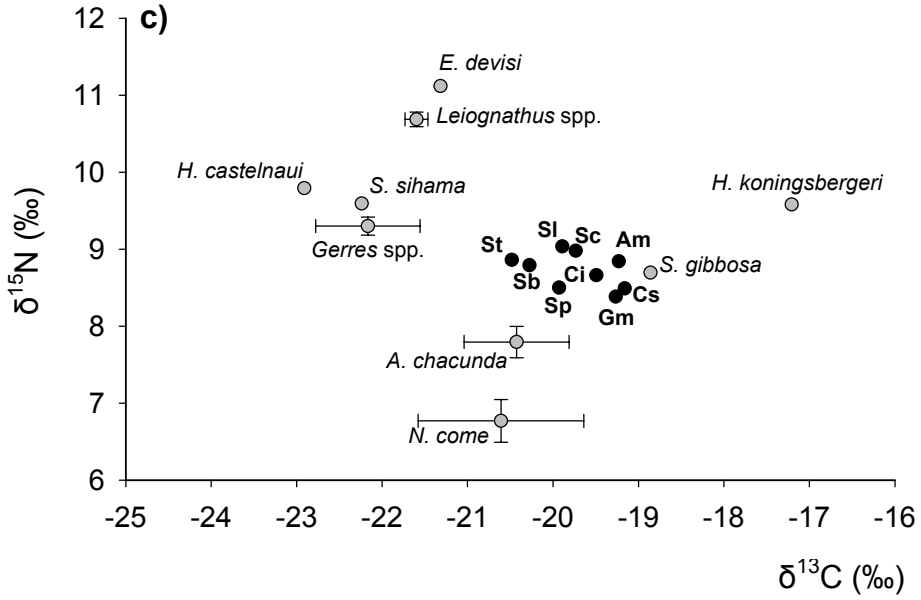

Fig. 4.8. (cont) Corrected $\delta^{13}C$ and $\delta^{15}N$ of fish consumers (black symbols, bold) and original values of potential food sources (grey symbols) for Deluge Inlet. **a)** Small invertebrate feeders with zooplankton, benthic peracarids and *Acetes* and shrimp post larvae; **b)** macrobenthic carnivores and minor piscivores with molluscs (○), peracarids (△), polychaetes (⊙), *Acetes* and shrimp postlarvae (◇), prawns (◈), and crabs (□); **c)** major piscivores with clupeoids, ponyfish, silverbiddies and whiting. Ab = *A. berda*; Ah = *A. hyalosoma*; Bb = *B. butis*; Ci = *C. ignobilis;* Cs = *C. sexfasciatus*; Gm = *G. minuta;* Ll = *L. lentjan*; Lr = *L. russellii*; Pk = *P. kaakan*; Sb = *S. barracuda*; Sc = *S. commersonnianus;* Sl = *S. lysan*; Sp = *S. putnamae;* Ss = *S. sihama*; St = *S. tala*; Tc = *T. chatareus.* Error bars correspond to standard errors, where organisms of same taxonomic group that had similar $\delta^{13}C$ and $\delta^{15}N$ values were grouped (**a** and **b**), or standard errors for a species (**c**). Species or groups of species mentioned in text are indicated. Note the differences in the *y* axis.

Major piscivores formed a tight group (ranges: $\delta^{13}C$ = 1.65‰; $\delta^{15}N$ = 1.09‰), suggesting similar dietary mixes. Corrected isotope values of these species fell close to the planktivorous *S. gibbosa* and the phytodetritivorous *A. chacunda* (Fig. 4.8c), but were higher in $\delta^{13}C$ and lower in $\delta^{15}N$ than other planktivores such as *H. castelnaui, E. devisi*, and leiognathids, and macrobenthic carnivores such as *S. sihama* and *Gerres* spp. Corrected isotope values of major piscivores were also lower in $\delta^{13}C$ and $\delta^{15}N$ than the planktivore *H. koningsbergeri*, and higher in $\delta^{15}N$ than the phytodetritivore *N.*

come. Hence, several combinations of sources can explain the piscivores' isotope values, and it is likely that these species feed on mixture of fish species. However, clupeoids such as *A. chacunda*, *N. come*, *H. castelnaui* and *S. gibbosa* appear to be among the most important components of their diet.

4.3.2.2. Food Webs in Victoria, Half Moon and Blacksoil Creeks

Animals from Victoria Creek were well separated in $\delta^{13}C$ (Fig. 4.9a). Several species, including the penaeid prawn *P. merguiensis* and the mud crab *Scylla serrata*, as well as a number of fish, had low $\delta^{13}C$ values within, or close to, the limits of mangrove $\delta^{13}C$, suggesting a major contribution of mangroves to nutrition.

Among fish, different detritivorous species had different $\delta^{13}C$ and $\delta^{15}N$ values (Figs. 4.9a and 4.10a). *N. come* and *A. chacunda* had very low $\delta^{13}C$, with values indicating a dependence on carbon of mangrove origin (Fig. 4.9a). These species were also higher in $\delta^{15}N$ than expected for primary consumers, with values similar to those of species of higher trophic levels (Fig. 4.9a). In contrast, the two mullet species, *Liza subviridis* and *Valamugil* sp., as in Deluge Inlet, had relatively low $\delta^{15}N$ and high $\delta^{13}C$ (Figs. 4.9a and 4.10a), with $\delta^{13}C$ values that suggest the incorporation of more ^{13}C enriched material such as benthic algae and C_4 producers. The herbivore garfish *Arrhamphus sclerolepis,* as the garfish *H. quoy* from Deluge Inlet, had also high $\delta^{13}C$, with values similar to the two mullet species, and within the range of C_4 producers (Fig. 4.9a and 4.10a).

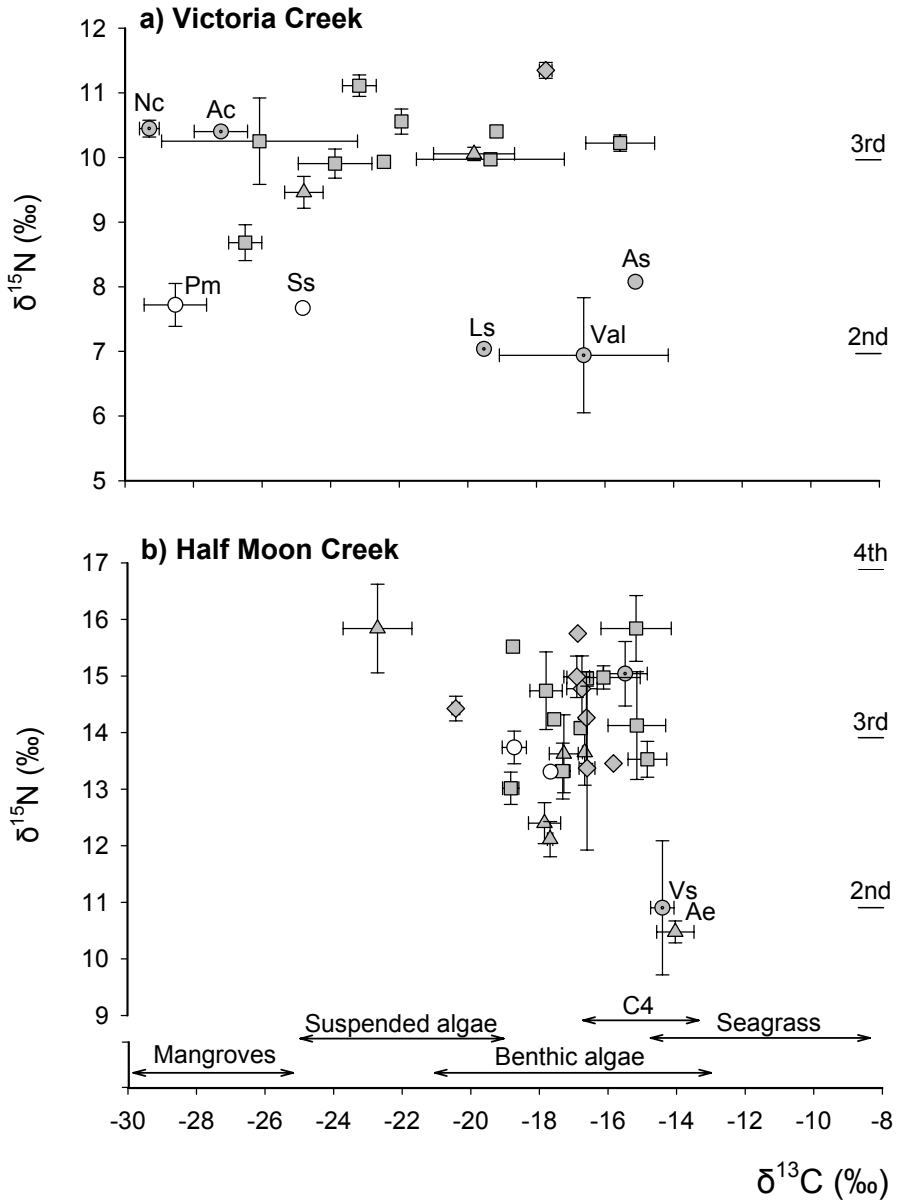

Fig. 4.9. Mean $\delta^{13}C$ and $\delta^{15}N$ of decapods (white symbols) and fish (grey symbols) from **a)** Victoria, **b)** Half Moon and **c)** Blacksoil Creeks. Arrows indicate $\delta^{13}C$ ranges of the different producer categories (see text). $\delta^{15}N$ levels for each trophic level are indicated on the right of each graph. Fish: ○ - herbivores; ⊙ - detritivores; ▽ – omnivores; △ - planktivores; □ - carnivores (macrobenthic carnivores and minor piscivores); ◇ - major piscivores. Species mentioned in text are also indicated: Ac = *A. chacunda*; Ae = *A. endrachtensis*; As = *A. sclerolepis*; Ls = *L. subviridis*; Nc = *N. come*; Pm = *P. merguiensis*; Sa = *S. analis*; Ss = *S. serrata*; Val = *Valamugil* sp.; Vs = *V. seheli*. Note the differences in the *y* axis.

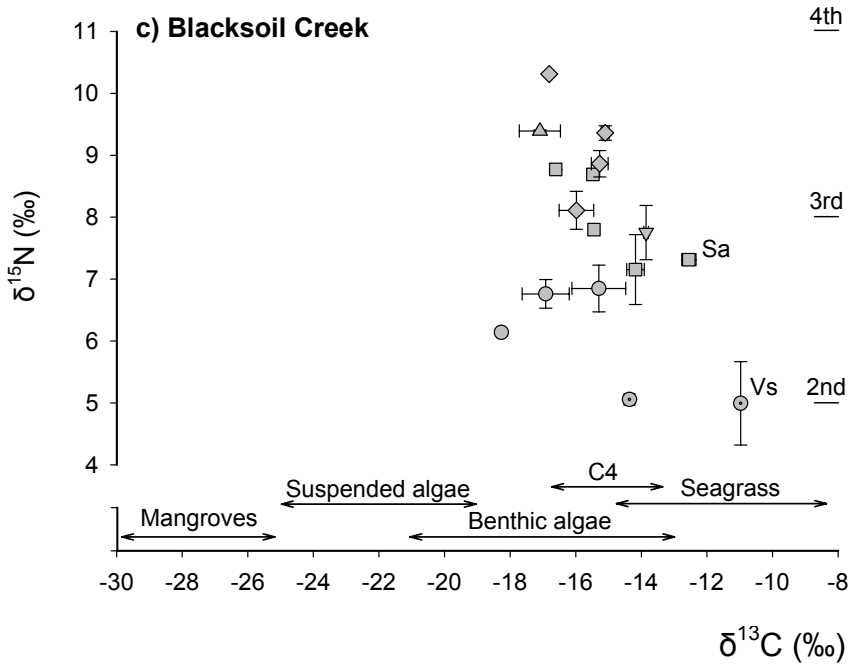

Fig. 4.9. (cont.). Mean $\delta^{13}C$ and $\delta^{15}N$ of decapods (white symbols) and fish (grey symbols) from **a)** Victoria, **b)** Half Moon and **c)** Blacksoil Creeks. Arrows indicate $\delta^{13}C$ ranges of the different producer categories (see text). $\delta^{15}N$ levels for each trophic level are indicated on the right of each graph. Fish: ○ - herbivores; ⊙ - detritivores; ▽ – omnivores; △ - planktivores; □ - carnivores (macrobenthic carnivores and minor piscivores); ◇ - major piscivores. Species mentioned in text are also indicated: Ac = *A. chacunda*; Ae = *A. endrachtensis*; As = *A. sclerolepis*; Ls = *L. subviridis*; Nc = *N. come*; Pm = *P. merguiensis*; Sa = *S. analis*; Ss = *S. serrata*; Val = *Valamugil* sp.; Vs = *V. seheli*. Note the differences in the *y* axis.

Carnivorous fish from Victoria Creek had a broad range of $\delta^{13}C$ (Figs. 4.9a and 4.10b), in contrast to the tight clustering of $\delta^{13}C$ of high trophic level consumers from Deluge Inlet. As with detritivores, there were species such as the macrobenthic carnivore *Terapon jarbua* and small *Gazza minuta* juveniles that had low $\delta^{13}C$, within the range of mangrove $\delta^{13}C$, and at the same time species such as *Gerres erythrourus* had values within the range of C_4 producers (Fig. 4.10b). Unlike at Deluge Inlet, $\delta^{15}N$ values of carnivores were similar between species (Figs. 4.9a and 4.10b). In fact, these species

seemed to be distributed in almost discreet trophic levels (Fig. 4.9a), which coupled with the well separated $\delta^{13}C$ values suggests a low levels of omnivory and of diet overlap at this site. In contrast to the situation at Victoria Creek, in Half Moon and Blacksoil Creeks different fish species had similar $\delta^{13}C$ and, as carnivores from Deluge Inlet, were distributed in a continuum in the $\delta^{15}N$ scale (Figs. 4.9b, c, 4.11 and 4.12), suggesting high levels of omnivory and a significant overlap in diet between species.

Fish from Victoria Creek had a relatively narrow range in $\delta^{15}N$, between 6.9‰ and 11.4‰, corresponding to only 1.5 trophic steps (Fig. 4.9a). However, species of higher trophic levels were absent from samples from this estuary, although they are common in the area (Baker & Sheaves 2005, 2006) and hence it was not possible to calculate trophic length for this system. In Half Moon and Blacksoil Creeks however, food webs seemed to have a trophic length similar to Deluge Inlet, with fish $\delta^{15}N$ suggesting the presence of 1.7 and 1.8 trophic steps between *Valamugil* spp. and the piscivore of highest $\delta^{15}N$ for Half Moon and Blacksoil Creek respectively (Fig. 4.9b, c). If *Valamugil* spp., as in Deluge Inlet, has a trophic level of ~2.3 (see above), then food webs in these areas have 4.0 to 4.1 trophic levels.

In Half Moon Creek, the planktivore *Atherinomorus endrachtensis* and the detritivore *Valamugil seheli* were very enriched in ^{13}C (Fig. 4.9b and 4.11a). Since no C_4 producers occur in substantial densities at Half Moon Creek to be important contributors to fish diet, these high $\delta^{13}C$ values must be a result of incorporation of carbon of benthic algae or even of seagrass origin. A similar situation was present for *V. seheli* from Blacksoil Creek (Fig. 4.9c and 4.12a) as well as for small whiting *Sillago analis*, suggesting that seagrass beds in adjacent waters are likely to have an important input into food webs in these areas.

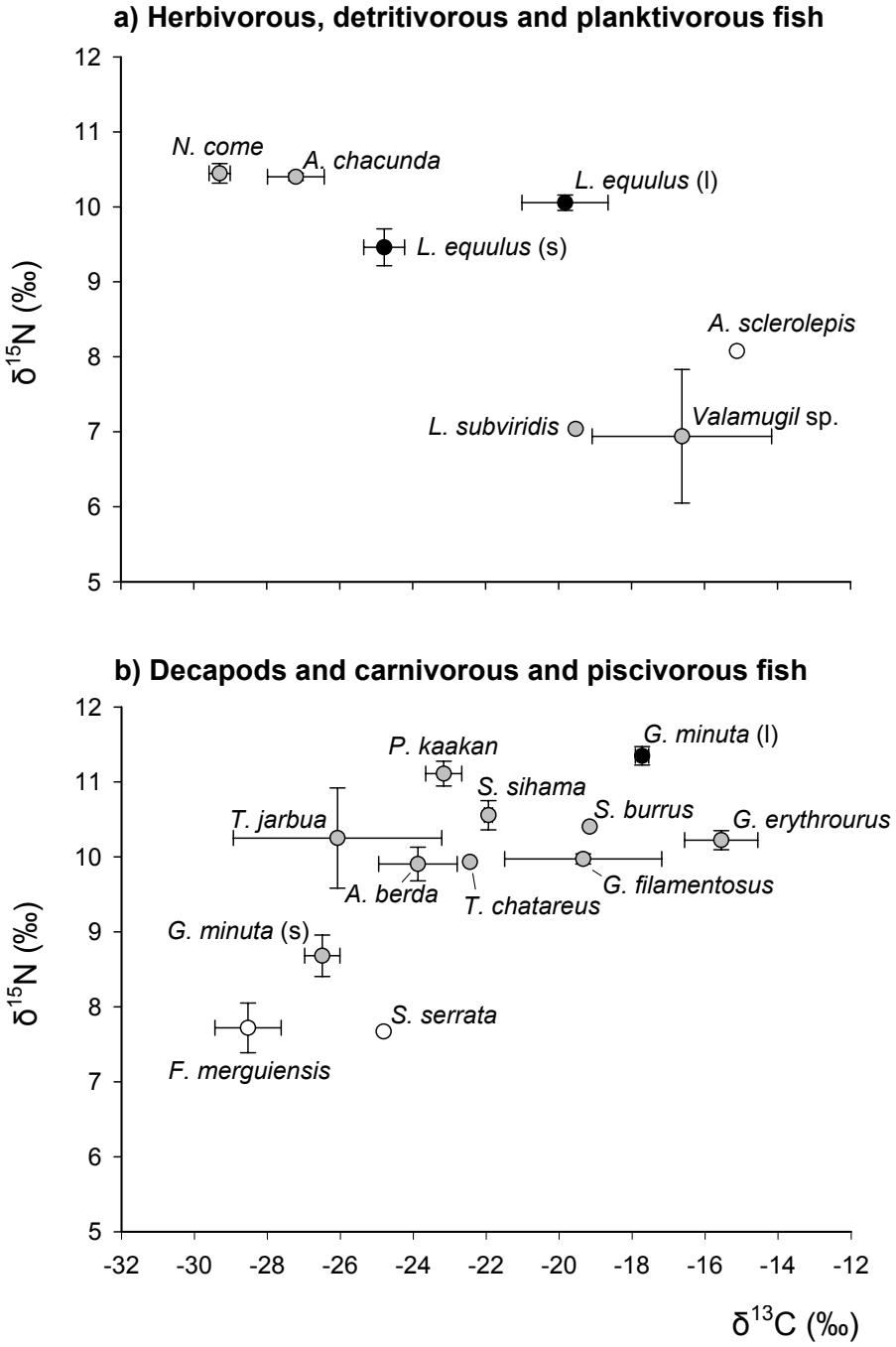

Fig. 4.10. Mean (± SE) carbon and nitrogen stable isotopic composition of consumers from Victoria Creek. **a)** Herbivorous (○), detritivorous (◎) and planktivorous (●) fish species. **b)** Decapods (○), carnivorous fish (◎) (macrobenthic carnivores and minor piscivores) and major piscivores (●). s/l - smaller and larger size class.

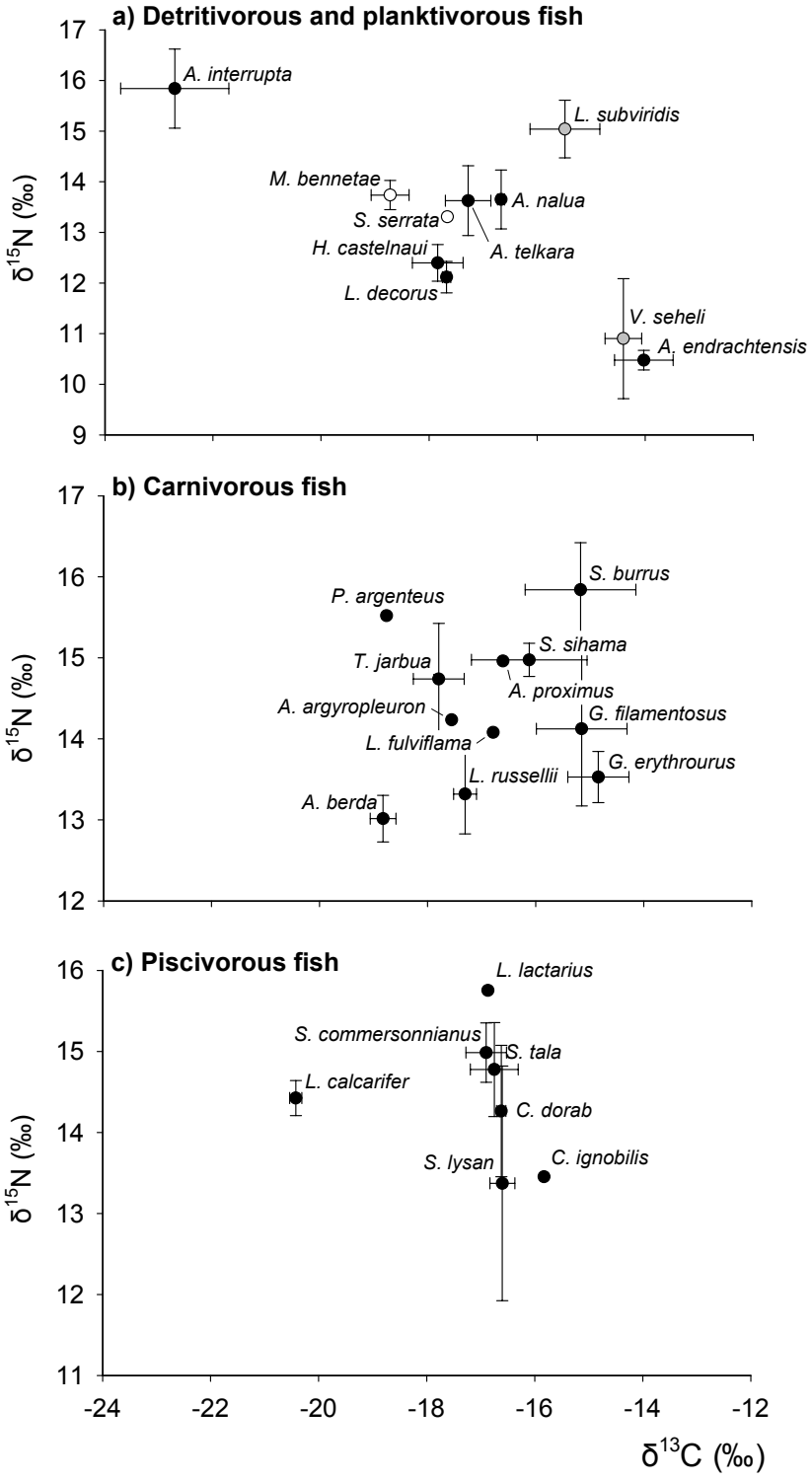

Fig. 4.11. Mean (± SE) carbon and nitrogen isotope composition of consumers from Half Moon Creek. **a)** Decapods (○) and detritivorous (◍) and planktivorous (●) fish. **b)** Carnivorous fish. **c)** Major piscivores. Note the differences in the *y* axis.

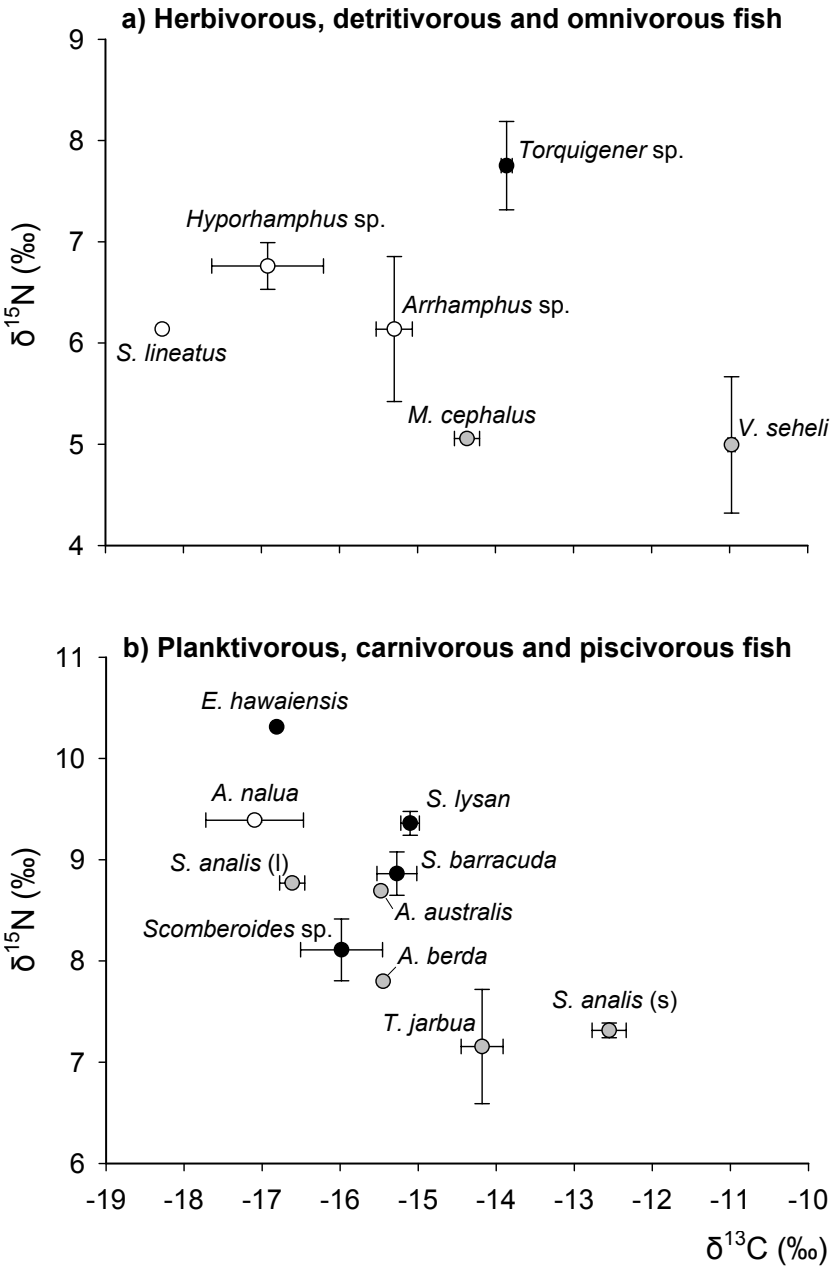

Fig. 4.12. Mean (± SE) carbon and nitrogen isotope composition of fish found in Blacksoil Creek. **a)** Herbivorous (○), detritivorous (◍) and omnivorous (●) species. **b)** Planktivorous (○), carnivorous (◍) and major piscivorous (●) fish species. Note the differences in the *y* axis.

In contrast to Deluge Inlet, highly mobile piscivores from Half Moon Creek had variable carbon and nitrogen isotopic composition (Fig. 4.9b and 4.11c). The barramundi *Lates calcarifer* had $\delta^{13}C$ values lower than all other major piscivores (Fig. 4.11c), and for $\delta^{15}N$, 11 of the 15 major piscivores formed a relatively tight group with values between 14.2 and 15.8‰, while the remaining four individuals had lower values, between 11.9 and 13.5‰. Differences were present even within the same species: the two doublespotted queenfish *S. lysan* collected had very different $\delta^{13}C$ (11.9 and 14.8‰); one of the three wolf herring *Chirocentrus dorab* individuals had a lower $\delta^{15}N$ of 12.7‰, while the other two were more enriched (14.5 and 15.5‰); and one of the four barred queenfish *Scomberoides tala* (13.1‰) had also lower $\delta^{15}N$ values than the remaining three (14.6 to 15.8‰).

4.4. DISCUSSION

Fish species composition analysed from each estuary appeared to be a comprehensive representation of the most common species in those systems, comprising the common species recorded in a major study by Sheaves (2006) of nine estuaries along the North Queensland coast, which included Deluge Inlet, Victoria Creek and Blacksoil Creek. Moreover, in all four estuaries considered, fish samples were dominated by juveniles, a result also in agreement with Sheaves (2006).

4.4.1. Detailed Analysis of the Sources of Energy and Food Web Structure in the Near-Pristine Estuary of Deluge Inlet

Incorporation of ^{13}C depleted carbon of mangrove origin into other aquatic producers was evident at Deluge Inlet, with both microphytobenthos and seagrass having $\delta^{13}C$ values lower than values reported for other marine coastal areas by France (1995b) and Hemminga & Mateo (1996) respectively. This phenomenon has been described for estuarine suspended producers (Bouillon et al. 2000, Dehairs et al. 2000) and seagrass (Lin et al. 1991, Hemminga et al. 1994), and was reported earlier in this thesis for the Ross River wetland pools (Chapters 2 and 3). This effect has also been found to decrease in intensity with increasing distance from the mangrove forest (Lin et al. 1991, Dehairs et al. 2000). Deluge Inlet opens to Hinchinbrook Channel, one of Australia's largest mangrove swamps, where water residence time can be as great as 20 days due to the unique hydrology of the area (Wolanski et al. 1990). Consequently, mixing between coastal and offshore waters is slow, and aquatic primary producers are likely to be faced with a medium where isotopic composition is heavily influenced by the presence of the dominant (Alongi et al. 1998) mangrove carbon, leading to more ^{13}C depleted tissues than producers in other more open areas.

However, and in contrast to seagrass and microphytobenthos, zooplankton collected in this area had $\delta^{13}C$ values within the range reported for marine suspended producers (France 1995b). This discrepancy may be explained by the fact that sampling was conducted at high tide during a period of spring tides. Hence, the sample may have been collected from a 'parcel' of marine water penetrating the estuary on the top of the tide. Because this is probably a transitory event, it is unlikely that plankton-feeding organisms resident in the estuary would assimilate enough 'offshore' zooplankton to

substantially influence their carbon isotope composition. This could account for the fact that sessile suspension feeders such as oysters and mussels, as well as the specialist copepod feeding clupeid fish *H. castelnaui* (Knott 2006), postlarval caridean shrimps, and the planktivorous shrimp *A. sibogae*, which are able to actively maintain their positions within estuary (Kimmerer et al. 1998, Omundsen et al. 2000), had much lower $\delta^{13}C$ values than the zooplankton collected. These low values strongly suggest that the food chains leading to these species are at least in part dependent on mangrove derived carbon, either from direct consumption of mangrove particulate matter by zooplankton, or because the zooplankton's phytoplankton food source was photosynthesising in an estuarine environment where the isotopic profile of dissolved CO_2 was heavily influenced by the presence of large quantities of ^{13}C depleted decomposing mangrove detritus.

On the other hand, the three major planktivorous clupeids, *H. castelnaui*, *H. koningsbergeri* and *S. gibbosa,* had a quite different carbon isotopic composition, suggesting they were feeding on prey supported by different primary producers. This reflects the observation that these species, although morphologically similar, have different dietary preferences, with *H. castelnaui* and *S. gibbosa* feeding mainly on copepods and other zooplankton, while the diet of *H. koningsbergeri* includes substantial quantities of benthic associated prey such as brachyura megalopae and polychaetes (Knott 2006).

Although isotope profiles of *H. castelnaui* and *H. koningsbergeri* accord with these differences in feeding behaviour, *S. gibbosa* had higher $\delta^{13}C$ than expected if it fed mostly on plankton, with $\delta^{13}C$ values closer to *H. koningsbergeri*. This is probably a result of species-specific differences in habitat preferences. Although feeding on similar

prey, *S. gibbosa* occurs mainly in shallow muddy and sandy banks, while *H. castelnaui* occurs mainly along edges in shallow mangrove habitats (Knott 2006). Hence, the relatively high $\delta^{13}C$ values of *S. gibbosa* could be a result of feeding on seagrass epifauna, since a range of organisms such as copepods, ostracods and amphipods regularly migrate from the sediment into the water column in seagrass habitats (Walters & Bell 1986). *H. castelnaui,* on the other hand, feeds mostly at high tides along the mangrove banks (Knott 2006), and hence is likely to consume more ^{13}C depleted mangrove associated epifauna.

Although precise details of energy sources and trophic pathways can be gleaned from the analysis of stable isotope composition of estuarine organisms, there can be differences in the degree of dependence on the various types of food sources within a trophic group, complicating the interpretation of stable isotope results. This was particularly evident for invertebrate primary consumers from Deluge Inlet, which showed different $\delta^{13}C$ values distributed through the entire spectrum (see Fig. 4.4). Although more difficult to detect, it is likely that this variability is also present at higher trophic levels. On the other hand, similar values of isotope composition can arise from two very distinct situations: a species may consume one food source exclusively, meaning that its signature is a direct reflection of this exclusive consumption; or a species may consume a range of different sources, the combination of which results in values similar to those of the first species. Therefore, it can be difficult to determine if the isotopic composition of a species reflects a specialized diet, or an average diet. This can further hinder the identification of the main trophic pathways and complicate the study of trophic organisation in these systems.

Nevertheless, based on the evidence of trophic links suggested by stable isotope results for this site, it was possible to construct a general model for the Deluge Inlet food web, where the main trophic chains transporting energy from primary producers are represented (Fig. 4.13). In doing this, and given the issues discussed above, we need to keep in mind that at the real food web is likely to be a more complex version of this simple model.

The most ^{13}C depleted trophic chain in Deluge Inlet seems to be based on mangrove carbon and probably also microphytobenthos (Fig. 4.13), which is incorporated by several invertebrate phytodetritivores (mainly molluscs, trophic level 2) (see Fig. 4.4), that are in turn consumed by macrobenthic carnivores (trophic level 3) (see Fig. 4.8b). Some of these carnivorous fish might be consumed by major piscivores (trophic level 4) (Fig. 4.13), although stable isotope data suggest that this trophic link is not very strong (see Fig. 4.8c).

Another important trophic chain, based on estuarine plankton, is also present (Fig. 4.13). Isotope values of the planktivores *A. sibogae*, caridean post larvae and *H. castelnaui* indicate the presence of ^{13}C depleted estuarine plankton in the area (see above). Hence, the planktonic food chain transports carbon from these suspended producers to small plankton feeders such as *A. sibogae* and caridean post larvae (trophic level 2), which support large zooplankton feeders such as *Leiognathus* spp. and *Ambassis* spp. (trophic level 3) (see Fig. 4.8a). These species in turn contribute to the diet of large piscivorous fish (trophic level 4) (see Fig. 4.8c).

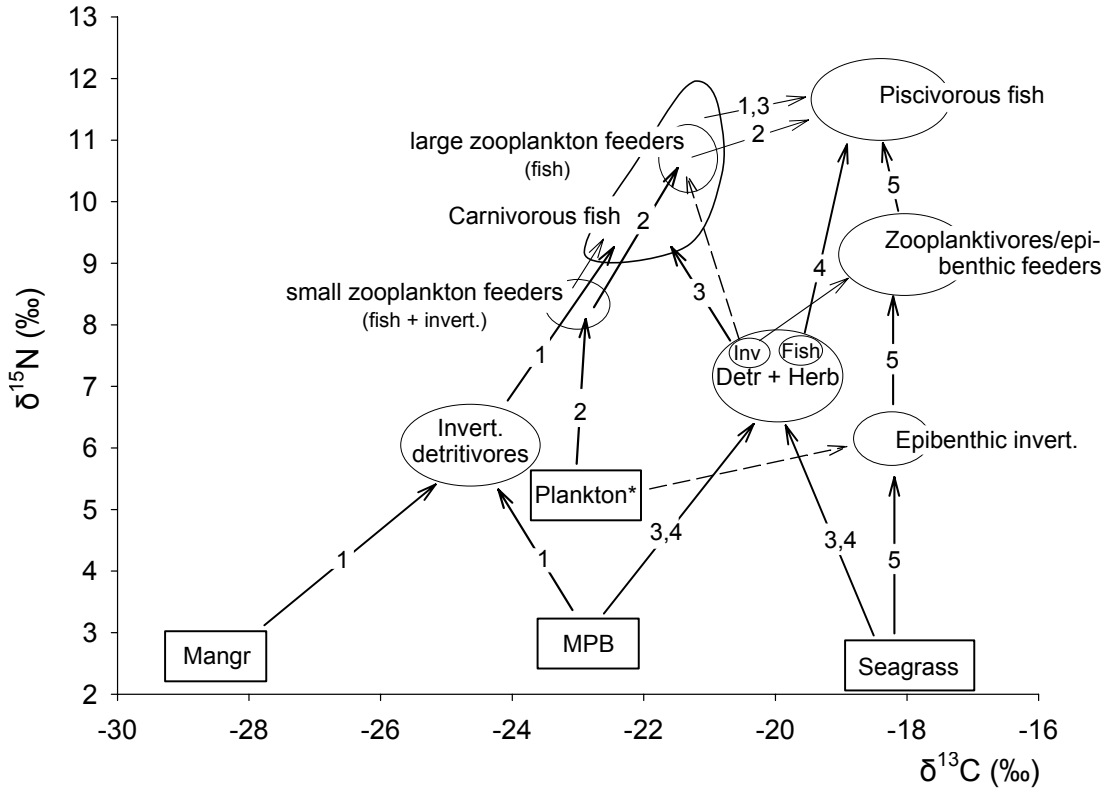

Fig. 4.13. General model for the Deluge Inlet food web showing the main trophic pathways based on stable isotope results from this study. Squares correspond to the ultimate carbon sources, and ellipses to consumers. Shapes delimitate isotope values of all or most species within the trophic group. Arrows indicate main trophic links. Darker arrows suggest stronger links, dashed arrows weaker, and light arrows indicate links of intermediate importance, as suggested by stable isotope analysis. The five main trophic chains are indicated: (1) mangrove-microphytobenthos based; (2) plankton based; (3) and (4) seagrass-microphytobenthos based; and (5) seagrass based. See details in text. Primary producers: Mangr = mangroves; MPB = microphytobenthos. Consumers: Invert. detritivores = invertebrate detritivores; Detr + Herb = detritivores and herbivores. * - plankton not sampled in the present study.

Two trophic pathways based on carbon from both microphytobenthos and seagrass origin are also present (Fig. 4.13). One transports energy to herbivorous and detritivorous invertebrates (trophic level 2) (see Fig. 4.4), which are in turn consumed by macrobenthic carnivores (trophic level 3) (see Fig. 4.8b), and the second transports

carbon to herbivorous and detritivorous fish (trophic level 2) (see Fig. 4.7), which are consumed by major piscivores (see Fig. 4.8c).

A fifth trophic chain, based mainly on seagrass carbon (Fig. 4.13), transports carbon from these producers to seagrass epifauna such as amphipods (trophic level 2) (see Fig. 4.4), which in turn support species such as *S. gibbosa* and *H. koningsbergeri* (trophic level 3; see above) (see Fig. 4.8a). In turn, these species serve as an important part of the diet of major piscivores (trophic level 4) (see Fig. 4.8c). Hence, carbon from primary producers is transported up the food chain to major piscivorous fish through different trophic pathways (Fig. 4.13), mostly through 3 trophic links, indicating that this system has ~4 trophic levels, concurring with the value indicated by the difference in $\delta^{15}N$ between the detritivorous mullet *Valamugil* sp. and the piscivore of highest $\delta^{15}N$.

Therefore, a substantial body of information on energy sources and trophic pathways could be gathered from the analysis of Deluge Inlet food web, in great part due to the presence of sources with distinct $\delta^{13}C$ values such as mangroves (low $\delta^{13}C$ values) and seagrass (high $\delta^{13}C$ values) in close proximity. This detailed analysis illustrates the high level of complexity of estuarine food webs, where carbon from different sources can be transported up the food web through different trophic pathways, and where trophic pathways can be relatively linear, or merge at higher trophic levels (see Fig. 4.13). Moreover, with this study, as in Chapter 2, it is again demonstrated that background knowledge on diet and behaviour of the different components of the food web is necessary to avoid erroneous conclusions. This was particularly evident in relation to plankton based food chains (see above).

It is also clear that it is crucial to collect as great number of species as possible from the range of available habitats to accurately characterise food webs in these areas. For example, for Deluge Inlet, as in the Mangrove pool in the Ross River (Chapter 2), only a limited number of species showed a clear evidence of incorporation of mangrove carbon into their tissues. If those species had not been collected and analysed, no input of mangrove carbon would be detected for this system, and important aspects of energy sources and trophic pathways would be missed, leading to a flawed understanding of the energetic processes taking place in this area.

4.4.2. Sources of Energy for Estuarine Communities

Comparison of Fish Isotope Composition Between Estuaries

The incorporation of mangrove carbon into estuarine organisms depends on the availability of local versus imported sources (Bouillon et al. 2004b), as well as on the type and extend of the wetland vegetation (Wafar et al. 1997, Odum 2000), the hydrology of the area, topography and shape of the estuary (Lee 1995, Polis et al. 1997, Twilley 1998, Teal & Howes 2000). In the present study, even though aquatic primary producers such as plankton and microphytobenthos were not collected at each estuary, and although the ranges of isotope values characteristic of each type of producers were taken from the literature, the comparative approach used clearly indicated that material from terrestrial wetland origin was incorporated into adjacent aquatic food webs. Although the similarity in $\delta^{13}C$ values of aquatic producers meant it was not possible to separate the specific contributions of each particular aquatic producer, the great disparity between the $\delta^{13}C$ values of mangroves and those of salt

marsh/aquatic producers made the identification of the input of mangrove carbon possible.

This study also indicates that the degree of incorporation of mangrove carbon into estuarine food webs relates directly to the extent of mangrove vegetation adjacent to the estuary: in Deluge Inlet, where dense mangrove forests are present, fish had very low $\delta^{13}C$ values, indicating an important contribution of mangrove carbon to their diet. In Victoria Creek, a wide range in $\delta^{13}C$ was detected, which probably reflects the incorporation of both ^{13}C depleted carbon of mangrove origin, and ^{13}C enriched carbon of sugarcane origin. In Half Moon Creek, where mangrove forest is less extensive, $\delta^{13}C$ values were slightly higher than at Deluge Inlet. In Blacksoil Creek, where the downstream sampling area consists of extensive sand flats with few mangrove trees along the banks, fish had the highest $\delta^{13}C$ values, suggesting a major dependence on benthic producers, a situation commonly seen on temperate mud and sandflats (Heip et al. 1995, MacIntyre et al. 1996, Underwood & Kromkamp 1999).

Results also suggest that considerable areas of mangrove need to be present for a substantial incorporation of mangrove carbon to be detectable. For example, although there are dense mangrove forests in Half Moon Creek, these only represent an area of ~3.7 km^2, much smaller than in Deluge Inlet or Victoria Creek. If stable isotope values for this site were analysed in isolation, it would be hard to detect any incorporation of mangrove carbon, since animals had relatively high $\delta^{13}C$ values, closer to aquatic benthic producers and terrestrial C_4 producers (see Figs. 4.3 and 4.9b). However, the pattern of increased depletion in ^{13}C with increased mangrove area suggests that

mangrove carbon does influence food webs in these systems, and consequently that there is likely to be a small incorporation of mangrove carbon even at Half Moon Creek.

The use of stable isotopes in the study of estuarine food webs is facilitated by the differences in $\delta^{13}C$ between the different producers present in these systems (France 1995b). In the present study, the widest difference in $\delta^{13}C$ between producers occurred at Victoria Creek, where ^{13}C depleted mangroves and other C_3 terrestrial producers occur in proximity to ^{13}C enriched C_4 sugarcane plantations. Accordingly, fish species from Victoria Creek showed the widest range in $\delta^{13}C$, indicating taxon-specific differences in trophic pathways. Two distinct energy pathways seem to dominate in this area, both likely to be based, at least in an important part, on terrestrial wetland carbon; one probably based mainly on mangrove carbon, and the other on sugarcane carbon. The presence of two distinct co-occurring pathways of carbon transfer within the same area has also been documented for other systems (e.g. France 1995c, Paterson & Whitfield 1997). Although C_4 macrophytes have often been found to contribute little to aquatic food webs (Hamilton et al. 1992, Forsberg et al. 1993, Bunn et al. 1997) and to have a lower nutrient content (Caswell et al. 1973) and lower digestibility (Wilson & Hacker 1987, Wilson & Hattersley 1989) when compared to C_3 plants, an incorporation of carbon from these ^{13}C enriched producers seems likely at Victoria Creek, appearing as the most parsimonious explanation for the high variability in $\delta^{13}C$ values found in fish from this system.

Stable isotope analysis also suggests the likelihood of incorporation of seagrass carbon by the herbivore *A. sclerolepis,* which had $\delta^{13}C$ values close to C_4 producers and seagrass. Given its morphology (long beak and small mouth lacking cutting teeth

(Froese & Pauli 2007)), it is not likely that this species feeds on terrestrial C_4 producers. Hence, although no seagrass beds are present in the estuary, the ^{13}C enriched $\delta^{13}C$ values of this species reflect the utilisation of carbon of seagrass origin, most likely transported into the estuaries from adjacent seagrass beds (Hyndes & Lavery 2005). In fact, seagrass is often the main source of carbon for this species (Connolly 2003, Waltham & Connolly 2006) and in Victoria Creek drifting seagrass is frequently carried into the area by the tides and wind (pers. obs.).

Incorporation of ^{13}C enriched carbon from sugarcane plantations

An incorporation of ^{13}C enriched carbon from sugarcane plantations was detected at Victoria Creek, where detritus feeding fish had unusually high $\delta^{13}C$ values, consistent with a strong influence of sugarcane carbon. Hence, it is possible that for systems such as Victoria Creek, where extensive areas of rainforest and mangrove wetland have been replaced by sugarcane plantations, $\delta^{13}C$ can be used as a proxy to determine the likelihood of herbicide and insecticide pollution. Since animals' carbon isotope composition represents the sources of energy assimilated over a period of time, even when pollutants are not present in measurable quantities in the systems at the time of sampling, animals' $\delta^{13}C$ indicative of a strong contribution of sugarcane carbon may also be indicative of large inputs of agro-chemicals. The usefulness of this approach depends, of course, on the extent to which inputs of sugarcane carbon are correlated with inputs of agro-chemicals. Further studies should be conducted to address this possibility.

Incorporation of ^{15}N enriched sewage-derived material

As with $\delta^{13}C$, fish $\delta^{15}N$ values were also useful to detect the incorporation of material resulting from anthropogenic activities, in this case of ^{15}N enriched nitrogen of sewage origin. In fact, the high $\delta^{15}N$ values of fish from Half Moon Creek are probably the result of incorporation of ^{15}N enriched nitrogen from a wastewater treatment plant sited adjacent to the creek. Sewage contamination has been found to lead to ^{15}N enrichment of aquatic fauna in lacustrine (Cabana & Rasmussen 1996, Lake et al. 2001), riverine (deBruyn et al. 2003, Steffy & Kilham 2004, Ulseth & Hershey 2005) and estuarine (McClelland & Valiela 1997, Schlacher et al. 2005, Hadwen & Arthington 2007) systems, as $\delta^{15}N$ of sewage origin is between 10 and 25‰ (Kendall 1998).

Evidence of fish movement could also be interpreted from the analysis of $\delta^{15}N$ values. Although several studies have successfully used stable isotopic analysis to study the movement of animals between habitats or ecosystems (Hobson 1999, Harrod et al. 2005, Herzka 2005), the analysis of $\delta^{13}C$ is generally used for this purpose. Nevertheless, $\delta^{15}N$ has been found to be useful in cases involving sewage input (Rau et al. 1981, Hansson et al. 1997). In the present study, the relatively low $\delta^{15}N$ of a number of major piscivores from Half Moon Creek in relation to most individuals from the same group (with differences being present even within a species) suggests that these animals have recently moved into the area from adjacent, unpolluted, estuaries or coastal waters, and that the nitrogen composition of their tissues had not equilibrated with the local environment at the time of sampling. Moreover, individuals with the lowest $\delta^{15}N$ had values similar to major piscivores from the near pristine Deluge Inlet, further supporting this movement hypothesis.

Differences in $\delta^{15}N$ were also detected among the three estuaries where no input of nitrogen of anthropogenic origin was present, as fish from Deluge Inlet and Victoria Creek were more enriched in ^{15}N than in fish from Blacksoil Creek. This is probably a result of greater nitrogen availability in the nutrient rich mangrove soils of Deluge Inlet and Victoria Creek, when compared to nutrient poor (Alongi 1988, Alongi 1994, Bruinsma 2001) saltpan and sandy areas surrounding Blacksoil Creek. In fact, nitrogen isotope composition of plants has been found to be positively correlated to nitrogen availability (Garten 1993), and this composition is reflected in the tissues of aquatic organisms that rely on their production for nutrition. Consequently, as is the case with carbon, it seems that nitrogen from terrestrial sources (in this case mangroves and sugarcane plantations) is incorporated by aquatic animals in open estuarine areas.

4.4.3. Trophic Structure

Trophic length. Results from the present study suggest that although food webs in estuarine areas of Tropical Australia are complex, the number of trophic levels is relatively constant among systems. Even though it is not possible to be certain that trophic levels and trophic lengths calculated correspond to the real values, these can be used as a means of comparison between sites, since $\delta^{15}N$ values of a mullet species (*Valamugil* spp.) provided the baseline in all cases.

$\delta^{15}N$ values of *Valamugil* sp. from Deluge Inlet indicate that this species' trophic level is approximately 2.3. In fact, mullet species generally consume benthic organisms along with the ingested phytodetritus (Blay Jr 1995, Moorthy et al. 2002, Blanco et al. 2003)

and hence have an effective trophic level higher than 2. Based on this information, it was possible to ascertain that food webs had approximately 4 trophic levels in the four systems considered. Even though no large piscivores (e.g. carangids) were collected at Victoria Creek and hence it was not possible to calculate the exact trophic length for this estuary, $\delta^{15}N$ values suggest the presence of at least 1.5 trophic levels between *Valamugil* sp. and the small leiognathid *G. minuta*, indicating that the food web has at least 3.8 trophic levels, and a trophic length certainly higher than this value, most likely around 4.

Vander Zanden & Fetzer (2007), in a literature review on trophic length in 219 aquatic systems (calculated based on $\delta^{15}N$ analysis), also reported that marine systems have in general ~4 trophic levels. However, the authors also found that trophic length spanned two full trophic levels within marine habitats, indicating that there is a significant variability in trophic length in these areas. In that review however, only six out of a total of 47 marine systems considered are located in tropical areas, and those six varied in food chain length from ~3.4 to ~4.4 trophic levels (Vander Zanden & Fetzer 2007). Such variability was not observed in the present study. This might be a consequence of the standardised method of calculating trophic length considered. In contrast, in the studies considered by Vander Zanden & Fetzer (2007) trophic length was calculated using different taxa of primary consumers. It seems therefore important to develop an universal protocol for calculating trophic length in estuarine areas, so that food web parameters such as trophic length and trophic positions can be validly compared between studies.

The similarity in trophic length among estuaries may have important implications in terms of conservation and management of these areas. Although species composition

can not be used as an indication of level of impact or estuary health, as fish faunas can be very variable even among systems located in close proximity (Sheaves 2006), perhaps the analysis of aspects of trophic organization such as trophic length, which ultimately reflects energetic processes, can lead to the development of more effective ways of measuring ecosystem condition. However, further studies are needed to verify this constancy in trophic length across estuaries in Tropical Australia.

Another potential approach to the analysis of patterns of trophic organization in estuaries can be based on the comparison of carbon and nitrogen isotope composition of different species across systems. In fact, a relatively small number of fish species consistently occurs in North Queensland estuaries (Sheaves 2006), including silverbiddies (*Gerres* spp.), whiting (*Sillago* spp.), ponyfish (*Leiognathus* spp.) and mullet (*Valamugil* spp. and *Liza subviridis*). The analysis of the distribution of stable isotope values of such species in the $\delta^{13}C$ vs. $\delta^{15}N$ plane, coupled with the study of changes in isotope composition of individual species between estuaries should be useful to identify similarities and differences in trophic structure between estuaries, which might be valuable to characterise trophic structure in these areas. However, due to time constraints this aspect was not included in this thesis.

***Omnivory and diet overlap*.** For Deluge Inlet, Half Moon Creek and Blacksoil Creek, there was evidence of a high level of omnivory (omnivores: species that feed at more than one trophic level (Pimm & Lawton 1978)) and diet overlap between fish species, indicated by the similarity in carbon isotope composition of species of higher trophic levels, coupled with the continuous distribution of $\delta^{15}N$ values along the $\delta^{15}N$ scale.

Omnivory is a very important aspect of a food web, contributing to the structural stability of animal communities and increasing the stability of food webs by decreasing the possibility of trophic cascades (Fagan 1997, McCann & Hastings 1997, McCann et al. 1998, Balcombe et al. 2005). Only at Victoria Creek, a system where a great part of natural surrounding lowland vegetation has been replaced by sugarcane plantations, do results indicate the presence of well separated trophic chains and discrete trophic levels, suggesting lower levels of omnivory.

The conversion of natural vegetation to sugarcane plantations can affect estuarine food webs in many ways, including through the modification of temperature and light regimes, the chemistry of the water, the input of dissolved and particulate terrestrial organic matter, riverbed disturbance and input of terrestrial invertebrates (Riley et al. 2004). The apparent low level of omnivory at Victoria Creek is therefore likely to be a result of impacts of anthropogenic activities over the ecosystem. Although it is difficult to determine the specific effects of each of these processes over the different food web compartments, it is clear that these can have an important impact over the entire food web. However, since only a limited number of estuaries were considered in this study, it is not possible to generalize or unambiguously attribute causality. More agriculture impacted systems need to be analysed for an adequate characterization of the consequences of such impacts. Such characterization could be useful to help predict, measure and possibly mitigate the impacts of agriculture and other anthropogenic activities over estuarine communities.

4.4.4. Conclusion

Results from this study confirm that carbon fixed by terrestrial wetland macrophytes such as mangroves and sugarcane enter the aquatic food webs and contribute to the support of invertebrate and fish communities in tropical estuarine systems. Moreover, results also indicate that anthropogenic impacts over estuarine catchments are reflected in the structure of adjacent estuarine food webs. It is therefore important to protect the entire assemblage of habitats in these areas, as any modification of riparian habitats can have impacts not only through changes in availability of food and refuge, but also by changing the origin of the ultimate source of carbon used by estuarine organisms, which can have important consequences over the entire estuarine food web, as appears to be the case for Victoria Creek.

In the estuaries considered, food webs were very complex and differed in both sources of energy and trophic structure. However, the fact that around four trophic levels were present in all systems indicates that this aspect of trophic structure is likely to be conservative across estuaries in North Queensland. If this is the case, trophic length and other aspects of trophic structure can be used to analyse the condition of estuarine systems. There is therefore a great potential for stable isotope analysis to be used to assess ecosystem health in estuarine systems, but further baseline studies need to be conducted in order to validate this hypothesis.

Chapter 5

Seasonality in Sources of Energy for Aquatic Communities in Intermittently Connected Estuarine Areas

5.1. INTRODUCTION

Flooding is critical in structuring communities in riverine and estuarine systems (Bayley 1995, Loneragan & Bunn 1999), with many fish and invertebrates depending on floods to complete their life-cycles (e.g. Fitzgerald et al. 1998, Gelin et al. 2001, Jaywardane et al. 2002). For example, in Tropical Australia, a number of economically and recreationally important fish species including the barramundi *Lates calcarifer*, the mangrove jack *Lutjanus argentimaculatus* and the giant herring *Elops hawaiensis*, use upstream estuarine wetlands and freshwater reaches at different stages of their life-cycles (Russell & Garrett 1983, Russell & Garrett 1985, Russel & McDougall 2005).

Rivers in Australia's Dry Tropics have highly seasonal flow regimes, with most flows occurring in the wet season, between November and May (McMahon et al. 1992). This seasonality leads to clear seasonal cycles in water biochemistry, terrestrial runoff, habitat availability, etc. The occurrence of appropriate environmental conditions at specific times of the year is crucial for the health and persistence of the different

habitats and the biotic communities they support (Loneragan & Bunn 1999, Ward et al. 1999, Grange et al. 2000, Sheldon et al. 2000).

During the wet season, waterways form a continuum of interconnected areas, and aquatic animals are able to move between habitats and access regions that may be inaccessible during the dry season. In the dry season however, many waterways are reduced to a string of isolated pools, where animals are trapped until the next connection occurs. In estuarine areas, this pattern of connection and disconnection periods is further complicated by the additional marine tidal connections that interact with freshwater flows to produce complex connectivity regimes (Sheaves & Johnston 2006b). Hence, estuarine pools can also become temporarily isolated from each other and from the rest of the estuary, with the type and periodicity of connection depending on the fluvial regime, tide magnitude, pool elevation, distance to the river, and spatial configuration of the landscape (Sheaves & Johnston 2006b).

The seasonality in hydrologic conditions has direct consequences for the functioning and dynamics of aquatic food webs, not only in providing physical connectivity and allowing movement of organisms between habitats, but also in allowing connectivity at an energetic level, in allowing access to alternative sources of energy and in mediating the flows of carbon through systems. For example, in the wet season, there may be a significant input of energy of terrestrial origin into aquatic food webs, with floodwaters transporting terrestrial material from the floodplain into the waterways, a process summarised for freshwater systems by the Flood Pulse Concept (FPC) (Junk et al. 1989). In the dry season however, autochthonous sources such as plankton and benthic algae may have a greater importance, a process then described by the Riverine Productivity Model (RPM) (Thorp & Delong 1994).

Stable isotopic analysis of carbon is particularly useful in the study of food webs and sources of energy in estuarine areas due to the large differences in $\delta^{13}C$ between C_3 terrestrial producers (including mangroves) and aquatic producers (France 1996). If ^{13}C depleted terrestrial material transported in with the floods is important for aquatic food webs, aquatic animals should show lower $\delta^{13}C$ values after the wet season. On the other hand, if autochthonous material is more important in the dry season, carbon isotope composition of animals should then shift away from terrestrial signatures.

The objective of this study is to investigate the seasonal variations in the importance of autochthonous and allochthonous sources of energy for aquatic communities in intermittently connected estuarine areas in the Australian Dry Tropics. Hence, stable isotopic analysis is used to (i) identify differences in sources of carbon for aquatic animal communities between locations, (ii) identify seasonal changes in sources of carbon for the different locations, and (iii) investigate the sources of energy and trophic pathways in areas with different ecological characteristics, including pools located in near pristine systems and those in systems subjected to various anthropogenic impacts such as urban development, forestry plantations and cattle pasture.

5.2. METHODS

5.2.1. Study Sites

Six intermittently connected estuarine pools located in five systems on the east coast of Tropical Australia were examined. Three were located in North Queensland: Saltwater

pool in Saltwater Creek and Curralea and Paradise Lakes in Ross Creek; and three in Central Queensland: Munduran, Gonong and Twelve Mile pools in Munduran, Gonong and Twelve Mile Creeks respectively (Figure 5.1).

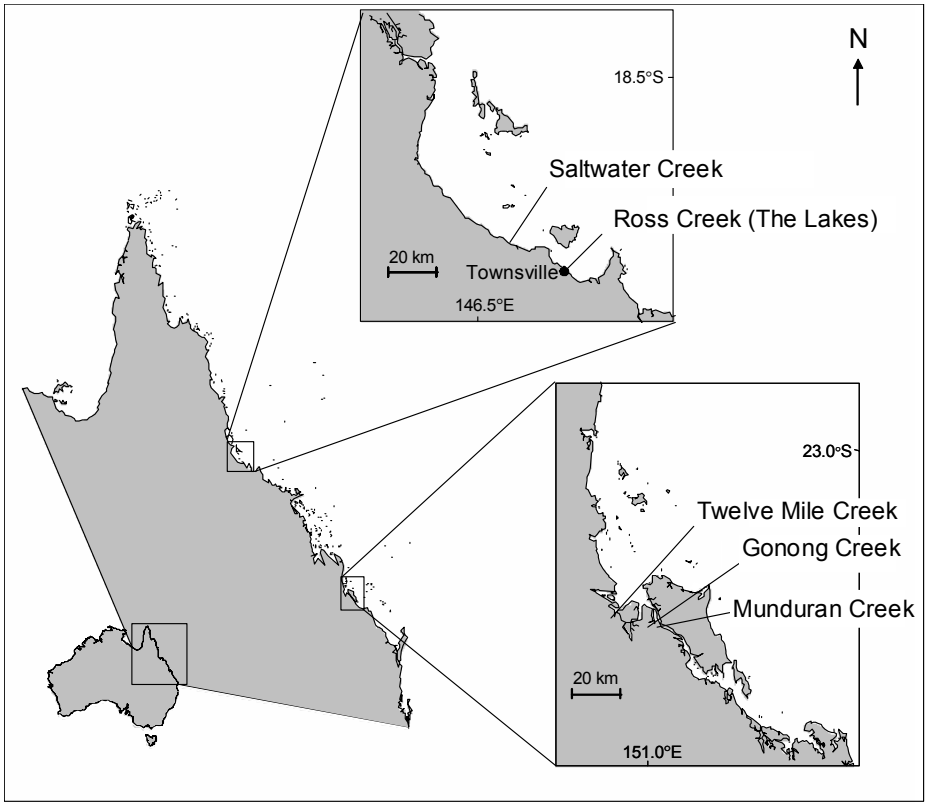

Fig. 5.1. Map showing the geographic location of the study areas.

Although both areas feature a summer wet and winter dry season, the details of rainfall pattern in North and Central Queensland are different (Fig. 5.2). In North Queensland, seasonal differences in rainfall are more pronounced, with heavy rains during the relatively short wet season followed by a long dry season, with almost no rainfall (Fig. 5.2). In contrast, Central Queensland has lower overall rainfall with less pronounced seasonal differences. Moreover, Central Queensland was going through a drought

period at the time of this study, and as a result the monthly precipitation in the summer months was lower than average (Bureau of Meteorology 2007). Nevertheless, this precipitation lead to a significant flow, allowing the connectivity between the different habitats in the three systems in Central Queensland (Sheaves & Johnston 2006b).

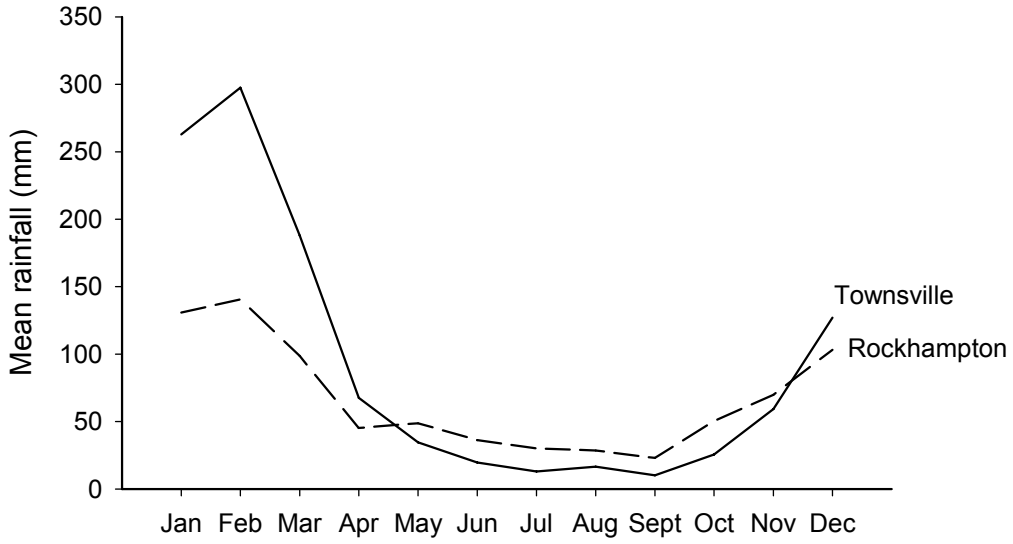

Fig. 5.2. Mean rainfall (mm) recorded for Townsville (averages from 1940 to 2004) and Rockhampton (averages from 1949 to 2004) (Bureau of Meteorology 2007), to illustrate the differences in rainfall pattern between North and Central Queensland respectively.

Saltwater Creek, 43 km north of the City of Townsville, runs through a near-pristine State Forest. Riparian vegetation is mainly native grasses and tea tree (*Melaleuca* sp.) forest. The estuarine section of the creek is 1.76 km long and forms a series of intermittently connected pools during periods with no freshwater flow. Sampling was conducted in the most downstream of these pools (Saltwater pool). This pool is 525 m long and 25 m wide, and connects to the estuary by tides over 2.9 m, therefore

retaining water throughout the year. It is shallow, with an average depth around 0.5 m and maximum depth of 1.3 m during disconnection periods. The pool substrate is a mix of very coarse grained sediment, pebbles and boulders, usually covered with a layer of epilithic algae. A scattering of small *Avicennia marina* and *Rhizophora stylosa* mangrove trees is present in the most downstream end of the pool.

Curralea and Paradise Lakes (jointly referred to as The Lakes) are two artificial impoundments connected to Ross Creek, in the City of Townsville (Fig. 5.1). The Lakes are surrounded by urban development, and are both connected to Ross Creek by a single 1500 m long canal. Tidal flow into the Lakes is restricted by tide gates at the mouth of the canal, with the gates closing over both the tops and bottoms of tides, producing an attenuated tidal range. The Lakes were constructed for flood mitigation and as contaminant traps for urban stormwater runoff (Johnston & Sheaves 2006b). Paradise Lake has a maximum depth of 2.4 m, is about 950 m long and varies in width between 50 m and 150 m. While Paradise Lake is directly connected to Ross Creek by the canal, Curralea Lake is connected to this canal by a further 116 m long, 1.5 m diameter pipe and a small floodway, which further restricts tidal connections and water turnover. Curralea Lake has a maximum depth of 3.0 m and is roughly L shaped, being 455 m long and 155 m wide on its longer arm, and 310 m long and 80 m wide on its shorter arm.

The sediment on the bottom of both Lakes is unvegetated and composed of a thick homogenous layer of anoxic mud. The banks are steep and made of concrete, and generally covered with a layer of green filamentous algae. Although most of the perimeter of Curralea Lake has no riparian vegetation, there is some vegetation associated with private residences, and a small area with *A. marina* and *R. stylosa*

mangrove trees. In Paradise Lake, a ~450 m long fringe of regenerating *A. marina* and *R. stylosa* mangroves is present. Both lakes are surrounded by a dense grass meadow mainly composed by the C_4 salt couch *Sporobolus virginicus*, urban lawns of C_4 grasses and sedges such as *Isolepis nodosa.* The C_3 succulent *Sesuvium portulacastrum* and the C_4 *Suaeda australis* are also present, but in very low densities.

Munduran Creek, located to the south of the Fitzroy River delta (Fig. 5.1), has a topography in which transverse rock bars result in a series of natural impoundments during the neap tides in periods of no freshwater flow. Sampling was conducted at the most upstream extremity of tidal incursion, in a pool separated from the estuary proper by a rock and gravel bar, and only connected to the estuary by the highest spring tides (>5.2 m) or during periods of freshwater flow. This pool is approximately 350 m long and about 18 m wide at its widest point, and has a maximum depth of 1.8 m when disconnected. The sediment is mainly composed of very coarse pebbles interspersed with muddy areas. It is surrounded by State Forest and has a narrow mangrove border (*A. marina, Aegiceras corniculatum* and *R. stylosa*), interspersed with native grasses and *Eucalyptus* woodland.

Gonong pool, at the upstream extent of tidal influence in Gonong Creek, in the Fitzroy delta (Fig. 5.1), is a permanent pool similar to that at Munduran Creek. It is disconnected from the rest of the estuary by a cobble and gravel bar about 50 m long and, as with Munduran, is connected to the estuary by the highest spring tides and during periods of freshwater flow. The pool is approximately 450 m long and 20 m in width at its widest point, and has a maximum depth of 2.1 m when disconnected. The

sediment is very coarse, mainly composed of pebbles with small areas of clay. The pool is bordered on its eastern side by National Park and on its western side by a forestry plantation. Gonong pool has an intermittent mangrove border on the National Park margin (*A. corniculatum, A. marina* and *R. stylosa*), and extensive areas of native grasses are present throughout the area.

Twelve Mile pool is an isolated estuarine pool on Twelve Mile Creek, also in the Fitzroy River delta. As with Munduran and Gonong pools, Twelve Mile pool represents the most upstream section of the estuary, and is connected to a series of upstream freshwater pools during periods of freshwater flow. However, Twelve Mile pool has a much lower frequency of tidal connection, only connecting on a few of the highest spring tides of the year (2-4 times a year), as tidal waters have to cross about 3 km of saltpan from Inkerman Creek for connection to take place. Due to this low frequency of connection, and the pronounced seasonality in precipitation, this pool attains its maximum level during the rainy season, after which the water level steadily decreases as the water evaporates (Sheaves & Johnston 2006c). In 2004, this resulted in a decrease from a maximum depth of 4.0 m in February, down to 3.5 m in July and 2.9 m in November. This variation in depth resulted in a pronounced decrease in the amount of submerged vegetation along the pool margins.

Twelve Mile pool is bordered by a narrow band (maximum width ~0.5 m) of the reed *Juncus* sp., beyond which the surrounding vegetation consists of a dense grass meadow mainly composed of the salt couch *S. virginicus.* Other sedges, rushes and salt marsh succulents are also present but in low densities. The pool is bordered on its northern side by pasture and on its southern side by a habitat reclamation area, of previously grazed land, from which cattle are now excluded. Few mature trees are

present, and mangroves are absent. At full level, this pool is around 800 m in length and 10-15 m in width for most of its length, with a maximum depth of 4.0 m. This pool maintained low salinities (< 10 ppt) throughout the sampling period.

5.2.2. Sample Collection, Processing and Analysis

Producers and animals were collected as described in Chapter 2. For fish capture however, additional fishing gears were used, including seine nets (12 mm mesh size), cast nets (6 and 18 mm mesh size), monofilament gill nets (25, 50, 100, 200 mm mesh sizes), fish traps and hook and lines. Due to the low salinities in Twelve Mile pool, several insect species were also present, which were sampled from the submerged vegetation with dip nets, and from the substrate with a benthic sledge. Insects were sorted and analysed using the same protocols as for other small invertebrates (see Chapter 2).

Samples were processed and analysed as described in Chapter 2. However, in this case some of the samples were analysed at the CSIRO Marine Research Laboratories in Hobart, Tasmania.

5.2.3. Sampling Design

Each pool was sampled for fish and invertebrates on two occasions: about three months before the wet season (pre-wet), and two to four months after the wet season

(post-wet). This time lag allowed a period of time under different conditions for the isotope composition of animal tissues to begin to reflect any change in nutritional source (Hesslein et al. 1993, Gorokhova & Hansson 1999). This design was used to give an indication of the origin of energy used during the dry (pre-wet samples) and wet (post-wet samples) seasons. Saltwater pool and The Lakes were sampled in November 2004 (pre-wet) and March 2005 (post-wet), while Munduran, Gonong and Twelve Mile pools were sampled between May and July 2004 (post-wet) and in November 2004 (pre-wet).

Since Twelve Mile showed very pronounced differences in environmental conditions between seasons (see details in Section 5.2.1), aquatic producers were collected both in the pre- and post-wet seasons. In the remaining locations however, producers were generally collected only on one sampling occasion, with the resulting values being used for both seasons. Due to cost constraints, no more than two samples were analysed for most animal species.

5.2.4. Data Analysis

Differences in Sources of Energy Between Locations and Seasons

Differences in sources of energy for aquatic food webs were analysed by comparing $\delta^{13}C$ values between locations and seasons using a classification and regression tree (CART) (De'ath & Fabricius 2000) based on mean $\delta^{13}C$ values of fish species. Invertebrates were not included since few species occurred at more than one or two locations.

Seasonal Variations in Sources of Carbon for Aquatic Food Webs

Differences in sources of carbon between seasons were investigated more explicitly for the fish species that occurred at a same location in both seasons. For this purpose, a CART was used to analyse the shifts in fish $\delta^{13}C$ between the pre- and post-wet season. Here, the dependent variable was the difference in mean $\delta^{13}C$ between seasons, and season and location were the independent variables. The input data consisted of zeros for the pre-wet season, i.e. to the starting point with which the effect of the wet season was measured; and values for the post-wet season corresponded to the differences in $\delta^{13}C$ between seasons for each species. Hence, a split between seasons with zero in the pre-wet values and the isotopic difference in the post-wet would indicate a significant seasonal change, while a lack of a split would indicate that the post-wet differences did not differ substantially from zero, i.e. that there were no changes in $\delta^{13}C$ between seasons.

Bivariate plots of seasonal shifts in $\delta^{13}C$ and $\delta^{15}N$ were also used to enable the analysis of both fish and invertebrates. In this case, $\delta^{15}N$ was also included because changes in $\delta^{15}N$ can indicate differences in incorporation of material of sewage (Costanzo et al. 2001, Costanzo et al. 2003) or fertilizer (Valiela et al. 2000, Costanzo et al. 2003) origin.

Sources of Energy and Trophic Pathways

Sources of Energy. For each site, the importance of the different sources of carbon was qualitatively analysed by comparing $\delta^{13}C$ values of animals with those of

producers. In most cases, values of locally collected producers were considered. In Saltwater pool however, since no producers other than epilithic microalgae were collected, the ranges in $\delta^{13}C$ characteristic of the different producer categories were used for the comparison, as described in Chapter 4. Hence, the range considered as indicative of planktonic producers was -22 ± 3‰ (mean ± SD), for benthic producers -17 ± 4‰ (France 1995b) and for C_4 producers -16.7 to -13.3‰ (see Chapter 4). Since a range of C_3 plants occur in these areas in addition to mangroves, $\delta^{13}C$ values of 39 individual plants of 19 species collected adjacent to estuaries along the Central and North Queensland coast (unpubl. data) were used, resulting in a range of -30.2 to -25.2‰.

Trophic Pathways. For each location and for each season, stable isotope analysis of carbon and nitrogen was used to identify trophic relationships and define the main trophic pathways. $\delta^{15}N$ values of organisms were used as an indication of trophic position (Vander Zanden & Rasmussen 1999). In most cases, trophic length was also calculated based on the difference in $\delta^{15}N$ between the detritivorous fish of lowest $\delta^{15}N$ and the species of highest $\delta^{15}N$, as described in Chapter 4. The only variation was that in this Chapter a mullet species was not used as a baseline at all locations because these species did not occur in all areas and in all seasons. In Saltwater pool, where the food web was very simple, trophic length was calculated based on the direct identification of trophic relationships between different species.

5.3. RESULTS

A total of 41 fish species was analysed, 28 in the pre-wet and 32 in the post-wet season. This included a freshwater species, *Nematolosa erebi*, captured in Curralea Lake and in Twelve Mile pool. Twenty invertebrate species were also analysed. About half of these species were collected in Twelve Mile pool, where a high diversity of insect larvae and other invertebrates generally associated with freshwater was present. The assemblage of fish species analysed reflects well the species composition in these areas: for the Fitzroy pools (Munduran, Gonong and Twelve Mile), it includes more than 80% of all species collected in each the area during five intensive sampling occasions carried out between July 2004 and May 2005 by Sheaves et al. (2006). For The Lakes, more than 70% of the most common species identified between November 2004 and March 2006 by Johnston & Sheaves (2006b) are represented for each location. In Saltwater pool, shallow depths and clear water ensured that individuals of all species observed were captured.

5.3.1. Differences in Sources of Carbon Between Locations and Seasons

Classification and Regression Tree Analysis

Fish $\delta^{13}C$ values varied between locations and seasons (Fig. 5.3). According to the 1-SE rule, a six-leaf CART (explaining 46% of the variability) was selected 40% of the time (Fig. 5.4). The CART indicated clear differences between locations, with fish from Munduran and Gonong having lower $\delta^{13}C$ than fish from the other sites (Fig. 5.4), probably as result of a greater incorporation of ^{13}C depleted carbon of terrestrial origin in these forested areas. Most of the variability is explained by this first split in the data.

$\delta^{13}C$ values were higher in fish from Twelve Mile pool, higher again in Curralea and Paradise Lake and highest at Saltwater Pool (Fig. 5.4).

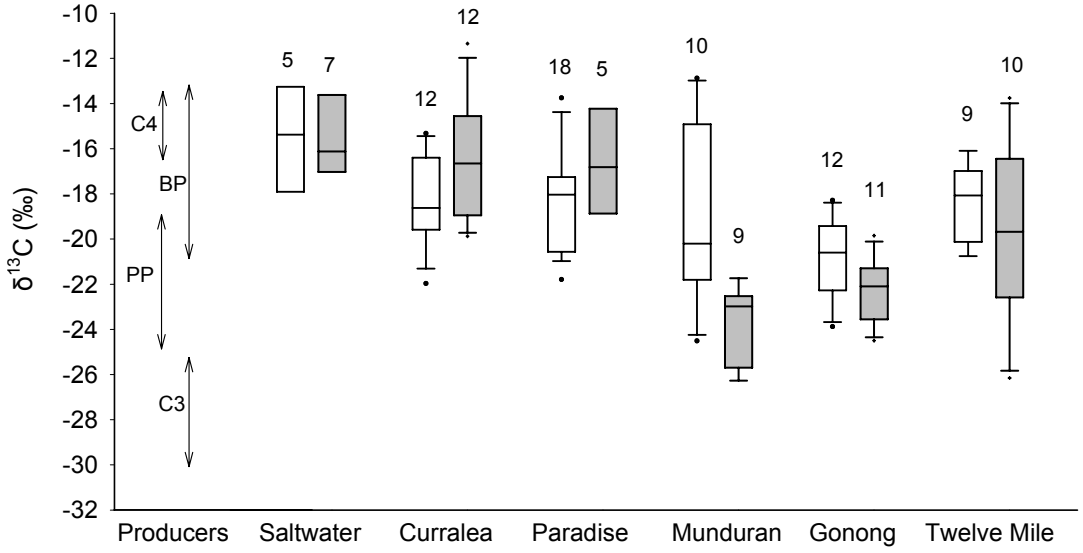

Fig. 5.3. Box plots showing the median (line within boxes), interquartile ranges (indicated by boxes), 10^{th} and 90^{th} percentiles (whiskers) and outliers (•) of $\delta^{13}C$ values of fish from the different pools collected in the pre-wet (white boxes) and post-wet (grey boxes) seasons. Graphs based on the average $\delta^{13}C$ of fish species. Arrows indicate range in $\delta^{13}C$ of the different classes of producers (see text). BP = benthic producers; C3 = C_3 plants; C4 = C_4 plants; PP = planktonic producers. Numbers above boxes indicate sample size (number of species).

There were also clear seasonal differences in fish $\delta^{13}C$ at Munduran and Gonong, and at Curralea and Paradise Lakes, but the shifts were in opposite directions (Fig. 5.4). At Munduran and Gonong fish collected in the post-wet season had lower $\delta^{13}C$ values than those collected in the pre-wet season (Fig. 5.4), suggesting a greater incorporation of ^{13}C depleted terrestrial carbon after the wet season. In contrast, for Curralea and Paradise Lakes fish collected after the wet season had slightly higher

$\delta^{13}C$ values than fish collected before the wet season (Fig. 5.4), possibly due to greater incorporation of ^{13}C enriched carbon from C_4 producers after the wet season.

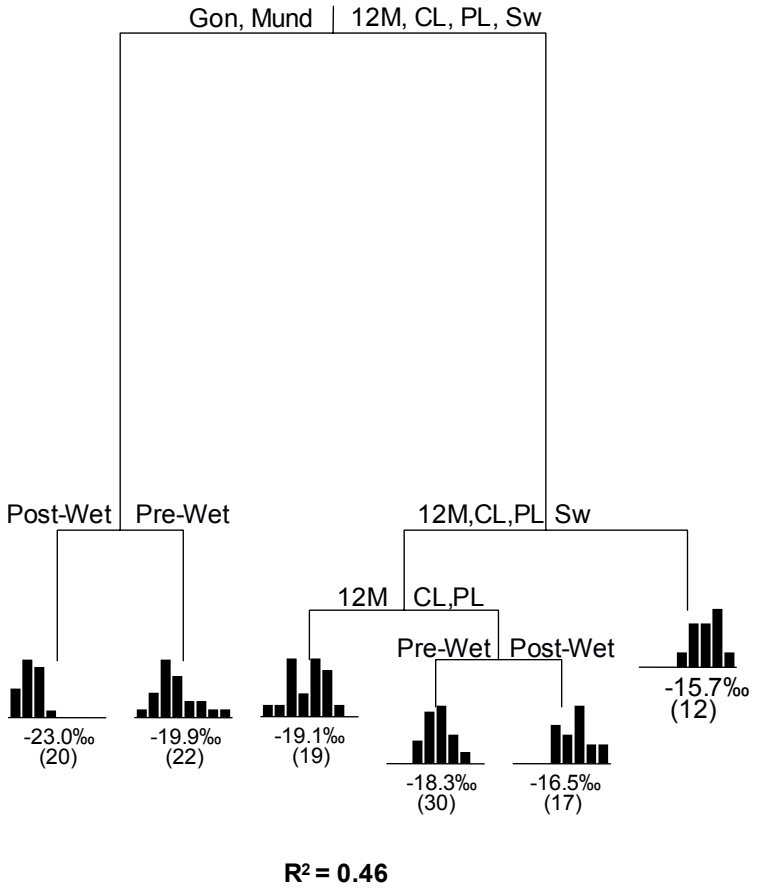

Fig. 5.4. Six-leaf classification and regression tree explaining fish $\delta^{13}C$ based on location and sampling season. Model calculated based on the average $\delta^{13}C$. Histograms of distribution of $\delta^{13}C$ are also presented, and mean $\delta^{13}C$ and sample size (in brackets) for each group are indicated. 12M = Twelve Mile; CL and PL = Curralea and Paradise Lakes; Gon = Gonong; Mund = Munduran; Sw = Saltwater.

Considering only fish species that occurred at a site in both seasons lead to a more definitive picture of seasonal change. Here, a three-leaf CART (explaining 49% of the variability) was selected 97% of the time according to the 1-SE rule, indicating that fish

from Munduran, Gonong and Twelve Mile shifted from higher $\delta^{13}C$ values in the pre-wet season to lower values at the post-wet season, while fish from Saltwater and Curralea and Paradise Lakes did not show any change in carbon isotope composition between seasons (Fig. 5.5).

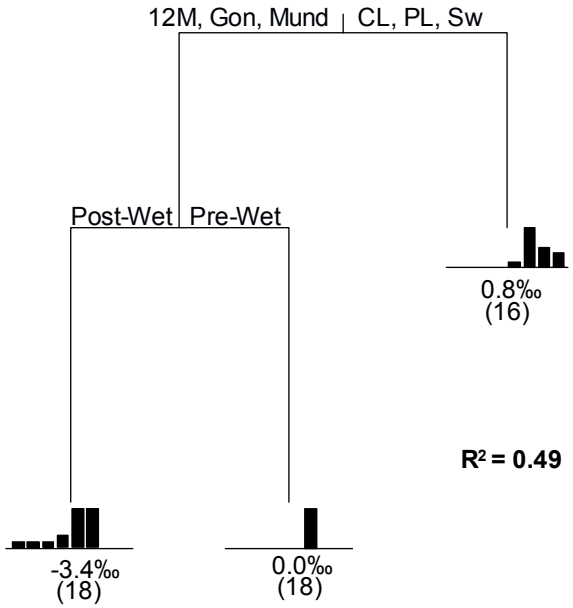

Fig. 5.5. Multivariate CART explaining the changes in fish $\delta^{13}C$ between the pre-wet and post-wet seasons for the different sites. Model calculated based on differences in $\delta^{13}C$ between the post-wet and the pre-wet season for all fish species that occurred at both seasons at each site. Histograms of distribution of the values of shifts in $\delta^{13}C$ are also presented, and mean shift in $\delta^{13}C$ and sample size (in brackets) for each group are indicated. 12M = Twelve Mile; CL and PL = Curralea and Paradise Lakes; Gon = Gonong; Mund = Munduran; Sw = Saltwater.

Graphical Comparison of Animal $\delta^{13}C$ and $\delta^{15}N$ Values Between Seasons

In Munduran and Gonong pools, a change from higher $\delta^{13}C$ values at the pre-wet season to lower values after the wet season was clear for all detritivore and

macrobenthic carnivore fish species (Fig. 5.6a, b). Only for the herbivore *Selenotoca multifasciata* (both locations) and the planktivore *Herklotsichthys castelnaui* (Gonong), $\delta^{13}C$ was similar between seasons (Fig. 5.6a, b). This adds weight to the idea that energy is entering the food web through the detritus food chain, as only detritivores and macrobenthic carnivores, i.e. species that ultimately rely on detrital material transported with the flood waters, showed a shift in $\delta^{13}C$, but not herbivores or planktivores, which rely on energy from other sources. At Twelve Mile, the pattern of isotopic shift was similar to that at Munduran and Gonong, with most animals having lower $\delta^{13}C$ after the wet season (Fig. 5.6c). For $\delta^{15}N$, there was no particular trend in change between seasons for Munduran, Gonong or Twelve Mile (Fig. 5.6a, b, c).

Although only a small number of species were analysed from Curralea and Paradise Lakes, all showed an increase in $\delta^{13}C$ from the pre-wet to the post-wet season (Fig. 5.6d, e), likely to be a result of a greater incorporation of ^{13}C enriched carbon from C_4 salt marsh plants after the wet season. In contrast to Munduran, Gonong and Twelve Mile where $\delta^{15}N$ values were stable over time, in Curralea and Paradise Lakes there were consistent increases in $\delta^{15}N$ from the pre-wet to the post-wet season (Fig. 5.6d, e), suggesting an increased incorporation of ^{15}N enriched nitrogen of urban runoff during the wet season. In Saltwater pool, in line with the CART analysis (Figs. 5.4 and 5.5), there was no clear indication of seasonal change in $\delta^{13}C$, although $\delta^{15}N$ tended to be higher after the wet season (Fig. 5.6f).

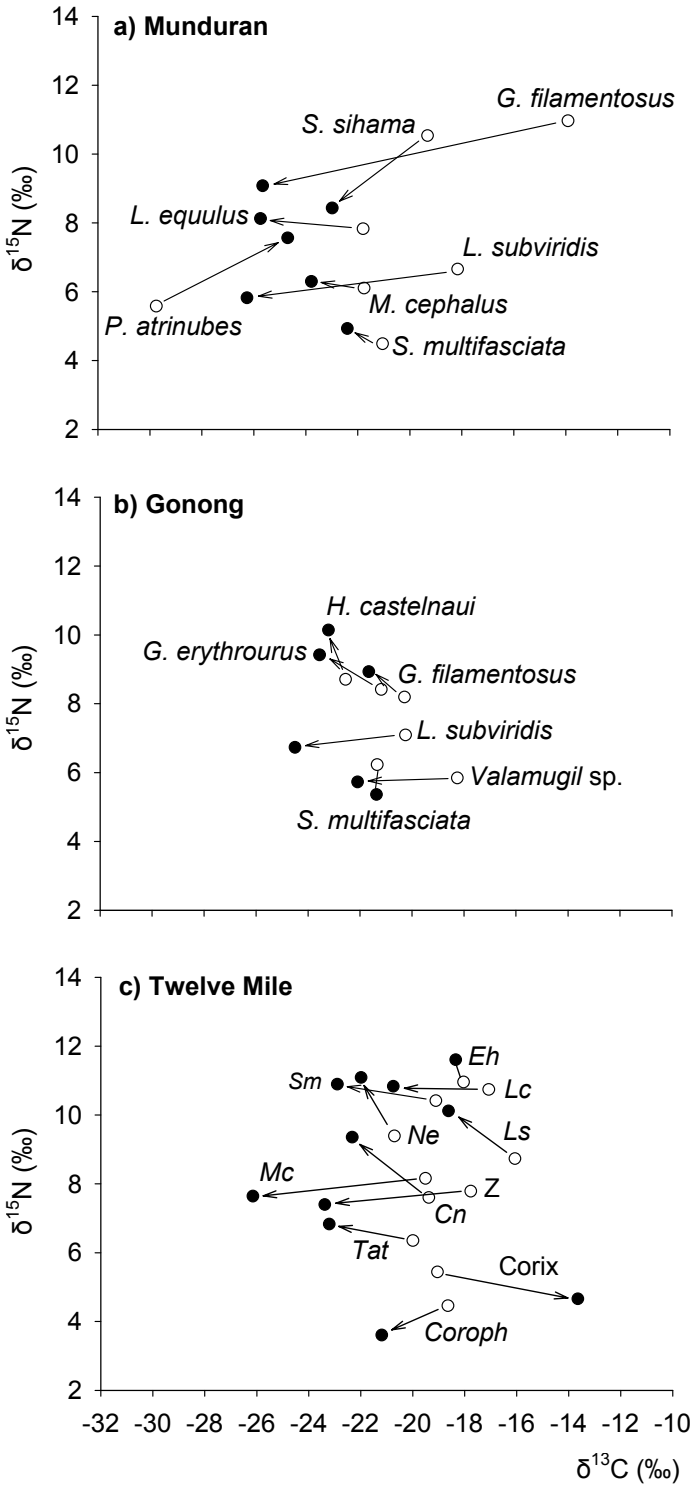

Fig. 5.6. Change in mean $\delta^{13}C$ and $\delta^{15}N$ between the pre- (white symbols) and post-wet (black symbols) seasons for animal species collected during both seasons in **a)** Munduran, **b)** Gonong, **c)** Twelve Mile, **d)** Curralea Lake, **e)** Paradise Lake and **f)** Saltwater. *Cn* = *C. nilotica*; Corix = corixids; *Coroph* = *Corophium* sp.; *Eh* = *E. hawaiensis*; *Lc* = *L. calcarifer*; *Ls* = *L. subviridis*; *Mc* = *M. cephalus*; *Ne* = *N. erebi*; *Sm* = *S. multifasciata*; *Tat* = *Tatea* sp.; *Z* = zygoptera larvae.

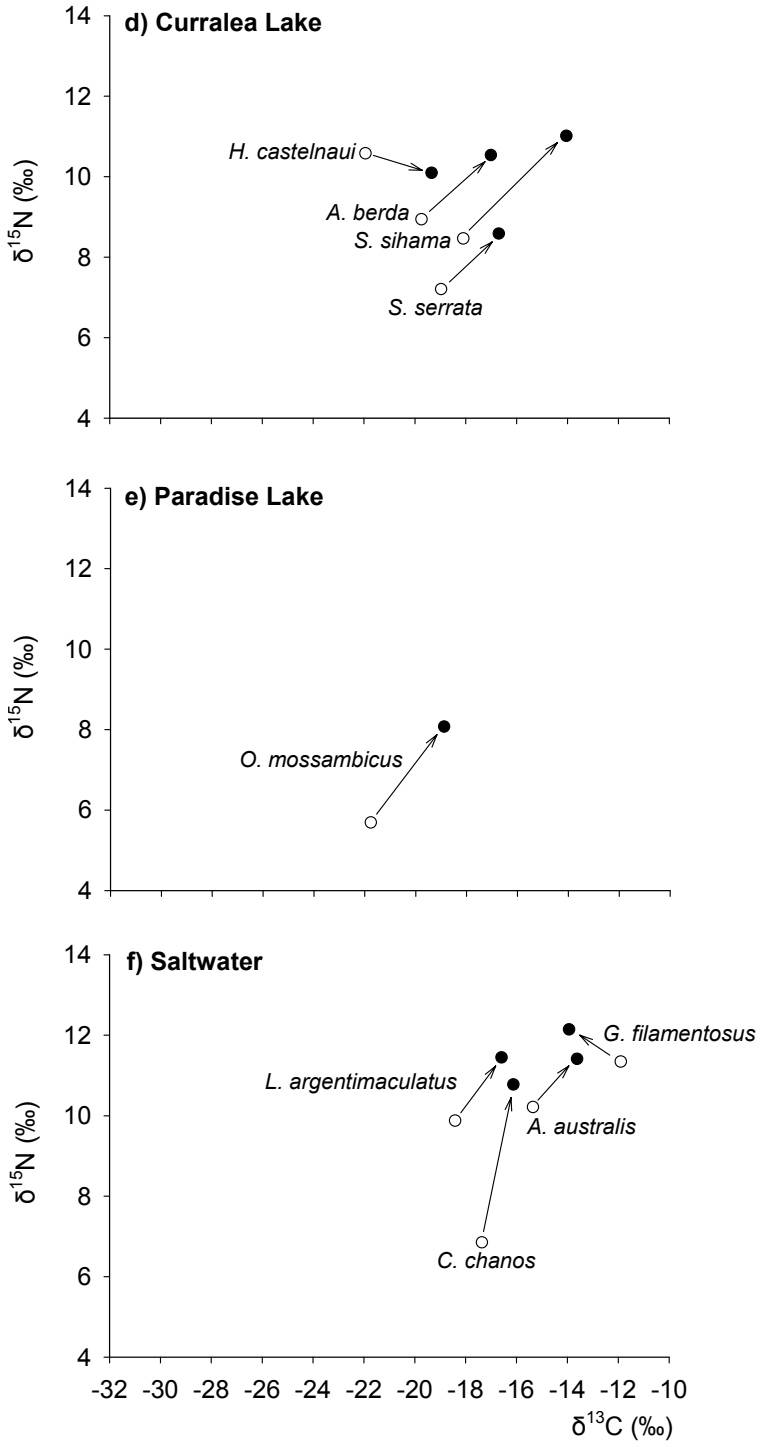

Fig. 5.6. (cont.) Change in mean $\delta^{13}C$ and $\delta^{15}N$ between the pre- (white symbols) and post-wet (black symbols) seasons for animal species collected during both seasons in **a)** Munduran, **b)** Gonong, **c)** Twelve Mile, **d)** Curralea Lake, **e)** Paradise Lake and **f)** Saltwater. *Cn = C. nilotica*; corix = Corixids; *Coroph = Corophium* sp.; *Eh = E. hawaiensis*; *Lc = L. calcarifer*; *Ls = L. subviridis*; *Mc = M. cephalus*; *Ne = N. erebi*; *Sm = S. multifasciata*; *Tat = Tatea* sp.; Z = zygoptera larvae.

5.3.2. Sources of Energy and Trophic Pathways

To determine the specific sources of energy and identify the main trophic pathways present in these areas, carbon and nitrogen isotope composition of primary producers and consumers collected at each system were compared graphically, both for the pre- and the post-wet season.

Saltwater. In both the pre- and post-wet season, most species from the Saltwater pool had very high $\delta^{13}C$, with values within the range of benthic algae and C_4 grasses (Table 5.1; Fig. 5.7a). Some species were even more enriched in ^{13}C than these producers. Only *L. calcarifer* (collected only in the post-wet season) had a low $\delta^{13}C$ value within the range of C_3 producers, and was well separated from the other species (Fig. 5.7a).

Invertebrates had $\delta^{13}C$ values close to epilithic algae (Fig. 5.7a), but also similar to C_4 terrestrial producers. However, given the low density of C_4 producers in the area, it is not likely that these were the main contributors to diets of aquatic animals. The amphipods *Corophium* sp. and Leptocheliid tanaids were similar in $\delta^{15}N$ to epilithic algae, while the natant shrimps *Palaemonetes atrinubes* and the penaeid prawn *Metapenaeus bennetae* had $\delta^{15}N$ values 4.3‰ higher than these producers (Table 5.1; Fig. 5.7b), a difference that corresponds to ~1.4 trophic steps. Hence, both $\delta^{13}C$ and $\delta^{15}N$ suggest that these decapods ultimately depend exclusively on benthic producers, either by direct consumption, by consuming benthic organisms such as amphipods and tanaids or possibly a mixture of both (Fig. 5.7b). The herbivore *Siganus lineatus* and the detritivore *L. subviridis* also had $\delta^{13}C$ values that appear to indicate exclusive dependence on epilithic algae (Fig 5.7c).

Table 5.1. Size range and carbon and nitrogen isotope composition of organisms collected in Saltwater pool. *n* = number of samples analysed. When *n* = 2, the range is indicated, and when *n* > 2 mean ± SE is presented. Sizes indicate total length (in 5 mm size classes for fish). Numbers between brackets indicate number of individuals included in samples composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Epilithic algae	2	-	-14.6 to -14.0	4.8 to 5.0
Consumers				
Pre-wet				
Invertebrates				
Corophium sp.	1(5)	4	-14.8	5.4
Leptochellid tanaids	1(~50)	4	-14.9	6.4
Metapenaeus bennetae	2	25-27	-11.5 to -11.8	9.0 to 9.2
Palaemonetes atribunes	4	20	-12.3 ± 0.4	9.2 ± 07
Fish				
Acanthopagrus australis	2	55-110	-15.8 to -14.9	9.8 to 10.6
Chanos chanos	1	160	-17.4	6.8
Gerres filamentosus	1	70	-11.9	11.4
Lutjanus argentimaculatus	4	90-105	-18.4 ± 1.0	9.9 ± 0.6
Liza subviridis	1	100	-14.6	8.3
Post-wet				
Fish				
Acanthopagrus australis	2	55-75	-14.0 to -13.2	11.0 to 11.8
Chanos chanos	1	125	-16.1	10.8
Gerres filamentosus	2	60-65	-14.2 to -13.6	12.1 to 12.2
Lutjanus argentimaculatus	1	110	-16.6	11.5
Lates calcarifer	1	225	-25.9	9.6
Siganus lineatus	2	75	-13.6 to -12.8	6.4 to 9.2
Selenotoca multifasciata	2	60-70	-20.1 to -14.0	4.0 to 6.4

The macrobenthic carnivores *Acanthopagrus australis* and *Gerres filamentosus* had similar carbon and nitrogen isotope composition, with values suggesting that these species feed mainly on a mix of peracarid and natant crustaceans (Fig. 5.7d), which are in turn dependent on epilithic algae. *A. australis* and *G. filamentosus* were also the species with the highest $\delta^{15}N$ (Table 5.1), indicating a short and simple food web in Saltwater pool, with only about 3.5 trophic levels.

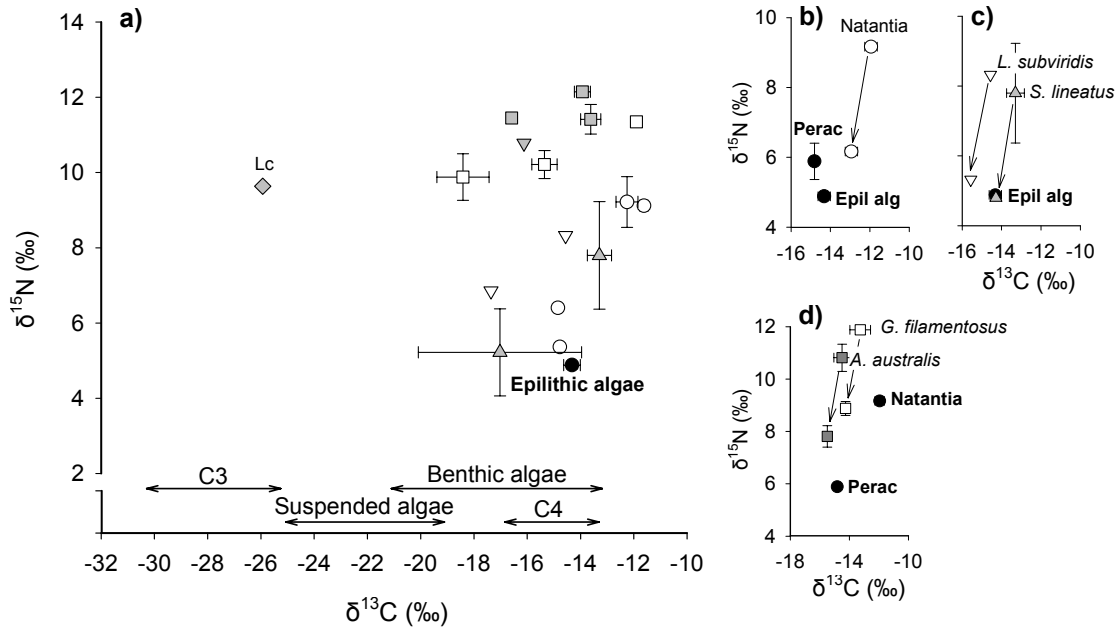

Fig. 5.7. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of organisms collected from Saltwater pool. **a)** $\delta^{13}C$ and $\delta^{15}N$ values of epilithic algae, invertebrates (circles) and herbivorous (upward triangles), detritivorous (downwards triangles), macrobenthic carnivorous (squares) and piscivorous (diamonds) fish collected in the pre-wet (white symbols) and post-wet (grey symbols) season. Arrows indicate the range in $\delta^{13}C$ of the different classes of producers (see text). C3 and C4 = plant species of C_3 and C_4 metabolism. The ^{13}C depleted *Lates calcarifer* (Lc), a species mentioned in text, is also indicated. b), c), d) - Diagrams showing $\delta^{13}C$ and $\delta^{15}N$ (mean ± SE) of potential food sources (bold; black symbols) and of consumers before and after correction for fractionation for one trophic level. Arrows indicate the direction of fractionation. **b)** Natant crustaceans (*P. atrinubes* and *M. bennetae*) with epilithic algae and peracarids; **c)** *S. lineatus* and *L. subviridis* with epilithic algae; **d)** *G. filamentosus* and *A. australis* (data pooled between seasons) with peracarids and the natant crustaceans *P. atrinubes* and *M. bennetae*. Epil alg = epilithic algae; Perac = peracarid crustaceans (*Corophium* sp. and Leptocheliid tanaids).

Curralea and Paradise Lakes. As in Saltwater, animals from both lakes were very enriched in ^{13}C (Tables 5.2 and 5.3), and most species had $\delta^{13}C$ values close to benthic algae and plankton (Figs. 5.8 and 5.9). However, some fish species had $\delta^{13}C$ values similar or even higher than the most ^{13}C enriched producers, the C_4 plants *S. virginicus*, *I. nodosa* and *S. australis*, indicating a likely contribution from these sources.

These species included the two herbivores from Curralea Lake, the banded scat *S. multifasciata* and the spotted scat *Scatophagus argus* (Table 5.2, Fig. 5.8), and *S. multifasciata* and the phytodetritivore *L. subviridis* from Paradise Lake (Table 5.3, Fig. 5.9).

In Curralea Lake, benthic algae had very high $\delta^{15}N$ (Table 5.2, Fig. 5.8), much higher than $\delta^{15}N$ of most consumers, suggesting that these producers did not have an important contribution to animal nutrition. However, it is possible that the ^{15}N enriched benthic algae was collected from an area with localized input of sewage waters, and so did not accurately reflect the overall $\delta^{15}N$ of the lake's benthic algae. In contrast, benthic algae collected in Paradise Lake had low $\delta^{15}N$ (Table 5.3, Fig. 5.9).

In both lakes, invertebrates and herbivorous and detritivorous fish had generally lower $\delta^{15}N$ values (Figs. 5.8 and 5.9). However, at higher trophic levels there was no clear separation between trophic guilds. This is especially true for Curralea Lake (Fig. 5.8). Here, in the pre-wet season, the largest difference in $\delta^{15}N$ was found between the detritivorous mud herring *Nematolosa come* and the predatory giant herring *E. hawaiensis* (Table 5.2), corresponding to 1.3 trophic steps and hence suggesting a food web with 3.3 trophic levels. In the post-wet season, the difference between the detritivorous milkfish *Chanos chanos* and the benthivorous crescent perch *Terapon jarbua* and the piscivorous trevally *Caranx ignobilis* also indicates the presence of 3.3 trophic levels, suggesting that trophic length did not vary between seasons (Fig. 5.8).

Table 5.2. Size range and nitrogen and carbon isotope composition of organisms collected in Curralea Lake. *n* = number of samples analysed. When *n* = 2, the range is indicated. Sizes indicate total length (in 5 mm size classes) for fish and carapace width for crabs.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Avicennia marina	1	-	-27.7	7.8
Benthic green algae	1	-	-18.4	10.2
Plankton	1	-	-18.5	2.6
Sporobolus virginicus	1	-	-14.6	4.6
Suaeda australis	1	-	-14.9	9.2
Consumers				
Pre-Wet				
Invertebrates				
Portunus pelagicus	1	125	-19.4	5.9
Scylla serrata	1	135	-19.0	7.2
Fish				
Acanthopagrus australis	1	75	-19.7	9.0
Acanthopagrus berda	1	50	-19.7	8.9
Elops hawaiensis	2	195	-19.7 to -18.5	10.2 to 10.8
Gerres erythrourus	2	50-65	-16.7 to -15.3	8.2 to 8.4
Herklotsichthys castelnaui	2	65-100	-22.3 to -21.6	9.6 to 11.6
Herklotsichthys	1	74	-15.7	9.5
Liza subviridis	2	120-125	-15.9 to -14.7	6.8 to 7.4
Nematolosa come	2	115-120	-18.5 to -18.2	6.3 to 6.8
Oreochromis mossambicus	1	114	-17.5	8.1
Pelates sexlineatus	1	60	-18.9	8.4
Platycephalus fuscus	1	130	-18.6	9.2
Sillago sihama	1	100	-18.1	8.5
Post-Wet				
Invertebrates				
S. serrata	1	100	-16.7	8.6
Fish				
Acanthopagrus berda	2	70-80	-17.9 to -16.2	10.5 to 10.6
Arothron manilensis	1	210	-19.9	8.9
Chanos chanos	2	280-300	-17.6 to -15.8	6.5 to 8.1
Chelonodon patoca	2	65-70	-18.7 to -18.0	9.5 to 9.5
Caranx ignobilis	1	115	-16.2	11.0
Gerres filamentosus	2	50-55	-17.7 to -14.6	10.6 to 10.9
Herklotsichthys castelnaui	2	55-65	-20.5 to -18.3	10.08 to 10.1
Nematolosa erebi	2	235-240	-20.1 to -18.2	8.6 to 9.4
Sillago sihama	1	100	-14.0	11.0
Scatophagus argus	1	135	-13.5	6.6
Selenotoca multifasciata	2	65	-12.1 to -10.6	4.5 to 4.8
Terapon jarbua	1	70	-16.6	11.3

Table 5.3. Size range and carbon and nitrogen isotope composition of organisms collected in Paradise Lake. *n* = number of samples analysed. When *n* = 2, the range is indicated. When *n* > 2, mean (± SE) is presented. Sizes are in total length (in 5 mm size classes for fish).

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Avicennia marina	1	-	-27.5	6.4
Green benthic algae	1	-	-17.4	5.2
Isolepis nodosa	1	-	-13.3	3.7
Sporobolus virginicus	1	-	-13.4	2.7
Suaeda australis	1	-	-15.1	6.8
Typhus sp.	1	-	-28.3	5.9
Consumers				
Pre-wet				
Invertebrates				
Penaeus merguiensis	2	30-43	-19.9 to -16.9	7.4 to 7.5
Fish				
Acanthopagrus australis	2	60	-14.8 to -14.0	10.3 to 11.1
Acanthopagrus berda	1	60	-17.5	10.3
Anodontostoma chacunda	2	110	-17.7 to -17.4	5.8 to 6.0
Chanos chanos	1	175	-20.8	6.5
Elops hawaiensis	1	355	-19.8	11.7
Gerres erythrourus	1	65	-17.5	8.2
Gerres filamentosus	2	85-104	-17.0 to -16.8	7.7 to 8.7
Leiognathus equulus	2	90-114	-20.6 to -20.7	7.8 to 8.5
Liza subviridis	2	55-155	-14.0 to -13.4	6.3 to 7.0
Lutjanus argentimaculatus	1	170	-20.9	10.7
Mugil cephalus	1	460	-20.5	9.0
Nematolosa come	2	120-180	-18.6 to -18.4	7.5 to 8.0
Oreochromis mossambicus	1	210	-21.8	5.7
Sardinella gibbosa	3	70-75	-20.0 ± 0.5	9.4 ± 0.1
Scomberoides commersonnianus	3	200-325	-17.7 ± 0.1	11.1 ± 0.1
Siganus lineatus	1	155	-16.8	8.6
Sillago sihama	2	105-110	-17.7 to -16.9	9.1 to 9.2
Thryssa hamiltonii	2	85	-19.0 to -17.7	10.4 to 10.5
Post-wet				
Fish				
Oreochromis mossambicus	2	70-380	-21.9 to -18.9	6.7 to 8.1
Pelates sexlineatus	1	110	-17.3	9.9
Platycephalus fuscus	1	150	-16.8	10.6
Selenotoca multifasciata	2	80-90	-14.3 to -10.7	5.3 to 7.4
Terapon jarbua	1	120	-15.9	11.1

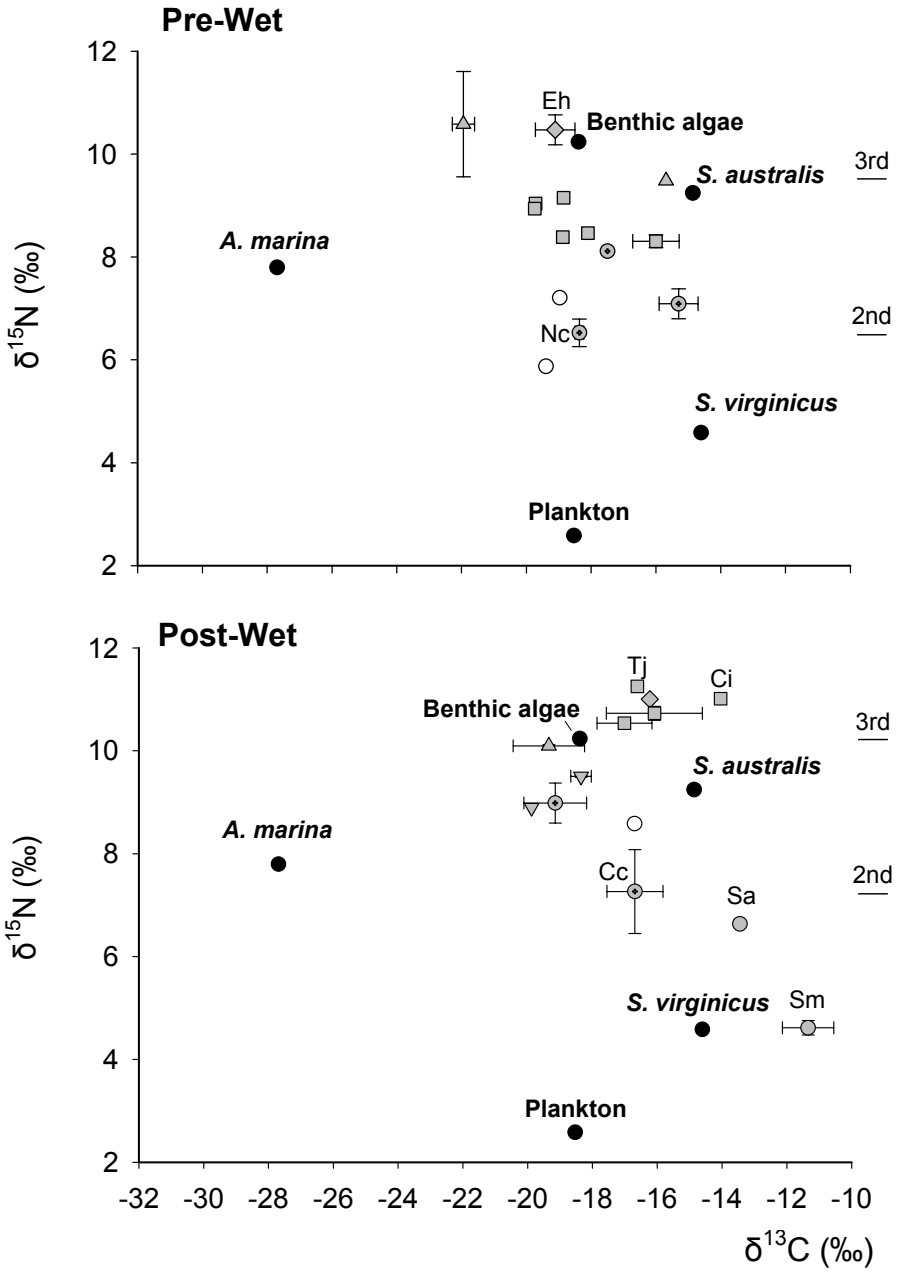

Fig. 5.8. Mean $\delta^{13}C$ and $\delta^{15}N$ (± SE) of producers (black symbols), crabs (white symbols) and fish (grey symbols) collected in Curralea Lake in the pre- and post-wet season. Fish: ○ - herbivores; ⊙ - detritivores; ▽– omnivores; △ - planktivores; □ - macrobenthic carnivores; ◇- piscivores. $\delta^{15}N$ values for each trophic level are indicated to the right of each figure. Species mentioned in text are also indicated: Cc = *C. chanos*; Ci = *C. ignobilis*; Eh = *E. hawaiensis;* Nc = *N. come;* Sa = *S. argus;* Sm = *S. multifasciata;* Tj = *T. jarbua*.

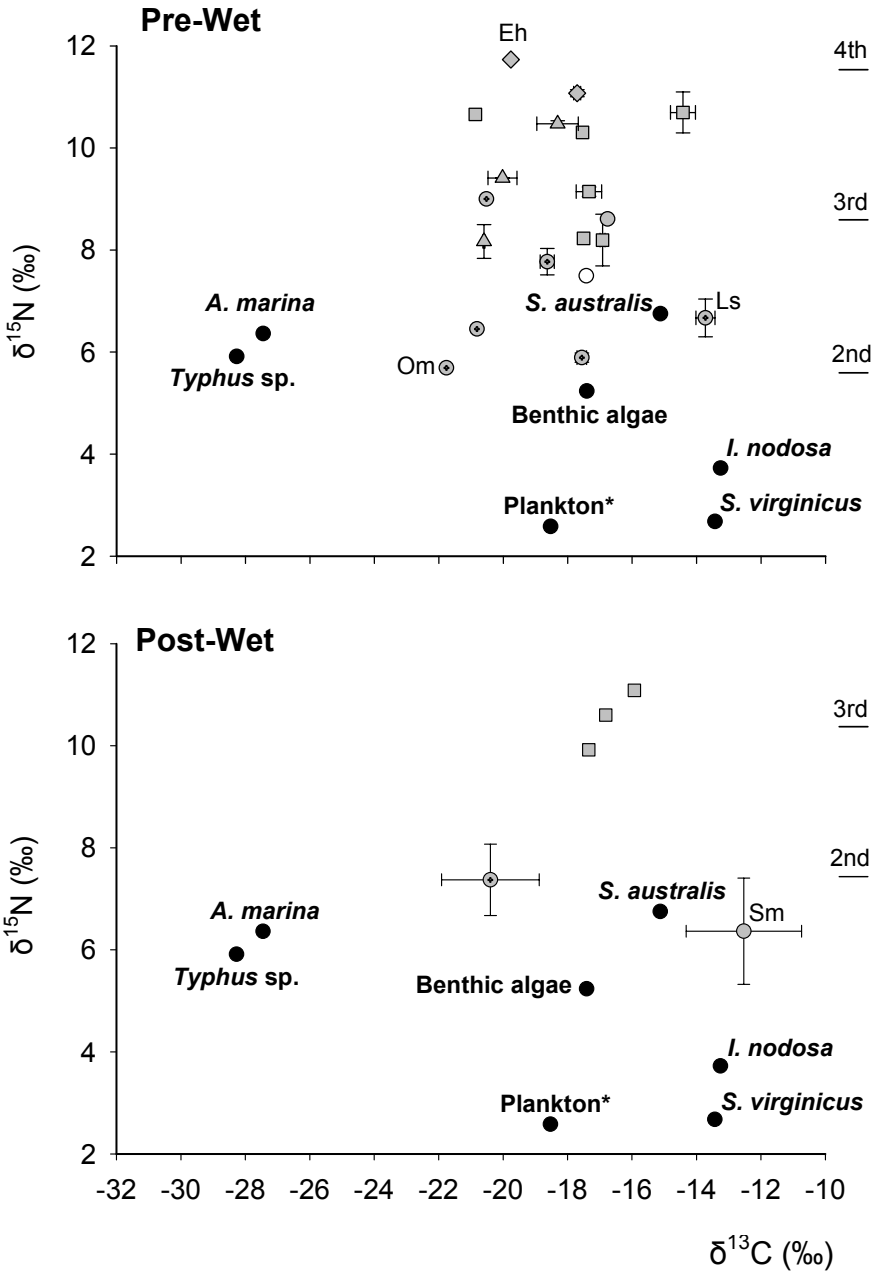

Fig. 5.9. Mean $\delta^{13}C$ and $\delta^{15}N$ (± SE) of producers (black symbols), invertebrates (white symbols) and fish (grey symbols) collected in Paradise Lake in the pre- and post-wet seasons. Fish: ○ - herbivores; ⊙ - detritivores; △ - planktivores; □ - macrobenthic carnivores; ◇- piscivores. $\delta^{15}N$ values for each trophic level are indicated to the right of each figure. Species mentioned in the text are also indicated: Eh = *E. hawaiensis*; Ls = *L. subviridis*; Om = *O. mossambicus*; Sm = *S. multifasciata*. (*) plankton not analysed at this site; $\delta^{13}C$ and $\delta^{15}N$ values taken from Curralea Lake.

In Paradise Lake, a $\delta^{15}N$ difference of 6‰ was found between the phytodetritivorous Mozambique tilapia *Oreochromis mossambicus* and the piscivorous *E. hawaiensis* in the pre-wet season (Table 5.3), corresponding to two trophic steps and suggesting a longer food web of four trophic levels (Fig. 5.9). It was not possible to calculate trophic length for the post-wet season since not many species were analysed for this season.

Munduran. Very little living plankton was present in Munduran pool throughout 2004. In both pre- and post-wet seasons, seston was mostly composed of suspended particulate organic matter of terrestrial origin, having $\delta^{13}C$ values close to C_3 plants such as the mangrove *A. corniculatum* (Fig. 5.10). Additionally, C/N ratios of seston were very high (>10), indicating the presence of refractory material. Therefore, only terrestrial producers or microphytobenthos were likely to play a major role in animal nutrition in this area.

Carbon isotope composition of animals collected in the pre-wet season formed two groups, one between -24.5 and -21.1‰, and the other between -16.6 and -12.4‰ (Fig. 5.10). The most ^{13}C depleted group had $\delta^{13}C$ values closer to microphytobenthos, while the most ^{13}C enriched was closer to C_4 producers such as the saltbush *Atriplex muelleri* (Fig. 5.10). For the mullet *Liza subviridis* and the withing *Sillago sihama*, different individuals belonged to the different groups (see Fig. 5.10). In the post-wet season, animals had more homogeneous $\delta^{13}C$ values, ranging from -26.3 to -21.6‰.

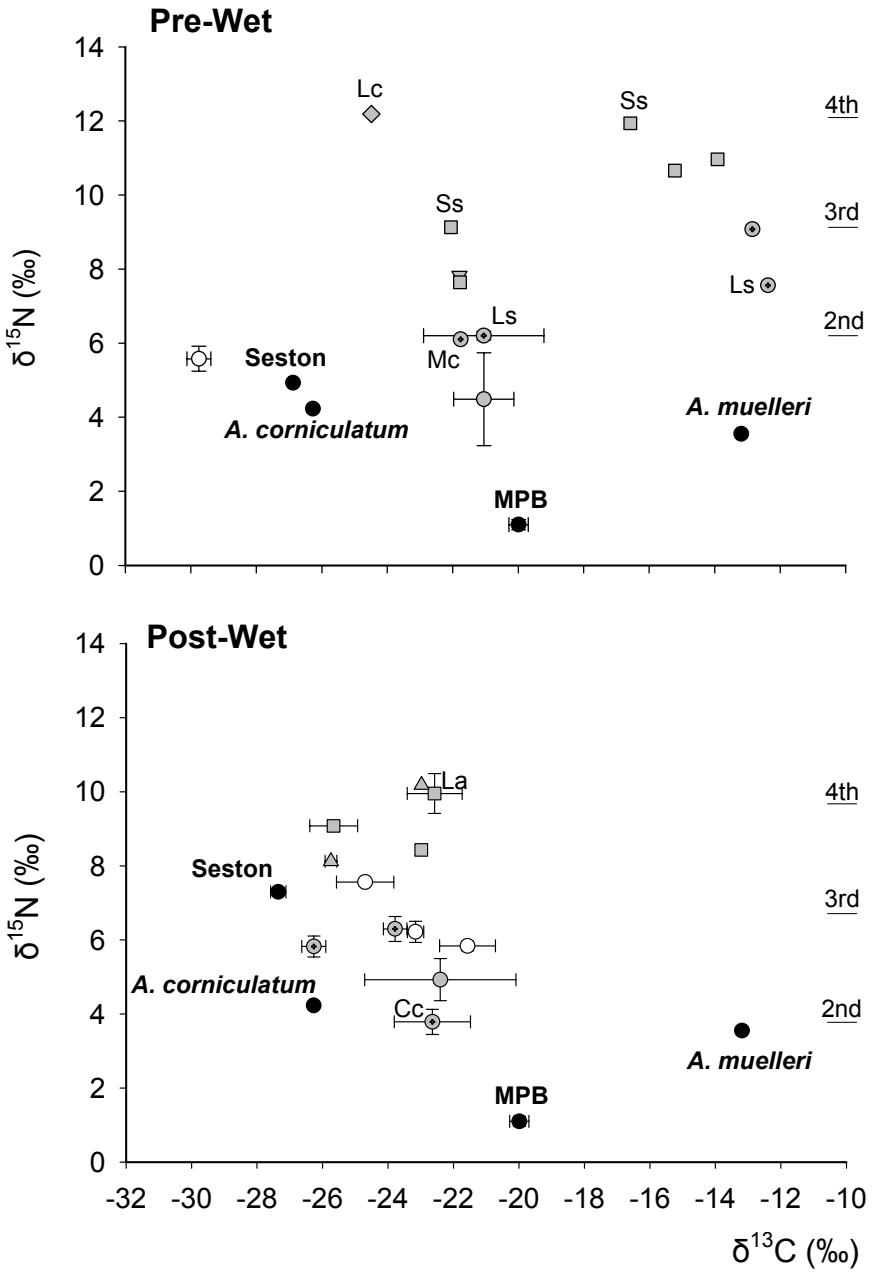

Fig. 5.10. Mean $\delta^{13}C$ and $\delta^{15}N$ (± SE) of producers (black symbols), shrimps and prawns (white symbols) and fish (grey symbols) collected in Munduran pool in the pre- and post-wet season. Fish: ○ - herbivores; ⊙ - detritivores; △ - planktivores; □ - macrobenthic carnivores; ◇- piscivores. $\delta^{15}N$ values for each trophic level are indicated to the right of each figure. In the pre-wet season, *L. subviridis* (Ls) and *S. sihama* (Ss) individuals are represented separately because a large difference in $\delta^{13}C$ between individuals was present. Other species mentioned in the text are also indicated: Cc = *C. chanos;* Lc = *L. calcarifer;* La = *L. argentimaculatus;* Ls = *L. subviridis*; Mc = *M. cephalus*. MPB = microphytobenthos.

At both pre- and post-wet seasons, invertebrates and fish primary consumers had lower $\delta^{15}N$ values than animals of higher trophic levels (Fig. 5.10). In the pre-wet season, $\delta^{15}N$ ranged from 6.1‰ for the mullet species *Mugil cephalus* and *L. subviridis* to 12.2‰ for the piscivore barramundi *L. calcarifer* (Table 5.4), a range that corresponds to two trophic steps, suggesting that the food web in this pool had around four trophic levels. In the post wet season, a similar difference of 2.1 trophic levels was found between the detritivorous milkfish *C. chanos* and the mangrove jack *L. argentimaculatus* (Table 5.4), again indicating the presence of four trophic levels.

Gonong. Almost no plankton or seston was present in Gonong pool throughout 2004. On the other hand, benthic organic matter found in the bottom of the pool had very low $\delta^{13}C$ and $\delta^{15}N$ (Table 5.5), with values that indicate an origin from ^{13}C depleted C_3 producers, most likely decomposing leaves of the mangroves *A. corniculatum*, or terrestrial species such as *Acacia* spp. and *Casuarina* spp. trees, which had low $\delta^{15}N$ (Fig. 5.11). Therefore, as in Munduran pool, only terrestrial producers or microphytobenthos were likely to be important contributors to animal nutrition in this area.

Animals had a relatively narrow range in $\delta^{13}C$ in both seasons. In the pre-wet season, animal $\delta^{13}C$ varied from -23.9 to -16.9‰, values intermediate between C_3 and C_4 terrestrial producers and close to microphytobenthos (Fig. 5.11). In the post-wet season, animals had slightly lower $\delta^{13}C$ values, ranging from -24.5 to -19.9‰, which can be an indication of a greater incorporation of ^{13}C depleted carbon of C_3 origin (Fig. 5.11).

Table 5.4. Size range and $\delta^{13}C$ and $\delta^{15}N$ values of organisms collected in Munduran pool. *n* = number of samples analysed. When *n* = 2, the range is indicated and when *n* > 2, mean (± SE) is presented. Sizes indicate total length (in 5 mm size classes for fish).

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Terrestrial sources				
Aegiceras corniculatum	1	-	-26.3	4.2
Atriplex muelleri	1	-	-13.2	3.6
Aquatic sources				
Pre-wet				
Seston	1	-	-26.9	4.9
Post-wet				
Microphytobenthos	3	-	-20.0 ± 0.1	1.1 ± 0.3
Seston	2	-	-27.6 to -26.9	7.3
Consumers				
Pre-wet				
Invertebrates				
Palaemonetes atrinubes	2	30	-30.1 to -29.4	5.2 to 5.9
Fish				
Acanthopagrus australis	1	55	-21.8	7.7
Gerres erythrourus	1	75	-15.2	10.7
Gerres filamentosus	1	85	-13.9	11.0
Lates calcarifer	1	205	-24.5	12.2
Leiognathus equulus	1	65	-21.8	7.8
Liza subviridis	2	95-120	-22.9 to -19.2	6.1 to 6.3
L. subviridis	1	185	-12.4	7.6
Mugil cephalus	1	200	-21.8	6.1
Nematolosa come	1	175	-12.8	9.1
Selenotoca multifasciata	2	85-95	-22.3 to -19.8	3.6 to 5.4
Sillago sihama	2	170-195	-22.1 to -16.6	9.1 to 11.9
Post-wet				
Invertebrates				
Metapenaeus bennetae	2	46-60	-22.4 to -20.7	5.7 to 6.0
Palaemonetes atrinubes	2	13	-25.6 to -23.8	7.6
Penaeus merguiensis	3	65-86	-23.2 ± 0.3	6.2 ± 0.3
Fish				
Chanos chanos	2	215-230	-23.8 to -21.5	3.5 to 4.1
Gerres filamentosus	4	50-80	-25.7 ± 0.7	9.0 ± 0.1
Leiognathus decorus	1	55	-23.0	10.2
Leiognathus equulus	2	70-80	-25.9 to -25.6	8.1 to 8.1
Liza subviridis	3	115	-26.3 ± 0.4	5.8 ± 0.3
Lutjanus argentimaculatus	2	300-305	-23.4 to -21.7	9.4 to 10.5
Mugil cephalus	2	230-235	-24.1 to -23.4	6.0 to 6.6
Selenotoca multifasciata	3	70-90	-22.4 ± 2.3	4.9 ± 0.6
Sillago sihama	1	225	-23.0	8.4

Table 5.5. Size range and $\delta^{13}C$ and $\delta^{15}N$ results of organisms collected in Gonong pool. *n* = number of samples analysed. When *n* = 2, the range is indicated. When *n* > 2, mean (± SE) is presented. Sizes are in total length for fish (5 mm size classes) and prawns, and carapace width for crabs.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Terrestrial sources				
Acacia sp.	1	-	-26.3	1.4
Aegiceras corniculatum	1	-	-27.6	3.1
Avicennia marina	1	-	-25.8	2.4
Casuarina equisetifolia	1	-	-29.8	-0.1
Enchylaena tomentosa	1	-	-29.8	7.2
Epaltes australis	2	-	-28.7 to -27.4	3.3 to 3.6
Heliotropium indicum	1	-	-28.6	1.5
Rhizophora stylosa	2	-	-27.4 to -27.3	1.3 to 1.6
Sida subspicata	1	-	-27.1	7.8
Sporobolus virginicus	1	-	-16.7	2.3
Suaeda sp.	1	-	-26.3	4.6
Urochloa mutica	1	-	-14.7	3.1
Aquatic sources				
Benthic organic matter	2	-	-28.8 to -27.9	0.3 to 0.5
Microphytobenthos	1	-	-19.0	0.3
Consumers				
Pre-wet				
Invertebrates				
Metopograpsus latifrons	4	21-28	-19.0 ± 0.8	7.0 ± 0.2
Paracleistostoma wardi	2	7-10	-20.1 to -19.34	3.6 to 3.9
Uca signata	2	12	-17.0 to -16.9	5.2 to 5.9
Fish				
Acanthopagrus australis	1	60	-19.1	8.2
Gerres erythrourus	2	75-85	-21.6 to -20.6	8.4 to 8.4
Gerres filamentosus	1	50	-20.3	8.2
Herklotsichthys castelnaui	1	70	-22.6	8.7
Leiognathus equulus	1	80	-23.9	9.2
Liza subviridis	1	95	-20.3	7.1
Lutjanus	1	175	-20.3	9.4
Sardinella sp.	2	65-70	-23.6 to -22.8	8.5 to 9.8
Selenotoca multifasciata	1	65	-21.3	6.2
Terapon jarbua	2	70-80	-18.9 to -18.3	8.1 to 8.3
Unidentified Gobid	2	15-20	-21.1 to -20.6	7.2 to 7.7
Valamugil sp.	2	75-85	-19.2 to -17.3	5.5 to 6.2
Post-wet				
Invertebrates				
Penaeus merguiensis	2	57-60	-20.5 to -20.2	6.1 to 6.4
Fish				
Ambassis sp.	1	50	-21.3	10.3
Chanos chanos	2	200-205	-20.4 to -19.3	5.0 to 5.4
Gerres erythrourus	3	45-55	-23.6 ± 0.8	9.4 ± 0.2
G. filamentosus	2	50-55	-21.7 to -21.6	8.6 to 9.2
Herklotsichthys castelnaui	3	80-85	-23.2 ± 0.1	10.1 ± 0.2
Leiognathus decorus	1	55	-23.7	9.4
Liza subviridis	3	80-110	-24.5 ± 0.3	6.7 ± 0.4
Mugil cephalus	1	180	-21.2	8.9
Selenotoca multifasciata	4	65-80	-21.4 ± 1.2	5.4 ± 0.5
Sillago sihama	2	120-130	-24.4 to -21.4	6.9 to 8.3
Valamugil sp.	3	120	-22.1 ± 0.5	5.7 ± 0.3

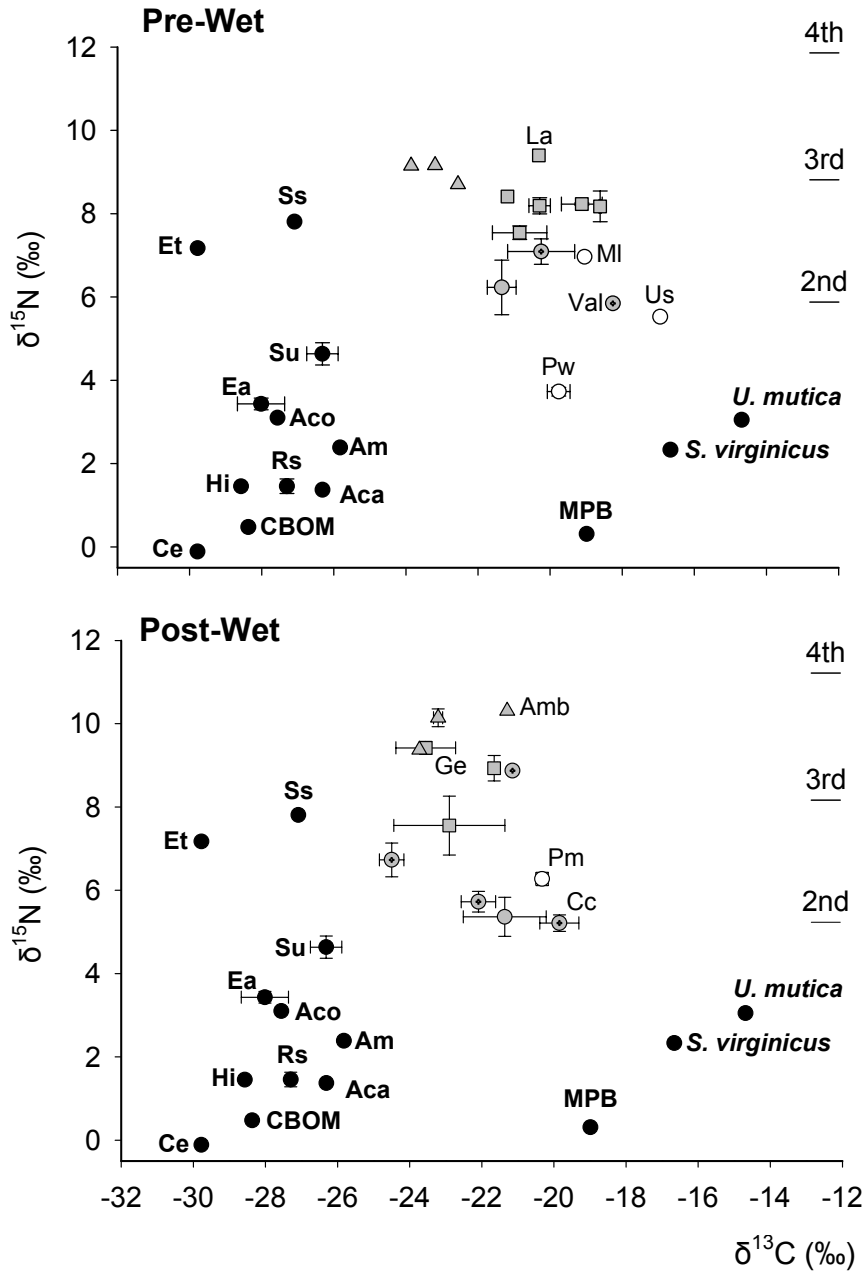

Fig. 5.11. Mean $\delta^{13}C$ and $\delta^{15}N$ (± SE) of producers (black symbols), decapods (white symbols) and fish (grey symbols) collected in Gonong in the pre- and post-wet season. Fish: ○ - herbivores; ⊙ - detritivores; △ - planktivores; □ - macrobenthic carnivores. $\delta^{15}N$ values for each trophic level are indicated to the right of each figure. Animal species mentioned in text are indicated: Amb = *Ambassis* sp.; Cc = *C. chanos*; Ge = *G. erythrourus*; La = *Lutjanus argentimaculatus*. Ml = *Metopograpsus latifrons,* Pm = *P. merguiensis*; Pw = *Paracleistostoma wardi*, Uc = *Uca signata*. CBOM = coarse benthic organic matter; MPB = microphytobenthos. C_3 plants: Aca = *Acacia* sp.; Aco = *A. corniculatum;* Am = *A. marina;* Ce = *C. equisetifolia;* Et = *E. tomentosa,* Eh = *E. australis*, Hi = *H. indicum;* Rs = *R. stylosa;* Sa = *S. australis;* Ss = *S. subspicata.* For full species names, please refer to Table 5.5.

In the pre-wet season, a maximum difference in $\delta^{15}N$ of 3.6‰ was found between the mullet *Valamugil* sp. and the mangrove jack *L. argentimaculatus* (Table 5.5), corresponding to 1.2 trophic links and indicating a food web with ~3.2 trophic levels (Fig. 5.11). A close difference in $\delta^{15}N$ (4.0‰) was found between *L. argentimaculatus* and the average for the three crab species, *Metopograpsus latifrons, Paracleistostoma wardi* and *Uca signata* (5.4‰), the probable food sources for *L. argentimaculatus* (Sheaves & Molony 2000), again indicating a relatively short trophic length. Note that *L. argentimaculatus* and crabs had very similar $\delta^{13}C$ values (-20.3 and -18.6‰ respectively), again suggesting the presence of a strong trophic relationship between these species.

In the post-wet season, the greatest difference in $\delta^{15}N$ was found between the detritivore *C. chanos* and the planktivorous glass perchlet *Ambassis* sp. (Table 5.5), corresponding to 1.7 trophic links and suggesting a food web with ~3.7 trophic levels (Fig. 5.11). However, *C. chanos* and *Ambassis* sp. are in different trophic chains, one being a detritivore and the other a planktivore. Differences in nitrogen isotope composition between other species also indicate a shorter trophic length. For example, a difference in $\delta^{15}N$ of 3.2‰ was present between the penaeid prawn *Penaeus* (*Fenneropenaeus*) *merguiensis* and the most ^{15}N enriched carnivorous fish *G. erythrourus* (Table 5.5), corresponding to lightly more than one trophic level. Since *P. merguiensis* is of trophic level ~1.5 (Chong & Sasekumar 1982, Robertson 1988) (Chapter 3 of this thesis), this food chain must have around 3.5 trophic levels, a value lower than the 3.7 suggested by the difference in $\delta^{15}N$ between *C. chanos* and *Ambassis* sp. Nevertheless, it seems that trophic length in this area was slightly longer after the wet season.

Twelve Mile. A wide range of animals was collected at Twelve Mile pool, both in the pre- and post-wet season (Table 5.6). When $\delta^{13}C$ and $\delta^{15}N$ values of these species and of available producers were graphed to identify the main sources of carbon, only producers considered to be potential important contributors were considered. These included the C_4 producers *S. virginicus* and *A. muelleri*, as well as the C_3 reed *Juncus* sp. and suspended aquatic producers. It was not possible to collect benthic producers as Twelve Mile pool was very turbid, which limited benthic productivity. Additionally, the pool edges were near vertical and hence that for most of the year no shallow areas were available for benthic production.

In the pre-wet season, animals had a narrow range in $\delta^{13}C$ (Fig. 5.12), with values intermediate between C_4 producers and plankton and *Juncus* sp., suggesting that a mixture of different sources contributes to animals' diets. Note that seston collected at this site was highly refractory (C/N ratio of 20), and hence it is not considered as a plausible source for aquatic consumers. *S. virginicus* seems to make an important contribution for most species (Fig. 5.12). However, the C_4 saltbush *A. muelleri* does not seem to be important in either the pre- or post-wet season, having $\delta^{15}N$ values too high to contribute to any species' nutrition (Fig. 5.12).

Incorporation of carbon of plankton origin was also detected for the planktivore *Ambassis telkara* in pre-wet season, which was 2.4‰ higher in $\delta^{13}C$ and 2.7‰ higher in $\delta^{15}N$ than zooplankton collected (Table 5.6; Fig. 5.12). However, given the high $\delta^{15}N$ of zooplankton, it seems that most invertebrate and fish species rely mainly on other sources, probably on a mix of detritus of *S. virginicus* origin and other sources, such as algae (although these were not collected in this season) (see Fig. 5.12).

Table 5.6. Size range and $\delta^{13}C$ and $\delta^{15}N$ results (mean ± SE) of organisms collected in Twelve Mile pool. *n* = number of samples analysed. When *n* = 2, the range is indicated. Sizes indicate total length (in 5 mm size classes for fish). Numbers in brackets indicate number of individuals included in samples composed by more than one animal.

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Producers				
Terrestrial sources				
Atriplex muelleri	2	-	-15.7 to -15.3	13.5 to 14.0
Cattle faeces	2	-	-16.2 to -15.2	5.0
Einadia hastata	2	-	-30.2 to -28.0	5.8 to 6.0
Halosarcia indica	2	-	-28.4 to -27.0	15.4 to 15.7
Sclerolaena muricata	2	-	-26.3 to -28.3	8.2 to 7.7
Sesuvium portulacastrum	3	-	-26.4 ± 0.8	8.3 ± 0.7
Sporobolus virginicus	3	-	-15.0 ± 0.6	7.4 ± 0.4
Aquatic sources				
Pre-wet				
Phytoplankton (> 53 µm)	1	-	-26.1	5.6
Seston (>125 µm)	1	-	-21.9	4.6
Zooplankton	1	-	-23.1	9.8
Post-wet				
Green filamentous algae	2	-	-22.9 to -22.7	4.3 to 4.9
Plankton (> 53 µm)	1	-	-29.1	6.4
Plankton (>125 µm)	1	-	-23.8	5.9
Consumers				
Pre-wet				
Invertebrates				
Anisoptera larvae	2(3)	10-15	-18.6 to -17.9	7.3 to 7.4
Caridina nilotica	4	15	-19.4 ± 0.1	7.6 ± 0.1
Corixidae	1(5)	7	-19.1	5.4
Corophium sp.	3(~20)	4	-18.6 ± 0.3	4.5 ± 0.1
Tatea sp.	1(5)	5-6	-20.0	6.4
Thiara sp.	1(5)	6	-23.2	6.8
Zygoptera larvae	1(5)	10-15	-17.8	7.8
Fish				
Ambassis telkara	2	45-70	-21.3 to -20.2	11.7 to 13.4
Elops hawaiensis	2	270-330	-18.1 to -18.0	10.6 to 11.4
Lates calcarifer	2	205-475	-17.6 to -16.6	10.5 to 11.0
Liza subviridis	1	205	-16.1	8.7
Mugil cephalus	4	250-440	-19.5 ± 0.7	7.9 ± 0.7
Nematolosa erebi	3	165-185	-20.7 ± 0.5	9.4 ± 0.4
Selenotoca multifasciata	3	145-150	-19.1 ± 13	10.4 ± 0.5
Unidentified Goby	2	20	-18.4 to -17.0	9.9 to 10.5
Valamugil sp.	2	30-35	-17.1 to -16.6	8.2 to 8.4
Post-wet				
Invertebrates				
Caridina nilotica	2	15	-22.7 to -21.9	9.2 to 9.5
Chironomids	3(~20)	10	-24.8 ± 0.1	7.3 ± 0.3
Corixidae	2(5)	7	-14.5 to -12.8	4.0 to 5.4
Corophium sp.	3(~20)	4	-21.2 ± 0.6	3.6 ± 0.3
Macrobrachium sp.	3	50	-22.3 ± 0.5	10.5 ± 0.4
Tabanid larvae	1(10)	5	-24.2	8.6

Table 5.6. (cont.) Size range and $\delta^{13}C$ and $\delta^{15}N$ results (mean ± SE) of organisms collected in Twelve Mile pool. *n* = number of samples analysed. When *n* = 2, the range is indicated. Sizes indicate total length (in 5 mm size classes or fish). Numbers in brackets indicate number of individuals included in samples composed by more than one animal

Species	*n*	Size (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Invertebrates (cont.)				
Tatea sp.	1(5)	5-6	-23.2	6.8
Trichoptera larvae	2(~20)	8	-23.9 to -23.0	6.4 to 6.6
Zygoptera larvae	2(5)	12-15	-24.8 to -22.0	7.1 to 7.7
Fish				
Anguilla reinhardtii	1	430	-16.6	10.6
Arrhamphus sclerolepis	3	140-145	-16.1 ± 0.5	10.9 ± 0.2
Elops hawaiensis	4	300-535	-18.4 ± 0.4	11.7 ± 0.3
Gerres filamentosus	2	130-160	-22.5	12.4
Lates calcarifer	3	235-305	-20.8 ± 2.4	10.8 ± 0.5
Liza subviridis	3	250-280	-18.6 ± 0.4	10.1 ± 0.4
Mugil cephalus	3	265-333	-26.2 ± 0.2	7.6 ± 0.5
Nematolosa erebi	2	160	-22.0 to -20.7	10.1 to 11.1
Rhinomugil nasutus	1	105	-13.8	8.2
Selenotoca multifasciata	2	120-165	-24.4 to -21.4	10.0 to 11.8

During the post-wet season, animals had more variable $\delta^{13}C$, ranging from -26.15‰ for the detritivore *M. cephalus* to -13.75‰ for the pop-eye mullet *Rhinomugil nasutus* (Table 5.6). These values suggest great differences in diet between species, ranging from an almost exclusive incorporation of carbon of plankton and/or *Juncus* sp. by *M. cephalus*, and of *S. virginicus* by the insect eater (Harrison & Senou 1997) *R. nasutus* (Fig. 5.12). Due to the similarity in carbon and nitrogen isotope composition of plankton and *Juncus* sp., it was not possible to separate the contributions of these two types of producers to animals. However, given the high planktonic productivity throughout the year (pers. obs.), it is likely that carbon fixed by planktonic algae contributes significantly for the food web both in the pre-wet and post-wet seasons. Although *S. virginicus* still appears to be important for some species, for a number of other species it appears to be of little importance (Fig. 5.12). As in the pre-wet season, in the post-wet season *A. muelleri* does not appear as an important contributor for any species.

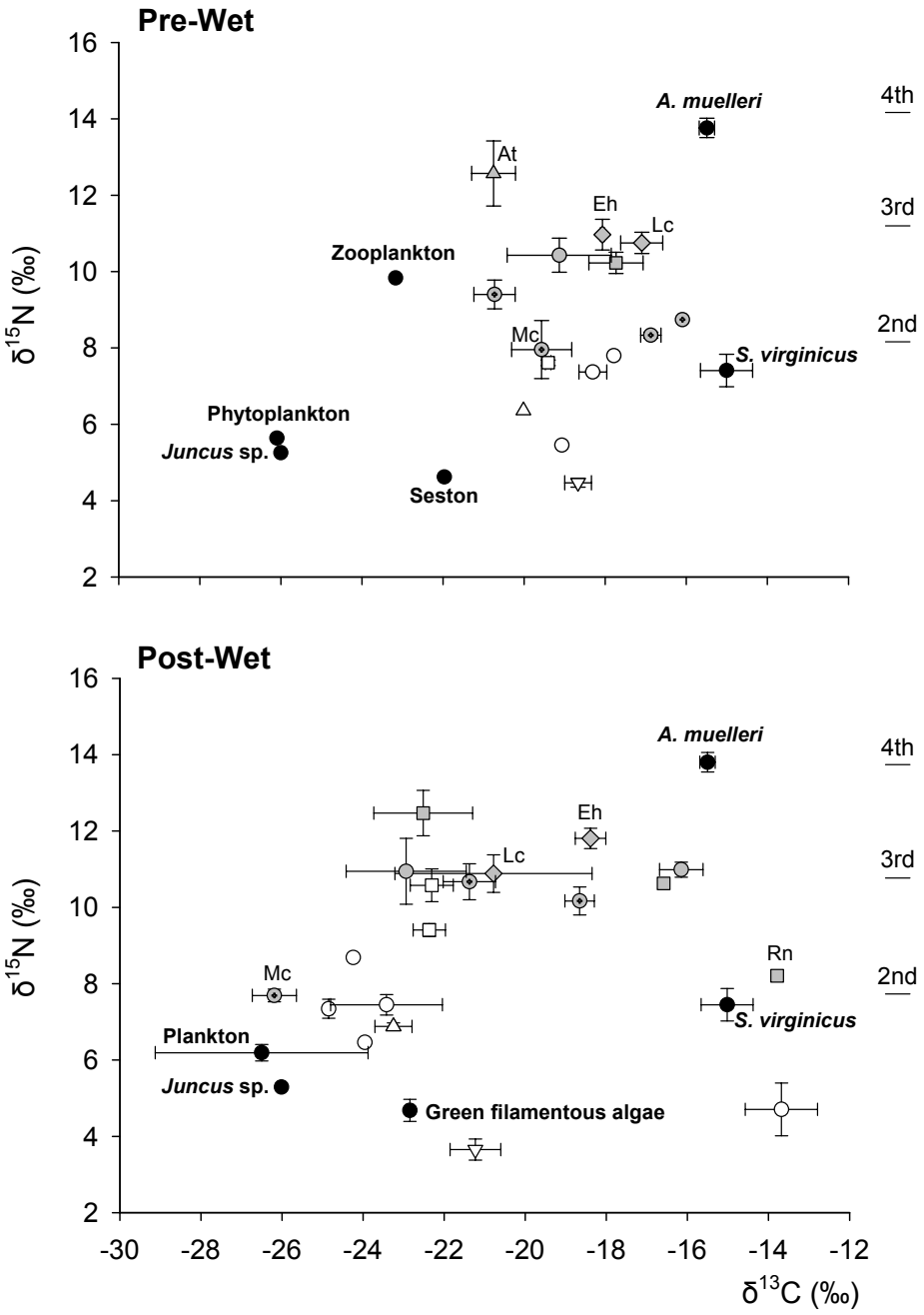

Fig. 5.12. Mean $\delta^{13}C$ and $\delta^{15}N$ (± SE) of producers (black symbols), invertebrates (white symbols) and fish (grey symbols) collected in Twelve Mile pool in the pre- and post-wet seasons. Invertebrates: ○ - insects; △ - gastropods; ▽ - *Corophium* sp. □ - decapod crustaceans. Fish: ● - herbivores; ⊙ - detritivores; ▲ - planktivores; ■ - macrobenthic carnivores; ◆- piscivores. $\delta^{15}N$ values for each trophic level are indicated to the right of each figure. Species mentioned in text are also indicated: At = *A. telkara*; Eh = *E. hawaiensis*; Lc = *L. calcarifer*; Mc = *M. cephalus*; Rn = *R. nasutus*.

Overall, the food chains at Twelve Mile Creek seem to be very short, with three or only slightly more than three trophic levels (Fig. 5.12). Even highly predatory species such as *L. calcarifer* and *E. hawaiensis* had a trophic level of only around three (Fig. 5.12). These species had $\delta^{15}N$ values similar to those of several detritivorous and herbivorous species (Fig. 5.12). Although in the pre-wet season *A. telkara* had $\delta^{15}N$ that indicate a trophic level higher than three (Fig. 5.12), this species is a planktivore and when its $\delta^{15}N$ values are compared to phytoplankton (difference of 6.9‰, corresponding to 2.3 trophic levels) and zooplankton (difference of 2.7‰, corresponding to 0.9 trophic steps), results indicate that this species has a trophic position only slightly higher than 3, a trophic level similar to that calculated based on the detritivore of lowest $\delta^{15}N$.

5.4. DISCUSSION

5.4.1. Sources of Energy

Results of this study suggest that terrestrial material is often important for aquatic communities from intermittently connected estuarine areas, and that there can be a seasonal variation in the relative importance of terrestrial and aquatic productivity for these communities. However, this importance varies from location to location, depending on the site-specific hydrological and ecological conditions.

Rainfall is crucial for the transport of terrestrial energy into aquatic systems (Junk et al. 1989, Douglas et al. 2005). However, it seems that there is a threshold where freshwater flow becomes a limiting factor for the input of terrestrial carbon into these systems. For example, for the forested areas of Munduran and Gonong of the Fitzroy

Delta, where the rainy seasons are not very intense, the negative shifts in carbon isotope composition of fish from the pre-wet to the post-wet season suggest a seasonal variation in sources carbon, with ^{13}C depleted terrestrial carbon more important after the wet season. This suggests that terrestrial material washed into the waterway during the low intensity wet season flows tended to accumulate in the pool beds, where it was incorporated into the tissues of aquatic animals. In contrast, no input of material of terrestrial origin was apparent in the shallow pool in Saltwater Creek. This difference correlates with differences in geomorphology and rainfall patterns. Saltwater Creek is at the border of the wet and dry tropics. Hence, little terrestrial material accumulates in the bed of this shallow pool due to the heavy wet season flows that effectively transport most of this material downstream. Moreover, this pool is hard bottomed with a smooth profile, lacking structural heterogeneity to trap sediment, further limiting the deposition of terrestrial material. Hence, at each location, a balance between rainfall and geomorphology appears to regulate the transport and accumulation of terrestrial material into the pools.

In Munduran and Gonong, only detritivores and macrobenthic carnivores showed a shift towards lower $\delta^{13}C$ values between the pre- and post-wet seasons, again indicating that a substantial proportion of energy for these species is based on imported terrestrial material, entering through the detritus food chain. Hence, during the pre-wet season, food webs seemed to be based mainly on benthic producers, but after the wet season the importance of C_3 terrestrial producers increased as terrestrial material was transported into the pools with flood waters. On contrary, herbivores and planktivores, which are not members of detrital food chains, had similar $\delta^{13}C$ values between seasons. A similar situation was found by Wantzen et al. (2002) for the

Pantanal wetland in Brazil, where the change in $\delta^{13}C$ was greater for detritivorous fish than for other trophic groups, and is also in agreement with Marczak et al. (2007) who, in a meta-analysis from 115 datasets from 32 studies, reported that detritivorous species were in general the most affected by the introduction of new material into a system. In contrast, in Saltwater pool, where no accumulation of terrestrial material was possible due to the heavy flows and shallow topography, despite relatively heavy shading, the food web seems to be based almost exclusively on benthic producers throughout the year.

Unlike Munduran, Gonong and Saltwater pools, which are relatively narrow and well shaded, The Lakes and Twelve Mile pool are larger and have almost no shading. While in shaded systems the waters are generally very clear because aquatic productivity is limited by the shading (Boston & Hill 1991, Hill & Dimick 2002), in larger and more open areas this regulation is reduced and aquatic producers become more important (Bunn et al. 1999, Finlay 2001, McCutchan Jr & William Jr 2002). This appeared to be the case in both Curralea and Paradise Lakes and in Twelve Mile pool, where the waters were often very green and highly productive (Johnston & Sheaves 2006a, pers. obs.), and carbon isotope composition of animals suggests a major dependence on autochthonous sources of carbon. In The Lakes, these autochthonous sources are probably composed of both benthic and planktonic primary producers. However, a lack of shallow water limits benthic productivity in Twelve Mile, meaning that planktonic producers must be the major contributors.

Curralea and Paradise Lakes also differ from Saltwater, Munduran and Gonong pools in being surrounded by dense grass meadows and suburban lawns composed of C_4 species, rather than forests dominated by C_3 species. Therefore, any substantial incorporation of terrestrial C_4 material washed in by rainfall should result in a shift in animals' $\delta^{13}C$ values from lower values in the pre-wet season to higher values in the post-wet season. However, it is difficult to draw definitive conclusions because $\delta^{13}C$ values of C_4 producers are close to those of aquatic producers. Nevertheless, this shift towards higher $\delta^{13}C$ values was observed for animals collected at The Lakes. In addition, some herbivorous and detritivorous fish species had carbon isotope composition that indicates an almost exclusive dependence on *S. virginicus* at both lakes. Therefore, although food webs in these areas are mainly based on aquatic producers, carbon from terrestrial origin is also incorporated into the aquatic organisms.

As in Munduran and Gonong, animals in Twelve Mile pool shifted from more ^{13}C enriched $\delta^{13}C$ values in the pre-wet season to more ^{13}C depleted values in the post-wet season. It is likely these changes in animals' isotope composition are a result of a greater incorporation of carbon from the ^{13}C depleted reed *Juncus* sp. in the post-wet season, since a band of submerged *Juncus* sp. develops around the water edges in the rainy season. Nevertheless, an important incorporation of carbon from the C_4 species *S. virginicus* was also detected for some species in both seasons.

In this system, the input of *S. virginicus* and C_4 pasture grasses into the aquatic food web may be amplified by the presence of cattle, which scatters faeces throughout the

area, including in the pool margins. Cattle faeces had $\delta^{15}N$ values 0.9‰ lower than the salt couch *S. virginicus,* the most abundant grass species, indicating that this is probably also the most grazed species (a $\delta^{13}C$ fractionation slightly less than -1‰ has previously been reported for herbivore faeces in relation to their diet (Sponheimer et al. 2003, Codron et al. 2005)). However, given the direction of change of animals' $\delta^{13}C$ values, this input seems to be relatively small in comparison to that of *Juncus* sp. Consequently, although in the wet season a vast meadow of C_4 grass is submerged and despite the introduction of C_4 material in the form of cattle faeces into the pool, energy from the narrow fringe of ^{13}C depleted C_3 reeds *Juncus* sp. bordering the pool edges seems to have a greater contribution to aquatic animals in Twelve Mile pool.

Previous studies have documented that herbivorous insects, when given a choice, prefer to consume C_3 to C_4 plant species (e.g. Scheirs et al. 2001, Clapcott & Bunn 2003). A similar situation could be true for aquatic invertebrates, which would explain the detected incorporation of C_4 plants in The Lakes, where C_3 plants occur in very low densities, and explain the lower importance of C_4 plants in Twelve Mile creek, where carbon of C_3 origin is available.

Taken together, these results indicate that food webs in intermittently connected estuarine areas in Tropical Australia can function in accordance with to the FPC or the RPM, with the dominant process depending on a complex interaction between local environmental conditions and season. Hence, the same system can rely mostly on transported energy during the relatively short rainy season, and on locally produced energy on the rest of the year. For these systems, a model taking into consideration the seasonal variations in sources of energy in these areas would be more appropriate than either the FPC or RPM.

Although several studies have found a significant and, in times, crucial input of terrestrial detritus into aquatic food webs in forest freshwater systems (e.g. France & Steedman 1996, France 1997, Herwig et al. 2004), this is the first study to document a similar phenomena for intermittently connected estuarine areas. This input represents an ecotonal coupling between the terrestrial environment and aquatic animals in estuarine wetlands, highlighting the tight linkages between these systems. Understanding these linkages is crucial for understanding the importance of environmental freshwater flows to estuarine ecosystems (Livingston 1997) and needs to be taken into account when planning projects that involve alteration of hydrology regimes of rivers and creeks, and the modification of wetlands and their adjacent habitats.

5.4.2. Trophic Structure

Fish species richness in the estuarine wetland pools considered in this study is relatively low. Thirty species have been reported for Curralea Lake and 33 for Paradise Lake (Johnston et al. 2005, Johnston & Sheaves 2006a, b), while in the Fitzroy catchment 25 species have been reported for Munduran, 22 for Gonong and 22 for Twelve Mile Creek (Sheaves et al. submitted). Despite that no study has focused on the fish fauna of Saltwater Creek, all the eight species observed in the shallow, clear waters of the pool were collected. Although the numbers of species are low compared to open tropical and subtropical estuaries within the same biogeographic region (91-128 species; Robertson & Blaber 1992), intermittently open estuarine areas generally have lower fish species diversities than permanently open areas (Pollard

1994, Harrison & Whitfield 2006). Nevertheless, several species of economical and recreational importance were found to use these habitats including the barramundi *L. calcarifer*, the mangrove jack *L. argentimaculatus,* eels *Anguilla* spp. and the giant herring *E. hawaiensis.*

These low diversity pools differed in both dominant sources of energy and trophic structure. The number of trophic levels varied between 3.2 for Gonong pool to 4 for Paradise Lake and Munduran pool. This maximum trophic length of four trophic levels is similar to that found for open estuarine areas in North Queensland (see Chapter 4), and corresponds to the maximum number of trophic levels found in most natural systems (Pimm 2002), both terrestrial and aquatic. Several factors are likely to have a role in determining trophic length and food web complexity in intermittently connected areas, including species composition, colonization and extinction history (Post 2002a, Brose et al. 2004), resource availability (Pimm 2002, Thompson & Townsend 2005), body size of the different components of the food web (Cohen et al. 1993, Cohen et al. 2003, Layman et al. 2005), and type and level of environmental disturbances (Marks et al. 2000, Ruetz III et al. 2005, Spiller & Schoener 2007).

For the particular areas considered in this study, species composition is directly limited by the extreme variations in physical and chemical conditions of the water (Sheaves et al. in review), which can only be tolerated by a small number of species (Griffiths 2001, Ray 2005). On the other hand, the relative isolation of these pools limits animals' movements between habitats, thereby limiting colonization processes and hence the complexity of food webs. Moreover, these pools are relatively small in area extent, and ecosystem size has been found to limit food chain length, with larger areas supporting longer food chains (Cohen & Newman 1988, Post et al. 2000, Brose et al. 2004,

Thompson & Townsend 2005). However, this did not seem to be the case over the range of pools analysed in this study, as for instance even the relatively small Munduran pool had a trophic length similar to that detected in open estuarine systems analysed in Chapter 4.

At the level of individual pools, a unique set of factors will limit trophic complexity and food chain length, depending on the system-specific ecological conditions. For example, the food web in Saltwater pool was very simple, with a short trophic length, probably as a result of a low availability of food, as planktonic productivity in this area is very low (pers. obs), and the periods of heavy rain do not allow a deposition of detritus of terrestrial origin into the pool. Therefore, only a simple food web based on epilithic algae could develop, with short, linear food chains and little complexity, where a strong trophic pathway could easily be traced through two trophic links.

In contrast, the short trophic length in Curralea Lake was probably not a result of a shortage of nutrients, as the waters are very productive throughout the year (Johnston & Sheaves 2006a). Instead, short food chain length in this location probably reflects the specifics of the interplay between extinction and re-colonization factors (Barbour & Brown 1974, Magnuson et al. 1998). Curralea Lake has a more limited connection with Ross Creek than Paradise Lake, where a longer trophic length was detected, with four trophic levels. Curralea Lake often suffers anoxia events due to the resulting limited water exchange, leading to regular fish kills which significantly reduce the number of species (Johnston & Sheaves 2006a, b). Hence, extinction and colonization history is likely to be the main factor limiting trophic length in this system.

Trophic length in Twelve Mile pool was also very short, and stable isotope results indicate that even highly predatory species such as the barramundi and the giant herring fed directly on primary consumers, resulting in a trophic level of only ~3. This is in agreement with Sheaves & Johnston (2006a) who found that the detritivore *N. erebi* was the preferred prey for *L. calcarifer* in Twelve Mile pool, comprising ~80% of the prey consumed.

In this pool, a vast area of wetland vegetation is inundated during the wet season, supporting a diversity of invertebrates such as shrimps, insects and snails (unpublished data), and allowing fish to move into the submerged vegetation and feed on a varied diet. Hence, fish showed well separated $\delta^{13}C$, suggesting that a wide range of food sources was available at this time, and that different species specialised in feeding on different sources. This movement of fish to feed on invertebrates inhabiting vegetation areas after the rise of the waters has been described for other systems (e.g. Dudgeon 1983, Wantzen et al. 2002, Balcombe et al. 2005).

For most of the year however, the area of submerged vegetation is greatly reduced and, with it, the invertebrate community abundance (unpublished data). At that time, the low diversity and availability of food sources seems to lead to high levels of omnivory and diet overlap between fish species, which was reflected in the narrow range of $\delta^{13}C$ values of fish collected in the pre-wet season. Sheaves & Johnston (2006d) also found that individuals of several fish species collected in Twelve Mile pool were in poor condition before the wet season, and in better condition after the wet season, adding weight to the idea that more energy was available after the wet season.

In contrast to all other areas, trophic length in Gonong pool was longer after the wet season. In this case, this was possibly a result of the hydrologic disturbance caused by flooding, which allowed the movement of both predators and prey between habitats, altering the fish species assemblage and resulting in an increase in trophic length. However, within a system, trophic length can vary with changes in trophic structure caused by the introduction or removal of top or intermediate predators, variation in the incidence of omnivory by top predators, and changes in trophic position of intermediate predators (Post et al. 2007). Because a panoply of factors can mediate the occurrence of any of these situations, especially in small intermittently connected areas such as those considered in this study, it is very difficult to be certain about the factors controlling trophic length in these systems.

Animal movement

As well as providing information on sources of energy and trophic pathways, stable isotope composition of animals also provided evidence of animal movement. For example, in the pre-wet season in Munduran pool, when inputs from stream flow had been absent for ~10 months, fish formed two groups of distinct $\delta^{13}C$. One group had $\delta^{13}C$ values much higher than would be expected given the common producers present in the area. These ^{13}C enriched animals had values that indicate a major dependence on C_4 plants such as the salt couch *S. virginicus* or other pasture grasses. Since there had been no recent inflow from upstream, and cattle grazing areas dominated by ^{13}C enriched C_4 plants are present downstream of Munduran pool, it appears likely that those fish had recently moved from downstream areas. Differences between groups

were not a result of differences in diet between species since for two species, the mullet *L. subviridis* and the northern whiting *Sillago sihama*, different individuals were found to have very distinct $\delta^{13}C$ values.

As in Munduran, $\delta^{13}C$ values of animals from Saltwater pool also suggested animal movement, with the low $\delta^{13}C$ value of the lone *L. calcarifer* suggesting recent movement from upstream freshwater reaches, where aquatic producers are more depleted in ^{13}C than in marine areas (France 1995b), or from an area with a greater input of ^{13}C depleted material of terrestrial origin. Similarly, in Twelve Mile pool, while the two *L. calcarifer* individuals collected before the wet season had close $\delta^{13}C$, the three individuals collected after the wet season showed well separated $\delta^{13}C$ values (-24.6, -21.3 and -16.3‰). More variable $\delta^{3}C$ values are expected after connections periods, and are an indication of a recent movement from other areas.

5.4.3. Conclusion

Results from this study suggest that, as in freshwater systems (Douglas et al. 2005), the hydrology regime is a major factor controlling the sources of energy in intermittently connected estuarine areas, controlling the amount of terrestrial material available to aquatic animals throughout the year, and allowing the presence of an energetic connectivity between the terrestrial and aquatic environments. The resulting seasonal input of material of terrestrial origin can in turn be of a great importance in regulating trophic structure and dynamics in these areas. Results also indicate that, within the same system, aquatic food webs may rely alternatively on autochthonous and

allochthonous sources of energy, depending on the season, and that a combination of the Flood Pulse Concept (Junk et al. 1989) and the Riverine Productivity Model (Thorp & Delong 1994) is needed to account for spatio-temporal variations in energetic processes taking place in these areas.

Chapter 6
General Discussion

Tropical estuarine wetlands such as mangroves and salt marshes are highly productive (Qasim & Wafar 1990) and have traditionally been considered to be exporters of organic matter to adjacent coastal and offshore areas (Teal 1962, Odum 1968). However, over the last two decades a number of studies have suggested that terrestrial wetland productivity is not as important as once thought, and a debate on the main sources of energy fueling estuarine food webs has emerged. While some studies indicate that terrestrial wetland producers are important in providing energy for estuarine communities, others suggest that the contribution of such producers is limited and that aquatic productivity is more important (see review by Lee 1995, Weinsten & Kreeger 2000). The objective of this thesis was to assist in resolving this contention for estuarine systems in Tropical Australia, and to analyse the mechanisms of energy transfer from primary producers to top consumers. In this Chapter, the main findings of this study are summarised and discussed. Directions for future research and management implications are also presented.

6.1. MAIN FINDINGS OF THIS STUDY

Importance of terrestrial wetland carbon for estuarine food webs

Identifying the sources of energy fuelling estuarine communities is crucial for understanding the organization and functioning of food webs in these areas. Although several studies have focused on the question of sources of energy (e.g. Loneragan et al. 1997, Bouillon et al. 2002a, Bouillon et al. 2004b), to date no study has provided evidence that unambiguously supports a general model describing the importance of imported and local sources of energy for estuarine communities, leaving the debate unresolved. Results from the present study indicate that terrestrial wetland productivity is incorporated into estuarine food webs, but this importance varies both temporarily and spatially, depending on the biotic and abiotic conditions of the area.

For a certain area, the incorporation of terrestrial wetland carbon into aquatic food webs is primarily dependent on the relative availability of carbon of terrestrial and aquatic origin (Polis et al. 1997, Bouillon et al. 2004b) (Chapters 4 and 5; Figure 6.1). Given the nature of the factors regulating the input of terrestrial and aquatic productivity into estuarine food webs, sources of energy are more constant in open areas such as the mouths of rivers (see Chapter 4), and more variable in relatively isolated areas such as the upstream reaches of estuaries and intermittently connected estuarine floodplain pools (see Chapter 5). This is most likely because open areas are subjected to the regular tidal mixing, while in more upstream areas there can be a greater temporal variability in ecological conditions, including salinity, connectivity and productivity.

On one hand, the availability of terrestrial carbon seems to be directly dependent on the type and extent of terrestrial wetland vegetation (e.g. Polis et al. 1997, Wafar et al. 1997, Odum 2000) (Chapters 4 and 5), which varies between systems and along the estuarine gradient, and is dependent on factors such as hydrology, landscape, topography and geomorphology of the area (Lee 1995, Polis et al. 1997, Twilley 1998, Odum 2000, Teal & Howes 2000) (Fig. 6.1). For example, among the open estuarine areas analysed in Chapter 4, there seemed to be a greater incorporation of ^{13}C depleted mangrove carbon at Deluge Inlet and Victoria Creek, the estuaries with the greatest areas of mangrove forest, than at Half Moon and Blacksoil Creeks, where mangrove forests, as well as any other wetland vegetation, were less extensive.

On the other hand, the availability of autochthonous energy is regulated by a different set of physical and biological factors (Fig. 6.1). Aquatic productivity is primarily dependent on the availability of light (Boston & Hill 1991, Hill & Dimick 2002), which in the most upstream reaches of estuaries can be mainly effected by shading from the forest canopy (Chapter 5). Hence, ecosystem size and shape are important factors influencing aquatic productivity in these areas, by directly controlling the relative proportion of open and shaded habitats in forest areas (Chapter 5). Moreover, factors such as nutrient availability (Flindt et al. 1999), turbidity levels and water depth (Murphy 1962, Krause-Jensen & Sand-Jensen 1998) can also be important in regulating photosynthetic levels, and substrate type may also affect the community of benthic producers (Rizzo & Wetze 1985) (Chapter 5; Fig. 6.1).

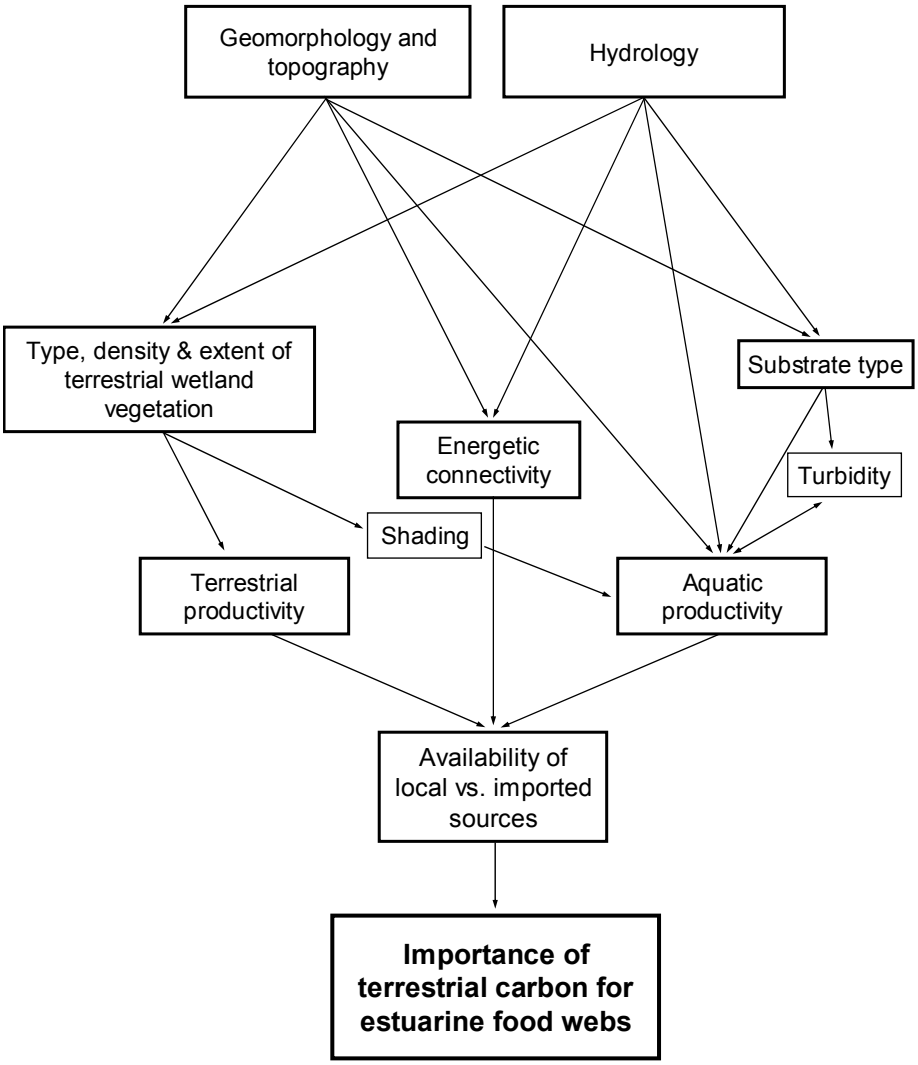

Fig. 6.1. Simplified conceptual model on the physical and ecological factors regulating the importance of terrestrial wetland producers for estuarine food webs in Tropical Australia.

However, the availability of terrestrial vs. aquatic carbon for estuarine communities is dependent not only on the productivity of the different habitats, but also on the energetic connectivity between the terrestrial and aquatic environments (Fig. 6.1). This connectivity is in turn regulated by several factors such as the spatial arrangement of

habitats, and hydrologic, geomorphologic and topographic characteristics of the area (Chapters 4 and 5; Fig. 6.1), which can operate at different temporal and spatial scales. This is well illustrated in Chapter 5 where a greater incorporation of carbon of terrestrial origin by aquatic animals was detected after the wet season in Munduran and Gonong pools, i.e. after the flooding waters provided a vehicle for connectivity between terrestrial and aquatic habitats, transporting carbon of terrestrial origin into the estuarine pools. In contrast, the heavy wet season did not allow the deposition of terrestrial material in Saltwater pool. This flushing of terrestrial material was further enhanced by the topography of Saltwater pool, which is unfavorable for the deposition of terrestrial material, highlighting the importance of the interaction between the effects of environmental flows and topography (Polis et al. 1997, Witman et al. 2004).

Animal movement can also be an important vector of energetic connectivity between areas (see review by Hobson 1999, and Rubenstein & Hobson 2004). For example, a percentage of fish collected in the pre-wet season in the forested area of Munduran (Chapter 4), had carbon isotope compositions suggesting recent migration from downstream areas surrounded by C_4 pasture areas (see Fig. 5.9). This energetic coupling between systems based on animal movement has been documented in several studies (e.g. Maruyama et al. 2001, Harrod et al. 2005), and can be of great significance for food webs in the receiving systems, allowing the input of energy that can be crucial for the functioning and dynamics of local food webs (Polis et al. 1996, Winemiller & Jepsen 1998). This dependence on donated nutrients underlines the importance of maintaining the natural patterns of physical and energetic connectivity between different habitats in these highly dynamic systems, as these can be involved

in energetic processes crucial for the stability of local food webs and persistence of estuarine communities through time.

Food web structure

While it is vital to identify the ultimate sources of energy supporting estuarine food webs, it is also important to understand the processes of energy flow and the main trophic pathways in these systems. Trophic length, or the number of energy transfers from primary producers to top consumers, is a fundamental food web parameter (Pimm 2002). In this study, all four open estuarine areas considered (Chapter 4) had similar trophic lengths, with approximately 4 levels, suggesting that trophic length is relatively constant for these areas. However, further studies need to be conducted over a wider range of systems in order to confirm this hypothesis. If however such constancy is verified, the analysis of trophic length may become a useful tool to characterise estuarine food webs in Tropical Australia and can potentially be used to describe ecosystem health in these areas.

It was also clear that omnivory is widespread in estuarine systems (Chapters 2, 3, 4 and 5), and that the diet of several fish and invertebrates can change substantially according to the environmental conditions (Chapters 2, 3 and 5). Omnivory is common in terrestrial and marine ecosystems (Diehl 1993, McCann & Hastings 1997, Williams & Martinez 2000) and has been found to increase the stability of food webs (Fagan 1997, McCann & Hastings 1997, McCann et al. 1998). In the open estuarine systems analysed in Chapter 4, greater levels of omnivory were found at Deluge Inlet, Half

Moon Creek and Blacksoil Creek food webs than at the agriculture impacted Victoria Creek. Additionally, Victoria Creek was also the only system where different trophic pathways did not seem to merge at high trophic levels, suggesting low levels of diet overlap between species. The low levels of omnivory and diet overlap at this system may be a result of the replacement of great extensions of natural wetland by sugarcane plantations, and hence be an indicative of a significant anthropogenic impact. Therefore, there seems to be a great potential to investigate the use of food web parameters such as trophic length, level of omnivory and diet overlap in the description and classification of ecosystem health.

In contrast to the situation in the open estuarine areas (Chapter 4), trophic length differed substantially between intermittently connected areas (Chapters 2 and 5), and even between seasons within the same system (Chapter 5). In general, intermittently connected areas had shorter and more variable trophic lengths than open estuarine areas, with 3.3 to 4 trophic levels. This agrees with the review by Vander Zanden & Fetzer (2007) who concluded that streams generally have shorter trophic lengths (mean ~3.5 trophic levels) than marine and lake ecosystems (mean ~4.0 trophic levels). Since the intermittently connected estuarine areas considered in this study are more similar in shape, size and frequency and type of disturbance to streams than to lake or marine areas, it is likely that these are also similar in trophic organisation to streams. Food chain length is also more variable in stream areas than in more stable marine and lake areas (Vander Zanden & Fetzer 2007), a pattern also seen in the present study, that probably reflects the greater environmental variability in these areas when compared to marine and lake systems.

Other aspects of trophic organization such as trophic pathways and levels of omnivory also differed between systems in intermittently connected areas (Chapters 2 and 5) and, in some cases, between seasons within a system (Chapter 5). This variability was probably a result of seasonality and of differences in ecological conditions between systems. Differences in trophic structure are often a result of differences in species composition (Power et al. 1995), which in turn depends on species-specific toleration to fluctuations in environmental conditions such as salinity and temperature (Griffiths 2001, Ray 2005) and on site-specific colonisation and extinction histories (Barbour & Brown 1974, Magnuson et al. 1998) (Chapter 5; Fig. 6.2). In the Australian Dry Tropics, this is directly regulated by seasonality in hydrologic conditions (Chapter 5), which regulates the movement of energy and animals between habitats. Colonisation and extinction is also dependent on factors such as habitat type and availability, and the availability of food in the different food web compartments (Fig. 6.2). All these factors interact in intricate ways to produce complex outcomes.

It is also likely that a different set of factors will determine the structure of the food web in each system, depending on the site-specific ecological conditions. This complexity makes it difficult to ascertain the exact processes controlling food web structure and complexity in these systems. There is therefore a great need to develop and implement further food web studies in different estuarine systems, to help clarify the general mechanisms involved in regulating trophic structure in these areas.

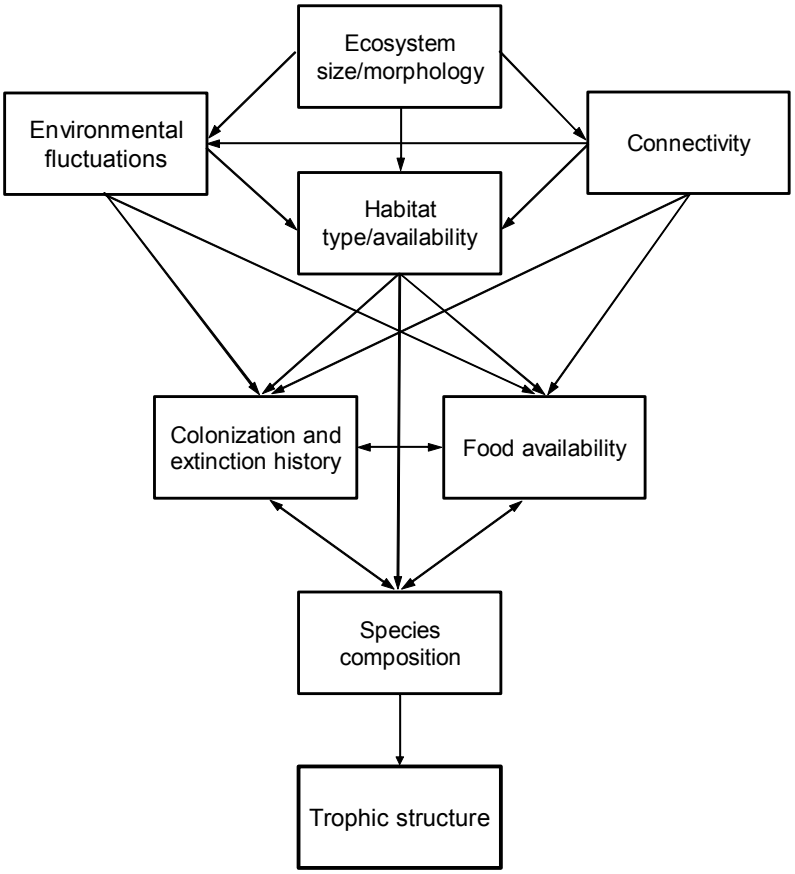

Fig. 6.2. Summary model on the factors influencing food web structure in estuarine areas. Arrows indicate the directions of the influence.

6.2. MANAGEMENT IMPLICATIONS

This study suggests that there is an incorporation of terrestrial wetland carbon into adjacent aquatic food webs in estuarine systems, and that such incorporation can affect the structure and dynamics of aquatic food webs. The study also indicates that, in agreement with previous studies (Pringle 2001, Bunn & Arthington 2002, Douglas et al. 2005), hydrologic connectivity is a key factor in regulating food web structure and

dynamics in these systems. It is therefore important to maintain the hydrologic regimes as close to the natural conditions as possible, in order to maintain the ecological condition in these areas.

Given the connectivity between the different areas, from aquatic to terrestrial habitats, from the most upstream reaches to the estuary mouths, it is clear that it is necessary to protect the whole assemblage of habitats in order to preserve the trophic functioning of the different components as close to natural as possible. This holistic approach to conservation, involving the protection of different habitats, has been previously recognized as necessary for the conservation of marine communities (Stevens 2002). Only then can the ecological health of these highly dynamic systems be maximised, and with it the economical (Costanza et al. 1997) and health (McMichael 1997) benefits provided.

6.3. DIRECTIONS FOR FUTURE RESEARCH

Stable isotopic analysis has been increasingly used in the study of food webs over the last two decades (Schindler & Lubetkin 2004), with the intent to identify the main sources of energy for animal communities (e.g. Lugendo et al. 2006), to quantify the transport of material through food webs (e.g. Hadwen & Bunn 2004), or simply to describe a species' diet (e.g. Waltham & Connolly 2006). In most studies, stable isotopic data is analysed qualitatively. In general, this involves the graphical comparison of stable isotope values of consumers with those of potential food sources (e.g. Herwig et al. 2004, Richoux & Froneman 2007).

Nevertheless, some quantitative approaches have been developed, including linear mixing models based on mass balance equations (Schwarcz 1991, Phillips 2001), concentration dependent mixing models (Phillips & Koch 2002) and more recently the IsoSource mixing model (Phillips & Gregg 2003), which has been found to be useful in cases where multiple potential food sources are present (e.g. Connolly et al. 2005b, Hall-Aspland et al. 2005, Benstead et al. 2006). However, these models have a number of limitations, which arise from the frequent presence of a great number of potential food sources, from similarities in isotope composition between potential sources, from the actual relevance of the sources selected, from uncertainties in trophic fractionation, etc. (Phillips 2001, Phillips & Gregg 2001, 2003), and only in exceptional circumstances can provide accurate results. This is illustrated in Chapters 2 and 3 where in several cases IsoSource results led to inconclusive or implausible solutions, as well as in Chapter 3, where great differences in IsoSource solutions resulted when considering different trophic levels. These differences also exemplify the potential effect of the natural variability in isotopic fractionation, which adds up with each trophic step.

Isotope tracers have also been used to detect the incorporation and study the transport of material through food webs (e.g. Hershey et al. 1993, Hall 1995, Winning et al. 1999, Herman et al. 2000). While this methodology can be useful to study trophic processes in experimental units or in parts of a system, it is not very useful in the study of large, highly dynamic systems such as estuaries, where tides and currents constantly mix and dilute material from different origins. Moreover, this technique can also be difficult to apply to large and relatively mobile species such as fish. Hence, it is not very useful to trace trophic pathways through to top consumers or to describe food webs in detail.

This was the first study to use CART models in the analysis of stable isotope data. This innovative and objective approach proved to be very useful in the identification of the main factors affecting the isotopic composition of consumers (Chapters 3 and 5), and in the characterisation of changes in fish isotope composition with season (Chapter 5). There is therefore a great scope for the use of CART analysis to answer a range of ecologic questions based on stable isotope analysis. Nevertheless, there is still a great need to develop better, more quantitative approaches to the analysis of stable isotope data.

Finally, further studies on sources of energy and food web organisation in tropical estuarine systems need to be conducted to improve our understanding on how these systems function and to help predict and mitigate the impacts of human activities and Climate Change over estuarine communities. In fact, in a review on global patterns of aquatic food chain length by Vander Zanden & Fetzer (2007), it was clear that the number of relatively detailed aquatic food web studies is very limited for tropical systems. Only ~8% of the studies available were conducted in tropical areas, and of these only six (32%) correspond to marine systems, which include not only estuarine areas, but also coastal shelf and pelagic/open ocean. This illustrates the great void of information on energetic processes taking place in tropical estuarine systems around the world, and stresses the importance of this study in contributing for the knowledge on sources of energy and food web structure and dynamics in these areas.

Chapter 7

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