Assessment of the importance of different near-shore marine habitats to important fishery species in Victoria using standardised survey methods, and in temperate and sub-tropical Australia using stable isotope analysis

Jeremy Hindell, Gregory Jenkins, Rod Connolly and Glenn Hyndes

Project No. 2001/036

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October 2004

2001/036

ISBN 1 74146 474 9

Preferred way to cite:
Hindell JS, Jenkins GP, Connolly RM and Hyndes G (2004) Assessment of the importance of different near-shore marine habitats to important fishery species in Victoria using standardised survey methods, and in temperate and sub-tropical Australia using stable isotope analysis. Final report to Fisheries Research and Development Corporation Project No. 2001/036. Primary Industries Research Victoria, Queenscliff.

Published by Primary Industries Research Victoria, Marine and Freshwater Systems, Department of Primary Industries, Queenscliff, Victoria, 3225.

Formatted/designed by Primary Industries Research Victoria Queenscliff

Printed by PIRVic Queenscliff, Victoria

Table of Contents

LIST OF TABLES

LIST OF FIGURES

NON-TECHNICAL SUMMARY

2001/036 Title: Assessment of the importance of different near-shore marine habitats to important fishery species in Victoria using standardised survey methods, and in temperate and sub-tropical Australia using stable isotope analysis

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Objectives:

1. To increase our understanding of fisheries/habitat links using a combination of standardised survey methods in Victoria, and isotope analyses across southern Australia and Queensland
2. To identify the importance of different nearshore habitats for important fish species from recruitment to older-life stages, for individual habitats at broad scales and habitat mosaics at finer scales
3. To improve the quality of data derived from isotope analyses by including a greater range of potential sources of primary production
4. To understand the transfer of primary production from important habitats to food chains of fish that occur outside that habitat, and also the sources of primary production for fish inhabiting habitat mosaics

5. To integrate existing near-shore habitat data-sets with detailed descriptions of fish/habitat associations in a spatial information system (GIS) that can be easily accessed by a variety of user groups

Non Technical Summary:

OUTCOMES ACHIEVED

Results from the present study will be valuable in the future detection of environmental perturbations, providing a baseline data set against which disturbance effects can be assessed. Information on habitat use, and how multiple habitats interact with each other, will put managers in a stronger position to argue for the preservation of important nursery habitat. Results from this project may also be important in advising on the appropriateness of marine park designs to ensure, among other things, fisheries sustainability.

The first part of this project was a basic survey of fish use of intertidal habitats such as mangroves, mudflats and saltmarshes, which previously had hardly been considered in temperate Australian coastal waters.

Mangroves (*Avicennia marina*) and mudflats were used by at least 41 species of fish. Juvenile stages of 41% of the species were sampled and economic species were common. Mangrove habitat in temperate Australian waters supports a richer juvenile fish assemblage than adjacent mudflats, but there is little difference between habitats for the subadult/adult assemblage. Ultimately, the 'value' of mangrove habitats to fishes depends strongly on the time and place.

Saltmarshes were difficult to sample because of unpredictable amounts of water cover. Saltmarsh flats were generally only covered with water during low-pressure weather systems. Most fish caught in this habitat were not of commercial value. Water temperature, salinity, depth or barometric pressure did not explain variability in the number of fish species present or fish abundance. Fish species in the saltmarsh flats also live in other habitats such as seagrass, and the observed patterns of habitat use seemed to partly relate to feeding behaviour.

The second part of the fish-habitat survey work aimed to see how the use of habitats by fish changed within different parts of the habitat, and also with respect to the location of other habitats.

A combination of experimental and survey methods were used to see whether fish use of mangrove habitat varied between the mudflats, the edge of the forest, and the interior of the forest. Numbers of fish were lower on the mudflats than in the forest or along the edge; number of fish species was greater along mangrove edges than the forest and mudflats; weight of fish was greater at the edge and mudflat than in the forest. Predation by other fish was did not appear to influence this pattern. Differences in the numbers and types of fish among these zones suggest that the number of fish species may increase where habitat becomes more patchy (as can happen when habitat is lost), as this creates relatively more habitat "edge". However, this could have a negative affect on abundances and number of species of resident mangrove fishes.

We also looked at how the numbers and types of fish changed in either seagrass or mangrove habitat with respect to distance from each other. Numbers and variety of fish in seagrasses and mangroves went up or down with the distance between these habitats, depending on the fish species in question. This suggests the need to consider habitats as elements of the wider landscape. Fish using mangroves appeared to respond more strongly to proximity to seagrass than the response shown by fish using seagrass to proximity to mangroves.

Assessing the importance of near-shore marine plants to the nutrition of fisheries species in temperate and sub-tropical Australia using stable isotope analysis

Stable isotope analyses are a novel method of quantifying the structure of coastal food webs, relying on different food sources having distinct natural isotope abundances that can be used to trace the source of production through the food chain. The use of stable isotopes is based on the concept that 'you are what you eat'. In this study we used mainly carbon and nitrogen isotopes, although some sulfur analyses were also done. Stable isotope signatures of carbon (and sulfur) change little through different levels of a food chain, so the 'signatures' in a high level consumer (e.g. fish) will be similar to those of the plants at the bottom of their food chain (e.g. seagrass). Nitrogen isotopes change among trophic levels as the lighter isotope is lost through metabolism, leading to differences in nitrogen signatures of between 3 and 5 units per trophic level.

The stable isotope studies were done across southern Australia so that we could better understand whether similar fisheries species were supported by alternative sources (plants) in different places. Analyses were initially (first summer and winter) done separately for each State. In the second (and last) summer we coordinated our sampling and analyses to focus attention on assessing the base for nutritional support of a single fisheries species – King George whiting.

In Victoria, 20 species of commercially and/or recreationally valuable fish were sampled. Values of $\delta^{13}C$ and $\delta^{15}N$ varied little between times of the year. The feasibility source modelling failed to show particularly strong contributions to fisheries species by a single source. The mangrove-saltmarsh complex contributed very low proportions (generally less than 10%) to fish nutrition, but the other sources generally contributed between 13 and 17 %.

In WA, a range of primary producers contributed to the production of benthic invertebrates that constitute major prey for fisheries species. The contribution of primary producers varied among invertebrate groups, indicating that the dependence of certain fish species on particular primary producers will depend on their main prey. Since the source of production varied considerably among invertebrate-prey groups, the flow-on of those sources to fish is also likely to be variable. Those fish that mainly consume amphipods will have a greater reliance on saltmarsh vegetation, whereas those consuming shrimp and crabs will have a greater dependence on seagrasses and the green algae *Cladophora*.

In South Australia, there was a very strong reliance on foodwebs based on seagrass (e.g. juvenile King George whiting, *Sillaginodes punctata*, blue swimmer crab, *Portunus pelagicus*). A surprising result was the reliance on seagrass material by yellowfin whiting (*Sillago schomburgkii*), which spends most time over other habitats.

Queensland work confirmed the importance of seagrass as the basis of nutrition in the inshore waters of Moreton Bay for 2 key crab species (blue swimmer crab, *Portunus pelagicus*, and mud crab, *Scylla serrata*). These results mean that a renewed emphasis can be placed on management for the protection of seagrass meadows, based on their role in the feeding ecology of fisheries species. Additional trials using sulfur isotopes were run in Queensland. Sulfur was more effective than carbon and nitrogen in distinguishing the importance of different plant and algae sources in fisheries foodwebs.

The occurrence of King George whiting across southern Australia afforded a unique opportunity to assess the base for nutritional support of a fisheries species across continental scales. In WA, whiting nutrition was supported most by benthic microalgae and green algae. In SA, carbon and sulfur analyses showed that *Heterozostera* and *Heterozostera* epiphytes were the principal sources. In Victoria, carbon and carbon + sulfur modelling both showed that *Heterozostera* was the principal base for nutritional support. Across southern Australia the base for nutritional support of a fisheries species depends strongly on the

regions from which the fish was caught, and sulfur isotopes are a useful method of elucidating the most important source from a pool, which, based on carbon isotopes, is inseparable.

KEYWORDS: Mangrove, mudflat, saltmarshes, fish, zonation, landscape, seagrass, stable isotope, base for nutritional support, carbon and sulphur stable isotopes, commercial

Acknowledgments

This research would not have been possible without generous funding from the Fisheries Research and Development Corporation (FRDC 2001/036) and Fisheries Victoria. Staff listed in Appendix 2 provided valuable support. Earlier versions of this report were improved by comments from anonymous reviewers and staff listed in Appendix 2. Nathan Waltham from Gold Coast City Council ran the final season's mud crab survey in Queensland. This work was done using the facilities at Marine and Freshwater Systems (DPI), Griffith University and Edith Cowan University.

FINAL REPORT

01/036 Assessment of the importance of different near-shore marine habitats to important fishery species in Victoria using standardised survey methods, and in temperate and sub-tropical Australia using stable isotope analysis

Background

This is a collaborative study between Drs G. Jenkins and J. Hindell, and Mr A. Longmore (Vic), Dr G. Hyndes (WA), and Dr R. Connolly (Qld). This project complements a study by Dr G. Skilleter and Dr N. Loneragan (application 2001/023: "Spatial arrangement of estuarine and coastal habitats and the implications for fisheries production and diversity"). Although the overall study essentially encompasses discrete studies for each State, the joint application allows for a more cost-effective and targeted study. The study can be divided into two main components: (1) an intensive quantitative study of fish focusing on economically important fishes and their habitat requirements in Victoria, including broad-scale and fine-scale habitat mosaic components; and (2) a stable isotope study to determine the source of production for important fish across the entire southern Australian coast.

HABITAT REQUIREMENTS

Both the Victorian Fisheries Act (1995) and the Commonwealth Environment Protection Act (1999) are based on the principles of Ecologically Sustainable Development (ESD). To apply the principles of ESD effectively we need much better knowledge than we currently have of those habitats that are critical for the long-term survival of fish. This part of the project will be restricted to Victoria, where, to date, our understanding of fish/habitat links has been mainly restricted to one habitat - seagrass, at one particular life stage - juveniles (Edgar & Shaw 1995a, Jenkins et al. 1997b). There is a growing consensus amongst fisheries scientists that alternative marine habitats, including mangroves, algal beds and saltmarshes, may also be important nursery habitats for commercially important marine fishes. An example of this is the finding that shallow reef-algal habitats may be equally as important to juvenile King George whiting as seagrass (Jenkins & Wheatley 1998). Information on the importance of mangrove habitats comes entirely from tropical environments (Robertson & Duke 1987, Sheaves 1992, Laegdsgaard & Johnson 1995); information on saltmarshes as nursery areas in Australia is very limited, especially in temperate waters (Connolly et al. 1997). The importance of alternative habitats as nursery areas for juvenile fish in Victoria has received very little attention and further research is urgently required. Information gained will be relevant to similar habitats across southern Australia and therefore the usefulness of the results will extend beyond Victoria.

In parallel with the study in Victoria, similar sampling will be done in Queensland as part of the Skilleter and Loneragan project (FRDC 2001/023). By using standardised sampling gear and methods we will allow one of the first rigorous comparisons of direct habitat use by important fishes in temperate and sub-tropical waters.

Apart from their role as habitat for juveniles, coastal habitats can be important for other life stages of fisheries species. Very few marine fishes, and none of commercial importance along the southern

Australian coast, remain in a single habitat for their entire life (Kailola et al. 1993). Depending on the age of the fish and local environmental conditions, the importance of different habitats as spawning sites and foraging habitats, and as refuge from environmental and biological perturbations, will vary (Lincoln Smith & Jones 1995). Our understanding of how commercially important fish use different habitats as they grow and age, however, is generally poor.

Apart from broad-scale considerations of habitat utilisation, there is increasing realisation that mixed patches of habitats ("habitat mosaics") may have different properties in supporting fish populations to individual habitat patches. At present, there is almost no information about the importance of the particular arrangement of the different patches of habitat within different mosaics on the abundance and diversity of finfish and crustacean communities. For example, it is unclear whether an area of seagrass adjacent to intertidal mangrove provides habitat of better quality for juvenile fish than a similar area of seagrass adjacent to intertidal mud. Our approach will be to understand the broad-scale utilisation of a number of habitat types by important fish species, and then to reduce our scale of interest to habitat mosaics.

The application of geographical information system (GIS) technology in marine habitat and fisheries management is potentially very useful. However, to date, although spatial information systems have been used to integrate existing fisheries habitat and environmental data sets, the next logical step of combining this information with distributions of fish and their use of habitats has not been taken. The Marine and Freshwater Resources Institute is currently creating a GIS database of various habitats along the Victorian coastline (FRDC 2000/157). A primary outcome from this work will be the improvement of existing GIS models predicting when and where fisheries species occur.

The survey work in Victoria is designed to answer several important questions: a) how do different habitats vary in their importance as nursery habitats for juveniles of economically important fish?; b) how do fish/habitat associations vary with fish ontogeny, i.e. growth and age?; and c) how does the strength of fish/habitat links change within- and amongst bays and amongst habitat types?; d) how does the arrangement of patches of different habitats in "habitat mosaics" effect habitat utilisation by important fish species. Additionally, information on habitat use by commercial fish at each site will be added to the Victorian habitat GIS.

TROPHIC LINKS

Studies on the dietary composition of fish through gut content analyses have traditionally been used to examine food webs and trophic linkages in aquatic ecosystems. But such an approach rarely considers the ultimate source of energy (plant production) and provides limited information on the interactions between the various primary producers and consumers in an ecosystem. Analysis of gut contents often provides only a snapshot of the diet of fish at a particular time, and the food consumed by fish varies considerably over time (hours, days, seasons), during the life cycle of the fish (juveniles to adults) and among habitats (Hyndes et al. 1997).

Stable isotope techniques are now recognised as a useful tool to identify and trace food/energy sources in coastal ecosystems (e.g. Peterson and Fry 1987, Loneragan et al. 1997, Jennings et al. 1997, Pinnegar and Polunin 2000). This approach allows the linkages between fish and the plant production in different coastal habitats to be determined by measuring the natural isotopic ratios, typically $^{13}C/^{12}C$ and $^{15}N/^{14}N$, of the different primary producers and consumers. Since ^{13}C exhibits only slight enrichment in tissue from primary producers to the various consumer levels, $^{13}C/^{12}C$ typically is considered useful for tracing the source material (e.g. mangrove, seagrass, saltmarsh, phytoplankton etc.) in the food web (Peterson and Fry 1987). In comparison, ^{15}N displays a stepwise enrichment of approximately 3‰ between primary

producer and each of the different consumer levels. The measurement of $^{15}N/^{14}N$ ratios has therefore been used to provide an estimate of the number of trophic levels in the food web. The combination of these isotopes is therefore very useful in determining the importance of different habitats to fisheries species.

A major advantage of isotope studies over traditional methods of establishing habitat links is that it can indicate where the nutritional base for a species is separate from the typical habitat occupied by the species. For example, seagrass detritus may underpin food chains to commercial fish in habitats such as unvegetated sand (Shaw & Jenkins 1992) or even the offshore pelagic environment (Thresher et al. 1992). Isotope studies also provide a method for determining the nutritional base of species occurring in habitat mosaics; this would not be possible with traditional dietary analysis unless "indicator" species for certain habitats were eaten.

This part of the project is complementary to two existing projects. The first is an ARC Small Grant project by Hyndes examining the influence of transported plant material on the trophic dynamics in nearshore unvegetated areas in WA. The second is a FRDC grant to Connolly using stable isotope analysis to determine the importance of seagrass to economically important fish and crustacean species occurring outside seagrass, in southern Queensland. Both projects are developing novel methods for analyses of inconspicuous food sources such as benthic microalgae that have often been ignored in past isotope studies. These methods will be further developed into routine, cost-effective techniques in the first year of the current proposal. In the second and third years, a major survey examining stable isotopes in sources of production, invertebrates, and fish will be carried out across southern Australia and in southern Queensland. This will represent the first broad-scale study of fish-habitat links using isotope analyses in Australia and will allow us to generalise about fish-habitat links for important species at a continental scale.

In Victoria and South Australia, the selection of a network of marine protected areas means there is an urgent need to rank the relative economic value to fisheries of different nearshore habitats. An important part of that is to demonstrate the contribution that plant production in each habitat makes to food webs sustaining fisheries production in that habitat or elsewhere.

In terms of the isotope component of this proposal we have taken the pro-active step of combining what was originally to be three separate proposals on stable isotopes, spanning four States, into one collaborative effort. This should result in standardisation of methods across States, economies of scale, and greater generality of the results. The importance of different habitats as the production source in food chains leading to important fish will be examined in the four States. In Victoria and Queensland we will additionally examine the food production sources for fishes utilising habitat mosaics.

In Victoria and Queensland (through the Skilleter and Loneragan study), the combination of both components of the study will allow the assessment of habitats that are utilised by important species directly (both broad-scale and fine-scale habitat mosaics), and indirectly through export of nutrition at a broad-scale or at the scale of mosaics (isotope sampling), giving a complete synopsis of habitat importance. Thus, the combination of the two approaches in Victoria and Queensland are entirely complimentary, and will give an enhanced outcome for our understanding of habitat utilisation by important species.

Need

The need for a greater understanding of the habitat requirements of important fishery species has been highlighted in recent reviews for FRDC. Cappo et al. (1998) emphasised that knowledge of the role of a diversity of habitats in healthy fisheries production is inadequate. Cappo et al. (1998) also emphasise the concept of a 'critical chain of habitats', with shifts between several habitat types as fish mature, suggesting that this may be fundamental to understanding life histories of important fishery species. The R & D approaches recommended by Cappo et al. (1998) including, "a shift in focus of community studies from single vegetated habitat types to 'chain of habitats' and regional sampling of alternative habitats with a suite of gears", and, "development and use of innovative biomarkers (e.g. Stable isotopes)", are directly addressed by this proposal.

Similarly, Butler & Jernakoff (1999) made a number of recommendations for research that are addressed in this proposal. These include studies of alternative habitats to seagrass to determine the relative importance of different habitats to fishery production, and stable isotope studies are recommended to trace the contribution of material exported from seagrass beds to fishery species elsewhere. Furthermore, Butler & Jernakoff (1999) suggest that habitat utilisation by older life stages of fishery species should receive greater emphasis.

There is clearly a need to develop an understanding of the links between important fishes and various inshore habitats, including mangroves, saltmarshes, seagrasses, rocky reef/algae, bare sand, to effectively manage our coastal fisheries. Fish may move from one habitat to another at various stages of their life cycles. Furthermore, plant material transported from other habitats could provide an important nutrient source to drive the food chain for important fishery species in key habitats. Any impacts on one habitat may therefore have a flow-on effect on fish assemblages in other habitats.

Victoria, South Australia and Western Australia are currently selecting a set of representative MPAs, and it is vital for the fishing industry to be involved in an informed decision making process. The relative importance of different nearshore habitats and areas to fisheries production is essential to this process.

Objectives

1. To increase our understanding of fisheries/habitat links using a combination of standardised survey methods in Victoria, and isotope analyses across southern Australia and Queensland
2. To identify the importance of different nearshore habitats for important fish species from recruitment to older-life stages, for individual habitats at broad scales and habitat mosaics at finer scales
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Chapter 1. Spatial and temporal variability in the assemblage structure of fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate Australian embayments

INTRODUCTION

Mangrove forests are highly productive, unique ecological environments that support rich assemblages of species via the provision of both a physical habitat and a source of nutrients (Hogarth 1999, Little 2000, Kathiresan & Bingham 2001). Pneumatophores, prop roots and trunks increase the available hard substratum for colonisation by unicellular diatoms (e.g. bluegreen cyanobacteria), micro/macro algae (e.g. Rhodophyta) and faunal epibionts, and may trap sediments and organic material (Chapman & Underwood 1995, Hogarth 1999). Crustaceans and molluscs are considered to be the most abundant and conspicuous invertebrate fauna in mangrove habitats (Hogarth 1999), and together with the epibiota, support diverse assemblages of fish, many species of which are linked directly, or indirectly, to valuable fisheries (Robertson & Duke 1990a).

Mangrove habitats contain diverse and abundant assemblages of fish. For example, studies of fish in mangroves have recorded 79 species (33 families) in Taiwan (Kuo et al. 1999), 55 spp. (22 families) in Mexico (Gonzalez-Acosta et al. 1999), 76 spp. in Florida (Ley et al. 1999), 60 spp. in Madagascar (Laroche et al. 1997), and 42 spp. in Australia (Halliday & Young 1996). Many (up to 73%) of the species of fish sampled in mangrove habitats are of commercial interest (Laroche et al. 1997), although patterns vary strongly with season (Laegdsgaard & Johnson 1995, Laroche et al. 1997) and amongst locations within a region (Robertson & Duke 1990a, Louis et al. 1995). Marine species appear to be the most common species of fish sampled in mangroves, estuarine species are the next most abundant, and freshwater species generally make up less than 10 % of the species collected (Pinto & Punchihewa 1996). Species richness and abundance of juvenile and adult fishes is often greater in mangrove habitats compared with alternatives such as unvegetated sand, seagrass or mudflats (Laegdsgaard & Johnson 1995, Clynick & Chapman 2002, Nagelkerken & van der Velde 2002), although the larger numbers of fish in mangroves than mudflats recorded by Clynick and Chapman (2002) were driven by a single species of gobiid. These patterns, however, depend strongly on the lifestages (size-classes) of the fishes sampled (Robertson & Duke 1987, de la Moriniere et al. 2002) and the species (Nagelkerken et al. 2000b).

One of the strongest paradigms in mangrove ecology promotes the role of mangroves in the provision of nursery habitat for juvenile fish and crustaceans. This paradigm is based on the observations by many studies of a rich fauna of juvenile fish in mangroves (Kathiresan & Bingham 2001), greater species richness and abundance of juvenile fish in mangroves compared with alternative habitats such as mudflats and/or seagrass (Nagelkerken & van der Velde 2002), post-settlement life-cycle migration from mangroves to alternative habitats such as coral reefs (de la Moriniere et al. 2002), and, in the few experimental assessments, the provision of food and reduction of predation by structural aspects of mangrove habitat (Laegdsgaard & Johnson 2001). Mangroves also appear to be valuable to older

lifestages, some of which have juveniles in other habitats (de la Moriniere et al. 2002). Larger fishes use mangrove habitats for feeding and shelter (Kathiresan & Bingham 2001), and many species are targeted by artisanal (de Boer et al. 2001) and commercial (Ley et al. 2002) fishers. These lines of evidence have helped to strengthen the resolve to protect these habitats, particularly in the tropics. With the exception of the work by Bell et al. (1984) and Clynick and Chapman (2002), however, there is virtually no information on the species richness and abundances of fish (including which lifestages and when) using temperate mangroves.

Clynick and Chapman (2002) suggested that inadequate and confounded sampling designs have limited the interpretation of patterns suggesting the importance of mangroves to fishes. Many studies have only sampled mangrove habitats (Kuo et al. 1999), or have sampled alternative habitats with different methods (Morton 1990), and therefore the relative importance of mangroves to specific size classes remains unclear (de la Moriniere et al. 2002). Studies are needed that use several different types of gear, each likely to catch a different suite of fishes, to best assess the range of lifestages and species of fish using mangroves. Furthermore, the same sampling design should be employed through time, at a range of locations and in alternative habitats, to assess the spatial and temporal generality of patterns.

Of the approximately 38 species of mostly tropical mangrove found in Australia (58 % of the world total), only a single species (*Avicennia marina*) grows in the temperate state of Victoria. This species grows here at the southernmost latitude of any mangrove in the world (38º45'S) and trees are stunted, 1-3 m in height compared with ≈ 30 m for *A. marina* on Hinchinbrook Island, tropical Australia (Harty 1997). In Victoria, A. marina has been cleared for agriculture and urbanisation, used as building materials, and burnt to make lime and soap (Harty 1997), however, *A. marina* forests still cover around 41 km2 of intertidal mudflat (almost 30 % of the total intertidal mudflat along Victoria's 1720 km coastline). The value of mangroves as habitat for marine animals, especially fish, has been transferred in theory from tropical systems, where it is relatively well studied, to temperate latitudes. Unfortunately, there is little empirical data on which species, when, and at what lifestages, fish use mangroves at their most temperate latitudes.

Given the dearth of information on the assemblages of fish using mangrove habitat in temperate waters, the first step in this work was to assess the diversity and abundance of fishes in mangroves and compare these with an alternative habitat with a similar regime of tidal inundation, mudflats. To best assess how the variability in space and time influences patterns between mangrove and mudflats, we compared fish catches at several locations within each of two large embayments through time (quarterly). To enable us to address at which lifestages fish were using each habitat, we employed a suit of gear types, including an active gear – seine, and 2 passive gears – gill and fyke nets.

MATERIALS AND METHODS

Study sites

Our study was done at 3 sites in each of 2 large embayments along the Victorian coastline (Fig. 1). Hastings, Warneet and Newhaven were chosen in Western Port (WP); Port Welshpool, Toora and Yanakie were chosen in Corner Inlet (CI). Both embayments are large; the perimeter and water area (area of inundation) are 197 km and 469 km2 in WP and 280 km and 377 km2 in CI respectively (OZESTUARIES 2000). The embayments are well flushed by semi diurnal tides (range ≈ 2.3 m), and are composed of several 'main' channels interspersed amongst large areas of intertidal flats measuring 387 km2 in CI and 90 km2 in WP (Table 1, Fig. 1). CI is largely unmodified (OZESTUARIES 2000); there has been some minor clearing of vegetation around the northern section, however, the southern half of the catchment has been proclaimed as national parkland. WP is 'modified' (OZESTUARIES 2000); much of the remnant vegetation in the catchment has been cleared for farming, and considerable areas of the

shoreline have come under pressure from urbanisation. The salinities in both embayments are largely marine in nature (33-38 ‰). There is more seasonal variability in salinities in CI than WP. Water temperatures in the shallow areas of the embayments may reach 28ºC during the warmest part of the day during summer, but generally vary between 9ºC in the winter and 18ºC overnight in the summer.

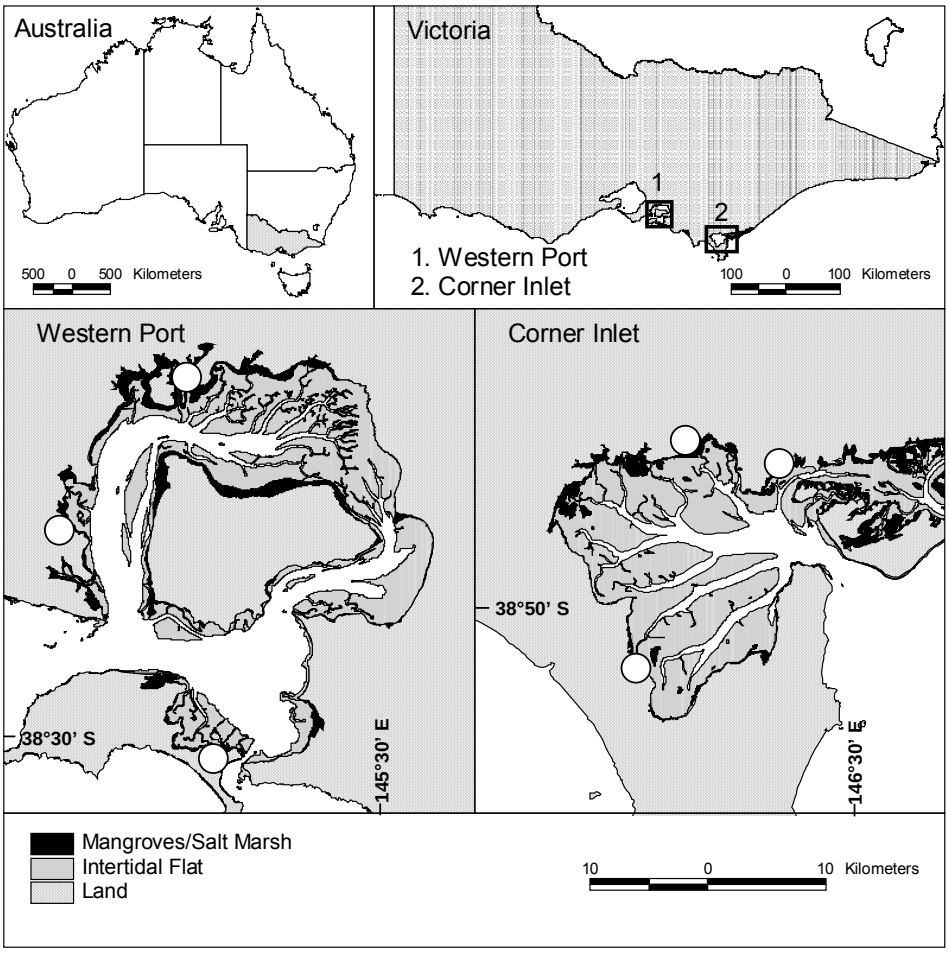

Figure 1. Location of study sites within Western Port (Hastings – H, Newhaven – N, Warneet – W) and Corner Inlet (Welshpool – W, Yanakie – Y, Toora – T). Inset: Location of study region within Australia.

Avicennia marina in WP and CI covers areas of 15 and 18 km2 respectively (Table 1). In WP, individual mangrove trees grow to a substantially larger size (3 – 4 m) compared to those in CI (1 – 2 m). In both embayments, however, the relatively small size of the plants creates a largely impenetrable barrier to human movement, even at low tide. The stands of mangroves are 'broken' by intertidal mudflats up to 500 m in width. There is little difference in the degree and frequency of inundation between the mangrove and mudflat regions selected within each location. The gradient of the shoreline is similar, both habitats are flooded at similar stages of the tidal cycle, and the depth in each habitat within a location (and that at which the nets were set) could not be differentiated. Mangrove habitats within the tropics in Australia and overseas are characterised by channels that funnel water off the mangrove as the tide recedes, but channels are largely absent from the mangrove habitat in WP and CI.

Study design

Sampling was done at quarterly intervals between January 2002 and November 2002. During each quarter (hereafter referred to summer, autumn, winter and spring), each location within each bay was sampled on a single (and separate) day. Sampling was done over a period of 4 days of spring or neap tides to maximise the degree to which fish would be able to use the intertidal habitats. We also limited our sampling to the period directly after sunrise to reduce variation due to diel factors.

Collection of fish

Fish were caught using three different types of gear: experimental gill nets, fyke nets and a beach seine net. Because of the largely impenetrable nature of the mangrove habitat, we were forced to focus our attention on catching fish at the mangrove fringe; the junction between the seaward edge of the mangrove canopy and the beginning of an area dominated by pneumatophores, which, for *Avicennia marina* in Victoria, are short (< 10 cm) 'aerial' roots projecting out of the substratum from axial roots. The prop-root zone often extends a further 10-15 m seaward from the mangrove fringe.

Gill nets were used to target larger (> 15 cm) mobile fishes. The experimental gill nets were 1.5 m deep, 35 m long, and composed from 5 panels, each of which was 7 m long and of a different mesh size. Each panel was sewn together so that they formed a single continuous net. The 5 mesh sizes (2.5, 3.8, 5.0, 6.3, 7.6 cm stretch mesh) potentially enabled us to sample fish from a variety of size classes and morphologies. Gill nets were set directly along the mangrove fringe, parallel to the shoreline. We were careful to follow the contours of the mangrove fringe to maximise the likelihood of sampling mangrove associated fishes.

Fyke nets were used to target smaller fishes, which are less likely to be caught in gill nets. The main 'bag' of each fyke net was made with 4 square rings (70 cm × 70 cm), and a wing (10 m long × 70 cm deep) was attached to each side of the 'bag'. A honey comb mesh (6 mm diameter holes) was used. Fyke nets were set along the mangrove fringe. They were not set to catch fish coming out of the mangroves via small channels, but to sample fish moving out of the mangrove 'flats' with the receding tide.

The pneumatophore zone was sampled with a beach seine net (10 m long × 2 m deep × 1mm mesh, with a 10 m long rope attached to each end), which was hauled directly along the mangrove fringe. The steps in setting the seine net are well described in Hamer and Jenkins (1996). Briefly, the end of one rope was set at the mangrove fringe. We then motored backwards along the fringe in a small punt to set-out the rope. At the bridle end of the rope, we began setting the seine net as we motored away from the mangrove fringe at 90º to our initial course (the mangrove fringe). Once the net had been set perpendicular to the mangrove fringe, we returned to the starting point, feeding out the second rope (the position the end of the first rope had been set), and gradually hauled the net into the boat. This procedure enabled us to repeatedly sample an area of approximately 75 m^2 (Hamer & Jenkins 1996).

All gears were also used to sample fish over the mudflats. The nets were set/hauled over mudflat habitat in the same orientation and at approximately the same depth, within a location, as in the mangroves. Four replicates of the gill and fyke nets were set in each habitat (mangrove and mudflat) within a particular site around 1-2 hr before high tide. At high tide, 3 replicate shots of the seine net were run in each habitat. The times at which gill and fyke nets were set and retrieved were recorded so that we could standardise catches by the time fished (which generally varied between 2.5 and 3.5 hr). The gill and fyke nets were retrieved just before all of the water had retreated from the mangrove fringe.

Statistical analysis

All data were checked for normality and homogeneity of variances using box plots and plots of residuals (Quinn & Keough 2002). Data were log10(x + 1) transformed where appropriate and reassessed. The species of fish sampled in this study probably varied in their 'catchability' between gear types, so the univariate analyses have been done for each gear type separately. Variability in a) total numbers of fish, and b) total numbers of species (both adjusted for fishing time where appropriate) was analysed with a 4-factor partially nested analysis of variance (ANOVA). Bay, Habitat and Time of year were treated as fixed factors. Site was nested within bay and was treated as a random factor. Single factor ANOVAs and Tukey's tests were used to explore significant interactions between main effects. Variability in the abundances of 2 species of fish (*Tetractenos glaber* and *Aldrichetta forsteri*) was analysed with 3-factor ANOVAs; Bay, Habitat and Time of the year were treated as fixed factors, the numbers of fish were averaged across nets within a site and site was treated as a replicate in the analysis.

RESULTS

In the course of this study, 8189 fish, representing at least 41 species were sampled (Table 2). Marine, estuarine and freshwater species represented 78, 17 and 5 % respectively of the total species sampled. Juvenile stages from 17 species (41 % of all species) were also caught. Eighteen species (44 %) of commercial/recreational interest were sampled from mangrove and mudflat habitat, of which 44 % were juvenile stages. With the exception of a few species of gobies about whose ecology we know little, few other species of fish sampled could be considered to be residents of the mangroves. Several species of fish (*Urocampus carinirostris*, *Hyporhamphus regularis*, *Mugilogobius paludis*, *Myxus elongatus*, *Platycephalus laevigatus*, *Aracana ornata*) were only sampled over mudflats, while 5 species (*Pseudaphritis urvillii*, Atherinid postlarvae, *Eubalichthys mosaicus*, *Girella tricuspidata*, *Arripis trutta*) were only sampled in mangrove habitat. Although the focus of this study was on teleost/chondrichthyian fishes, juveniles of a species of loliginid squid (*Sepioteuthis australis*, Quoy & Gaimard 1833) were also sampled from mangroves.

The fyke net sampled at least 28 species, the second greatest diversity (but the highest number of individuals) of fishes sampled by any gear in the study (Table 1). The majority of these were juvenile stages, although adults from several species (e.g. *Macquaria colonorum* and *Hyporhamphus melanochir*) were also caught. Semi-pelagic fishes, such as *Arripis truttacea*, *Aldrichetta forsteri* and *Hyperlophus vittatus* were commonly sampled with fyke nets, as were benthic gobiids and semi-demersal tetradontids. Abundances of fish sampled with the fyke net varied inconsistently between habitats (ANOVA habitat × site{bay}, $df_{4,144}$, MS = 0.473, $P = 0.012$) and times of the year (ANOVA site{bay} × time, $df_{12,144}$, MS = 0.515, $P < 0.001$) amongst sites (Fig. 2). More fish were sampled in mangrove than mudflat at all sites, but these patterns were statistically significant at only 4 sites (Hastings, $P = 0.017$; Welshpool, $P < 0.001$; Yanakie, $P = 0.005$; Toora, $P < 0.001$). The inconsistency through time between sites was driven largely by more fish sampled in summer compared with autumn, winter and spring ($P < 0.001$), and autumn compared with spring only ($P < 0.001$) at Yanakie. The number of species sampled with the fyke net (Fig. 3) also varied inconsistently through time between sites (ANOVA site × time, $df_{12,144}$, MS = 0.022, $P = 0.021$). Significantly more species of fish were sampled with the fyke net in mangrove habitats than mudflats (ANOVA, $df_{1,4}$, MS = 17.824, $P = 0.013$).

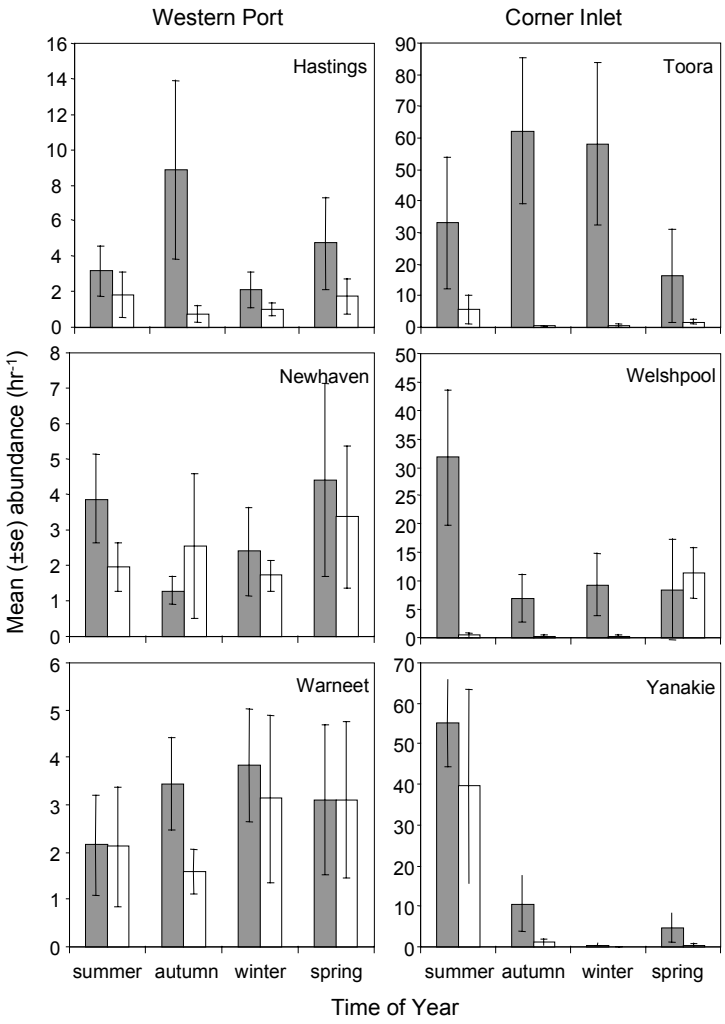

Figure 2. Mean (± se) total abundance of fish caught in the fyke net (adjusted for fishing time - hr^{-1}) within each habitat type (mudflat and mangrove) during each combination of season, embayment and site.

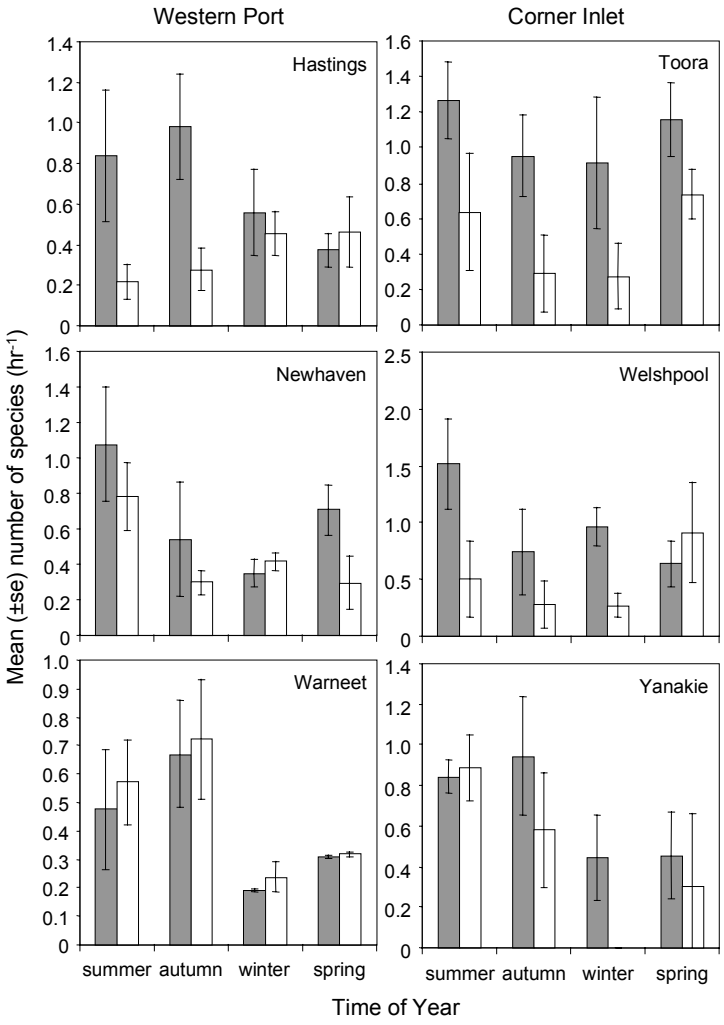

Figure 3. Mean (± se) number of species of fish caught in the fyke net (adjusted for fishing time - hr^{-1}) within each habitat type (mudflat and mangrove) during each combination of season, embayment and site.

The gill nets were most effective at sampling larger fishes (SL > 15 cm), and no fish smaller than 10 cm were sampled with this gear. The total numbers of fish sampled with the gill net also varied inconsistently between times of the year (ANOVA time × site{bay}, $df_{12,144}$, MS = 0.176, P <0.001) and habitats (ANOVA habitat × site{bay}, $df_{4,144}$, MS = 0.102, P = 0.028) amongst sites (Fig. 4). Significantly more fish were sampled in mudflats than mangroves at Newhaven (P < 0.001), Yanakie (P = 0.002) and Welshpool (P = 0.014), although more fish were sampled in mangroves than mudflats at Toora (P = 0.001), and the numbers of fish were similar between habitats at Hastings and Warneet (P > 0.05). The number of species sampled with the gill nets varied inconsistently between times of the year amongst sites (ANOVA time × site{bay}, $df_{12,144}$, MS = 0.015, P = 0.038; Fig. 5).

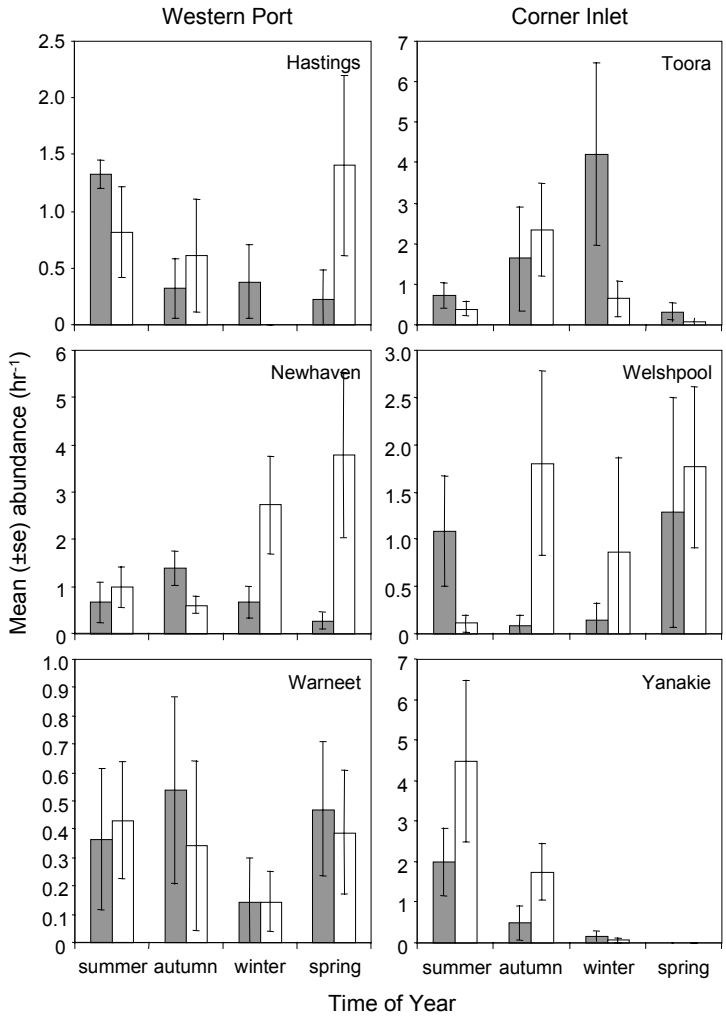

Figure 4. Mean (± se) total abundance of fishes caught in the gill net (adjusted for fishing time - hr^{-1}) within each habitat type (mudflat and mangrove) during each combination of season, embayment and site.

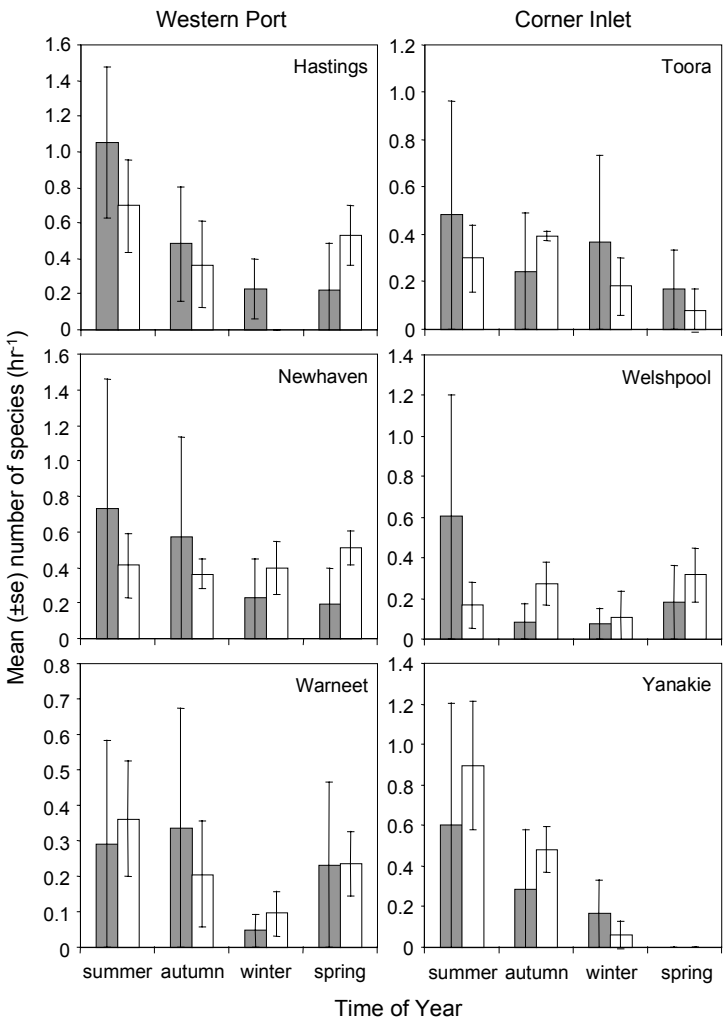

Figure 5. Mean (± se) number of species of fish caught in the gill net (adjusted for fishing time - hr^{-1}) within each habitat type (mudflat and mangrove) during each combination of season, embayment and site.

The seine net sampled mostly early post-settlement and juvenile stages of fish from at least 29 species. Most of these fishes were benthic (e.g. species from the family Gobiidae), although there were also semi-demersal species of atherinids and a sillaginid sampled. The numbers of fish sampled with the seine net varied inconsistently between habitats amongst times of the year across bays (ANOVA habitat × time × bay, $df_{3,12}$, MS = 0.564, P =0.043; Fig. 6). In both embayments, there was a pattern of more fish in mangroves than mudflats in summer and autumn, little difference between the habitats in winter, and more fish in mudflat than mangroves in spring, but this pattern was statistically significant only in summer and spring in CI ($P > 0.05$). The species richness of fishes sampled with the seine net varied inconsistently between habitats through time (ANOVA habitat × time, $df_{3,12}$, MS = 0.224, $P = 0.001$; Fig. 7). The numbers of species did not vary between habitats from summer to winter ($P > 0.05$), but more species were sampled from mudflats than mangroves in spring ($P = 0.005$).

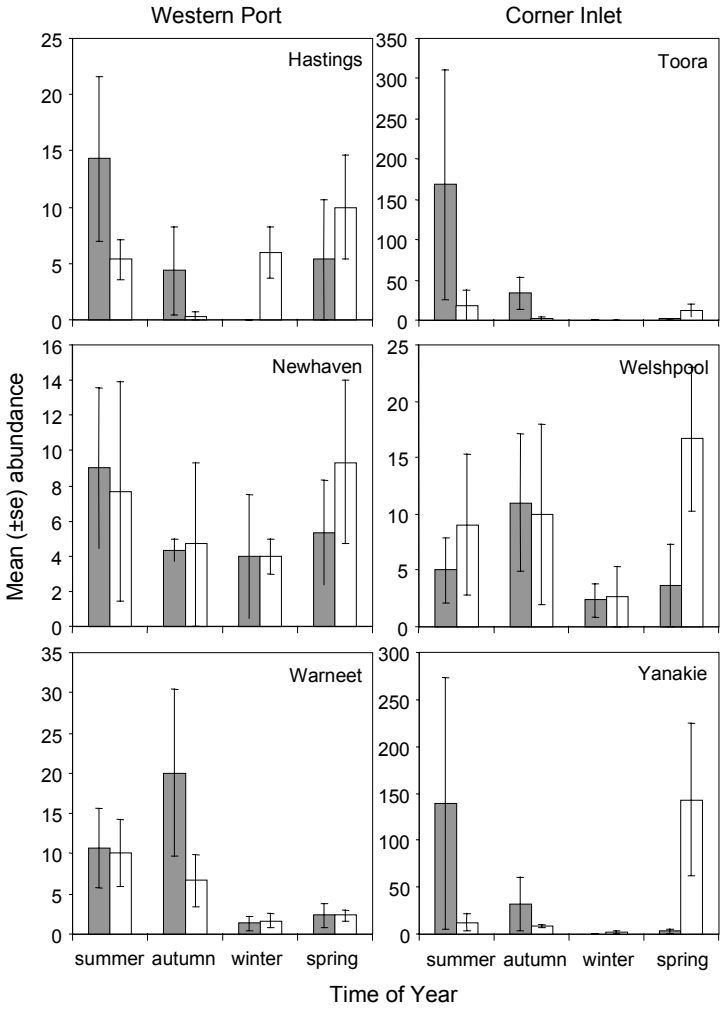

Figure 6. Mean (± se) total number of fish caught in the seine net within each habitat type (mudflat and mangrove) during each combination of season, embayment and site.

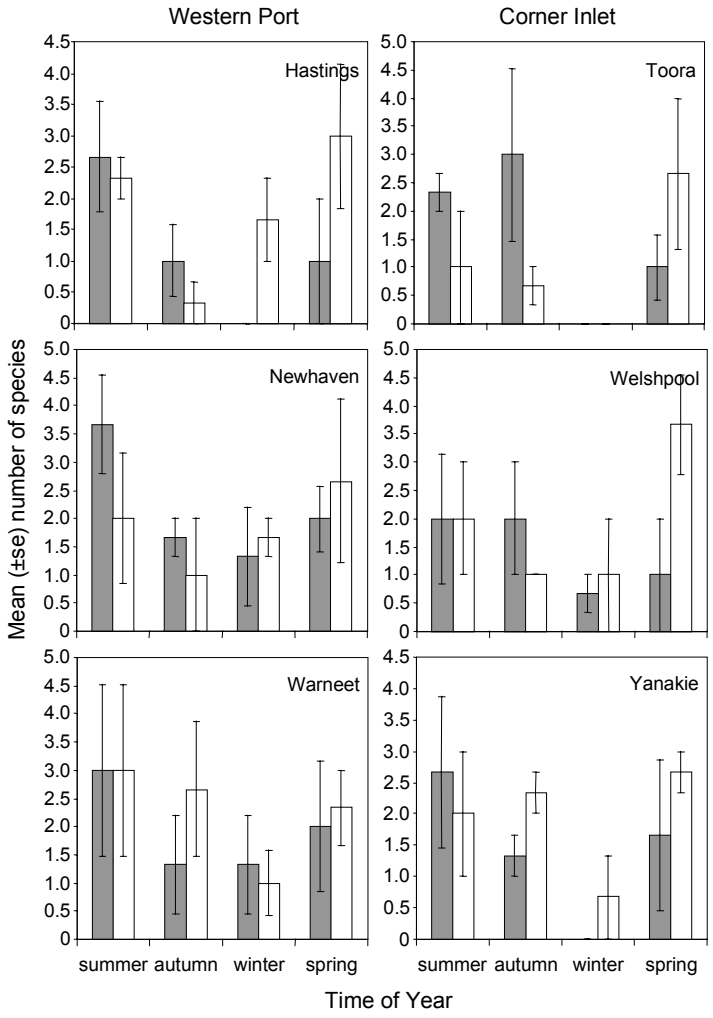

Figure 7. Mean (± se) number of species of fish caught in the seine net within each habitat type (mudflat and mangrove) during each combination of season, embayment and site.

Two of the three most common species (*Tetractenos glaber* and *Aldrichetta forsteri*; Table 1) were caught consistently enough to analyse statistically; catches of atherinids were large but highly patchy, and were not analysed statistically. The number of individuals of each of these species also varied between bays, through time and between times of the year (Fig. 8). Slightly more *T. glaber* were caught in mangroves than over mudflats using the fyke net (ANOVA, $df_{1,32}$, MS = 0.105, $P = 0.047$; Fig. 8), and their numbers varied inconsistently between times of the year in each bay (ANOVA time × bay, $df_{3,32}$, MS = 0.108, $P = 0.011$; Fig. 8); in WP, the numbers of *T. glaber* sampled with the fyke net did not vary between times of the year, but in CI, more *T. glaber* were sampled in summer than autumn ($P = 0.003$), spring ($P = 0.045$) and winter ($P = 0.001$). The numbers of *A. forsteri* sampled with the fyke net were greater in CI than WP (ANOVA, $df_{1,32}$, MS = 0.506, $P = 0.011$; Fig. 8), and in mangroves compared with mudflat, although habitat differences varied inconsistently between times of the year (ANOVA habitat × time, $df_{3,32}$, MS = 0.280, $P = 0.015$); over mudflats, the numbers of *A. forsteri* did not vary between times of the year ($P > 0.05$), but in mangroves, more juvenile *A. forsteri* were caught in autumn than summer ($P = 0.001$) and winter ($P = 0.008$). Most *A. forsteri* sampled with the gill net were adult stages (> 25 cm SL), but their numbers did not vary significantly with the time of year, the type of habitat or the embayment (Fig. 8).

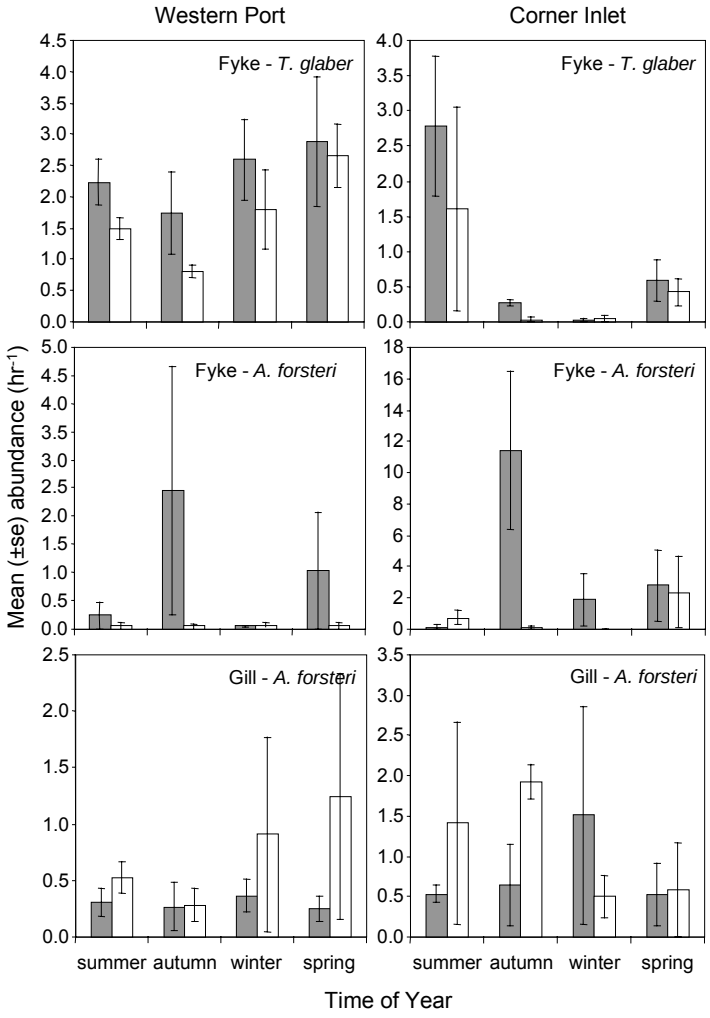

Figure 8. Mean (± se) total abundance of smooth toadfish (*Tetractenos glaber*) and yellow-eye mullet (*Aldrichetta forsteri*), adjusted for fishing time (hr^{-1}), sampled in the fyke and gill nets within each habitat type (mudflat and mangrove) during each season in each embayment.

DISCUSSION

Tropical mangroves are generally characterised by a rich, diverse and abundant assemblage of fish (Kathiresan & Bingham 2001). Research in tropical mangroves has recorded 54 to 135 species of juvenile/adult fish (Tongnunui et al. 2002) and up to 54 species of fish larvae (Barletta-Bergan et al. 2002). Relatively few species may dominate total abundances, for example the mugilid *Liza macrolepis* made up to 70 % of the total numbers of fish in mangrove creeks of Northern Taiwan (Kuo et al. 1999), and the density and biomass of fishes using mangroves may be as high as 3.5 fish m^3 and 10.9 $g.m^3$ respectively (Robertson & Duke 1990a). Less work has been done at temperate latitudes, but the available evidence suggests that there are fewer species and lower abundances of fish. Near Sydney, Australia, Clynick and Chapman (2002) sampled just 17 species (8 families) from mangrove and adjacent mudflat habitat, while Bell et al. (1984) sampled 46 species (24 families) in the lower reaches of a mangrove creek. During the course of our study, we sampled 37 species, and a single species of atherinid (*Leptatherina presbyteroides*) made up almost half (48 %) of all fishes sampled. The abundances of fish sampled in our study using fyke

nets were quite high (up to 450 fish/shot), and while it is not possible to give a density of fish for this method, sampling by Skilleter and Loneragan (unpublished data) using the same nets in subtropical Australia have caught similar densities of fish. In association with the work of Clynick and Chapman (2002) and Bell et al. (1984), our study suggests that assemblages of fish using temperate mangroves are less species rich, but the abundance of fishes using mangroves appears to be as high as those measured in the tropics. Like the work from the tropics, just a few species contribute most to the total numbers of fish.

Intertidal mudflats are a dominant feature of estuarine systems, and while they may comprise a significant proportion of estuarine habitat available to fish, information on what fish use these habitats and when is sparse (Morrison et al. 2002). Overall, more species of fish (39 spp.) were sampled over mudflat than mangrove habitats in this study (7 Species were sampled over mudflats exclusively), but just 28 % of all fish sampled were from mudflats. Some of these species were only present in unvegetated mudflats as adults (ie *Macquaria colonorum*), others only as juveniles (ie *Sillaginodes punctata*), and some as both adults and juveniles (ie *Rhombosolea tapirina*). Despite the dominance of species such as *Leptatherina presbyteroides*, which represented 44 % of all mudflat-associated fishes, they were still almost twice as abundant in mangrove habitats, which implies that mangroves provide fish with 'resources' not available in mudflats, such as a refuge from predation/disturbance and or food. Morrison et al. (2002) found that small adults and juvenile fishes dominated samples of fish in temperate tidal mudflats, with some species moving 1000 m or more across the mudflat during flood tides. In contrast to work in the tropics, which suggests that resident species (those that remain within the mangrove) may comprise as much as 94.5% of fishes in mangrove systems (Ley et al. 1999), the species sampled in our study were unlikely to be resident in nature. There appears to be a dearth of refuges at low tide (e.g. permanent water holes within the mangroves or mudflats), and, except for a couple of species of gobiid (*Gobiopterus semivestitus*, *Pseudogobius olorum*) that appear to be reasonably sedentary and are potentially small enough to exist within grapsid crab burrows at low tide, fish must be migrating up to 100's m during flood tides, using shallow unvegetated habitats to feed (Inglis 1995) and/or avoid predation (Gibson & Robb 1996).

The families of fish sampled from mangroves in this study were, to some extent, consistent with those sampled in mangroves at more tropical latitudes and, at a more regional scale, with those sampled in alternative vegetated habitats (ie seagrass). Some of the most common families of fish sampled from mangroves in this study, such as the mugilids, tetradontids and gobiids, are common in mangroves in tropical Australia and overseas (Laegdsgaard & Johnson 1995, Kuo et al. 1999). Additionally, gobiids, atherinids and a clupeoid, which comprised most of the families of fishes sampled from mangroves in this study, were amongst the most common fishes sampled in seagrass habitats within the same embayments (and in some cases the same sites) by Jenkins et al. (1997b) and Edgar and Shaw (1995a). Conversely, research by Bell et al. (1984) in temperate, and Skilleter and Loneragan (unpublished data) in subtropical Australia, has sampled relatively large numbers of sparid juveniles from mangroves. Despite the abundance of sparid adults/juveniles in deeper water habitats within our system (P. Hamer unpublished data), we did not sample any from mangroves. At a more regional scale, we sampled few syngnathids, clinids or monacanthids, which are very common in local seagrass habitats (Edgar & Shaw 1995a, Jenkins et al. 1997b). While there is a degree of plasticity in habitat requirements (evidenced by the sharing of species between habitats) of some fishes, the relative differences in the abundances of many species between alternative habitats suggest species-specific differences in the importance of nearshore habitats, within and between regions.

Mangroves are valuable as nursery habitat for a wide range of fishes (Laegdsgaard & Johnson 1995). Compared with alternative habitats, particularly mudflats, mangroves are thought to have more food, provide protection from predators, and reduce environmental disturbance (Kathiresan & Bingham 2001). This paradigm is based largely on mensurative evidence (Robertson & Duke 1987, Laegdsgaard & Johnson 1995, Nagelkerken et al. 2000b, Vidy 2000), although recent work by Laegdsgaard and Johnson

(2001) suggests the nursery value of mangroves is at least partly attributable to the provision of food and shelter from predation. The results from our study are consistent with the idea that mangroves are valuable habitat for small and juvenile fishes, although this pattern is strongly influenced by the spatial scale and time at which the study is done, and the species sampled. Catches of fish in the fyke net were significantly greater in mangroves than mudflats at 4 of the 6 study sites, although fish were more abundant in mudflat than mangroves at 2 sites. Data from the seine net suggested that fish were more abundant in mangroves than mudflat during summer and autumn, although there was little difference in winter, and the reverse pattern was observed in spring. Positive associations of several species with mangroves, including juvenile *Aldrichetta forsteri* , adult/juvenile *Leptatherina presbyteroides* and juvenile *Hyperlophus vittatus* suggest that mangroves are valuable in the provision of habitat for small/juvenile fishes. These species are commonly observed in the stomachs of larger predatory fishes (Edgar & Shaw 1995b, Hindell et al. 2000b), and given the greater structural complexity of mangroves versus mudflats, our patterns are not inconsistent with a model of reduced predation via the provision of a structural refuge. Laegdsgaard and Johnson (2001) have also shown that the provision of food may be important, and this factor may also be important in contributing to the higher numbers of juveniles observed in mangroves. Conversely, the positive association of species such as *Favonigobius lateralis* and *Rhombosolea tapirina* with mudflat rather than mangrove habitat suggests that mangroves are not necessarily 'valuable' to all species of fish. We contend that for many species of fish, temperate mangroves are valuable in the provision of nursery habitat, but this pattern is highly species-specific and depends on where, at what time and how fish are sampled.

Mangrove forests are believed to be important to larger fishes as sites for feeding and as refuges from predation (Kathiresan & Bingham 2001). Some of these fishes use the mangrove throughout their life while others use mangroves only as adults (Blaber et al. 1989, Ley et al. 1999), and many species support artisanal, commercial and recreational fisheries (de Boer et al. 2001, Ley et al. 2002). Of the 10 species of large fish (those sampled with the gill net and fyke net) we sampled from mangroves and mudflats, only 3 species (*Kestratherina esox*, *Tetractenos glaber* and *Macquaria colonorum*) were more abundant in mangroves than mudflats. Tetradontids are often amongst the most common species sampled in tropical and subtropical mangroves (Bell et al. 1984, Clynick & Chapman 2002), feeding on mangrove associated meiofauna (Duncan & Szelistowski 1998). *M. colonorum* appears to fill a similar niche in temperate waters to that of various species of lutjanids, lethrinids and sparids in the tropics (Robertson & Duke 1990); highly predatory species which are closely associated with mangrove snags. *Kestratherina esox* is a highly piscivorous atherinid (Hindell et al. 2000b), and commonly occurs in habitats such as seagrasses with large numbers of juvenile fishes. These species support the role of mangroves as sites for feeding. Conversely, 3 species (*Aldrichetta forsteri*, *Platycephalus laevigatus* and *Contusus brevicaudus*) were more common in mudflats than mangroves. Mugilids are often the most dominant family sampled from mangroves (Kuo et al. 1999), which is consistent with our finding for the juvenile stages of *A. forsteri*. Adult *A. forsteri*, which were amongst the largest fish sampled in this study (≈ 30 cm SL), may not require the structural complexity supplied by mangroves as a refuge from predation, or may be foraging on a suite of prey which is less common in mangroves. Most (4 species; *Arripis truttacea*, *Hyporhamphus melanochir*, *Platycephalus speculator*, *Pomatomus saltatrix*) large species occurred in similar numbers in mangroves and mudflats; *A. truttacea*, and *P. saltatrix* are highly transient, predominantly piscivorous species; *H. melanochir* is relatively transient and commonly feeds on planktonic crustaceans and terrestrial insects; *P. speculator* is a demersal species that consumes mainly juvenile fish. Overall, we suggest that temperate mangroves are no more important in the provision of habitat for large fishes than mudflats, the equal use of these habitats by most large fishes suggests that it is the intertidal environment *per se* which is most important, probably as a foraging habitat.

The assemblage structure of fishes within and between mangrove habitats (and the alternatives) often varies strongly through time and at different locations (Clynick & Chapman 2002). Seasonal differences in species richness and abundance are common (Bell et al. 1984, Robertson & Duke 1987, Kathiresan 2000), although not always statistically significant (Robertson & Duke 1990). These differences are often attributed to ontogenetic changes in habitat preferences (Barletta-Bergan et al. 2002) or environmental parameters such as salinity or temperature (Lin & Shao 1999, Rueda 2001). There may also a be a significant amount of spatial variability in the use of mangroves by fish, which has been considered in the context of proximity of mangrove habitat to alternative habitats (Thollot 1992), position of mangrove habitat within an estuary (Ley et al. 1999), site-to-site variability (Clynick & Chapman 2002) and a combination of these (Skilleter & Loneragan 2003). Our study showed that the relative 'value' of mangroves compared with mudflat, based on species richness and abundances of fish varied strongly within embayments and through time. Salinity and temperature varied little between embayments (or sites), and the differences between times of the year were unlikely to have much biological importance. The spatially explicit recruitment of species such as *Favonigobius lateralis* (to mudflats) and *Aldrichetta forsteri* (to mangroves), ontogenetic shifts in habitat use by species such as *Rhombosolea tapirina*, and seasonal changes in local abundance of larger species such as *Pomatomus saltatrix*, *Arripis truttacea* and the platycephalids would contribute. The mechanisms underlying these patterns require further investigation, however, more attention must be given to assessing the spatial and temporal generality of mangroves as habitat for fishes in temperate Australia.

There is some debate as to whether nearshore habitats are important because of the type of habitat *per se*, or whether their importance arises because of the area within which they happen to occur. Nagelkerken and van der Velde (2002) suggest that, in the absence of estuarine influence, 'bay habitat dependence' is a more useful concept than that of 'estuarine dependence' (Lenanton & Potter 1987, Blaber et al. 1989). The application of a bay habitat dependence model is also more relevant in our system, where salinity was predominantly marine at ≈ 37 ppt. The work dealing with these concepts is based on the idea of comparing assemblages of fish inside and outside estuaries (Blaber et al. 1989), or the same habitat inside and outside embayments (or estuaries) (Nagelkerken & van der Velde 2002), but does not address the aspect of whether, depending on the location within an embayment, alternative habitats support different numbers of fish. If, for example, alternative habitats in different regions of the embayment contain similar numbers of fish, the concept of bay habitat dependence is supported. If, however, alternative habitats contain different numbers of fish, the concept of habitat dependence should be considered. Our work suggests that the relative importance of position (bay habitat dependence) versus provision (habitat dependence) depends on the location within which a study is done. At some of our sites, there was little difference in the assemblage structure of fish between habitats, which was consistent with the idea of bay dependence. At other locations, even within the same bay, mangroves were much more 'valuable' than mudflats, supporting the contention of habitat dependence. These patterns are consistent with the work of Jenkins et al. (1997b) and Jenkins and Hamer (2001), who found that the relative importance of seagrass compared with unvegetated sand, based on numbers of post-settlement *Sillaginodes punctata*, varies strongly with the location within Port Phillip Bay, Australia. The idea of bay habitat dependence, as it applies to the provision of habitat by mangroves in temperate embayments, depends strongly on the location within a bay, and further research is needed to assess the relative contributions of predation, food and environmental disturbance.

At least some of the spatial variability in our results could also have been attributed to among-site variability in the structural complexity of the mangroves and subsequent effects of these differences in structure on, for example, food and shelter (as above). We had no direct estimates of how the density or length of pneumatophores, or biological conditions associated with these, such as algal/invertebrate

cover, varied among sites. But these factors could generate some of the spatial variability in fish seen here, and is an area that requires further attention.

The stunted nature of the mangrove habitat at our study sites largely precluded setting equipment inside the mangrove forest. A question arises, however, as to whether we sampled fish associated with the mangroves, or whether we sampled fish associated with a component of the mangroves, in our case the pneumatophore zone. Both the fyke and gill nets were set directly along the mangrove fringe, so it is reasonable to assume that the fish caught in these gears were actually using the mangrove rather than just the pneumatophore zone. In contrast, the seine net sampled fish directly from the pneumatophore zone because it was impossible to operate the seine net on the landward side of the mangrove fringe. This raised 2 issues, however: it is possible that patterns in the use of fish between this and the unvegetated region represent either differences between the structure associated with the pneumatophores rather than the mangrove forest and/or differences in the effectiveness of seine nets in areas with and without pneumatophores. Recent work by Vance et al. (2002) suggests that abundances of penaeid prawns change with distance into mangrove forests, partly in response to local topography and patterns in water currents, and supports the idea that the pneumatophore zone of mangroves potentially supports different assemblages of fauna compared with the regions inside the mangrove forest. But, the seine net is also likely to be less effective at sampling small fishes that can avoid the net as it drags over the pneumatophores rather than directly along the substratum. Further research is needed that examines the degree to which assemblages of fish change depending on the position within a mangrove forest using gears that are less likely to vary among structural attributes.

Table 1. Summary of the areas of each habitat (mangrove and mudflat) with reference to the total area of inundation and perimeter of each embayment (OZESTUARIES 2000), and the mean (±se) seasonal salinity and temperature of each embayment (Corner Inlet and Western Port).

	Corner Inlet				Western Port			
Perimeter (km)	280				197			
Water area (km^2)	377				469			
Intertidal flats (km^2)	387				90			
Mangroves (km^2)	18				15			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Temperature (ºC)	18.0 (±0.4)	14.8 (±0.6)	9.1 (±0.3)	12.4 (±0.4)	19.2 (±0.5)	17.6 (±0.1)	10.9 (±0.2)	13.4 (±0.2)
Salinity (ppt)	37.2 (±0.4)	36.7 (±0.1)	33.6 (±0.5)	35.4 (±0.3)	37.0 (±0.3)	36.7 (±0.2)	35.5 (±0.1)	35.8 (±0.1)

Table 2. Number of each species collected in each combination of time of year (summer, autumn, winter and spring) and habitat (mangrove – M, mudflat – UV). Data were pooled across bays, sites and sampling gears. Species are presented in alphabetical order.

	Summer		Autumn		Winter		Spring	
Species	M	UV	M	UV	M	UV	M	UV
Banjo shark (*Trygonorrhina guanerius*)	1	1	-	-	-	-	-	-
Bluespot goby (*Pseudogobius olorum*)	48	8	138	13	4	13	28	43
Blue-spot spotted stingaree (*Urolophus paucimaculatus*)	-	-	-	-	-	2	1	-
Bridled leatherjacket (*Acanthaluteres spilomelanurus*)	2	-	-	1	-	1	-	-
Cobbler (*Gymnapistes marmoratus*)	-	1	1	-	-	-	2	-
Congolli (*Pseudaphritis urvillii*)	-	-	2	-	1	-	-	-
Estuary perch (*Macquaria colonorum*)	3	3	6	-	1	-	1	-
Galaxid (*Galaxias maculatus*)	-	-	-	-	7	1	26	-
Girdled goby (*Nesogobius* sp 1)	33	9	7	2	-	3	-	5
Glass goby (*Gobiopterus semivestitus*)	101	14	29	33	8	1	3	2
Globefish (*Diodon nicthemerus*)	3	-	2	1	-	-	2	2
Greenback flounder (*Rhombosolea tapirina*)	6	6	1	3	1	6	18	45
Hairy pipefish (*Urocampus carinirostris*)	-	-	-	-	-	2	-	2
Halfbridled goby (*Arenigobius frenatus*)	26	5	13	1	-	-	8	25
King George whiting (*Sillaginodes punctata*)	2	4	-	5	1	-	4	2
Longfin goby (*Favonigobius lateralis*)	1	9	9	46	5	16	4	42
Longsnout flounder (*Ammotretis rostratus*)	1	2	-	2	-	-	-	2
Luderick (*Girella tricuspidata*)	-	-	1	-	-	-	-	-
Mosaic leatherjacket (*Eubalichthys mosaicus*)	1	-	-	-	-	-	-	-
Ornate cowfish (*Aracana ornata*)	-	-	-	1	-	-	-	-
Pale mangrove goby (*Mugilogobius paludis*)	-	1	-	-	-	-	-	-
Pike-head hardyhead (*Kestratherina esox*)	20	5	1	2	2	-	-	-
Prickly toadfish (*Contusus brevicaudus*)	3	-	1	12	-	-	-	6
River garfish (*Hyporhamphus regularis*)	-	-	-	5	-	-	-	-
Rock flathead (*Platycephalus laevigatus*)	-	4	-	-	-	-	-	-
Sand mullet (*Myxus elongatus*)	-	-	-	1	-	-	-	-
Sandy sprat (*Hyperlophus vittatus*)	446	31	412	2	-	-	-	-
Sea mullet (*Mugil cephalus*)	1	1	-	-	-	-	-	-
Senator wrasse (*Pictilabrus laticlavius*)	-	-	-	-	-	1	-	-
Shortfin eel (*Anguilla australis*)	1	-	-	1	-	-	-	-
Silver fish (*Leptatherina presbyteroides*)	2062	580	183	4	404	9	185	460
Smooth toadfish (*Tetractenos glaber*)	263	125	93	43	139	102	137	137
Southern calamary (*Sepioteuthis australis*)	-	-	4	-	-	-	-	1
Southern sea garfish (*Hyporhamphus melanochir*)	-	1	1	1	4	-	-	1
Spotted pipefish (*Stigmatopora argus*)	-	-	-	-	-	-	-	-
Tailor (*Pomatomus saltatrix*)	-	-	2	2	-	-	-	-
WA salmon (*Arripis trutta*)	-	-	1	-	-	-	-	-
WA salmon (*Arripis truttacea*)	5	3	6	4	-	1	1	5
Widebody pipefish (*Stigmatopora nigra*)	6	16	-	-	-	-	1	-
Yank flathead (*Platycephalus speculator*)	4	3	-	-	-	-	-	1
Yellow eye mullet (*Aldrichetta forsteri*)	69	117	493	78	114	57	168	139
Monacanthid postlarvae	1	-	-	-	-	-	-	1
Atherinid postlarvae	3	-	-	-	-	-	-	-
Gobiid postlarvae	28	19	4	9	-	-	-	-
Odacid postlarvae	4	-	-	-	-	-	-	1
Total fish	3144	966	1411	273	691	215	589	922
Total species	28	24	23	24	13	14	16	20

Chapter 2. Fish use of saltmarsh flats in a temperate Australian embayment

INTRODUCTION

Saltmarshes, seagrass beds and mangrove forests are thought to be crucial elements of the nearshore marine environment. These biotopes are often referred to as 'nursery habitats' (Bell & Pollard 1989, Minello et al. 2003), where juvenile fishes, including those of commercial importance, are provided with protection from predators (Rozas & Minello 1998) and an abundant source of food (Zimmerman et al. 1984, Connolly 1994a). The implications of changes to seagrass beds and mangrove forests are relatively well understood (and subsequently predictable) given our knowledge of processes shaping the fauna that use them (Yanez-Arancibia et al. 1993, Jenkins et al. 1997b, Loneragan et al. 1997, Jenkins & Hamer 2001, Peterson et al. 2001). Unfortunately, despite the increased vulnerability of saltmarshes to extinction in some areas (Saintilan & Williams 1999), we know little about the nature and strength of links between saltmarsh habitats and the fauna, particularly fishes, which use them.

Saltmarshes are complex environments, comprised of a small number of specialised emergent terrestrial plants, marsh ponds, unvegetated pools and tidal creeks (Minello et al. 2003). The physical and biological characteristics of southern hemisphere saltmarshes are different from those in the northern hemisphere. Northern hemisphere saltmarshes occur in the low intertidal zone, are dominated by cord grasses (*Spartina* spp.), and are generally inundated daily by high tides; southern hemisphere saltmarshes occur higher in the intertidal zone and are dominated by succulent shrubs and herbs (Long & Mason 1983, Adam 1990). In temperate Australia, the saltmarsh flora often forms three distinct zones: the high marsh, mid marsh and low marsh. The low marsh, dominated by succulent beaded glasswort (*Sarcocornia quinqueflora*), and mid marsh vegetation, shrubby glasswort (*Schlerostegia arbuscula*), comprise the 'saltmarsh flat' (Environment 1990). The saltmarsh flats are inundated infrequently, mostly during spring high tides (Morton et al. 1987). In regions with a small tidal range, such as bays with narrow entrances (e.g.. Port Phillip Bay, Australia), the degree of inundation is driven primarily by low barometric pressure (Ranwell 1972).

Two models have been suggested to explain associations between fish and saltmarshes. First, saltmarshes provide an abundant source of prey for fish and macroinvertebrates (Weisberg & Lotrich 1982). Dietary analyses of fish in sub-tropical Australian saltmarshes suggest that saltmarshes are valuable in the provision of food for juvenile fishes (Morton et al. 1987, Morton et al. 1988, Sumpton & Greenwood 1990), and West and Zedler (2000) found that saltmarsh flats were important sources of food for fish in the USA. Secondly, the structure provided by saltmarsh plants is thought to provide small fish with a refuge from predators (Kneib 1987). The value of marshes in the mediation of predation is thought to interact in complex ways with distance from the edge, elevation and flooding patterns (Rozas & Zimmerman 2000). Experimental manipulations suggest that both growth rate and predation risk influence habitat use by fish in intertidal saltmarshes (Halpin 2000). To date, no study has assessed the dietary composition of fishes sampled from saltmarshes in temperate Australia to determine whether a) juvenile and small fishes are preying on benthic fauna associated with the saltmarsh, and/or b) piscivorous species are consuming juvenile fishes associated with saltmarsh.

Environmental attributes, including salinity, water temperature and depth are thought to influence the spatial and temporal patterns in fish use of saltmarsh habitats (Kneib 1987, Poulin & FitzGerald 1989, Minello et al. 2003). Physico-chemical variables have been shown to contribute more to the growth of

juvenile fishes than diet or structural attributes such as stem density (Baltz et al. 1998), and variation in salinity and temperature influences the assemblage structure of fish in saltmarsh pools (Poulin & FitzGerald 1989, Baltz et al. 1993, Minello et al. 2003). The depth of inundation and the distance fish move over the saltmarsh are often correlated (Thomas & Connolly 2001), with smaller fish occurring at a shallower depth and a shorter distance onto the marsh than larger fish (Kneib 1987, Minello et al. 2003). The assemblage structure of fish may also depend on diel period (Rountree & Able 1993, Hindell et al. 2000b). In saltmarsh habitats, Morton et al. (1987) found that larger fish only entered the tidal inlet at night, but little of the variability in fish abundance or species richness could be explained by diel period. Thomas and Connolly (2001) measured variability in the assemblage structure of fish between diel periods, but could only sample nocturnally in winter and diurnally in summer, and were unable to differentiate between seasonal versus diel effects. Hampel et al. (2003) suggest that diel period may interact with tidal regimes (depth), producing different assemblages between day and night on spring tides and little difference between diel periods during neap tides.

Port Phillip Bay contains large areas of seagrass and sheltered unvegetated habitat, which are important to juvenile and subadult species, including some of commercial importance, as foraging areas (Jenkins et al. 1997b, Hindell et al. 2000b, Jenkins & Hamer 2001). While saltmarsh flats are a conspicuous element of the nearshore semi-aquatic environment at several locations within Port Phillip Bay, their value to juvenile fishes has not been investigated. In the present study we assessed 1) which species and life stages of fish were using saltmarsh flats, 2) the spatial and temporal consistency in the patterns of fish assemblages with respect to diel periods and environmental variables, and 3) the diets of fish occurring on the saltmarsh flats in relation to local abundances of potential prey at varying distances onto the saltmarsh.

MATERIALS AND METHODS

Study Area

Our study was done on the southwest side of Port Phillip Bay, Victoria, Australia (Fig. 9). Unvegetated patches of mud and beds of seagrass (*Heterozostera tasmanica*) occupy the subtidal zones (Hamer & Jenkins 1996). Saltmarsh is common in the sheltered intertidal regions, which are protected from strong westerly winds. Tidal currents within this region of the bay are weak (Black et al. 1993), and the amplitude is less than 1 m (Jenkins & Hamer 2001).

The saltmarsh in this region of Port Phillip Bay is made up of three distinct zones that extend along the shoreline parallel to one another: low marsh (saltmarsh flats), mid marsh and high marsh. The low marsh occurs at the seaward edge of the saltmarsh, adjacent to the subtidal, and is composed of a low-lying beaded glasswort, *Sarcocornia quinqueflora*. *S. quinqueflora* spreads across the sediment in dense and sparse patches no higher than 10 cm and is commonly flooded. The mid marsh extends along the shoreline immediately landward of the low marsh, and is dominated by 1 m high stands of shrubby beaded glasswort (*Schlerostegia arbuscula*) interspersed with smaller shrubs of *Sueada australis*. This region of the saltmarsh is subject to only occasional inundation. The high marsh occupies the most landward position of the saltmarsh, is rarely inundated, and dominated by tussock grasses.

Meteorological events can be very important in determining the occurrence and degree of inundation of saltmarshes (Ranwell 1972). Preliminary sampling suggested that the inundation of saltmarsh flats in Port Phillip Bay is infrequent and to some extent independent of astronomical tidal regimes. During low-pressure systems (< 1013 hP), water levels increase inside Port Phillip Bay by water forcing, often as a result of strong (> 25 knots) westerly winds, and saltmarsh inundation occurs at high tide to depths 10 - 70 cm.

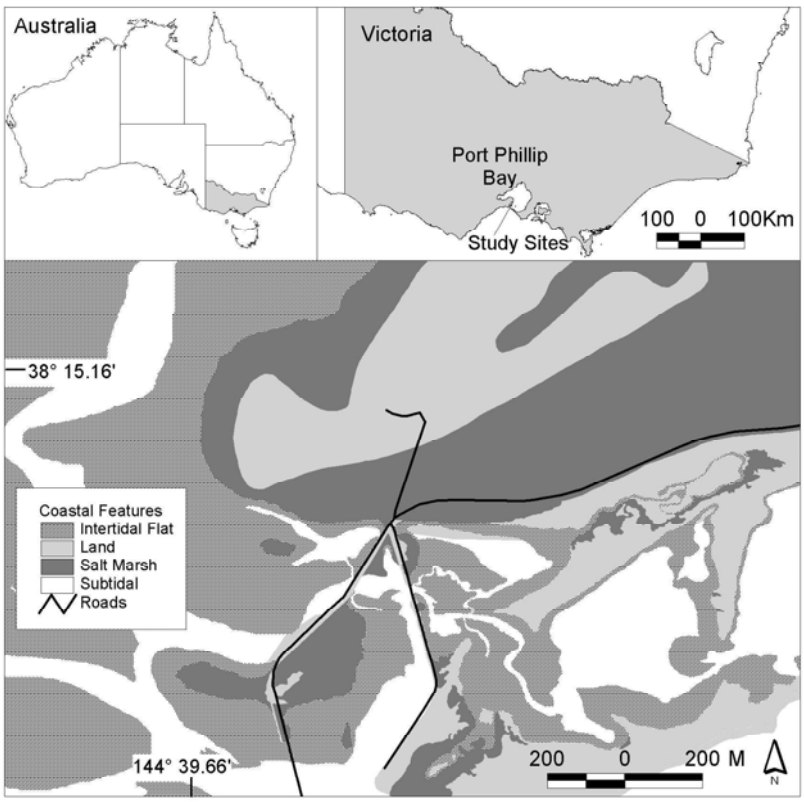

Figure 9. Location of the study region within Port Phillip Bay, Victoria. Inset: Location of Victoria within Australia, and location of Port Phillip Bay within Victoria.

Sampling Fish

Fish associated with the saltmarsh were sampled using seine and fyke nets on each sampling occasion day and night. Sampling was done over 18 inundation events (14 diurnal and 4 nocturnal) between August 2002 and May 2003, which represented all occasions of saltmarsh flooding (see Table 3). The sampling dates were initially chosen to correspond with spring high tides, but dates corresponding with tides of lower amplitude were sampled opportunistically during low-pressure weather systems. For each sampling event, 8 plots were chosen randomly from a 20 x 20 m grid, imposed on a map showing the area of saltmarsh, and allocated a net type (fyke or seine). Four plots were sampled with each gear type on each sampling occasion. Seine and fyke nets were randomly assigned to plots to avoid re-sampling and to ensure net types were interspersed.

Fyke nets (n = 4, 3 mm mesh, 70 cm high) were used to passively collect fish moving out of the saltmarsh. Each fyke net was set facing landward along the seaward edge of the saltmarsh. The bottom of each wing was weighted with lead rope, and the top was held buoyant with floats. Fyke nets were set approximately 1-2 hr before the expected high tide. The fyke wings were extended landward of the seaward edge of the marsh at a 45° angle to the fyke mouth, and the bottom of each wing was pushed into the sediment to ensure there were no gaps through which fish could escape. Setting the nets in this way ensured that the only fish sampled were those that had previously been on the saltmarsh. Fyke nets were retrieved when the water had drained off the saltmarsh flat. The times at which nets were set and retrieved were recorded.

Fish were actively sampled from the saltmarsh flat using a 1 mm-mesh seine net (2 m high × 10 m long, with 10 m ropes attached at each end). The steps of setting and retrieving this type of gear are described by Jenkins and Hamer (2001). Briefly, the length of the net was extended across the marsh flat. Each person walked away from the seine, parallel with the shore, until the ropes were fully extended. The two people hauled the seine net along the saltmarsh flat for 10 m by retrieving the length of rope. This method of setting the net ensured we consistently sampled an area of approximately 75 m^2. While there is a chance that seine nets under-estimate abundances of benthic fishes in structurally complex habitats such as pneumatophores (previous chapter), we considered that the saltmarsh sampled here provided no more of an impediment to sampling these species than seagrass, and was therefore a relatively reliable method of sampling most species, especially semi-demersal species such as atherinids and mugilids.

All fish were anaesthetised in 5 ml pure clove oil mixed with 500 ml seawater until no movement could be observed, and then preserved in 95 % ethanol. In the laboratory, all fish were removed from ethanol, press-dried, weighed (g) and their standard length (SL - from the tip of the snout to the posterior end of the caudal peduncle, mm) was measured. Fish were identified to species under a dissecting microscope.

Physico-chemical characteristics

Several physico-chemical characteristics of the saltmarsh were recorded so that we could assess the degree to which these were related to abundances of fish. Salinity (ppt), temperature (°C) and water depth (cm) were recorded at peak high tide after each seine net haul (n = 4) on each sampling occasion. Barometric pressure (hP) was recorded for each event to assess the influence of local meteorological events on the degree of inundation.

Dietary composition of fish

Dietary analysis was done on fish sampled from the saltmarsh on 4 sampling occasions during the day to assess whether they were feeding on saltmarsh-associated fauna. We chose to focus on samples collected during the day rather than the night because previous work has shown that juveniles from species such as *Sillaginodes punctata* feed mostly during the day (G. Jenkins unpublished data). A subsample of 15 individuals from each species collected from 4 different sampling events were analysed (see Table 3). To ensure subsamples were representative of size, 5 fish were chosen from each of 3 size groups, which were based on the size range for each species sampled. In the laboratory, fish stomachs, excluding intestines, were removed, press-dried and weighed (g). Due to the difficulty of differentiating between the stomach and intestine in *Atherinasoma microstoma* and *Favonigobius lateralis*, both regions of the gut were analysed. Individual prey were identified to the lowest taxa possible and counted. Distinguishable features (e.g. eye spots in gammaridean amphipods) were counted on partially digested individuals to avoid overestimation of abundance (Hyslop 1980). Each prey category was amassed, press-dried and weighed (g) (Hyslop 1980). The diets of fyke and seine net-captured fish were analysed separately because of the possibility that fish characteristics (i.e. size, diet) may vary between net hauls that sample single schools of fish. The index of relative importance (IRI) (Hyslop 1980) for each prey category was calculated by:

$$IRI = (N + W) \times O$$

Where N and W are the proportional contributions of abundance and weight respectively, and O is the proportional frequency of occurrence.

Abundance of potential prey

On the 4 sampling events from which fish were chosen for dietary analysis, samples of invertebrate fauna were collected from different regions across the edge of the saltmarsh to determine if fish were feeding on saltmarsh-associated invertebrates. At high tide, a corer (65 mm diameter × 150 mm long, plexiglass tube covered at one end with 100 μm mesh) was used to collect invertebrate fauna from 2 locations within each of 3 regions across the saltmarsh flat: unvegetated (UV) – 5 m seaward from the saltmarsh edge; vegetated (V) – 5 m landward from the marsh edge; edge (E) – at the unvegetated sand/saltmarsh interface (n = 3 cores in each location). Small diameter corers (~ 50 mm) have been found to be more effective than larger ones (150 mm) for sampling demersal invertebrates less than 2 mm in size (Edgar et al. 1994). The open end of the plexiglass tube was pushed approximately 10 mm into the sediment, collecting invertebrate fauna from immediately above and within the benthos. A steel plate (200 mm x 120 mm) was inserted under the core to prevent the loss of sediment and fauna, and the core and plate were lifted from the water. The contents were washed into a plastic bag with seawater and transported to the laboratory. Core samples were placed in 500 ml jars and preserved in 70 % ethanol.

In the laboratory, each sample was washed through a series of 3 nested sieves (1000 μm, 500 μm and 250 μm) to separate size groups of meiofauna. Juvenile fish from the species sampled in this study prey predominantly on epibenthic fauna in the 250 – 2000 μm size range (Edgar et al. 1994). Because of the amount of inorganic matter in the 500 and 250 μm samples, a sample splitter was used to reduce the amount of material we had to sort through (Elmgren 1973). The sample splitter was a PVC cylinder enclosed at the top by a fitted water-tight lid. The cylinder was divided at the bottom into 8 wedge-shaped chambers, each with a 5 mm hole plugged with a rubber stopper. The 500 and 250 μm samples were washed into the divider with seawater, inverted, rotated and placed on a flat surface to allow fine particles to settle equally amongst chambers for 10 min. Excess water was released. Four chambers were released to collect half of the 500 μm sample. One chamber was released to collect one-eighth of the 250 μm sample. Subsamples were collected in a glass jar, mixed with Rose Bengal to enhance our ability to see animals, and sorted. Animals in the 3 sieve samples were counted and identified to taxonomic order under a dissecting microscope.

Statistical Analysis

Fish samples were analysed separately for fyke (passive gear) and seine (active gear) nets because of the possibility that the different techniques sampled different assemblages of fish. The numbers of fish sampled with the fyke nets were adjusted by catch per unit fishing time (effort, hrs).

Univariate data

All data were checked for normality and homogeneity of variance with box plots and plots of the residuals. Non-normal and heterogenous data were $\log_{10}(x + 1)$ transformed and reassessed. Two-factor nested analyses of variance (ANOVAs) were used to assess whether species richness and fish abundance varied between diel periods. Sampling event (day) was nested within diel period. Variability in abundances and species richness of invertebrates sampled with the cores between regions of saltmarsh across days was analysed with a two-factor ANOVA; region of the saltmarsh (zone) and sampling day were treated as fixed factors. Linear regression analyses were used to determine the relationship between species richness and fish abundance (dependent variables) and salinity, temperature, depth and barometric pressure (independent variables). Data were analysed using mean values for each sampling event.

Multivariate data

The degree to which a) the assemblage structure of fish varied between diel periods, and b) fish diets were similar to invertebrates collected with the cores at different regions of the saltmarsh were assessed with non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity measures (Clarke & Warwick 2001). Stress-values, which indicate the difficulty associated with relating objects to each other within the ordination plot, below 0.1 were considered 'ideal,' however stress-values below 0.3 were accepted (Quinn & Keough 2002). Data on the assemblage structure of fish were 4th root-transformed to reduce the influence of numerically dominant species; dietary data and data from the cores were transformed to presence/absence because we were most interested in assessing the degree to which species sampled with the cores matched those in the diets. The *a-priori* null hypotheses were tested statistically with one-way analyses of similarity (ANOSIM). The *P*-value was nominated as 0.05. Where multiple pair-wise tests occurred, the *P*-value was adjusted using sequential Bonferroni corrections to reduce the experimentwise Type-I error rate (Quinn & Keough 2002). All multivariate analyses were done using Primer version 5.0 (Clarke & Warwick 2001).

RESULTS

Diversity and abundance of nekton in saltmarsh

A total of 2047 fish from 10 species was collected in our study (Table 4). All species were predominantly juvenile and sub-adult stages, ranging in size from 29 to 255 mm SL (Table 4). In 18 sampling events, 79 % of fyke and 93 % of seine net sets caught fish. Fyke nets caught a total of 689 individual fish from 10 species; seine nets sampled 1358 individuals from 6 species (Table 4).

The small-mouthed hardyhead (Atherinidae: *Atherinasoma microstoma*, Günther) was the most abundant species, 483 fish in fykes (70 %) and 1157 in seines (85 %)(Table 4). The long-finned goby (Gobiidae: *Favonigobius lateralis,* Macleay) represented 20 % (136 fish) of the fyke but just 0.8 % (11 fish) of the seine net catches. King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier), pike-headed hardyhead (Atherinidae: *Kestratherina esox*, Klunzinger), yellow-eye mullet (Mugilidae: *Aldrichetta forsteri*, Valenciennes), silver fish (Atherinidae: *Leptatherina presbyteroides*, Richardson), greenback flounder (Pleuronectidae: *Rhombosolea tapirina,* Günther), common jollytail (Galaxiidae: *Galaxias maculatus*, Jenyns), smooth toad fish (Tetraodontidae: *Tetractenos glaber*, Freminville) and common weedfish (Clinidae: *Heteroclinus adelaide*, Valenciennes) were also sampled. *G. maculatus*, *H. adelaide*, *R. tapirina* and *T. glaber* were only sampled with fyke nets (Table 4).

Diel variability

Atherinasoma microstoma, *Aldrichetta forsteri*, *Favonigobius lateralis*, *Kestratherina esox*, and *Sillaginodes punctata* occurred during both the day and night (Table 4). *Galaxias maculatus*, *Rhombosolea tapirina*, *Heteroclinus adelaide* and *Tetractenos glaber* only occurred during the day, while *Leptatherina presbyteroides* was only sampled at night (Table 4). Abundances of the most common species, *Atherinasoma microstoma*, did not vary between diel periods for either seine (2-factor nested ANOVA: $F_{1,8} = 0.305$, $P = 0.595$; Fig. 10) or fyke nets (2-factor nested ANOVA: $F_{1,15} = 0.031$, $P = 0.862$; Fig. 10). Similarly, there was little difference in the total number of fish sampled with the seine (2-factor nested ANOVA: $F_{1,8} = 0.438$, $P = 0.526$; Fig. 10) or fyke nets (2-factor nested ANOVA: $F_{1,15} = 0.013$, $P = 0.907$; Fig. 10) between diel periods. In contrast, more species of fish were sampled with the seine at night (2-factor nested ANOVA: $F_{1,8} = 8.18$, $P = 0.021$; Fig. 10), but the number of species sampled with the fyke net did not vary between diel periods (2-factor nested ANOVA: $F_{1,15} = 0.158$, $P = 0.696$; Fig. 10). There was a significant difference between diel periods in the assemblage structure of fish sampled with the seine net (ANOSIM: $R = 0.515$, $P = 0.017$), but there was

no significant difference in the assemblage of fish collected in fykes between diel periods (ANOSIM: R = 0.038, $P = 0.378$). There was little difference in fish length between diel periods for the most abundant species, *A. microstoma* (Table 4), and although larger *Sillaginodes punctata* and *Aldrichetta forsteri* occurred during the night (Table 4), there were too few fish sampled to perform any meaningful statistical analyses.

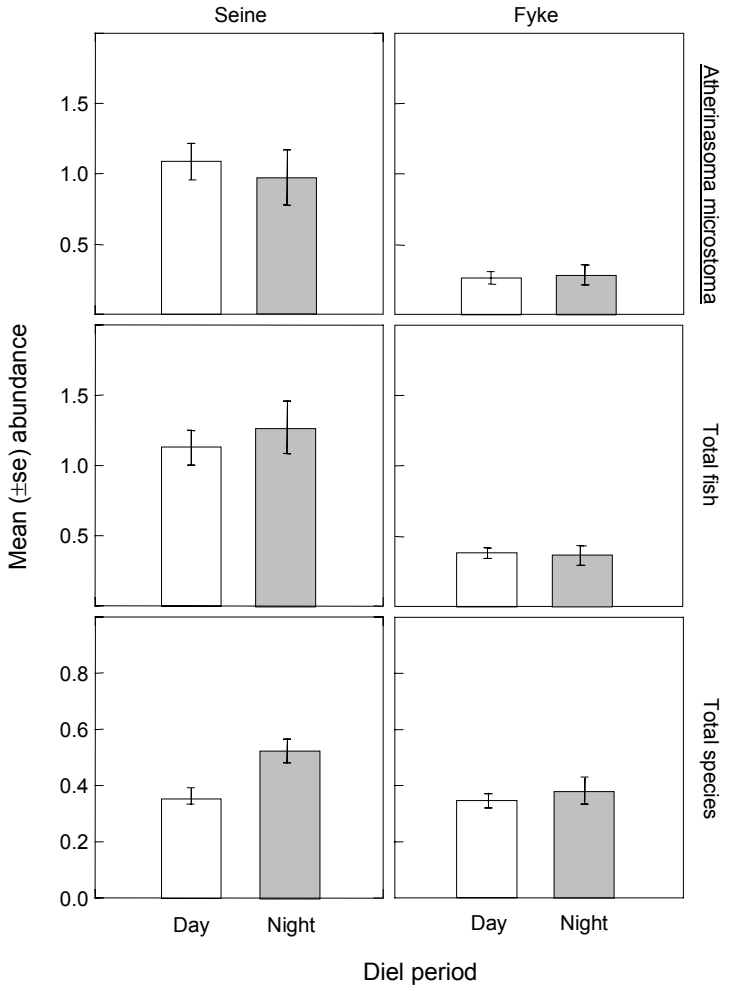

Figure 10. Mean (± se) abundance of Atherinasoma microstoma, total fish, and total species sampled with seine and fyke (hr^{-1}) nets during the day and night.

Physico-chemical variables

Water depth at the edge of the saltmarsh ranged from 10 to 63 cm ($\mu = 29 \pm 12$ cm). Barometric pressure ranged between 1008 hP and 996 hP ($\mu = 1003 \pm 5$ hP). Mean (± sd) salinity and temperature were 36 ± 2 ppt and 18 ± 4 °C, respectively. Linear regression analysis showed no significant relationship between abundances/species richness of fish sampled in fykes and seines, and salinity (ppt), water temperature, depth or barometric pressure ($P > 0.05$). Neither were there statistically significant relationships between depth, salinity, temperature, or air pressure and the number of *Atherinasoma microstoma* caught in fyke or seine nets ($P > 0.05$).

Dietary composition of fish in relation to 'prey' abundance

Dietary analysis was done on 309 fish including *Atherinasoma microstoma* (n = 211), *Aldrichetta forsteri* (n = 46), *Favonigobius lateralis* (n = 41), *Sillaginodes punctata* (n = 9) and *Heteroclinus adelaide* (n = 2) (Table 5). Eight major prey groups were identified in the diets of fish, 37 fish stomachs (12 %) were empty, and the relative importance of specific prey categories varied with the type of gear used to sample fish. Harpacticoid copepods were common in the guts of *Sillaginodes punctata*. *Aldrichetta forsteri* mainly consumed gammaridean amphipods or hemipteran insects. *Atherinasoma microstoma* consumed a broad range of prey, but diets were mostly composed of hemipteran insects or gammaridean amphipods (Table 5). *Favonigobius lateralis* preyed largely on gammaridean amphipods and polychaetes, and harpacticoid copepods were common, though to a lesser extent (Table 5). Insects (hemipterans) and insect larvae were consumed by *F. lateralis*, but most of their diet was made up of gammaridean amphipods. Gammaridean amphipods were the only taxa observed in the stomachs of *Heteroclinus adelaide*, although only 2 fish were sampled (Table 5).

A total of 6207 invertebrates were collected over 4 sampling periods from a total area ≈ 76 m^2 across 3 saltmarsh regions (Table 5). Potential prey were placed in 8 categories: gammaridean amphipods, harpacticoid copepods, other crustaceans (including isopods and mysid shrimp), molluscs (bivalves and gastropods), polychaetes, insects (including wasps, flies, ants and beetles), insect larvae and arachnids (Table 5). Nematodes were abundant in the core samples, but were excluded from analysis because they are not considered a common prey item for fish (Edgar & Shaw 1995b). Harpacticoid copepods, which are frequently consumed by fish (Jenkins et al. 1996), were the most abundant invertebrate category sampled across all regions of the saltmarsh (Table 5). There was no significant difference in the total abundance (ANOVA: $F_{2,9}$=0.285, P = 0.759) or species richness ($F_{2,9}$= 2.928, P =0.105) of invertebrates between the 3 regions of the saltmarsh (UV, E and V). Nor was there a significant difference in invertebrate numbers between sampling days ($F_{2,9}$ = 2.751, P = 0.117), but taxa richness varied significantly between sampling days ($F_{2,9}$= 6.434, P = 0.018). Using nMDS and ANOSIM, we could not differentiate between assemblages of potential prey sampled amongst the regions (UV, E and V) (R = 0.067, P = 0.135), so core samples were not differentiated according to region for comparison with fish diets.

The invertebrate groups identified in the diets of fish were also observed in the core samples across the saltmarsh/sand flat interface, but the degree of similarity between the dietary composition of some fishes and the core samples varied significantly between different regions of the saltmarsh (Fig. 11). Diets of *Atherinasoma microstoma* collected in a seine net were not consistent with potential prey collected from the vegetated (ANOSIM: R =0.338, P = 0.001; saltmarsh edge: R = 0.265, P = 0.001) or unvegetated (R = 0.283, P = 0.001) regions. Similarly, the diets of *Aldrichetta forsteri* collected in a seine net were not consistent with invertebrates collected at any of the regions of the saltmarsh (vegetated, R =0.588, P = 0.001; edge, R = 0.742, P = 0.001; unvegetated, R = 0.684, P = 0.001). The diet of Favonigobius lateralis collected in fyke nets was also not consistent with the assemblage of potential prey collected anywhere across the saltmarsh edge (edge, R = 0.505, P = 0.001; vegetated, R = 0.515, P = 0.001; unvegetated, R = 0.406, P = 0.001).

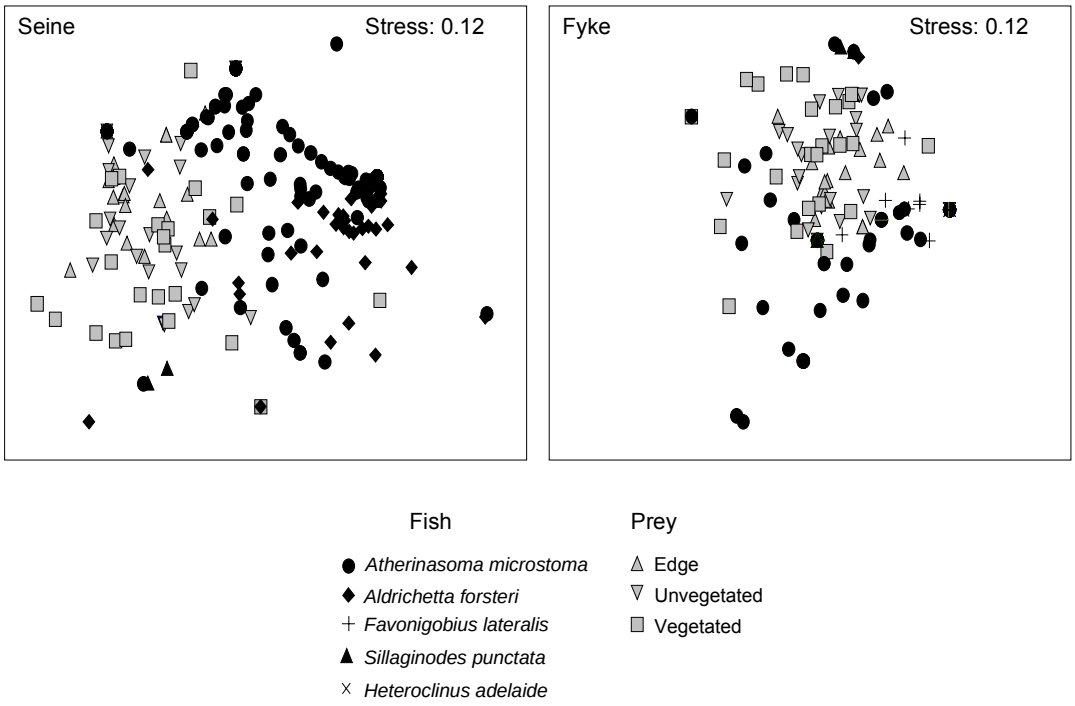

Figure 11. Two-dimensional ordination plot, based on Bray-Curtis dissimilarity measures, of the diets of abundant fishes (n > 6) sampled with seine and fyke nets, in relation to the potential prey sampled in the different regions of the saltmarsh (core samples).

DISCUSSION

Even though the frequency of inundation of saltmarsh flats in Port Phillip Bay was low, and marsh inundation depended less on astronomical tides and more on meteorological events, when flooded, the saltmarsh was frequently utilised by a range of fish. We sampled either diurnal or nocturnal periods on every occasion when the saltmarsh was flooded, 18 events in total. The tides in our study region are semidiurnal, therefore, the saltmarsh was often, but not always, depending on local changes in air pressure and tidal height, flooded twice in 24 hrs. Based on the average times of inundation of the saltmarshes, taken from the times used to adjust catches in the fyke nets, throughout the duration of our study (5040 hrs in total), saltmarshes were flooded for, on average, 3.5 hrs each high tide (7 hrs in a 24 hr cycle), or approximately 2.5 % of the time. Ten fish species occurred on the saltmarsh flats. Most of these were juvenile and small fishes (e.g. *Aldrichetta forsteri*, *Leptatherina presbyteroides*), and some form fisheries of considerable local economic value (e.g. *Sillaginodes punctata*). Similar fish taxa have been found in other studies of fish associated with saltmarshes in subtropical and temperate Australia (Morton et al. 1987, Connolly et al. 1997, Thomas & Connolly 2001). In the only other study of fish associated with saltmarsh in temperate Australia, Connolly et al. (1997) found that *Atherinasoma microstoma* and *Favonigobius lateralis* dominated the assemblages of fish sampled from saltmarsh flats.

The species of fish sampled in our study have also been recorded locally in shallow (< 2 m) seagrass (*Heterozostera tasmanica*) and over unvegetated sand (Jenkins et al. 1997b, Jenkins & Sutherland 1997, Hindell et al. 2000b). Previous studies have reported moderately lower abundances and species richness of fish in saltmarshes compared with mangroves and seagrass beds (Morton et al. 1987, Morton et al. 1988, Minello et al. 2003). Our study supports these findings in terms of species richness; fewer species

were sampled in the saltmarsh (10 spp.) compared with the work of Jenkins et al. (1997b), which reported 24 and 16 species of fish in seagrass and unvegetated habitat, respectively. Recent work by Baumgartner (unpublished data), who sampled 14 species of fish from intertidal mangroves, suggests that the habitat differences (i.e. seagrass versus saltmarsh) are not simply due to the inability of fish to penetrate intertidal regions. Even though species richness appears to be lower in saltmarshes compared with alternative habitats, the opposite pattern is apparent for fish abundances. We sampled 1348 fish with the seine net, with an average of ≈ 96 fish.haul^{-1}. Jenkins et al. (1997b) sampled approximately 60 fish.haul^{-1} using the same equipment (and sampling the same area ≈ 75 m^2) in local seagrass beds. These differences could simply reflect sampling artifacts, i.e. greater sampling efficiency in saltmarsh than seagrass. We could not find a study comparing seine net efficiency in saltmarsh and seagrass, but capture efficiency for several fish species in the same seine nets used in our study did not vary between artificial seagrass fronds with different morphologies (Jenkins and Sutherland 1997). The greater rigidity of saltmarsh stems compared with seagrass fronds might actually be predicted to reduce seine net efficiency, leading to patterns opposite to those observed. Despite the possibility that gear efficiency may influence the results, we believe the saltmarsh sampled in our study supports fewer species of fish, but total abundances may be greater than those sampled in habitats such as seagrass that have traditionally been considered to be valuable nursery habitat. Consequently, even though fish have access to saltmarsh for relatively short periods of time (i.e. 2.5 % of all time in our study), these habitats may be valuable for juvenile fishes.

Some of the species of fish sampled from saltmarsh in previous studies contribute to economically valuable fisheries. For example, mugilids, sillaginids and sparids form valuable fisheries around Australia, and juveniles from these families are relatively common in the subtropical saltmarsh (Thomas & Connolly 2001). Fishery species are also common in marsh habitats of North America (Rozas & Zimmerman 2000). Conversely, few commercial species have been found to use temperate Australian saltmarshes. Connolly et al. (1997) found that just a single species of commercial interest (*Aldrichetta forsteri*) used temperate saltmarshes, and it occurred in low numbers. In Port Phillip Bay, *Sillaginodes punctata* is an important commercial and recreational fisheries species, and the juveniles are closely associated with beds of seagrass and later with unvegetated patches of sand (Jenkins et al. 1997b, Jenkins & Sutherland 1997, Jenkins et al. 1998, Hindell et al. 2000a, Hindell et al. 2002). *S. punctata* has been collected in mangrove habitat (Baumgartner unpublished data), but recent work by Hindell and Jenkins (2004) suggests it is not common in this habitat. Our study is the first to consistently collect juvenile *S. punctata* from saltmarsh. Additionally, our study documents that juveniles from other commercially and recreationally valuable species, such as *Aldrichetta forsteri* and *Rhombosolea tapirina*, also inhabit saltmarshes. Saltmarshes may be more important than previously thought as habitat for economically valuable species in temperate Australia.

Environmental variables, such as salinity, temperature and turbidity are often correlated with attributes of fish assemblage structure in shallow estuarine habitats (Loneragan & Potter 1990, Cyrus & Blaber 1992), although habitat preferences of fish are not always explained by environmental variables (Laegdsgaard & Johnson 1995). In our study, neither abundances of fish or species richness varied significantly with temperature or salinity. Tidal periodicity and range are considered to be the primary determinants of the frequency and extent of flooding of saltmarshes, and a recent review by Minello et al. (2003) suggests that the nursery value of saltmarshes is at least partially dependent on tidal amplitude. In the present work, astronomical tides were less important in determining the extent of flooding of saltmarshes than local meteorological events. In fact, saltmarshes were only flooded during periods of low barometric pressure (< 1013), often associated with strong westerly winds and driving rain. With an increase in water depth (which in our study often correlated with decreasing pressure), a greater area of the saltmarsh is available for fish utilisation (Rozas 1995). Despite the marked variation in inundation depth on saltmarsh flats in our study, no relationship was found between water depth and fish or species

abundance. This is in contrast to work by Thomas and Connolly (2001) and Morton et al. (1987), who found water depth was positively related to species richness and abundances of some species, possibly as a result of the greater availability of 'habitat'. In our system, although flooding per se provides fish with access to saltmarsh, the degree to which saltmarshes are inundated appears to be inconsequential in shaping assemblages of fish.

The majority of surveys of fish using saltmarshes are done during the day (Peterson & Turner 1994, Connolly et al. 1997, Rozas & Minello 1998), and few studies have assessed how patterns of use vary between diel periods (Rountree & Able 1993). Our study showed that larger (SL > 90 mm) *Aldrichetta forsteri* and *Sillaginodes punctata* occurred exclusively at night. Previous work by Morton et al. (1987) and Rountree and Able (1993) has also shown that large individuals of several fish species occur during the night. Morton et al. (1987) suggested behaviour (i.e. predator avoidance) may have influenced diel size variation. Hindell et al. (2000b) found that atherinids were more abundant nocturnally in shallow seagrass beds in Port Phillip Bay, and suggested this pattern was driven by predator avoidance. It is also possible that the large fish sampled at night in our study reflects net avoidance during the day. Large fish may be capable of avoiding capture by swimming out of the way, but smaller fish may not have the physical capacity to avoid being caught by the active gear. Despite the exclusive occurrence of larger fishes in saltmarshes at night, our study showed little difference in fish assemblage structure between diel periods. Neither was there a significant degree of variability in species richness, fish abundance and abundances of the most common species (*Atherinasoma microstoma*) with diel period. The lack of diel variability in our response variables suggests that factors such as predator occurrence, prey availability or variation in physical conditions (e.g. temperature), which have been shown to vary between diel periods elsewhere (Rountree & Able 1993), may be less important in shaping diel patterns in the assemblage structure of fish in the temperate saltmarshes studied here.

Saltmarshes are considered to be a valuable nursery habitat because they provide juvenile fishes with protection from predation and adequate levels of food (Weisberg & Lotrich 1982, Halpin 2000). In the present study, most of the fish collected from saltmarshes were juveniles, and based on dietary analyses, piscivorous fishes were not present. These data are consistent with the idea that saltmarshes provide small fish with a refuge from predation.

Terrestrial invertebrates sometimes formed a large component of the diets of some species (e.g. *Atherinasoma microstoma*, *Aldrichetta forsteri*), and for most of the fishes sampled, we could not differentiate between the assemblages of prey consumed by the fish and the assemblages of potential prey sampled in the saltmarsh flats. For several species (e.g. *Heteroclinus adelaide*, $n = 2$; *Sillaginodes punctata*, $n = 9$), this pattern could be a by-product of the small sample sizes and the generalist nature of many estuarine fishes. For species such as *A. microstoma* ($n = 211$) and *A. forsteri* ($n = 46$), however, which were collected in relatively large numbers, our data are consistent with the idea that saltmarshes may be important as foraging habitat for small fishes. In contrast to previous work that has shown that meiofauna may be more abundant in vegetated than unvegetated habitats (Jenkins & Hamer 2001), the present study found that abundances of potential prey were similar between zones across the saltmarsh flat despite large differences in the degree of inundation and amounts of vegetation. This suggests that even though saltmarsh flats may be a foraging habitat for the fishes we collected, the similarity in prey abundances between regions of the saltmarsh raises the possibility that fish may have been feeding over the unvegetated areas adjacent to the saltmarsh flats. Future work should take a more spatially explicit approach to sampling fish before and after access to the saltmarsh flats to better estimate the importance of these areas in feeding.

'Aquatic' insects adapted to saline environments inhabit marine ecosystems, and hemipterans are amongst the most successful (Lehmkuhl 1979). For the most abundant fishes sampled in our study,

Atherinasoma microstoma and *Aldrichetta forsteri*, hemipteran insects were amongst the most common prey items, but these prey were amongst the least common invertebrates sampled in the cores. This apparent discrepancy between diets and prey abundance can be interpreted in several ways. It is possible that our method of sampling invertebrates underestimated abundances of hemipterans either because we did not sample far enough onto the saltmarsh, or the corer was not a useful method of sampling this taxa. Recent work has shown that hemiptera are present in the mid marsh zone of saltmarshes (Travers unpublished data). Alternatively, it is possible that fish are feeding on hemiptera that are floating on the surface of the water and have been 'washed-in' from other regions of the environment. Future research should attempt to separate the contribution of floating versus benthic sources of prey, and more attention needs to be placed on sampling potential prey from higher in the intertidal zone, even though this region may not be flooded very often.

Table 3. Summary of biological attributes measured (A – fish abundance, D – samples taken for fish diets, C- core samples) and approximate duration of inundation (estimated from the time fyke nets were fishing) for each sampling event.

Event	Date	Diel Period	Attribute	Flood time (hrs)
1	11/10/2002	Day	A	4.8
2	14/10/2002	Night	A	3.3
3	18/10/2002	Day	A	3.5
4	23/10/2002	Day	A	3.3
5	24/10/2002	Day	A	2.0
6	25/10/2002	Day	A	2.6
7	13/11/2002	Day	A	3.5
8	15/11/2002	Night	A	6.1
9	3/12/2002	Day	A	6.1
10	4/12/2002	Day	D, C, A	2.0
11	5/12/2002	Day	D, C, A	3.0
12	6/12/2002	Night	A	3.1
13	7/12/2002	Day	A	3.4
14	30/1/2003	Day	D, C, A	2.5
15	31/1/2003	Day	D, C, A	3.0
16	14/4/2003	Day	A	3.5
17	19/5/2003	Night	A	2.6
18	20/5/2003	Day	A	4.0

Table 4. Summary of frequency of occurrence (%), total number (n), mean (± sd) abundance (N) and the standard length (SL, mm) for each species of fish caught during each diel period (Day versus Night) across the 18 sampling events sampled with fyke and seine nets. * < 0.1. Means were calculated from 56 fyke and seine samples during the day, and 16 fyke and seine samples during the night.

				Day		Night	
Gear	Taxa	%	n	N	SL	N	SL
Fyke	Atherinidae						
	Atherinasoma microstoma	62	483	1.5 (2.8)	35.9 (13.5)	1.8 (3.2)	47.2 (13.3)
	Kestratherina esox	3	23	* (0.3)	68.9 (14.9)	0.2 (0.6)	78.5 (5.3)
	Leptatherina presbyteroides	4	3			* (0.05)	35.5 (0.7)
	Galaxiidae						
	Galaxias maculatus	7	14	0.1 (0.8)	37.7 (2.4)		
	Gobiidae						
	Favonigobius lateralis	40	136	0.6 (1.5)	31.8 (7.4)	* (0.1)	43.6 (14.9)
	Clinidae						
	Heteroclinus adelaide	4	4	* (*)	51.0 (21.5)		
	Mugilidae						
	Aldrichetta forsteri	6	9	* (*)	83.1 (77.6)	* (0.17)	255 (35.4)
	Pleuronectidae						
	Rhombosolea tapirina	6	5	* (0.13)	31.8 (7.5)		
	Sillaginidae						
	Sillaginodes punctata	9	11	* (0.1)	33.1 (7.9)	*	196
	Tetraodontidae						
	Tetractenos glaber	1	1	*	106		
Total fyke			689				
Seine	Atherinidae						
	Atherinasoma microstoma	93	1157	30.0 (36.1)	42.4 (11.0)	29.0 (52.9)	45.2 (16.2)
	Kestratherina esox	10	23			5.7 (5.8)	76.7 (14.5)
	Leptatherina presbyteroides	17	93			13.3 (10.5)	38.2 (9.5)
	Gobiidae						
	Favonigobius lateralis	17	11	2.0 (1.4)	36.71 (6.6)	1.0 (*)	41.3 (14.8)
	Mugilidae						
	Aldrichetta forsteri	22	61	9.5 (11.9)	41.9 (5.0)	1.3 (0.6)	46.5 (12.1)
	Sillaginidae						
	Sillaginodes punctata	17	13	2.0 (*)	29.5 (2.1)	1.8 (0.9)	92.7 (34.2)
Total seine			1358				
Total catch			2047				

Table 5. The proportional (%) abundance (N), proportional weight (W) and index of relative importance (IRI) of each prey category for each species sampled from saltmarsh habitat with the fyke and seine nets, and the proportional abundance of potential prey sampled with the cores in the edge (E), unvegetated (UV) and vegetated (V) regions of the saltmarsh. * includes isopods, mysid shrimp and decapods. ** represents values < 0.5.

			Marine Prey														Terrestrial prey								
			Gammaridean Amphipods			Harpacticoid Copepods			Other Crustaceans*			Molluscs			Polychaetes			Insects			Insect larvae			Arachnid		
Gear	Fish species	n	N	W	IRI	N	W	IRI	N	W	IRI	N	W	IRI	N	W	IRI	N	W	IRI	N	W	IRI	N	W	IRI
Fyke	*Aldrichetta forsteri*	5	20	95	4633	77	4	1624	2	1	60															
	Atherinasoma microstoma	85	7	0.2	217	22	**	157	28	**	66	2	**	2	2	100	102	23	**	683	14	0.01	98	2	**	4
	Favonigobius lateralis	37	36	49	6007	34	1	383							12	25	37	8		20	10	25	281			
	Heteroclinus adelaide	2	100	100	20000																					
	Sillaginodes punctata	7				55	1	1576	27	1	398				18	99	117									
Seine	*Aldrichetta forsteri*	41	1	0.1	8	5	**	34	67	2	674				2	87	89	21	9	2444	2	1	93	2	1	151
	Atherinasoma microstoma	126	7	47	2644	22	1	54	8	0	42	2	11	53	2	16	18	32	18	3052	24	4	178	2	1	22
	Favonigobius lateralis	4	47	28	3710										40	71	111	13	1	361						
	Sillaginodes punctata	2				55	25	7955	36	50	4318	9	25	1705												
Core	Edge		5			33			2			47			10			**			1			1		
	Unvegetated		4			53			5			19			18			**			**			**		
	Vegetated		1			44			5			18			19			2			8			1		

Chapter 3. Patterns of fish zonation in temperate mangroves, with emphasis on evaluating sampling artifacts

INTRODUCTION

Tropical mangroves are common in many estuaries and sheltered bays, and support rich assemblages of flora and fauna through the provision of shelter and stable substrata (Chapman & Underwood 1995, Lee 1999, Kathiresan & Bingham 2001). Many of the fish and invertebrates using mangroves support fisheries of considerable economic (Sasekumar et al. 1992) and social (de Boer et al. 2001) value, with fishery resources linked strongly to the 'health' of mangrove systems (Kathiresan & Rajendran 2002). Temperate mangroves are poorly studied in comparison to tropical systems, and there is little understanding of the importance of temperate mangroves as habitat for fish and invertebrates.

The relative value of mangroves, as compared with alternative (often adjacent) intertidal (e.g. mudflats, seagrass) and subtidal (e.g. coral reefs) habitats, to fish and invertebrates is well studied in the tropics (Blaber et al. 1989, Nagelkerken et al. 2000b, Mumby et al. 2004), and better studied for juvenile than adult lifestages (Robertson & Duke 1987). Mangroves are generally thought to be more important to juvenile fishes than sparsely vegetated mudflats or intertidal seagrasses. This idea is based largely on correlative data (Nagelkerken et al. 2000b, Hindell & Jenkins 2004), although recent experimental and review studies suggest mangrove structure minimises predation and maximises food availability (Laegdsgaard & Johnson 2001, Sheridan and Hays 2003). Conversely, Sheridan and Hays (2003) found that nekton densities were sometimes lower in mangroves compared with adjacent habitats. Only two studies have compared fish use of mangroves with unvegetated mudflats in temperate regions. Results were highly variable in time and space (Clynick & Chapman 2002, Hindell & Jenkins 2004), but there was often little difference in response variables (e.g. fish abundance) between the two habitats.

Comparisons of fish use among habitats provide gross estimates of habitat usage, but in anticipation of the need for a more process-based approach to attributing values of importance to mangroves as fisheries habitat (Sheridan & Hays 2003), and in recognition of the application of landscape-scale approaches to assessing fish-habitat relationships (Robbins & Bell 1994, Bell et al. 2001), there is a need for better understanding of spatially explicit patterns of fish use within habitats (among microhabitats). Mangroves have generally been treated as a single habitat unit, the value of which has been inferred from samples taken at one stratum (or zone), usually along the seaward edge (Hindell & Jenkins 2004), but fish and invertebrate assemblages may vary strongly with distance into mangrove forests. Fish abundances and biomass may be greater at 'inland' mangrove positions (Ronnback et al. 1999), with juvenile fish and prawns moving considerable distances into mangrove forests (Vance et al. 1996) depending on topography and current patterns (Vance et al. 2002). Conversely, assemblages of epibenthic nekton may be more abundant and diverse along the edge than inner forest regions of mangroves (Vance et al. 1996, Meager et al. 2003). Understanding how assemblages of fish differ between the edge and interior of mangroves, and how these patterns differ from adjacent habitats will have applications in improving sampling of mangroves *per se* and in understanding the consequences of habitat fragmentation.

Bottomless pop-up nets (sensu Connolly 1994b; also called bottomless lift nets, Rozas 1992a), hereafter referred to as pop nets, have been effective in sampling nekton from intertidal habitats such as saltmarshes and seagrass with high levels of structure, but have not been used in mangroves. Pop nets

are advantageous over alternative gears (e.g. throw, seine, drop, flume and block nets) because sampling efficiency is not reduced by dense vegetation, their use is not restricted to areas along navigable channels, and they can be set-off remotely (Kneib 1991, Rozas 1992b, Connolly 1994b). A potential drawback in using pop nets is that there is often significant disturbance of the sampling area by trampling and digging-in of net structure. This disturbance may attract or disperse fish and invertebrates, thereby confounding measures of association for a particular habitat type, but no study has attempted to address this issue experimentally.

There were 2 parts to this study. First, we assessed artifacts associated with setting pop nets (pop net artefact experiment) by investigating whether the disturbance of setting pop nets influenced local assemblages of fish in habitats of widely different structural complexity (intertidal seagrass versus intertidal unvegetated sand). Second, we compared fish assemblages among mangrove zones (pop net survey of fish in intertidal habitats), to (1) quantify densities of fish using mangrove forest (≈ 20-30 m landward of the seaward margin of the mangroves), mangrove edge (seaward margin of mangroves) and sparsely vegetated mudflat; (2) compare pop net catches to those of traditional gears such as beach seine nets; (3) examine whether inundation regimes influence assemblages of nekton using intertidal habitats.

MATERIALS AND METHODS

Study regions

The pop net artefact experiment was done in Port Phillip (144°38'57.594 E, 38°07'39.884 S – see Hindell et al. 2000), a large (1950 km^2), circular, semi-enclosed tidal embayment (Black et al. 1993), joined with the ocean of Bass Strait through a narrow rocky entrance. Tides in Port Phillip are semi-diurnal with a range of less than 1 m, currents are generally weak (Black et al. 1993), and there is little thermal or salinity stratification (Longmore et al. 1990). A study region was chosen in Port Phillip because it has large areas of intertidal seagrass (*Zostera muelleri* Irmisch ex Ascherson) amongst which are dispersed patches of unvegetated sand, we have excellent baseline data on fish-habitat associations here over the last 10 years (Jenkins & Black 1994, Jenkins & Wheatley 1998, Jenkins & Hamer 2001), and it was accessible in all weather conditions and enabled us to maximise the number of sampling occasions.

The pop net survey of intertidal habitats was done in Western Port (see Fig. 1), a tidally dominated system (semi-diurnal with a range of 2.3 m) with approximately 90 km^2 of intertidal mudflat, 15 km^2 of which is covered by a single species of mangrove, the grey mangrove (*Avicennia marina* Vierhapper). Individual trees here are smaller (< 3 m in height) than in the tropics, where this species may exceed 10 m (Harty 1997), and the stands of mangroves are largely restricted to protected regions of the bay where the substratum is muddy-sand. The study region in Western Port was chosen because it has large stands of mangrove, the substratum is firm enough to enable nets to be set by foot, and we have a good understanding of the local fish assemblages (Robertson 1980, Edgar & Shaw 1995a). The intertidal can be separated into 3 habitat zones: mangrove forest (≈ 20-30 m landward of the seaward edge of the mangroves); mangrove edge (seaward edge of the mangrove forest); and, intertidal mudflat (an area of the intertidal without mangroves at the terrestrial-marine confluence). Intertidal elevation gradually decreases from the mangrove forest to the edge, but the cycles and extent of tidal inundation were similar between the mudflat and the mangrove edge.

Study design

Pop net artefact experiment

The pop net artefact experiment assessed whether the disturbance of setting nets influenced fish assemblages using habitats of different structural complexity (seagrass, unvegetated sand). The design of

the pop nets was based on that of Connolly (1994b) and enabled nets to be constructed *in situ*. Each net had 5 × 5 m buoyant and weighted frames made from 20 mm PVC pipe (Fig. 12a). Silicone sealant was used to seal air inside the buoyant frame; steel rods (10 mm diameter by 4 m) were placed inside the weighted frame. The frames were attached to the top (buoyant frame) and bottom (weighted frame) of a net (20 m long × 1.2 m high with 1 mm mesh and a zip at one end to allow the net to be formed into an enclosure) by sliding 5 m lengths of frame into 'sleeves'. The 5 m frame components were joined via 20 mm PVC 'elbows'.

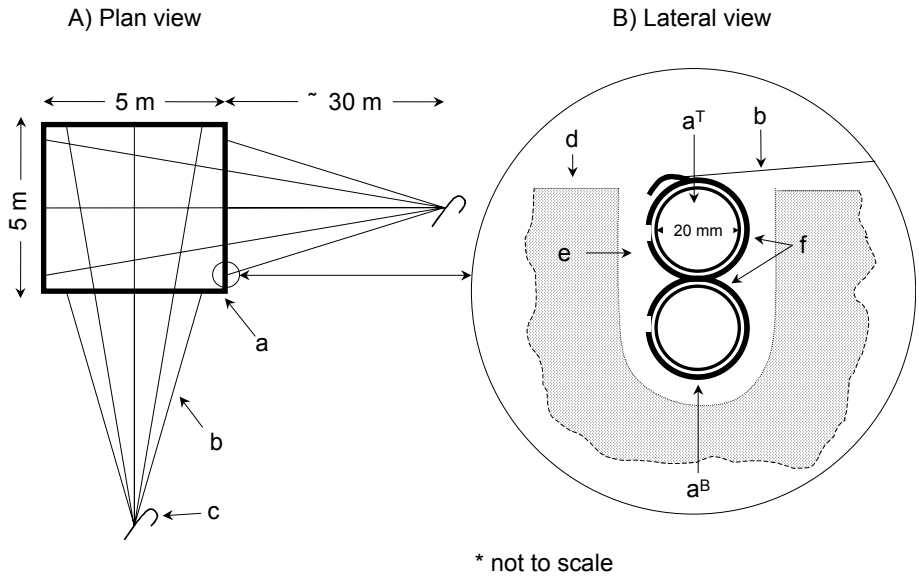

Figure 12. Design of pop nets showing a) view from directly above, and b) a cross section through the net frames seated within a channel. a – net frame (^{T} top - buoyant, ^{B} bottom - weighted), b – remote-release lines, c – pegs, d – surface of substratum, e – channel, f – plastic clips to hold top and bottom frame together before release.

On each of 5 different occasions (over 2 weeks), a single replicate of each of 3 net treatments (pop net + channel, channel only, unmanipulated) was set-up in seagrass and unvegetated sand at low tide. We could only set a single replicate of each treatment because of the short (2 hours) time available due to tidal inundation. The pop net + channel treatment consisted of a 5 × 5 m channel (5 cm deep and 10 cm wide) within which a pop net (including frames) was placed. The buoyant frame was attached to the weighted frame with 2, 20 mm plastic hose clamps (combined with a cable tie) placed at intervals along each side (Fig. 12b) and the net was held in the channel with steel pegs. The channel treatment was simply a 5 × 5 m channel of the same dimensions as above. The unmanipulated treatment was an area without any channel or pop net. Different plots of each habitat were used on successive occasions (i.e. nets were packed up and treatments re-applied to previously unmanipulated plots.

Fish using the treatments in each habitat were collected with a small beach seine net (10 m long × 2 m high with 1 mm mesh) at high tide. These nets have been used extensively to sample small and juvenile

fishes in seagrass and unvegetated sand habitat (Connolly 1994a, Jenkins et al. 1997b). The beach seine net was set around one corner of the treatment plot and hauled across to the opposite corner.

Pop net survey of fish in intertidal habitats

Pop nets were used to quantitatively sample fish in 3 mangroves zones (forest, edge, mudflat) on 7 different occasions. A different plot of each habitat was selected on each occasion (n = 7) so that nets were not repeatedly sampling the same area. Pop nets were set in the substratum according to the methods above (for pop net + channel). Care was taken to ensure there were no gaps through which fish could escape between the substratum and the weighted frame. A release mechanism, consisting of 20 kg monofilament line joined to plastic hose clamps at 3 positions along each side of the net (Fig. 12a), was attached to each pop net so that they could be set-off remotely. For each pair of opposing sides, lines were run to a single point 30 m away, which was marked with a buoy so that it could be found at high tide (Fig. 12a). The nets were built *in situ* so that they could be set around mangrove trees and other structures. At high tide, a person waded quietly to each buoy, and retrieved the steel peg with the lines attached. The monofilament lines were then simultaneously puled to release the buoyant frame, which rose to the surface within 1-2 seconds. Nets were monitored to prevent bird predation. When the tide had receded trapped fish were collected by hand.

A beach seine net (as in the pop net artefact experiment) was used to sample fish at high tide from mudflats so that we could compare this method with pop nets. The pneumatophore zone and mangrove forest could not be sampled with the seine net because of the high levels of structure. Setting and retrieving this seine net is well described by Jenkins and colleagues (Jenkins et al. 1997a, Jenkins et al. 1997b). Briefly, one of the 10 m ropes attached to the side of the seine net was set in a straight line, the net was then set at approximately 60° to the rope, and the final rope was set at approximately 60° to the net in the form of an equilateral triangle. The net was then hauled into a bin by 2 people, sampling an area of approximately 75 m^2. Water depth at the time of setting pop- and seine nets was recorded so that we could assess whether samples varied with the degree of tidal inundation.

In both the experimental and survey parts of our study, fish were identified to species and their length (from the snout to the caudal peduncle - SL, mm) was measured. In the pop net survey, the weight (g) of each fish was also recorded. Fish that could not be identified in the field were anaesthetised, preserved in ethanol and returned to the laboratory, where they were identified to species (Gomon et al. 1994), and their SL and weight measured. All work was done between October 2004 and January 2005.

Statistical analysis

Univariate data

All data were checked for normality and homogeneity of variances. Data that failed to meet these assumptions were transformed ($\log_{10} x + 1$) and reassessed.

For the pop net artifacts experiment, differences in fish abundance, species richness and abundance of gobiids (the most common family caught) among net treatments and between habitats were compared using 2-factor analyses of variance (ANOVAs). Net treatment and habitat were treated as fixed factors, sampling occasions provided the replication (n = 5). Differences among levels of fixed factors were assessed with *a posteriori* planned comparisons (Quinn & Keough 2002). Power analyses were used to assess our confidence in detecting a difference among net treatments if one actually existed (Quinn & Keough 2002), and were calculated based on an effect size of 100% (e.g. a doubling of fish numbers) using G*Power (Erdfelder et al. 1996). This effect size was within the range of variability recorded in previous

studies quantifying fish abundances in seagrass and unvegetated sand at our study region (Jenkins et al. 1997b, Hindell et al. 2000b).

For the pop net survey, fish abundance, biomass and species richness were adjusted by the area of habitat sampled - pop and seine nets sampled areas of 25 and 75 m^2, respectively. Differences in fish abundance, biomass and species richness among zone by gear combinations (i.e. pop net-forest, pop net-edge, pop net-mudflat, seine net-mudflat) were compared with 1-factor ANOVAs. Net by habitat combination was treated as a fixed factor and sampling occasions provided the replication (n = 7). Planned comparisons were used to assess whether variables (a) sampled with pop nets differed among zones, and (b) sampled only from mudflat differed between seine and pop nets. The relationship among variables (fish abundance, biomass and species richness) and water depth was analysed with regression analyses for zones and gear types separately. Probability values from these analyses were adjusted using a Bonferroni procedure (Quinn & Keough 2002) to reduce the type-I error rate. All univariate analyses were done with SYSTAT statistical software (Wilkinson et al. 1992).

Multivariate data

Similarity in the assemblage structure of fish among (1) net treatments and habitats (pop net artifacts experiment), and (2) habitats and gear types (pop net survey) were analysed with non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity measures (Clarke 1993, Clarke & Warwick 2001). Data were 4^{th} root-transformed to reduce the influence of numerically dominant species. *A priori* null hypotheses were tested statistically with analyses of similarity (ANOSIM), and similarity percentages (SIMPER) were used to calculate the relative contributions to differences by particular species. Where multiple pair-wise tests were done, *P*-values were adjusted using Bonferroni corrections to reduce the experimentwise type-I error rate (Quinn & Keough 2002). All multivariate analyses were done with Primer version 5.0 (Clarke & Warwick 2001).

RESULTS

Pop net artifacts

In assessing whether setting pop nets altered assemblages of fish associated with habitats of different structural complexity (seagrass and unvegetated sand), 464 fish from 14 species (9 families) were collected (Table 6). Assemblages of fish varied weakly between habitats (ANOSIM: Global R = 0.165, *P* = 0.044; Fig. 13), but not among net treatments (ANOSIM: Global R = -0.155, *P* = 0.990; Fig. 13). SIMPER showed that *Favonigobius lateralis* (36%), *Rhombosolea tapirina* (14%), *Heteroclinus perspicilatus* (11%) and *Nesogobius* sp. 1 (9%) contributed to 70% of the difference in assemblage structure between habitats.

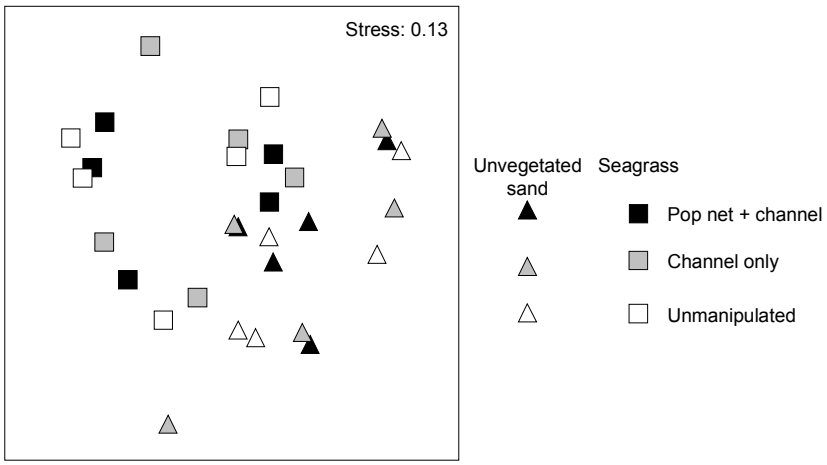

Figure 13. Multidimensional scaling plot, based on Bray-Curtis dissimilarity measures, comparing assemblages of fish among treatments of the pop net artifacts experiment (pop net + channel, channel only, unmanipulated) for each level of structural complexity (seagrass versus unvegetated sand). (n_{total} = 30).

There was little difference in total fish abundance, species richness and gobiid abundance among net treatments or between habitats (Table 7, Fig. 14). Only species richness differed significantly between habitats, with more species in seagrass than unvegetated sand (Fig. 14). Importantly, with respect to assessing whether setting pop nets in habitats of different structural complexity influenced fish samples, the interaction terms between pop net treatment and habitat were highly non-significant ($P > 0.586$) for all 3 variables. The statistical power to detect differences of 100% was adequate (Table 8). There was at least an 80% likelihood of detecting a significant ($P < 0.05$) change of 100% in abundances of fish (effect size) associated with the pop net + channel or channel only treatments compared to unmanipulated plots in seagrass and unvegetated sand. The power of the statistical analyses to assess whether species richness and abundances of gobiids varied between treatments was lower (40 – 50%) in unvegetated sand (Table 8), but 97% for species richness in seagrass.

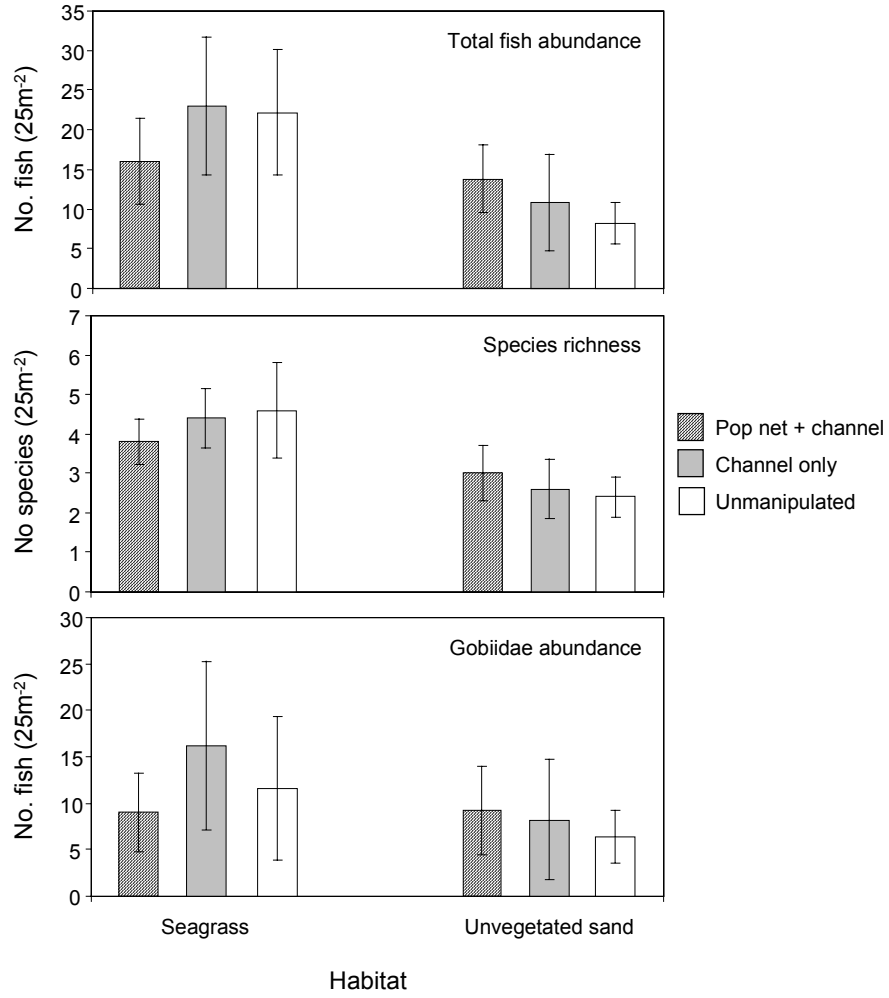

Figure 14. Mean (±se) total fish abundance, species richness, and gobiid abundance ($25m^{-2}$) among pop net experimental treatments (pop net + channel, channel only, unmanipulated) for each level of structural complexity (seagrass, unvegetated sand). (n_{total} = 30).

Pop net survey of fish use of intertidal habitats

The pop nets collected 15 species of fish from 9 families (Table 9). Benthic fishes such as gobiids (6 spp) dominated (42% of all fish caught), but semi-pelagic species (e.g. *Atherinasoma microstoma, Sillaginodes punctata and Aldrichetta forsteri*, *Arripis trutta* and *A. truttacea*) were also sampled. Many of the fishes, particularly the gobiids, were adult/subadult stages, but juvenile stages of *Sillaginodes punctata*, *Rhombosolea tapirina, Aldrichetta forsteri* and the arripids were also collected (Table 9).

The assemblage structure of fish differed strongly among habitats (ANOSIM: Global R = 0.603, *P* = 0.001; Fig. 15ab). Fish assemblages collected with the pop nets in the forest were different from those along the edge (ANOSIM: Global R = 0.357, *P* = 0.006; Fig. 15a) and mudflat (ANOSIM: Global R = 0.987, *P* = 0.001; Fig. 15a). SIMPER showed that the same 5 species (*Pseudogobius olorum*, *Atherinasoma microstoma*, *Mugilogobius paludis*, *Tetractenos glaber* and *Favonigobius lateralis*) explained at least 88% of the differences between forests and the other zones (edge and mudflat), 50% of which was due to *P. olorum*. The strong difference in assemblage structure between edge and mudflat (ANOSIM: Global R = 0.415, *P* = 0.001) was driven by 4 of the species from above, but *M. paludis* was replaced by *Arenigobius frenatus*. Assemblages of

fish collected over mudflat differed strongly between seine and pop nets (ANOSIM: Global R = 0.669, *P* = 0.001; Fig. 15b); *F. lateralis*, *T. glaber* and *A. frenatus* were more common in pop than seine nets (Table 9), and contributed more than 75% to the differences between gears.

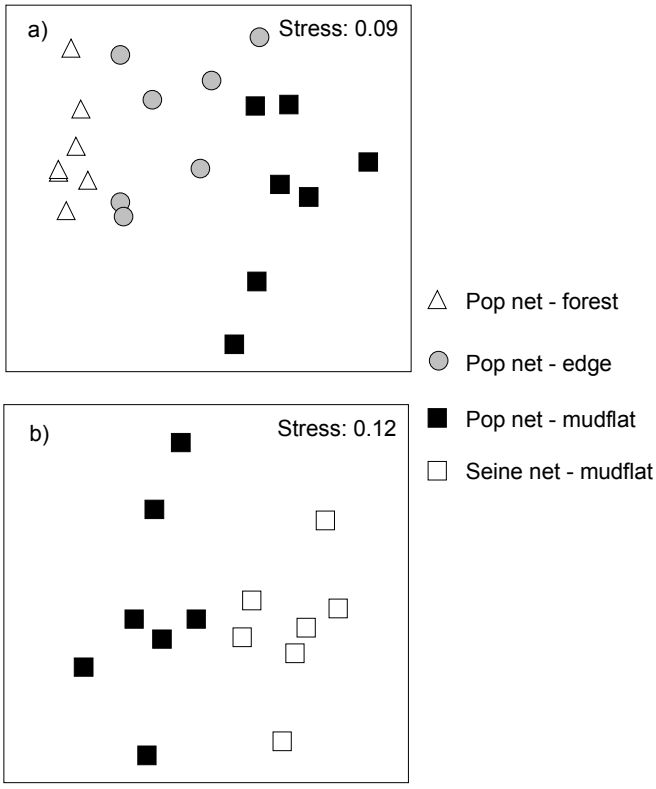

Figure 15. Multidimensional scaling plots, based on Bray Curtis dissimilarity measures, comparing assemblages of fish (a) among zones (forest, edge and mudflat) for pop nets only, and (b) between seine and pop nets in mudflat only. (n_{total} = 28).

Fish abundances (ANOVA: $df_{3,24}$, F = 9.790, *P* < 0.001) and species richness (ANOVA: $df_{3,24}$, F = 21.823, *P* < 0.001) differed significantly among zones, but fish biomass did not (ANOVA: $df_{3,24}$, F = 1.757, *P* = 0.185; Fig. 16). Fish abundances were greater in the forests (Planned Comparison - PC: $df_{1,24}$, F = 16.231, *P* < 0.001) and along the edge (PC: $df_{1,24}$, F = 6.835, *P* = 0.015) than in mudflats, but not significantly different between edges and forest (PC: $df_{1,24}$, F = 2.000, *P* = 0.170). There was no significant difference in fish abundance collected on mudflats between seine and pop nets (PC: $df_{1,24}$, F = 0.477, *P* = 0.496). Species richness was greater along edges than in forests (PC: $df_{1,24}$, F = 8.425, *P* = 0.008) or mudflats (PC: $df_{1,24}$, F = 20.805, *P* < 0.001), and differed little between forests and mudflats (PC: $df_{1,24}$, F = 3.743, *P* = 0.110), although the species composition was markedly different (see above). Significantly more species were sampled with the pop than the seine nets (PC: $df_{1,24}$, F = 21.871, *P* = 0.003).

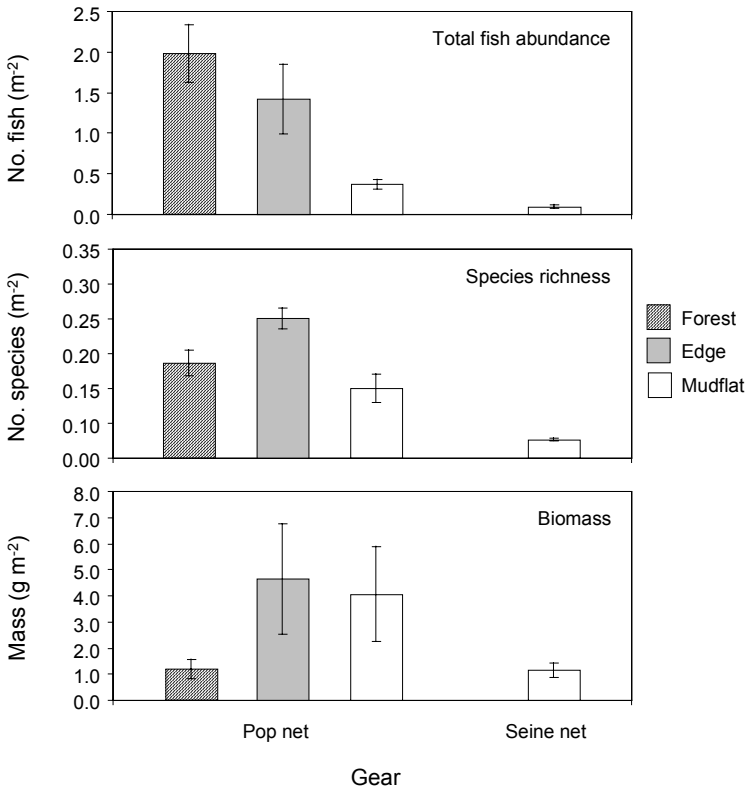

Figure 16. Mean (±se) total fish abundance, species richness and biomass (m^{-2}) among zones (forest, edge, mudflat) collected with pop and seine nets. (n_{total} = 28).

Fish abundance, species richness and biomass collected with the pop nets varied weakly with water depth, regardless of the habitat. Once the significance levels were adjusted (Bonferroni procedure), however, depth did not explain a significant amount of variability for any of the variables ($P > 0.016$).

DISCUSSION

Utility of pop nets in sampling fishes

Accurately quantifying abundances of fish in habitats with high levels of structure can be exceedingly difficult. Seine and trawl nets are largely limited to habitats with little 'rigid' structure such as seagrass and unvegetated sand. Fyke and gill nets, fish traps and underwater video are useful in sampling fish in habitats with high levels of physical structure, such as rocky/coral reefs and mangroves, but do not accurately measure density, only relative estimates of occurrence. Pop nets are advantageous over these gears in that they can be used to sample habitats with high levels of rigid structure *and* provide measures of density. Unfortunately, however, pop nets are effort-intensive to set up, and a consequence of this effort is that the area immediately adjacent to the net is greatly disturbed by, for example, human trampling and digging the net into the mud. This raises 2 questions, neither of which have been considered previously. First, does the disturbance influence estimates of assemblage structure by, for example, attracting some species and/or dispersing others? Second, are the effects of disturbance consistent between habitats of widely different structural complexity? The second point is pertinent given that the aim of many studies is to compare fish assemblages using alternative habitats, often with very different structural attributes. In our study, the disturbance of setting pop nets changed neither the

assemblage structure nor univariate measures of abundance (e.g. species richness or total numbers), regardless of the structural complexity of the habitat. Furthermore, these patterns were not simply a reflection of type II errors – concluding no effect when there actually was. Power analyses showed that we often had power in excess of 80% to detect changes in fish abundance among pop net treatments. Our results of no disturbance effect of setting pop nets enable subsequent differences (or lack there of) among habitats to be interpreted as habitat-specific processes rather than sampling artifacts.

Small (< 20 m) beach seines are commonly used to collect fish in soft sediments and provide reliable estimates of abundance for many nektonic taxa (Connolly 1994a, Jenkins et al. 1997b). Pop nets are also efficient methods of collecting small and juvenile fishes, and there is some evidence that they are actually better at sampling intertidal fishes than seine nets (Connolly 1994b, Rozas & Minello 1997). The pop nets in our study collected more species, greater biomass and larger numbers of fish than seine nets. The 'assessment of artifacts' component of our study showed that this difference was not simply due to sampling bias. As in the work of Connolly (1994b), the pop nets used in our study were highly effective in catching smaller sedentary species, particularly gobiids. Previous sampling in the same region with fyke and gill nets, however, collected few small fishes (Hindell & Jenkins 2004). Furthermore, in our study transient species such as *Arripis truttacea* and *Tetractenos glaber*, which move over scales of 100's to 1000's of m, were collected also, helping to dispel concerns that pop nets are restricted in sampling only small (< 5 cm) relatively sedentary (that move over scales of 10s of ms) species.

Assemblages of fish associated with temperate mangroves

Temperate mangroves are thought to have fewer species and lower abundances of fish than tropical systems (Clynick & Chapman 2002, Hindell & Jenkins 2004), possibly as a function of latitudinal trends in productivity (Saenger & Snedaker 1993, Alongi et al. 2000). Accurate estimates of density are rare in tropical/subtropical systems, and completely absent in temperate mangroves (until our study). In our study, total densities of fish in the forest (13.9 fish m^{-2}) exceeded those of Barletta et al. (2000) (2.8 fish m^{-2}). Mean densities of fish in the forest (2.0 fish.m^{-2}) and along the edges (1.4 fish.m^{-2}) in our study were also greater than those measured in the tropics by Vance et al. (1996) (1.0 fish m^{-2} in forest and 0.3 fish m^2 along mangrove edge), but less than Ronnback et al. (1999) (5.1 fish m^2). Notwithstanding potential differences in the gears used, total species richness was considerably lower in our study (15 spp overall and 8 spp inside mangroves) compared with Vance et al. (1996) along the creek/mangrove interface (26 spp) and Ronnback et al. (1999) (37 spp), but similar to Barletta et al. (2000) (14 spp). Our study represents the first quantitative estimates of fish density and species richness in temperate mangroves. While our study is consistent with previous work showing relatively low species richness in temperate systems (Clynick & Chapman 2002, Hindell & Jenkins 2004), fish densities are comparable to those measured in tropical and subtropical mangroves.

Variability in assemblages of fish using mangroves versus mudflats

Fish abundances and species richness in mangroves are often greater than those in adjacent mudflat (Kathiresan & Bingham 2001), and this pattern is thought to reflect greater provision of food and/or protection from predation via structure from mangrove structure (Laegdsgaard & Johnson 2001). The degree to which temperate mangroves support richer fish assemblages than adjacent mudflats depends strongly on location (Hindell & Jenkins 2004), but at most locations abundances and species richness are greatest in mangroves. Interpreting these patterns from previous tropical studies may have been difficult because fish assemblages using mangroves were often compared with those using alternative habitats at different depths or proximity to shore (e.g. Nagelkerken et al. 2000abc). In our study, however, large (100's m's) gaps between mangrove stands enabled us to sample mudflats with almost identical regimes

of tidal inundation and proximity to the shoreline. Although we collected a similar number of species between habitats, the taxa and fish abundances from mangroves were very different to those of mudflats. Small taxa dominated by gobiids occurred almost exclusively inside mangrove forests, whereas larger mobile species were common on mudflats. Fish abundances were > 4 times greater in mangroves than mudflats, while biomass showed the reverse pattern. Given the refuge role of mangroves, it is possible that small fishes may be confined to mangroves in our system by larger predatory fishes such as arripids, which are common along habitat edges and over unvegetated habitat (Robertson 1982, Hindell et al. 2000b). The larger fishes using mudflats, such as *Sillaginodes punctata*, may be too large for these predatory species to consume. Alternatively, mangroves may have lower abundances of infauna than adjacent habitats (Alongi & Sasekumar 1992). Many of the infaunal/epifaunal taxa important in the diets of fish use unvegetated mudflats (Edgar & Shaw 1995b), so greater biomass of fish (and larger size of fishes) using mudflat may also reflect energy budgets and local variability in the availability of prey.

The most abundant species collected from mudflats (*Sillaginodes punctata*, *Favonigobius lateralis* and *Tetractenos glaber*) in our study were consistently sampled from mudflats and seagrass beds throughout Western Port by Edgar and Shaw (1995a) and Robertson (1980). One of the most abundant species we collected in mangroves (*Pseudogobius olorum*) was common on mudflats adjacent to stands of mangroves in other regions of Western Port (Edgar & Shaw 1995a). The other abundant mangrove-associated fish, *Atherinasoma microstoma*, was not taken from unvegetated mudflats in either our study or by Robertson (1980), although in Robertson's study this species was common in seagrass. *Rhombosolea tapirina* was common across all habitats in our study, but previously only occurred over mudflats. The most conspicuous species sampled primarily from mangrove forests in our study (*Mugilogobius paludis*) was not recorded previously, and may be one of the few truly resident species in our temperate mangrove system.

The intertidal nature of mangroves may preclude their use by fish at low tide unless they can remain in deeper channels with residual water, take refuge in burrows, or have physiological adaptations enabling them to remain out of water (Barletta et al. 2000, Barletta et al. 2003). Fishes using forests in our study were dominated by small (< 30mm) gobiids, some of which (e.g. *Mugilogobius paludis*) are rarely caught outside mangroves (Robertson 1980, Edgar & Shaw 1995a). The mangroves in our study have few (if any) deeper channels with residual water at low tide, so 'resident' species must have physiological adaptations that enable them to cope with periods of emergence and/or seek refuge in burrows, buried in the mud or hidden in epiphytes attached to pneumatophores (Barletta et al. 2000). If fish were seeking refuge in crab burrows or were able to withstand extended periods of emergence, we would not have expected them to aggregate in the last remaining water at the lowest point of the pop net (the point from which they were collected). It is possible that some 'resident' species may follow the falling tide to the seaward edge of the mangroves, at which stage they seek refuge within epiphytes and in smaller water depressions, to minimise emergence times and desiccation. This is purely speculative, however, and further work is needed to better understand the fine-scale (m's) patterns of movement of intertidal fishes with tidal flooding regimes.

Zonation of fish assemblages in mangroves

Stands of mangroves are generally viewed as a single habitat, and sampling is commonly restricted to the edges of forests, often along the seaward edge of navigable channels. There is growing realisation, however, that fish assemblages vary greatly among micro-habitats within stands of mangroves. Ronnback et al. (1999) and Meager et al. (2003) have shown strong patterns of zonation for fish and invertebrates in tropical mangroves. Ronnback et al. (1999) found large differences in fish assemblages between micro-habitats (pneumatophore v prop roots) within mangrove forests, and richer assemblages

inside the forest than along the edge. Conversely, Vance et al. (1996) reported greater abundances and more species of fish along the mangrove fringe than at sites inside the forest. Meager et al. (2003) also observed greater numbers of epibenthic crustaceans at the mangrove edge than inner forest sites, and this pattern was not driven by microhabitat differences (vegetated versus cleared) between locations. Our results show that fish assemblages along mangrove edges are as different from those inside the mangrove forest as those in adjacent mudflats. Assemblages inside the forest were dominated by small taxa, particularly gobiids, whereas those along the edge consisted of more species and greater mean size. Fish abundance differed little between forest and edge, but species richness and biomass were lower in the forest than along the edge. Recent work by Vance et al. (2002) shows that differences in faunal abundances among regions within mangrove forests depend largely on local topography and water currents. In our study, water depth within a zone was a poor predictor of fish abundance, species richness, or biomass among sampling occasions. More likely, broad differences in physical structure, and the effects of this structure on productivity and faunal interactions (e.g. predation), are most important in shaping patterns of zonation of fish within mangrove forests.

The greatest species richness, biomass and abundances (the latter 2 in association with mudflats and forests respectively) of fish along the edges of mangroves in our study is consistent with work in tidal marsh systems showing significant edge effects. Invertebrate and vertebrate taxa may vary strongly about the edge of salt marshes, with species richness and abundance of nekton both increasing and decreasing with distance onto salt marshes (Peterson & Turner 1994, Minello et al. 2003). There can be strong links between infauna and nekton near the marsh edge when decreases in infaunal densities close to the marsh edge coincide with increased abundances of nekton predators (Whaley & Minello 2002), and strong positive relationships between nekton abundances and amounts of intertidal edge (Webb & Kneib 2002). While there can be a lot of variation in numbers of species and densities of nekton between locations within a marsh (Thomas & Connolly 2001, Osgood et al. 2003), the patterns depend on whether unvegetated or vegetated edge of the marsh is compared with the interior vegetated regions (Minello et al. 2003).

Coastal habitats such as mangroves are increasingly under threat from urbanisation, pollution and climate change (Alongi 2002). A consequence of these processes can be the fragmentation of existing habitat units, with concomitant increases in perimeter to area ratios as patch size decreases. There is a need to understand how the value of habitat changes with fragmentation (Forman & Godron 1986), and how assemblages respond to changes in landscape structure (McNeill & Fairweather 1993). Our results showed strong differences in fish assemblages between the edge and interior of mangroves. The fragmentation of mangroves (and subsequent increases in the relative amounts of edge to interior) is likely to increase the overall biodiversity of fishes using this habitat in our study region, but may detrimentally influence abundances of species resident within the mangrove forest.

Table 6. Summary of mean abundances (μN – fish m^{-2}) and mean lengths (μL – mm), total number of samples, total number of species and fish abundance (fish m^{-2}) among pop net treatments (pop net + channel, channel only, unmanipulated) in each level of structure (seagrass, unvegetated sand) in the pop net artefacts experiment. Figures in parenthesis represent standard errors. * only 1 fish caught.

	Seagrass						Unvegetated sand					
	Pop net		Channel		Unmanipulated		Pop net		Channel		Unmanipulated	
	μN	μL	μN	μL	μN	μL	μN	μL	μN	μL	μN	μL
Aldrichetta forsteri			0.09 (0.09)	94.9 (807)			0.04 (0.03)	79.4 (9.1)	0.03 (0.01)	52.0 (28.9)	0.02 (0.02)	107.5 (3.5)
Arenigobius frenatus	0.01 (0.01)	34.0 (*)	0.01 (0.01)	32.0 (*)	0.04 (0.03)	40.0 (13.1)						
Ammotretis rostratus							0.02 (0.02)	50.0 (0.01)			0.01 (0.01)	68.0 (*)
Favonigobius lateralis	0.26 (0.26)	25.9 (4.2)	0.54 (0.38)	24.4 (6.2)	0.38 (0.33)	24.4 (5.6)	0.31 (0.15)	36.2 (11.1)	0.23 (0.19)	35.8 (8.8)	0.19 (0.11)	39.1 (10.0)
Gymnapistes marmoratus	0.06 (0.04)	24.3 (2.6)			0.07 (0.04)	27.6 (3.2)						
Heteroclinus perspicilatus	0.05 (0.02)	48.7 (7.4)	0.09 (0.04)	50.2 (6.0)	0.07 (0.03)	50.9 (4.6)						
Lissocampus caudalis					0.02 (0.02)	49.0 (2.8)						
Meuschenia freycineti			0.01 (0.01)	47.0 (*)	0.04 (0.04)	41.4 (6.9)						
Nesogobius sp. 3	0.05 (0.02)	24.0 (1.5)	0.02 (0.02)	22.5 (0.7)	0.03 (0.03)	25.5 (1.3)	0.01 (0.01)	24.0 (*)	0.01 (0.01)	21.0 (*)		
Nesogobius sp. 1	0.05 (0.03)	29.0 (12.7)	0.07 (0.06)	34.6 (6.3)	0.01 (0.01)	42.0 (*)	0.05 (0.05)	41.8 (9.2)	0.08 (0.06)	37.5 (3.2)	0.06 (0.05)	36.1 (6.8)
Platycephalus speculator							0.03 (0.03)	50.8 (3.4)				
Rhombosolea tapirina	0.09 (0.04)	16.7 (6.9)	0.06 (0.03)	15.6 (2.8)	0.14 (0.07)	18.1 (3.9)	0.09 (0.04)	23.3 (10.3)	0.07 (0.04)	27.3 (15.7)	0.05 (0.03)	28.7 7.6)
Stigmatopora nigra	0.01 (0.01)	84.0 (*)			0.01 (0.01)	77.0 (*)						
Sillaginodes punctata	0.08 (0.08)	22.1 (0.7)	0.03 (0.01)	77.8 (37.3)	0.06 (0.05)	22.0 (0.8)	0.01 (0.01)	52.0 (*)				
Total Samples	5		5		5		5		5		5	
Total Species	9		9		11		8		5		5	
Total Abundance (fish m^{-2})	3.3		4.5		4.3		2.8		2.1		1.6	

Table 7. Summary of 2-factor analyses of variance comparing total fish abundance, species richness and gobiid abundance among net treatments (pop net + channel, channel only, unmanipulated) and between levels of structure (seagrass, unvegetated sand).

		Total fish abundance		Species richness		Gobiid abundance	
Source	df	F	*P*	F	*P*	F	*P*
Net treatment (N)	2	0.050	0.951	0.016	0.985	0.039	0.962
Habitat (H)	1	3.374	0.079	7.585	0.011	0.619	0.439
N × H	2	0.547	0.586	0.275	0.762	0.170	0.845
Error	24						

Table 8. Summary of statistical power analyses of changes of 100% (effect size) in the variables (total fish abundance, species richness, gobiid abundance) in the manipulated (pop net + channel, channel only) versus unmanipulated plots in each level of structure (seagrass, unvegetated sand). Mean values of variables (fish $25m^{-2}$) have been $log_{10}(x+1)$ transformed. Actual % differences between unmanipulated and manipulated treatments given in parenthesis. sd standard deviation. All analyses done at $F_{2,12} = 3.885$.

Habitat	Variable	Treatment			sd	Effect Size		
		Unmanipulated	Channel	Pop net	±	100%	λ	Power (%)
Unvegetated sand	Total fish abundance	0.84	0.82 (2)	1.03 (23)	0.40	1.65	14.125	85
	Species richness	0.34	0.33 (3)	0.42 (24)	0.23	0.67	6.840	53
	Gobiid abundance	0.68	0.60 (12)	0.79 (16)	0.56	1.36	4.926	48
Seagrass	Total fish abundance	1.21	1.19 (2)	1.09 (10)	0.40	2.42	30.361	99
	Species richness	0.61	0.62 (2)	0.56 (8)	0.23	1.21	22.329	97
	Gobiid abundance	0.80	0.93 (16)	0.83 (4)	0.56	1.59	6.808	53

Table 9. Summary of mean abundances (μN – fish m^{-2}) and lengths (μL – mm), total number of samples, mean water depth, total number of species, abundance (fish m^{-2}) and biomass (g m^{-2}) of fishes among habitats (forest, edge, mudflat) for each gear. Figures in parenthesis represent standard errors. * only 1 fish caught. ^{J} juvenile and ^{A} adult lifestages (based on sizes given by Gomon et al. 1994).

	Pop net						Seine net	
	Forest		Edge		Mudflat		Mudflat	
	μN	μL	μN	μL	μN	μL	μN	μL
Aldrichetta forsteri^{J}	-	-	-	-	-	-	0.001 (0.001)	59.0 (*)
Arenigobius frenatus$^{J A}$	0.029 (0.017)	36.2 (1.7)	0.091 (0.037)	38.7 (3.2)	0.063 (0.027)	43.4 (3.1)	-	-
Arripis trutta^{J}	-	-	0.006 (0.006)	75.0 (*)	-	-	-	-
Arripis truttacea^{J}	-	-	0.006 (0.006)	65.0	-	-	-	-
Atherinasoma microstoma$^{J A}$	0.246 (0.099)	20.4 (0.5)	0.154 (0.078)	20.1 (1.1)	-	-	-	-
Favonigobius lateralis $^{J A}$	-	-	0.126 (0.050)	30.8 (2.4)	0.120 (0.033)	29.9 (2.2)	0.020 (0.014)	21.9 (3.9)
Gobiopterus semivestitus^{A}	0.011 (0.011)	19.0 (1.0)	-	-	-	-	-	-
Mugilogobius paludis^{A}	0.171 (0.035)	27.8 (1.3)	0.006 (0.006)	40.0 (*)	-	-	-	-
Nesogobius sp. 1$^{J A}$	-	-	0.017 (0.017)	17.0 (0.6)	-	-	-	-
Omobranchus anolius^{A}	0.006 (0.006)	54.0 (*)	-	-	-	-	-	-
Pseudogobius olorum$^{J A}$	1.480 (0.273)	20.9 (0.2)	0.714 (0.310)	20.7 (0.3)	0.011 (0.011)	23.0 (2.0)	-	-
Rhombosolea tapirina$^{J A}$	0.017 (0.008)	20.7 (2.3)	0.029 (0.011)	36.0 (1.6)	0.023 (0.017)	22.9 (2.3)	0.010 (0.005)	27.4 (13.9)
Sillaginodes punctata^{J}	-	-	0.080 (0.023)	27.5 (1.2)	0.034 (0.024)	115.5 (4.2)	0.037 (0.013)	107.4 (11.5)
Siphaemia cephalotes^{A}	-	-	0.006 (0.006)	41.0 (*)	-	-	-	-
Tetractenos glaber^{A}	0.023 (0.012)	98.5 (2.4)	0.183 (0.081)	85.8 (3.6)	0.120 (0.062)	98.8 (2.5)	0.028 (0.007)	98.0 (3.5)
Total samples	7		7		7		7	
Mean water depth (cm)	0.6 (0.3)		0.9 (0.2)		0.9 (0.2)		0.8 (0.1)	
Total Species	8		12		6		5	
Total Abundance (fish m^{-2})	13.8		9.9		2.6		1.3	
Total Biomass (g m^{-2})	8.4		32.5		28.4		16.1	

Chapter 4. Effects of diel period, gear selectivity and predation on patterns of microhabitat use by fish in a mangrove dominated system in southeastern Australia

INTRODUCTION

Mangroves cover significant areas of the intertidal zone of protected bays and inlets throughout the tropics, where they support rich assemblages of algae, invertebrates, birds and fish (Alongi 2002). In the last 50 years, around 50% of the worlds mangroves have been destroyed by, and remain under threat from, human disturbance through urban development, farming and pollution (Alongi 2002). In Australia, most of our understanding of the value of mangroves to marine fauna, particularly fish, comes from the tropics. We have little understanding of faunal-mangrove associations at temperate latitudes.

High abundances of juvenile fish and invertebrates in mangroves has led to the idea that mangroves are valuable 'nursery' habitat (Robertson & Duke 1987, Laegdsgaard & Johnson 1995, Nagelkerken et al. 2001) because they provide a source of food and structure that provides a refuge from predators (Bell et al. 1984, Laegdsgaard & Johnson 2001). Conversely, not all mangroves have been shown to be important habitat (or more important than adjacent habitats) for juvenile and small fishes (Ley et al. 1999, Clynick & Chapman 2002, Hindell & Jenkins 2004). Regardless of the pattern, there is little experimental evidence to either support or refute the processes driving alternative patterns (Sheridan & Hays 2003). Experiments in subtropical Australia showed that juvenile fish (*Sillago* spp., *Liza argentea* and *Atherinomorus ogilbyi*) sought shelter in artificial pneumatophores in the presence of predators, and *Sillago* spp. were less susceptible to predation and had greater rates of feeding in mangroves than adjacent mudflats (Laegdsgaard & Johnson 2001). This work was done in subtropical Australia and focussed on between-habitat differences in food and predation, but, given the different structural zones within mangroves (microhabitats), experimental work is needed to assess the role of processes such as predation in structuring fish assemblages within temperate mangroves.

Structural attributes can vary in subtle ways among regions within habitats (microhabitats), leading to small-scale (meters to tens of meters) variability in faunal assemblages (Alevizon et al. 1985, Jernakoff et al. 1996). Mangroves also vary greatly in levels of structural complexity within patches (Ronnback et al. 1999, Ronnback et al. 2002), often growing in distinct bands at different distances from the waters edge (Underwood & Chapman 1995a, Clarke 2004). These patterns may influence local abundances of epifauna across regions (or microhabitats) within mangrove forests (Satumanatpan et al. 1999, Satumanatpan & Keough 2001). Despite the apparent delineation of areas within mangroves, most studies have treated them as a single habitat (Hindell & Jenkins 2004).

The strong patterns in change of structural elements within mangroves, and their potential effects on faunal assemblages highlights a need for spatially explicit sampling. Most studies, however, have sampled a single region of mangroves, such as channels (Pinto 1987, Chong et al. 1990) and creeks (Bell et al. 1984, Robertson & Duke 1987, Lin & Shao 1999), or along edges (Laroche et al. 1997, Hindell & Jenkins 2004). Additionally, mangrove nekton are commonly sampled with semi-quantitative 'passive' methods

such as gill and fyke nets, which are efficient methods of sampling nekton abundance but do not measure density. Stake, block and drop nets have been used to provide spatially explicit estimates of fish density (Thayer et al. 1987, Morton 1990, Lorenz 1999, Ronnback et al. 1999), but more recently bottomless pop nets (hereafter referred to as pop nets) have shown promise in quantifying densities of juvenile fishes within mangroves (Hindell & Jenkins in press). To date, few studies have assessed how faunal samples change between highly quantitative and qualitative methods, nor discussed the implications of sampling bias in shaping our understanding of small-scale faunal-habitat associations.

Recently, there have been greater efforts to describe patterns of microhabitat use by prawns (Vance et al. 1996, Ronnback et al. 1999, 2002, Vance et al. 2002), barnacles (Satumanatpan et al. 1999, Satumanatpan & Keough 2001) and crabs (Dahdouh-Guebas et al. 2002) within mangroves. Just 2 studies have investigated microhabitat use by fish within mangroves. Vance et al. (1996) found greater numbers of fish at the mangrove/channel fringe, where the structure in the water column was least. Ronnback et al. (1999) found fewer fish at the mangrove fringe and greater numbers deeper in the forest. Both studies found more fish in less structured *Avicennia* mangrove, smaller individuals inside mangroves than along the fringe, and few piscivorous fish deep in the forest. These patterns were consistent with a model of fish using the interior of mangroves as a refuge from predation, but no experiments were done to test this hypothesis.

Tethering mobile prey is useful in comparing predation rates in different habitats (Aronson et al. 2001, Haywood et al. 2003), particularly in demonstrating the refuge value of mangroves for fish (Laegdsgaard & Johnson 2001). Tethering, however, may alter an individuals behaviour and escape responses, making them more susceptible to predation (Peterson et al. 2001, Haywood et al. 2003). Prey lost from tethers are generally assumed to be eaten (Acosta & Butler 1997, Haywood et al. 2003), but predation rates may be overestimated if prey escape their tethers. Laegdsgaard and Johnson (2001) controlled for this by tethering fish inside cages in each habitat, providing an estimate of fish lost through means other than predation. Future studies comparing survival of tethered prey across habitats of different structure should employ a similar approach to separate predation effects from artefacts of tethering.

Fish-habitat associations often vary between diel periods (Rooker & Dennis 1991, Gibson et al. 1998, Nagelkerken et al. 2000a). In mangroves, diel migrations by some species are thought to reflect behaviour related to feeding or shelter (Laroche et al. 1997, Nagelkerken et al. 2000a). In the only study on diel fish variations in temperate mangroves, Clynick and Chapman (2002) found no difference in fish abundance and species richness between day and night samples. Different microhabitats within mangroves provide varying levels of food and shelter for fish (Ronnback et al. 1999), and while these patterns may facilitate strong differences in assemblages of fish across microhabitats between times of the day, no study has attempted to explore this relationship.

To increase our understanding of the role of temperate mangroves in supporting assemblages of fish, the present study aimed to (1) quantify abundances of fishes using mangroves in temperate Australia, (2) assess whether fish assemblages varied across mangrove microhabitats between diel periods, (3) measure the consistency in fish samples between quantitative and qualitative sampling methods, and (4) determine the importance of predation in shaping microhabitat use by fish within mangroves.

METHODS

Study Site

This study was done in the Barwon River Estuary, Victoria, Australia (Fig. 17), between September 2003 and April 2004. The estuary is tidally dominated, with semi-diurnal tides that range in height between 1 and 1.7 m above mean low water (OZESTUARIES 2000). Natural vegetation in the catchment has been

largely cleared for urbanisation, but a single species of mangrove, *Avicennia marina* (Forsskal) Vierhapper, covers large areas of the intertidal mudflat. The remaining intertidal region is largely unvegetated mud flat with a sparse covering of seagrass (Zosteraceae: *Zostera muelleri,* Irmisch ex Ascherson). The stands of *A. marina* are typical of those elsewhere in Victoria's bays and inlets – trees are stunted in growth (< 3m in height) and distributed in small discontinuous stands (Harty 1997). Victoria's mangroves generally lack the small but deep channels draining mangrove forests in tropical systems, and nekton associated with mangroves must therefore be sampled directly from the forest rather than tidal creeks and rivulets draining the intertidal flats. The mangroves are inundated each high tide, but the length of time and depth of inundation depends on tidal regimes and local climatic conditions. During low pressure weather patterns and strong westerly winds, the water level and mean tidal range inside Victoria's bays and inlets increases (Jenkins & Black 1994).

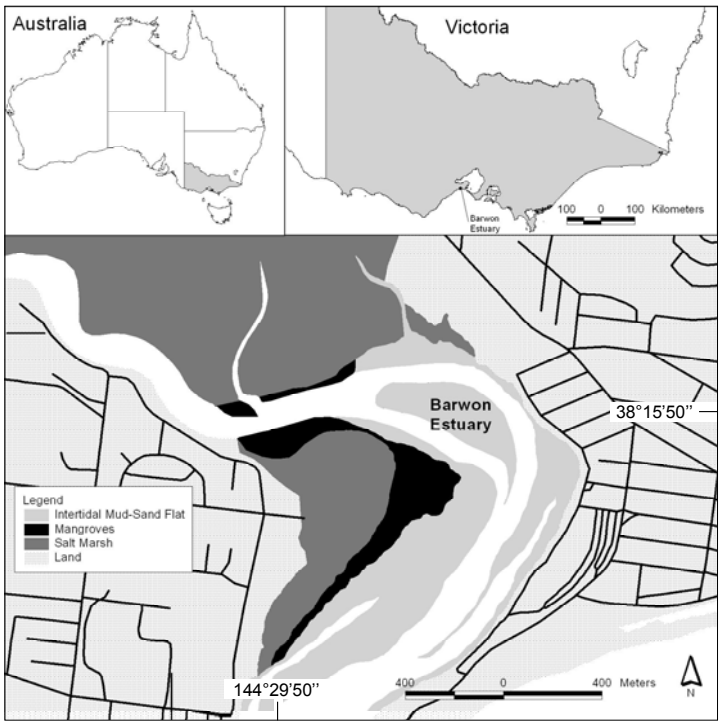

Figure 17. Location of the study area in the Barwon River. Inset: Location of the Barwon River in Australia. Sampling was done in and around the mangrove habitat (shown in black) throughout the study area.

The mangrove 'habitat' in our study area can be divided into three microhabitat types based on gross structural attributes: forest, pneumatophores, and channel. The forest is dominated by mangrove trees and dense pneumatophores (aerial roots of mangroves, mean length (± se) = 19.4 ± 5.4 cm, mean density (± se) = 78.8 ± 7.4 m^{-2}), and occurs in narrow bands ≈ 10 – 20 m seaward from the top of the intertidal. The pneumatophore microhabitat lacks mangrove trees but has many pneumatophores, which are similar in length (mean ± se = 16.0 ± 2.1 cm) but less dense (mean ± se = 38.4 ± 4.0 m^{-2}) than in the forest. Pneumatophores inside and outside the forest support a variety of algal (e.g. *Ulva* spp., *Enteromorpha*

spp., *Caloglossa* spp. and *Cantenella* spp.) and molluscan/crustacean taxa (e.g. *Eliminius modestus*, *Austrocochlea constricta*, *Bembicium auratum*). The channel microhabitat is defined by the absence of pneumatophores and trees and is the area immediately seaward (to 10 m) of the pneumatophore microhabitat.

Survey 1 - Variability in fish assemblages among microhabitats and between diel periods

To assess whether assemblages of fish varied among microhabitats within mangroves (forest, pneumatophore, channel) and between diel periods, fish in each microhabitat were sampled day and night on 5 separate occasions each. Sampling occasions were chosen which corresponded with spring tides to ensure that mangrove forests were flooded (Hindell & Jenkins 2004). On each sampling occasion (day or night), fish in each of the microhabitats were sampled with replicate (n = 2) fyke and gill nets (i.e. 6 fyke and 6 gill nets were set, 2 in each microhabitat). Care was taken to ensure nets of the same type were not set along-side one another within or among microhabitats. Fishing times of each net were recorded for each sampling occasion.

Fyke nets are a common method of sampling fish associated with mangroves, and are particularly useful in targeting small fish (Lin & Shao 1999, Clynick & Chapman 2002). The fyke nets used here are described in Hindell and Jenkins (2004). Briefly, nets were made from 4, 0.7 × 0.7 m aluminium frames, around which 6 mm black honeycomb mesh was attached. A 6 × 0.7 m length of the same mesh (wing) was attached to each side of the net opening. Floats and a lead line were attached to the top and bottom of the wings, respectively. Fyke nets were set so that the opening (and wings) faced landward in each microhabitat. Fyke nets were set and retrieved approximately 2 – 3 hrs before and after, respectively, mean high water. The maximum water depth at each fyke net was recorded so that we could further assess how variability in water depth in each microhabitat influenced fish assemblages. Fyke nets were set and collected on foot, taking care not to disturb surrounding pneumatophores.

Gill nets are efficient methods of sampling transient species with a variety of morphologies, particularly larger (> 15 cm total length) fishes (Hindell et al. 2000b). The gill nets used here are described in detail by Hindell and Jenkins (in press). Briefly, nets comprised 5, 7 × 1.5 m long panels of mesh, each of a different size (2.5, 3.8, 5.0, 6.3, 7.6 cm stretch mesh), joined to make a 35 m-long net. The different mesh sizes enabled us to target fish of different sizes because there is a high degree of size-selectivity for specific mesh sizes (Acosta & Appeldoorn 1995, Gray 2002). Floats and a lead-line were attached to the top and bottom, respectively, and 2, 3 kg weights were attached to each end to prevent the nets from moving with the currents. Gill nets were set along the centre-line of each microhabitat, parallel to the landward margin of the shoreline ≈ 2 hr before, and collected ≈ 2 hr after high tide. Gill nets were set and retrieved from a boat or on foot depending on the water depth.

Where possible, all fish were returned alive to the water after identification to species, and their weight (g) and length (SL – length from the tip of the snout to the posterior end of the caudal peduncle, mm) measured. If this was not possible, fish were anaesthetised and preserved in 90% ethanol. All fish were identified to species (Gomon et al. 1994), and their weight and length recorded.

Survey 2 – Fyke versus pop nets in mangroves

Gear selectivity can vary with habitat and water depth (Rozas & Minello 1997). It was possible that patterns observed in fish assemblages between microhabitats in the present study could reflect sampling efficiency. To assess whether differences in fish assemblages sampled with gill and fyke nets among microhabitats were 'real' or due to sampling bias, fyke and pop nets were used to sample fish on 5

additional occasions during the day. On each occasion, a single fyke and pop net was set in each of the forest and pneumatophore microhabitats. No nets were set in the channel because water depth and currents were unsuitable for sampling with pop nets. Survey 2 was done directly after completing survey 1 so that we could better compare the findings from the 2 surveys.

Pop nets are a highly quantitative method of sampling fish in intertidal habitats with high levels of structure (Rozas 1992a, Connolly 1994b). The operation and design of pop nets is well described by Connolly (1994b) and Hindell and Jenkins (in press). Briefly, each net had 5 × 5 m buoyant and weighted frames made from 20 mm PVC pipe. Silicone sealant was used to seal air inside the buoyant frame; steel rods (10 mm diameter by 4 m) were placed inside the weighted frame. The buoyant and weighted frames were attached to the top and bottom, respectively, of a net (20 m long × 1.2 m high, 1 mm mesh and a zip at one end to allow the net to be formed into an enclosure). With the top and bottom frames together (and the net in between) the pop nets were gradually pushed into the substratum until the top of the net was level with the surface, thereby reducing the need for a trench to be dug. A release mechanism, which consisted of 20 kg monofilament line attached to plastic clamps at 3 positions along each side of the net, was attached to each pop net so that they could be set-off remotely. For each pair of opposing sides, lines were run to a single point ≈ 30 m away, which was marked with a buoy so that it could be found at high tide. On high tide, 2 people (1 at each buoy) retrieved the steel pegs with lines attached and simultaneously pulled the monofilament lines to release the buoyant frame, which rose to the surface in 1 to 2 secs. Nets were monitored to prevent predation by birds on fish, and when the tide had receded, trapped fish were collected by hand, anaesthetised and preserved as above.

Predation across microhabitats within mangroves

Variation in predation pressure at different positions within mangroves is thought to explain changes in fish assemblages across microhabitats (Vance et al. 1996, Ronnback et al. 1999). To determine if predation varied across microhabitats within mangroves, the survival (fish remaining tethered) of juvenile *Aldrichetta forsteri* (Mugilidae) Valenciennes was measured in the forest, pneumatophore and channel with and without pressure from predation.

On each of 5 separate sampling occasions during the day, 3 juvenile (< 10 cm SL) *Aldrichetta forsteri* were tethered in each of 3 predation treatments (predator exclusion cage, cage control, no cage) in each microhabitat. Predator exclusion cages provided a means of assessing whether fish were missing from tethers through means other than predation. Cage controls assessed whether differences in survival between caged and uncaged areas were due to the structure of the cage. Uncaged treatments assessed 'natural' predation levels in each microhabitat. Each cage was constructed from a 1 × 1 × 0.3 m wooden frame enclosed by 1 cm green plastic mesh. This mesh size excludes fish preying on juvenile mugilids (Hindell et al. 2001). A 5 cm steel sheet was attached to the bottom of each cage so that it could be secured in the substratum. Cage controls were made from the same materials as exclusion cages but had 0.5 × 0.2 m holes cut in each side to allow predatory fish entry. *A. forsteri* were tethered to clips and attached to monofilament line (see below) that stretched between steel stakes attached to the cages (exclusions and controls) at opposing corners. Uncaged treatments lacked any cage structure but fish were tethered to the same length of monofilament line stretched between 2 steel stakes.

The 'predatory' and 'prey' species highlighted in the current study were based on stomach contents analyses of fish by Hindell et al. (2000b), Edgar & Shaw (1995b) and Robertson (1982). The western Australian salmon (*Arripis truttacea*, Cuvier), in particular, are voracious predators on juvenile and small fish from a wide variety of species including mugilids, and are often among the most abundant fishes in shallow estuarine habitats during the day (Robertson 1982, Edgar & Shaw 1995b, Hindell et al. 2000b).

Juvenile *Aldrichetta forsteri* were chosen as prey for three reasons: (1) they are common throughout the study system and are among the most common species sampled in temperate Australian mangroves (Hindell & Jenkins 2004); (2) they are a common prey species for predatory fishes such as *Arripis truttacea* and *Acanthopagrus butcheri* (Sparidae) Munro (Hindell et al. 2000b); and, (3) they are easy to tether, robust and tolerant to handling. On each occasion, *A. forsteri* were collected < 2 hrs before tethering with a 6 × 1.5 m, 10 mm seine net from nearby mudflats. Each fish was attached to a 15 cm length of 5 kg monofilament line which was tied to the bottom jaw of fish at one end and to a small clip at the other. When water depth in the forest reached ≈ 20 cm, fish were tethered in each cage treatment in each microhabitat (n = 27 fish on each sampling occasion). The standard length of each fish was measured prior to tethering to ensure that similarly sized fish were used in each treatment. The numbers of fish remaining in each treatment after ≈ 2 hrs (time of forest inundation) were recorded.

Data analysis

Univariate analysis

All data were checked for normality and homogeneity of variance using box and residual plots (Quinn & Keough 2002). Where data did not meet these assumptions, they were transformed (Log_{10} or arcsine) and reassessed. Fish abundances were always adjusted for time (fyke and gill nets) or area (pop nets) fished. Survival of tethered fish was adjusted by time of tethering.

In survey 1, variability in abundances, biomass and species richness (the number of species) between diel periods, and among sampling occasions and microhabitats was analysed using 3-factor partially nested analyses of variance (ANOVAs). Microhabitat (forest, pneumatophores, channel) and diel period (day, night) were treated as fixed factors, sampling occasion was treated as a random factor nested within diel period, and nets (fyke, gill) were analysed separately. The relationships between total species richness and abundance, pooled across diel periods and gear, and water depth were analysed using regression analyses. In survey 2, 2-factor randomised blocks ANOVAs were used to assess variability in fish abundances between microhabitats (fixed factor: pneumatophore, forest) and sampling occasions (random factor, 1 to 5) for each gear separately (fyke v pop nets). Tukey's tests were used to assess the degree to which dependent variables differed between levels of independent factors for both sets of analyses. In the predation experiment, variability in survival of juvenile fish between microhabitats and caging treatments (closed cage, open cage, no cage) was analysed with a 3-factor randomised blocks ANOVA. Non-significant ($P < 0.05$) differences among microhabitats and caging treatments were assessed with *post hoc* power analyses. An effect size (ES) of 66% was chosen to correspond with the loss of 2 fish from an experimental cage. Power analyses were done using GPower (Erdfelder et al. 1996). All univariate analyses were done using SYSTAT (Wilkinson et al. 1992).

Multivariate analysis

Multidimensional scaling (MDS), analysis of similarity (ANOSIM) and similarity percentages (SIMPER), based on Bray-Curtis dissimilarity indices calculated from fish abundances, were used to assess whether fish assemblages varied (1) among microhabitats and between diel periods (survey 1), and (2) between gear types and microhabitats (survey 2). In survey 1, analyses were first run on raw (non-transformed) data. The same analyses were then run on transformed (log(x+1)) data, and, if the results were the same regardless of whether the data had been transformed, then the results from the analyses of raw data were used (as was the case in this study). In survey 2, data were transformed to presence/absence because even though the gears used (fyke and pop nets) provide very different estimates of abundance (fyke – $fish.hr^{-1}$, pop – $fish.m^{-2}$), we still wanted to assess whether the overall assemblage structure differed between gear

types. Sampling occasions when no fish were sampled were removed from analyses. Multivariate analyses were done using PRIMER (Clarke & Warwick 2001).

RESULTS

Variability in fish assemblages among microhabitats and between diel periods (Survey 1)

A total of 693 fish (20 spp. from 15 families) were sampled over 10 sampling occasions (5 day, 5 night; Table 10). *Arripis truttacea* and *Aldrichetta forsteri* constituted 63% of all fish, while 6 species – brown trout (*Salmo trutta,* Linnaeus), tailor (*Pomatomus saltatrix,* Linnaeus), tommy ruff (*Arripis georgiana,* Valenciennes), sea mullet (*Myxus elongates,* Gunther), cod larvae (*Pseudophycis* spp.) and long snout flounder (*Ammotretis rostratus,* Gunther) were sampled only once (Table 10). Marine species represented 74% of all fish, freshwater and estuarine species accounted for 13%, and 12 species (76% by abundance) were of commercial importance (Kailola et al. 1993). Based on size-ranges in Gomon et al. (1994), 61% were juveniles. Gill nets sampled 450 fish mostly > 100 mm SL, such as *Acanthopagrus butcheri*, white trevally (*Pseudocaranx dentex,* Bloch and Schneider) and *A. truttacea*. Fyke nets were more successful at sampling fishes < 100 mm SL, such as the common jollytail (*Galaxias maculatus,* Jenyns), bridled goby (*Arenigobius bifrenatus,* Kner) and Tamar river goby (*Favonigobius tamarensis,* Johnston).

The fish assemblages sampled with fyke and gill nets varied strongly between diel periods and among microhabitats (Table 11, Fig. 18). For both gear types, the variability in fish assemblages among microhabitats was driven most by differences between the forest and the channel (Table 11, Fig. 18). The diel differences in assemblage structure for fishes sampled with the fyke nets were driven primarily by *Favonigobius tamarensis* (21%), *Galaxias maculatus* (20%) and *Aldrichetta forsteri* (17%), while *F. tamarensis* (27%), *Tetractenos glaber* (17%) and *G. maculatus* (16%) contributed most to assemblage differences between the forest and channel. For the gill net sampled fishes, *Arripis truttacea* (36%) and *Aldrichetta forsteri* (35%) contributed most to diel differences and differences between the forest and channel (*A. truttacea* 41%, *A. forsteri* 29%).

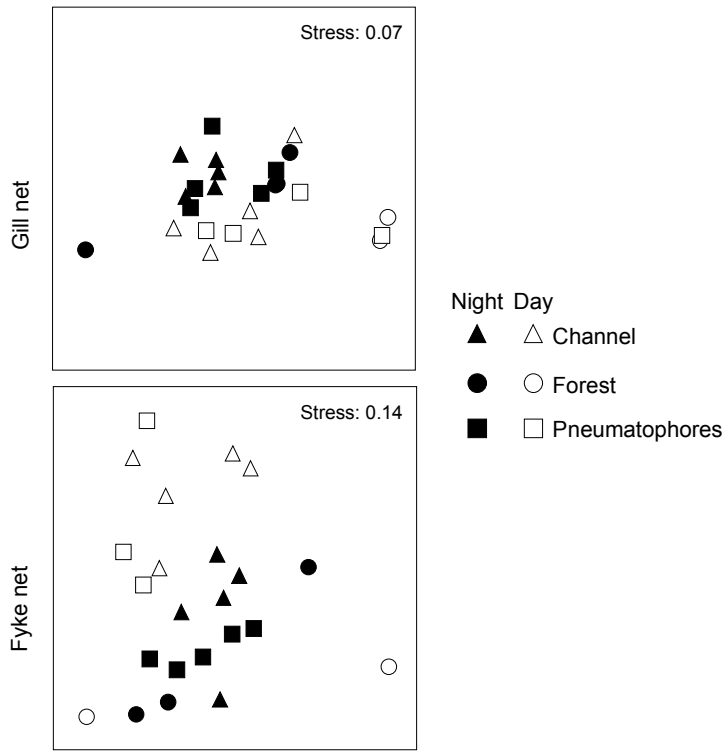

Figure 18. Multidimensional scaling plots, based on Bray-Curtis dissimilarity indices calculated from fish abundances, comparing microhabitats (channel, pneumatophores, forest) and diel periods (day, night) for each gear (gill, fyke) separately. 2 Night-Forest and 3 Day-Forest points are superimposed for both gears. 2 and 1 points are superimposed for Day-Pneumatophore fyke and gill nets, respectively. (total n = 30).

Fish abundances in fyke and gill nets varied inconsistently among microhabitats between sampling occasions and diel periods (Table 12, Fig. 19). Tukey's tests showed that fish were statistically more abundant ($P < 0.05$) when sampled with gill nets in the channel than the pneumatophores on 3 occasions (1 day, 2 night, Fig. 19), and in the channel than the forest on 8 occasions (4 day, 4 night, Fig. 19). On 3 night occasions more fish were sampled in the pneumatophores than forest. Fish abundances in the fyke nets were significantly greater in the channel than pneumatophores on 2 night and 3 day occasions, between the channel and forest on 6 occasions (3 day, 3 night, Fig. 19), and between the pneumatophores and forest on 6 occasions (2 day, 4 night, Fig. 19). There was a significant positive relationship between fish abundance and water depth in the pneumatophores and forest, but not in the channel (Table 13). The mean (± se) water depths (cm) in the forest, pneumatophore and channel were 49 (± 7), 66 (± 9) and 90 (± 7), respectively.

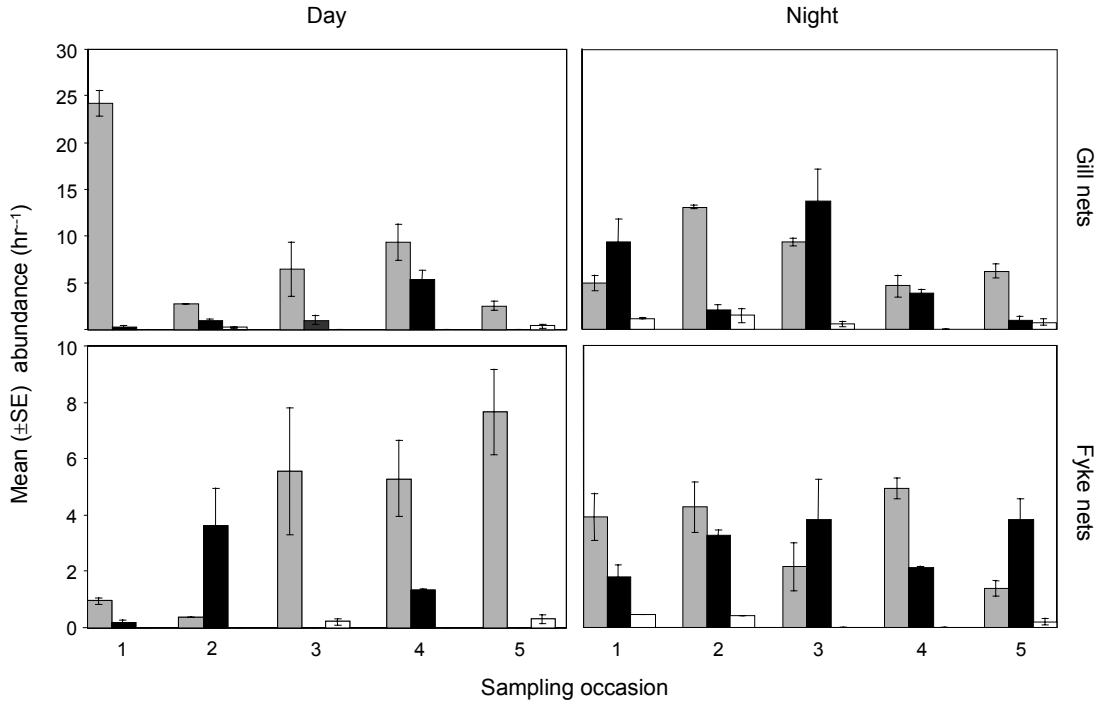

Figure 19. Mean (±SE) abundance of fish sampled in gill and fyke nets (hr^{-1}) during diel cycles (day, night) in each microhabitat (channel - grey, pneumatophores - black, forest - white) for each sampling occasion (total n = 120).

Fish biomass varied significantly among microhabitats between diel periods for both gill and fyke nets (Table 12, Fig. 20). Tukey's tests (statistically significant at $P < 0.05$) showed that fish biomass in gill nets was greater in the channel than the pneumatophores, which had greater biomass than the forest (Fig. 20). Fish biomass in the gill nets was also greater during night than day periods (Fig. 20). In the fyke nets biomass was greater in the channel and pneumatophores than the forest, but similar between the channel and pneumatophores (Fig. 20). Fish biomass was greater during night than day for both gear types (Fig. 20).

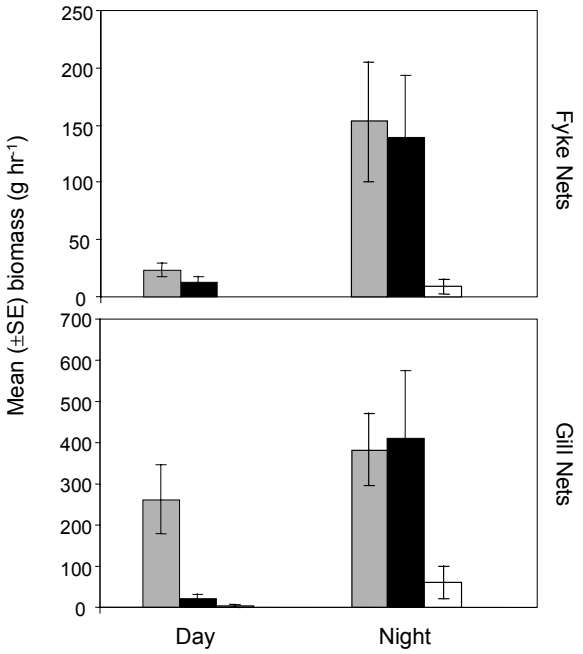

Figure 20. Mean (±SE) biomass of fish sampled in gill and fyke nets (hr^{-1}) during diel cycles (day, night) in each microhabitat (channel - grey, pneumatophores - black, forest - white)(total n = 120).

Species richness in the gill nets varied inconsistently among sampling occasions and microhabitats between diel periods, but in the fyke nets varied only among microhabitats through time (Table 12, Fig. 21). Using Tukey's tests (as above), species richness measured with gill nets was generally lower in the forest than the pneumatophores and channel, regardless of diel period. But differences between the pneumatophores and channel depended on the time of day – during day periods species richness was lower in the pneumatophores than channel, while at night species richness was similar among microhabitats. Like gill net samples, species richness in the fyke nets was often significantly lower in the forest than pneumatophores (1 day, 3 nights) and channel (3 days, 3 nights). On most sampling occasions, however, there was little difference between the pneumatophores and the channel (Fig. 21). There were no significant relationships between species richness and water depth in any of the microhabitats (Table 13).

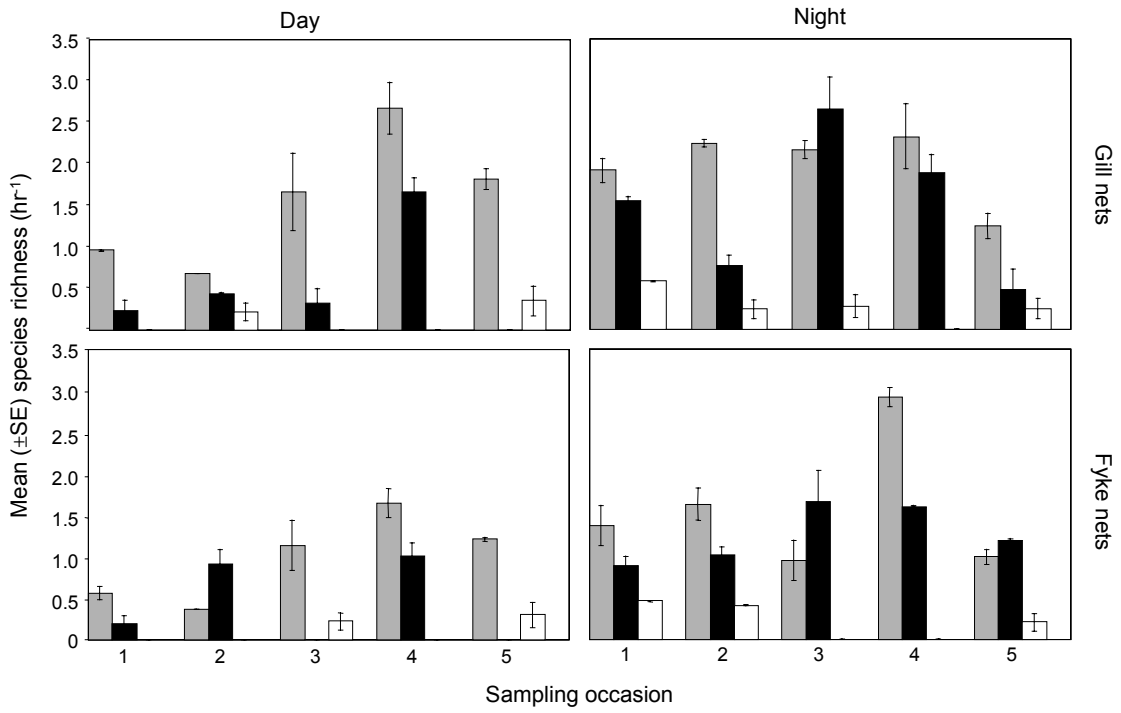

Figure 21. Mean (±SE) species richness sampled in gill and fyke nets (hr^{-1}) during diel cycles (day, night) in each microhabitat (channel -grey, pneumatophores - black, forest - white) for each sampling occasion (total n = 120).

Fyke versus pop nets in the mangroves (Survey 2)

Patterns in the fish assemblages across microhabitats (forest and pneumatophores) were similar for each gear (pop and fyke nets). Although only based on 5 replicates in each microhabitat, ANOSIM showed no difference in the species composition (based on presence/absence) sampled in the pop and fyke nets (R = -0.026, *P* = 0.544). Notwithstanding similarity in the assemblages, each gear sampled slightly different numbers of fish among microhabitats. Pop nets sampled 23 fish from 2 species (*Atherinasoma microstoma* and *Tetractenos glaber*) in the forest, and 108 fish from 8 species in the pneumatophores (Table 10). Fyke nets sampled similar numbers (n = 28) of fish to the pop nets in the forest (Table 10, Fig. 22), but 10 times more fish (n = 1102) in the pneumatophores. *A. microstoma* dominated catches in both nets (> 80%) in the pneumatophores (Table 10). Abundances of fish were greater (albeit weakly non-significant) in the pneumatophores than forest for both gears (Table 14, Fig. 22). Species richness was also greater in the pneumatophores than forest for both gears, but significantly so only for the pop nets (Table 14, Fig. 22). Neither fish abundances nor species richness varied significantly among sampling occasions (Table 14).

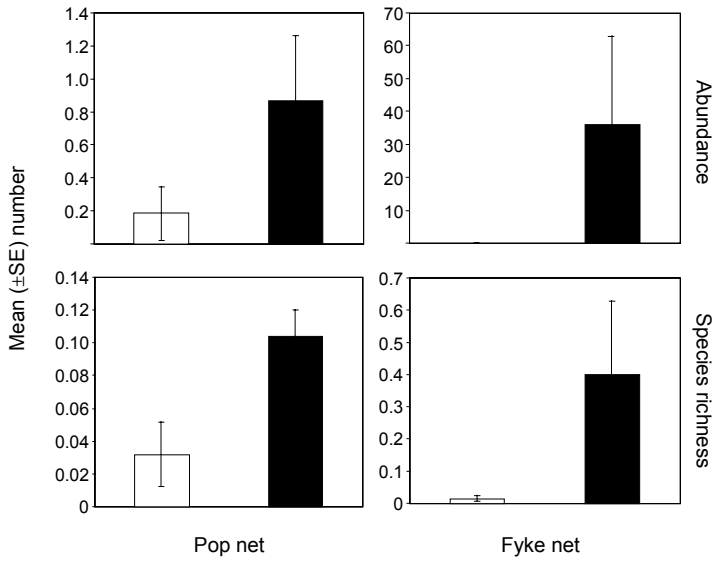

Figure 22. Mean (±SE) abundance and species richness of fish sampled with the pop (m^{-2}) and fyke (hr^{-1}) nets in the forest (white) and pneumatophores (black)(total n = 20).

Predation across microhabitats within mangroves

The survival of juvenile *Aldrichetta forsteri* did not vary significantly among microhabitats or cage treatments (Table 15, Fig. 23). Of 135 fish tethered, only 15 were 'lost' (Fig. 23); 5, 4 and 6 fish in the channel, pneumatophores and forest, respectively. Most (n = 9) fish were lost from uncaged plots, 2 from exclusion cages, and 4 from cage controls. The proportional survival of fish did not vary significantly among microhabitats or caging treatments (Table 15, Fig. 23).

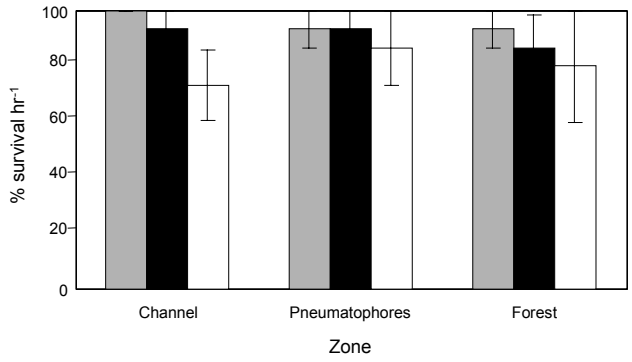

Figure 23. Mean (±SE) % survival (hr^{-1}) of juvenile *Aldrichetta forsteri* tethered within predation treatments (exclusion cages - grey, cage controls - black, uncaged - white) (total n = 45).

The lack of significant microhabitat or predator treatment effects was not simply due to type II errors. Power analyses revealed that if survival in the other microhabitats differed from that in the channel by 66% (i.e. 2 of the 3 tethered fish were lost), we had an 88% (F = 3.885, ES = 1.015, λ = 15.447) chance of detecting a significant effect; the actual difference between the channel and the pneumatophores was 4

and 2% between the channel and forest, respectively. Similarly, if survival in exclusion cages differed from the other treatments by 66%, we had a 95% (F = 3.885, ES = 1.157, λ = 20.090) chance of detecting significant effects. The actual differences in survival between exclusion cages and cage controls or uncaged treatments were 8 and 18%, respectively.

DISCUSSION

Interaction between microhabitat use of mangroves and diel period

The greatest abundances, biomass and species richness of fish in the present study were found in the channel adjacent to the mangroves. Forests supported fewer species and much lower numbers of fish, but this pattern varied strongly depending on the time of day. During the day and night most fish were sampled in the channel, but at night fish abundances increased in the pneumatophores and forest. Movement of fish between microhabitats with diel periods may be due to changes in predation pressure (Gibson & Robb 1996, Hindell et al. 2000b). In the present study, larger predators such as *Anguilla australis* and *Acanthopagrus butcheri* were sampled in all microhabitats at night but were largely absent during the day. Larger *Arripis truttacea* were also more common in the channel and pneumatophores at night, and these movements of predatory fish could maintain populations of smaller prey species such as *Aldrichetta forsteri* in habitats (and at depths) such as forest where predation pressure is likely to be minimised (Gibson & Robb 1996).

Alternatively, patterns in microhabitat use could be a function of variability in depth. Mangrove studies have traditionally compared fish abundances using mangroves and adjacent habitats without attempting to address the influence of water depth (Robertson & Duke 1987, Nagelkerken et al. 2000b). Meager et al. (2003), however, suggest that some epibenthic nekton (e.g. *Acetes sibogae*) may be significantly correlated with water depth depending on the microhabitat. In our study, species richness varied little with water depth regardless of microhabitat. Species abundances also varied negatively (but not significantly) with water depth in the channel, but were positively related to water depth in the pneumatophores and forest. While there was some cross-over in water depths between the day and night, the average water depth was actually greater at night than during the day. The interaction, therefore, in fish abundances between times of the day and among microhabitats could actually reflect differences in water depth rather than diel period *per se*. The mechanisms underlying diel changes in microhabitat use are purely speculative, but our observations highlight the need for spatially explicit approaches to assessing use of mangroves, with emphasis on separating effects of diel regimes and water depth.

The results from studies using a single gear to sample mangrove fishes may be restricted in their generality because of gear selectivity (Rozas & Minello 1997, Sheaves 2001). We attempted to reduce the degree to which differential gear selectivity influenced among-microhabitat patterns in fish assemblage structure by using multiple gear types (fyke, gill and pop nets). While patterns of increasing fish abundance and species richness from the forest to the channel can be interpreted as microhabitat 'selection', it is also possible that patterns could at least partially be attributable to differential gear selectivity among microhabitats. Lower fish abundance in forest than channel, for example, could be an effect of reduced gear effectiveness in the more complex structure. Although we must interpret the patterns from the current study cautiously because it was done in one region over a course of several months, we suggest that differential gear effectiveness due to variable structure was less important for 3 reasons. First, fyke and gill nets (passive gears) are favoured over alternative towed nets, such as trawls and seines, in habitats with high levels of structure (e.g. mangrove forests) because their effectiveness depends more on fish movement and less on the ability to manoeuvre the net through the structure to trap fish. Enclosure devices such as pop nets have even fewer variables influencing catch efficiency, which is not thought to vary substantially with the presence of structure (Rozas & Minello 1997). Second,

while there were some differences in the species of fish sampled by the different gears, the overall patterns of fewer fish in the forest than pneumatophores (surveys 1 and 2), and fewer fish in the pneumatophores than channel (survey 1), although not always statistically significant, were consistent between gears. Third, the water in our system was often highly turbid. This greatly reduced the visibility, and given that more fish were sampled in the channel during the day than night overall, suggests that fish may not have displayed significant gear avoidance.

Tropical mangroves are thought to support higher abundances and species diversity of fishes than temperate systems (Clynick & Chapman 2002, Hindell & Jenkins 2004), but differences in sampling methodologies often prevent informative comparisons across studies in estuarine systems (Rozas & Minello 1997, Connolly 1999), thereby masking broad-scale generality in findings. The present study is unique in that parallel work has been done elsewhere in subtropical and temperate Australia using similar (and in some cases the same) types of gear. Skilleter and Loneragan (unpublished data) sampled > 16,000 fish from 47 species in a single summer using the same fyke nets as we used here; their mean catches of juvenile and small fish (adjusted for fishing time) sometimes exceeded 700 fish hr^{-1}. In the present study, we sampled just 1954 individuals from 23 species in total (all gears including fyke nets combined), with maximum rate of capture of fish in fyke nets of 5.3 fish hr^{-1} (in the channel). Although we ran only 10 trials of the pop net, assemblages of fish sampled with this gear were also less rich than those reported in studies using highly quantitative methods in the tropics. Total densities of fish in our forest (0.18 fish m^{-2}) and pneumatophore (0.86 fish m^{-2}) microhabitats were lower than those of Barletta et al. (2000) (2.8 fish m^{-2}), Vance et al. (1996) (1.0 fish m^{-2} inside the forest) and Ronnback et al. (1999) (5.1 fish m^{-2} inside the forest). Conversely, a recent study by Hindell and Jenkins (in press) in a separate temperate Australian mangrove system recorded mean fish densities in the forest (2.0 fish m^{-2}) and pneumatophores (1.4 fish m^{-2}) that were comparable (and in some cases exceeded) those from the tropics. Species richness measured with the pop nets was also considerably lower in the present study (2 and 8 spp. in the forest and pneumatophores, respectively) compared with Vance et al. (1996) (26 spp. along the creek/mangrove interface), Ronnback et al. (1999) (37 spp.) and Barletta et al. (2000) (14 spp). The present study is consistent with previous work showing relatively low species richness in temperate systems (Clynick & Chapman 2002, Hindell & Jenkins 2004), but it is the first study to show that fish densities can also be significantly lower than those in tropical and subtropical mangroves.

Predation not a driver of microhabitat use by fish in temperate mangroves

Small and juvenile fish may use the interior of mangrove forests as a refuge from predation (Vance et al. 1996, Ronnback et al. 1999). The pattern of lower fish abundances, particularly small prey species such as *Galaxias maculatus, Favonigobius tamarensis* and *Atherinasoma microstoma*, inside forests than along the edge or channel in the present study was consistent with avoidance of shallow water and/or greater predation, despite the potential for increased structure to mediate predation effects in these microhabitats. In contrast to this model, our tethering experiments showed that rates of predation on juvenile *Aldrichetta forsteri* were low across all microhabitats. This suggests that predation was not important in determining patterns of fish use across microhabitats, at least during the day when we would expect to see greatest predation by birds and highly visual predatory fishes such as *Arripis truttacea*. In the absence of any predation effect, we suggest that the lower numbers of fish inside mangroves may be attributable to a lack of food, which in turn fits with models suggesting lower productivity of temperate mangroves (Alongi 2002). More attention should be given to assessing changes in the distribution of invertebrate prey across microhabitats to better assess the contribution of varying food supply on fish use of microhabitats within temperate mangroves.

Problems associated with tethering experiments, such as restricting escape behaviour and entanglement of tethers are well documented (Haywood et al. 2003). High survival of juvenile *Aldrichetta forsteri* across structurally different microhabitats suggests that tangling and behavioural changes caused by tethering were unlikely to have influenced rates of predation. Tethering studies often overlook the need to control for the loss of tethered organisms and assume they have been eaten (Acosta & Butler 1997, Haywood et al. 2003). Fish tethered in cages provide a useful means of testing the effectiveness of tethers by providing an estimate of the fish that have escape their tethers without being eaten. For example, Laegdsgaard and Johnson (2001) attributed greater predation to fishes on mudflats than seagrass or mangroves because tethered fish were not lost from predator exclusion cages. In our study, 2 fish were lost from closed cages, suggesting that fish had 'escaped' their tethers by means other than fish or bird predation. More fish were lost from uncaged and cage control treatments than exclusion cages, but the 2 losses from exclusion cages suggest that fish may have been removed from their tethers by invertebrate predators. Several species of grapsid crab are common in our study system and possibly prey on fish with restricted mobility. The results from our tethering study are not consistent with decreasing predation pressure by fish and birds with increasing structure of microhabitats within mangroves, and tethering studies in association with predator cages appear to be useful in elucidating non-target predation events.

Nursery value of temperate mangroves

Mangroves are widely cited as important nursery habitat for juvenile fish and crustaceans (Kathiresan & Bingham 2001), but there is growing uncertainty as to whether mangroves actually support larger numbers and facilitate the survival of post-settlement nekton (Sheridan & Hays 2003). The present study suggests that areas within mangroves support few small and juvenile fish compared with areas along the mangrove edge and in the channel. This pattern changes slightly during the night when more smaller fish appear to be using the pneumatophore and forest microhabitats.. The greater abundances of larger fish in these microhabitats at this time present some interesting possibilities for assessing changes in the refuge value of (and resource use in) habitats with diel periods. The view that mangrove structure provides smaller fish and invertebrates with a refuge from predation (Primavera 1997, Laegdsgaard & Johnson 2001) is also not supported here – the survival of fish did not vary across microhabitats. Based on the weak patterns of association with, and lack of predation effect in mangroves observed here, the mangrove microhabitats in out study system do not appear to be differentially important as habitat for juvenile and small fishes.

Table 10. Summary of fish sampled in (1) survey 1 among microhabitats (channel – Ch, pneumatophores – Pn, forest – F) during each diel period (day, night) pooled across gears, and (2) survey 2 among microhabitats using pop and fyke nets. N = number, W = weight (g), L = average length (mm), [C] commercial species. [J] juvenile and [A] adult lifestages sampled, respectively. ** weights < 1g. Figures rounded to whole numbers.

	Survey 1																		Survey 2			
	Day									Night									Pop		Fyke	
	Ch			Pn			F			Ch			Pn			F			Pn	F	Pn	F
Species	N	W	L	N	W	L	N	W	L	N	W	L	N	W	L	N	W	L	N	N	N	N
Anguilla australis[C J A]										11	4751	526	17	5129	464	1	280	380				1
Arripis georgiana[C J]													1									
Arripis truttacea[C J]	98	4479	133	2	19	83				80	6523	156	57	4472	154				2		1	
Atherinasoma microstoma[J A]							1	**	25	1	**	23	2	1	46				89	21	916	23
Pseudocaranx dentex[C J A]	2	87	125							14	1074	135	2	89	128							
Hyperlophus vittatus[C J]																					65	
Engraulis australis[C A]																					1	
Galaxias maculatus[J]	13	1	36	15	2	36	1	**	44	13	2	36	16	3	35	3	**	45				2
Girella tricuspidata[C A]													2	3610	377							
Arenigobius bifrenatus[A]	1									9			2									
Favonigobius tamarensis[A]	38	41	42	2	5	57				12	22	51	3	6	49				10			
Pseudophycis sp.[J]				1	**	21																
Aldrichetta forsteri[C J A]	63	3097	144	18	507	119				51	3637	161	57	3452	152	13	603	130	1		100	
Mugil cephalus[C J]	1	119	180																			
Ammotretis rostratus[A]													1	3	54				1			
Rhombosolea tapirina[C J A]	2	111	100																			
Pomatomus saltatrix[C J]	1	63	158																			
Salmo trutta[C J]	1	127	212																			
Gymnapistes marmoratus[A]	2	59	102																			
Sillaginodes punctata[C J]	9	178	130	2	46					3	127	154	3	125	164				1			
Acanthopagrus butcheri[C J A]	1	460	234							7	3203	227	6	2848	214	3	1622	280				
Stigmatopora nigra[A]																			1			
Tetractenos glaber[J A]	14	964	109	10	700	106	2	149	110	2	137	119	1	93	130				3	2	19	2
Average		39	131		25	70		37	59		95	159		116	164		125					
Total	246			50			4			203			170			20			108	23	1102	28

Table 11. Summary of multivariate analyses of similarity comparing fish assemblages among microhabitats (forest, pneumatophore, channel) and between diel periods (day, night) for each gear (gill, fyke) separately. (total n = 30). Bold when $P < 0.05$.

	Gill Net		Fyke Net	
Source	Global R	*P*	Global R	*P*
Diel	0.276	0.006	0.424	0.001
Microhabitat	0.261	0.010	0.196	0.037
Forest v Pneumatophore	0.135	0.139	0.287	0.061
Forest v Channel	0.798	0.001	0.46	0.004
Pneumatophore v Channel	-0.04	0.625	-0.034	0.551

Table 12. Results of 3-factor partially nested analyses of variance comparing fish abundance, biomass and species richness among microhabitats (forest, pneumatophore, channel) and sampling occasions (1-10) nested within diel periods (night, day) for each gear (fyke, gill) separately. Bold when $P < 0.05$. Data $\log_{10}$ transformed. (total n = 120).

		Abundance				Biomass				Species richness			
		Gill		Fyke		Gill		Fyke		Gill		Fyke	
Source	df	MS	*P*	MS	*P*	MS	*P*	MS	*P*	MS	*P*	MS	*P*
Diel (D)	1	1.429	0.108	0.650	0.042	45.730	0.003	29.349	0.003	0.335	0.076	0.477	0.007
Microhabitat (M)	2	8.459	<0.000	3.441	<0.000	72.145	<0.000	52.586	<0.000	1.447	<0.000	0.812	<0.000
D x M	2	0.639	0.265	0.433	0.226	5.290	0.258	4.247	0.281	0.086	0.015	0.083	0.228
Occasion {D}	8	0.437	0.022	0.111	0.524	2.462	0.555	1.661	0.519	0.081	0.006	0.035	0.056
M x Occasion {D}	16	0.443	0.008	0.265	0.029	3.583	0.283	3.086	0.103	0.015	0.797	0.051	0.003
Error	30	0.161		0.122		2.843		1.819		0.023		0.016	

Table 13. Regression analyses of the relationships between fish abundance/species richness and depth, regardless of gear or diel period, in each microhabitat. Bold when $P < 0.05$. Abundance data $\log_{10}(x+1)$ transformed. (total n = 10). Trend indicates the overall pattern of the relationship.

		Channel				Pneumatophores				Forest			
	df	R^2	MS	*P*	Trend	R^2	MS	*P*	Trend	R^2	MS	*P*	Trend
Abundance	1,8	0.117	0.266	0.332	–	0.438	3.436	0.037	+	0.579	0.798	0.011	+
Species richness	1,8	0.117	0.119	0.332	+	0.267	0.732	0.126	+	0.371	0.201	0.062	+

Table 14. Results of 2-factor randomised blocks analyses of variance comparing abundances and species richness of fish between microhabitats (forest and pneumatophore) and among sampling occasions (1 to 5) for pop and fyke nets separately. All data log10 (x+1) transformed (total n = 20). Bold where $P < 0.05$.

		Abundance				Species Richness			
		Pop		Fyke		Pop		Fyke	
Source	df	MS	*P*	MS	*P*	MS	*P*	MS	*P*
Microhabitat	1	0.081	0.155	1.939	0.096	0.00216	0.022	0.034	0.175
Occasion	4	0.017	0.665	0.378	0.532	<0.0003	0.223	0.011	0.554
Error	4	0.026		0.411		<0.0001		0.013	

Table 15. Results of a 3-factor randomised blocks analysis of variance comparing survival of tethered fish (n = 135) across microhabitats (forest, pneumatophore, channel), cage treatments (exclusion cage, cage control, uncaged) and sampling occasions (1 to 5). Data arcsine transformed (total n = 45).

Source	df	MS	*P*
Cage (C)	2	0.025	0.771
Microhabitat (M)	2	0.274	0.158
Occasion (O)	4	0.544	0.096
M × C	4	0.114	0.739
C × O	8	0.117	0.901
M × O	8	0.093	0.832
Error	16	0.230	

Chapter 5. Landscape-scale patterns in fish assemblages associated with seagrass beds at different distances from mangroves

INTRODUCTION

Some of the most influential theoretical contributions in ecology (ie. island biogeography, MacArthur and Wilson, 1967 and metapopulation theory, Levins 1970) have incorporated the effects of spatial arrangement of habitat patches on community structure and dynamics. In terrestrial systems, these theories have provided a framework for assessing the consequences of habitat fragmentation and design of nature reserves (Andren 1994, Horner-Devine 2003) by assessing patterns (and to a lesser extent processes) among habitat patches of differing structure, size and arrangement (Brandl & Tscharntke 2004). This approach, referred to as 'landscape ecology', considers different types of habitats and the linkages between them at a variety of spatial scales (Bell & Bradley 1994).

The most obvious consequence of habitat degradation in marine systems, through, for example processes such as climate change, pollution and fishing effects, is the fragmentation of habitats into smaller, more isolated patches (Sheperd et al. 1989, Andren 1994, Micheli & Peterson 1999, Alongi 2002, Stenbeck et al. 2002). Until recently, few studies had considered how the spatial arrangement of marine habitats affects the structure and dynamics of faunal communities (Bell & Bradley 1994). In estuarine systems there has been (and continues to be) a significant amount of research into the smaller scale (meters to 10s of meters) effects of patch size, shape and 'edge effects' on nekton (Sogard 1989, McNeill & Fairweather 1993, Eggleston et al. 1998). The results from this work have been largely 'patchy' themselves, with few consistent patterns (Connolly and Hindell unpublished review). Much less work has attempted to asses how fauna respond to habitat heterogeneity at the landscape scale, that is, change among habitat types such as seagrasses, mudflats, mangroves and saltmarshes as their proximity to one another varies over scales of 100s to 1000s of meters (Irlandi & Crawford 1997).

Seagrass and mangrove habitats provide an ideal environment for investigating landscape-scale patterns as they occur in a variety of spatial arrangements and provide visually discrete patches that can be mapped in the field using tools such as aerial photography (Sogard 1989). As both mangrove and seagrass provide valuable habitats for fish and invertebrates, understanding the effects of fragmentation is important.

Seagrasses are often the most conspicuous type of vegetation in sheltered marine embayments, where they support diverse and abundant communities of fish and invertebrates (Edgar & Shaw 1995a), particularly juvenile stages, through the provision of shelter and food. Studies of faunal assemblages in seagrass beds have largely concentrated on comparisons with adjacent, usually unvegetated sand and the role of structural complexity in influencing assemblage composition (Bell & Westoby 1986ab, Bell & Pollard 1989, Worthington et al. 1992) through modifying predation patterns, food availability, shelter and larval settlement (Heck & Orth 1980, Jenkins & Sutherland 1997, Upston & Booth 2003). While correlations between seagrass structure and fish abundances are evident within a bed (Bell & Westoby 1986a), these patterns tend to break down over larger spatial scales, for example different beds within an estuary (Bell & Westoby 1986b, Worthington et al. 1992). In examining why these patterns change, there has been greater focus on the role of seagrass landscapes in shaping patterns of faunal association.

Many studies suggest that the position of seagrass beds within an estuary is a more important predictor of community structure than seagrass complexity or patch size (Bell & Pollard 1989, Hovel & Lipcius 2002). When Bell et al. (1988) placed identical ASUs in three arms of a New South Wales estuary the different locations supported very different assemblages of fish. It is likely a combination of factors influence the variability in faunal composition among locations. For new recruits, local hydrodynamic factors influence the transport of larvae to the beds (Hamer & Jenkins 1996). Other factors that influence fauna include the distance to the mouth of the estuary (Bell & Westoby 1986b) and salinity (Loneragan et al. 1986). Just as these physical characteristics vary among positions within an estuary, so too does the proximity of habitats, but this is a little studied area of landscape ecology in marine environments. Sogard (1989) found that composition of faunal communities varied strongly with the proximity of artificial seagrass units (ASUs) to natural seagrass, while the proximity of natural seagrass to coral reefs and saltmarsh also influences the fauna colonising seagrass patches (Irlandi & Crawford 1997, Micheli & Peterson 1999, Nagelkerken et al. 2000ac). The position of seagrass beds in relation to alternative vegetation such as mangroves may have significant influences potentially increasing the abundance or diversity of assemblages, and needs to be examined further.

Through meetings with Skilleter et al (current FRDC project), the role of habitat mosaics (the spatial arrange of units) were discussed. Consensus was reached that seagrass and mangrove habitats are routinely examined separately, but may be intrinsically linked in 2 ways. First, the passive transport of dissolved and particulate materials from areas of high primary productivity (also called outwelling) provides a mechanism for the transfer of nutrients into adjacent habitats (Lee 1995, Bouillon et al. 2000, Bouillon et al. 2002). Second, many estuarine species use mangroves at high tide, probably as feeding areas, but retreat to subtidal areas when the tide recedes. Several predictions about the spatial distribution of animals among and between habitats can be made with reference to these models, and specifically, proximity of seagrasses to mangroves. If, for example, outwelling from mangroves enhances the productivity of adjacent seagrass beds, over broad (100s to 1000s of meters), among-site spatial scales, we would predict richer fish communities (i.e. greater abundances and more species) in seagrass close to than further from mangroves. Alternatively, a landscape in which mangroves and seagrass are close together might provide greater overall food (Sheaves & Molony 2000) and shelter resources (Hindell & Jenkins 2004), and thereby support greater numbers and more species of fish, than one where seagrasses are separated from mangroves by vast expanses of unvegetated sand and/or mud. Furthermore, over finer (10s to 100s of meters), within-site spatial scales, if there is intrinsic value to fish of mangroves associated with seagrass, then we predict that fish abundances and or species richness will be greater in seagrass associated with mangrove than seagrass along sandy beaches (non-mangrove).

The overall aim of this study was to assess whether the proximity of mangroves influenced assemblages of fish using seagrasses. More specifically, we had 2 main objectives: 1) assess whether the proximity of mangroves influenced fish assemblages in seagrass over broad (100s to 1000s of meters), among-sites within an embayment, spatial scales; and, 2) assess whether the presence and proximity of mangroves influenced fish assemblages in seagrass over finer (10s to 100s of meters), within site, spatial scales.

MATERIALS AND METHODS

Study system

Our study was done in Western Port Bay (see earlier chapters for description of this embayment).

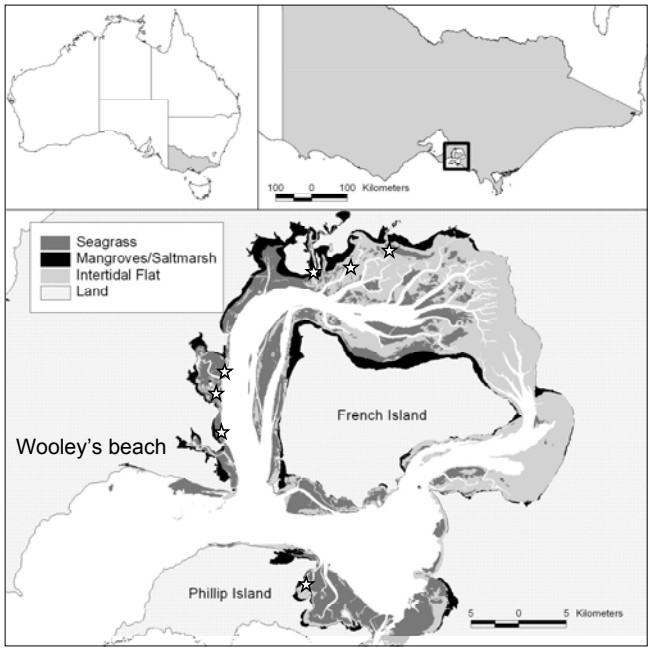

Figure 24. Approximate locations of study sites in Western Port, Australia. Inset: location of study area in Australia. Open stars indicate study sites.

Western Port is an area of high biological diversity, with a wide range of habitats including mangroves, saltmarsh, seagrass and deep water channels (Shapiro 1975), and is listed as a wetland of international importance under the Ramsar Convention. While 4 species of seagrass (*Heterozostera tasmanica, Zostera muelleri*, *Amphibolis antarctica*, and *Halophila australis*) are present, very sparse beds of *Z. muelleri* are the most extensive, covering approximately half of the intertidal mudflat (Blake 2001). Dense beds of *H. tasmanica* occur along the shallow (< 2-3 m) regions of the subtidal channels. Dense but short (trees rarely exceed 2-3 m in height) stands of mangroves (*Avicennia marina*) occur along 40% of the perimeter of Western Port (Shapiro, 1975), covering an area ≈ 15km^2 (OZESTUARIES 2000).

Broad-scale (100s to 1000s of meters), among site patterns in seagrass-associated fish

The first part of this study assessed whether assemblages of fish in seagrass varied with proximity to mangroves. Fish were sampled from beds of *Heterozostera tasmanica* at seven sites in WPB (Fig. 24). These sites were chosen for their accessibility, the presence of large (>300 m^2) areas of seagrass adjacent to mangrove dominated shore, and variation in proximity to the closest stand of mangroves. The distance from seagrass sites to the closest mangroves ranged from 110 to 855 m. All seagrass beds were located along the edge of channels at a mean (± sd) depth (m) of 2.3 (± 0.4).

No direct measures of structure were available for the mangroves in our study system (apart from those we measured ourselves in previous chapters), and it was outside the scope of the current project (for both money and time) to attempt to do so. But, the mangroves around the system have the same canopy height, and the high variability in the length and density of pneumatophores with distance into the forest appears to be consistent at all of our study locations.

Fish were sampled between 17th May and 4th July, 2004, within 3 hours of high tide using a small beach seine net (10 m long × 2.5 m high, with 1 mm mesh) with a 10 m long rope attached to each end. The net

was set from a small (3.5 m long) boat by modifying the methods of Hamer and Jenkins (1996). Briefly, the end of one rope was attached to an anchor, which was then 'set' in a patch of seagrass. We then motored backwards to set-out the rope. At the net-rope junction, we began letting-out the seine net as we motored backwards at 90° to our initial course. Once the net had been set, we returned to the point at which the first end had been anchored, feeding out the second rope as we went. Back at the starting point, the boat was anchored, and the net was retrieved by 2 people, one hauling on each rope. This procedure enabled us to repeatedly sample an area of approximately 75 m^2 (Hamer and Jenkins 1996). We repeated this process 5 times over different areas of seagrass at each of the study sites (5 non-overlapping replicate seine shots in each of 7 locations). GPS was used to record the latitude and longitude of each replicate sample. These positions were later plotted on a chart of the WPB using Arcview, and the distance from the closest stand of mangroves to each seagrass sample was measured.

Smaller-scale (10s of meters), within site patterns in seagrass-associated fish

The second part of this study assessed whether fish assemblages in seagrass varied with the proximity and/or presence of mangroves over smaller (10s of meters) spatial scales. This work was done at one site in WPB (Wooley's beach, which was also 1 of the 7 sites sampled in the first part of the study, see Fig. 24). As in Hindell and Jenkins (in press), this site was chosen because (1) the substratum is firm enough to set nets by foot, (2) we have an excellent understanding of the local fish assemblages (Robertson 1980, Edgar & Shaw 1995a, Hindell and Jenkins 2004, in press), (3) there is a sparse but consistent covering of *Zostera* over the intertidal mudflat and large dense beds of *Heterozostera* subtidally, and, (4) there are areas of beach with and without stands of mangroves.

The intertidal mudflat at this site can be separated into 2 main regions: (1) mangrove forest/sandy beach (extending approximately 20-30 m off-shore); and, (2) intertidal mudflat (extending approximately 200 m offshore). The density and length of *Zostera* may vary across the intertidal mudflat at this site (J. Hindell pers. obs), so artificial seagrass units (ASUs, 2 m long × 1 m wide, as per Jenkins et al. 1998) were used to standardise seagrass structure and patch size. These units are representative of the density and length of seagrass in Western Port (Bulthius 1983), and are rapidly colonised by seagrass fauna (Sogard 1989). ASUs were 'conditioned' before deployment by leaving them seaward of the mangrove fringe for 4 weeks to accumulate similar amounts of drift algae and epiphytes.

Replicate (n = 4) ASUs were placed haphazardly on the intertidal mudflat both 'near' to (within 5 m) and 'far' from (approximately 200 m) mangrove and sandy beach dominated shorelines. Steel pegs were used to anchor ASUs to the substratum. Replicate (n = 4) plots of 'natural' mudflat (the same size as the ASUs – 2 × 1 m) were also demarcated in each combination of shore type (mangrove beach, sandy beach) and proximity (near, far) to assess whether fish assemblages changed among treatments (proximity and shore type) depending on the type of substratum. Differential GPS was used to record the positions of each ASU and mudflat plot so that we could return to patches repeatedly.

Fish from the ASUs and mudflat were sampled with a small beach seine net (6 m long × 2 m high, with 1 mm mesh). One end of the net was attached to a pole, which was pushed into the substratum at one corner of the ASU/mudflat plot. The net was then set around the ASU/mudflat plot by 1 person. Once the ASU/mudflat plot was enclosed, the net was retrieved and all fish were collected. All replicate ASUs/mudflat plots in each proximity × shore type treatment were sampled over one 'high tide period'. Pilot sampling prior to the study showed that greater fish abundance and species richness occurred on either flooding or ebbing tides (A. McCallum unpublished data), with fewest fish and species caught at high tide. We therefore restricted sampling to a 2 hr period midway between mean low and high water on both incoming and outgoing tides. We were careful to sample at least one replicate ASU/mudflat plot in each treatment combination on flooding and ebbing tides. Sampling was repeated on 3 occasions in

September 2004. Each occasion was separated by several days and was haphazardly chosen from those when a complete tidal cycle (low-high-low) occurred during daylight hours.

General processing of fish samples

Where fish could be identified in the field, they were returned alive to the water after their standard length (SL - tip of the snout to the posterior end of the caudal peduncle) was recorded. Fish that could not be identified in the field were preserved in 95% ethanol and returned to the laboratory for measurement and identification. While the focus of this study was on teleost fishes, 2 species of squid were also caught and recorded. In the laboratory animals were removed from ethanol, press dried with paper towel to remove excess moisture, and measured for weight (g) and standard length (mm). Where more than 30 individuals occurred in a sample, a subsample of 30 was measured. Fish were identified under a dissecting microscope using Gomon et al. (1994). Squid were identified using Norman and Reid (2000).

Statistical analysis

Univariate analyses

Prior to statistical analyses, all data were checked for normality and homogeneity of variances with box plots and plots of residuals (Quinn and Keough 2002). Where variances were not homogeneous and/or distributions were not normal, data were transformed (log10(x+1)) and reassessed. All Univariate analyses were done using SYSTAT Version 10.

For the first part of our study, linear regression analyses were used to asses whether each of (1) fish abundance, (2) biomass, (3) species richness, (4) abundances of the 2 most common families, and (5) abundances of the 4 most common species sampled from seagrass varied with the distance (m) to the nearest mangroves. Sites (n = 7) were treated as replicates and seine samples (n = 5) were averaged within a site.

In the second part of our study, we first ran 3-factor analyses of variance to assess whether each of fish abundance and species richness differed between shore types (mangrove versus sandy beach), proximity (near versus far) and substratum (ASU versus mudflat). Shore type, proximity and substratum were treated as fixed factors, ASUs/mudflat plots were replicates (n = 4). ASUs/mudflat plots were sampled repeatedly on 3 occasions only to get a better estimate of overall fish abundances, and variables were averaged across occasions for individual ASU/mudflat plots. We chose not to use a repeated measures analysis because the inclusion of a 'time' factor would not have improved our assessment of the main effects (at the between subjects level), nor was time a factor of interest in our design.

Strong 3-way interactions between shore type, proximity and substratum were shown for both abundance and species richness. We therefore ran a series of planned comparisons to better assess the effects of proximity and shore type for ASUs and mudflat data separately. We first compared whether samples from mangrove-far differed from beach-far, and whether mangrove-near differed from beach-near. The results from this initial testing determined which of 3 scenarios would follow. First, if there were no differences we compared the average of 'far' samples to the average of 'near' samples. Second, if no difference was observed between beach types at the 'far' location but differences existed between shore types at the 'near' location (or vice versa), then the average of the 'far' proximities was compared to each 'near' shore type. Third, if differences were observed between shore-types at each proximity, then each shore type × proximity combination was tested against each other combination.

Multivariate analyses
Multidimensional scaling (MDS), analysis of similarity (ANOSIM) and similarity percentages (SIMPER), based on Bray-Curtis dissimilarity matrix calculated from species abundance data were used to assess whether fish assemblages varied between treatments. Analyses were run using untransformed and then transformed data. If there was no change in the results between transformed versus untransformed data, we chose to use untransformed data. We first assessed whether fish assemblages varied between substratum types (ASU, mudflat plots). With no statistically significant difference between substratum types ($P > 0.05$), fish assemblages were then compared among the 4 shore type × proximity treatments (mangrove-near, mangrove-far, beach-near, beach-far) pooling across substratum types. Multivariate analyses were done using Primer version 5.

RESULTS

Broad-scale (100s to 1000s of meters), among-site patterns in seagrass-associated fish

Natural seagrass beds sampled across WPB produced a total of 575 fish and squid from 18 families and 35 species (Table 16). Most fish were small (< 10 cm) sedentary species such as gobiids and syngnathids. The wide-bodied pipefish (*Stigmatopora nigra*) was the most abundant species (32% of all fish and squid caught). Other common species included the pygmy squid (*Idiosepius notoides*, 20%), the spotted pipefish (*Stigmatopora argus*, 10%) and the halfbridled goby (*Arenigobius frenatus*, 9%). Five species of commercial importance were caught – King George whiting (*Sillaginodes punctata*), six spine leatherjacket (*Meuschenia freycineti*), anchovy (*Engraulis australis*), rock whiting (*Haletta semifasciata*) and squid (*Sepioteuthis australis*). All of these fish were sub-adult lifestages based on the size ranges given by Gomon et al. (1994)(Table 16).

Fish assemblages in seagrass varied with proximity to mangroves. There was a positive (albeit not statistically significant) relationship between each of abundance and biomass of fish and distance from seagrass to mangroves (Table 17, Fig. 25). Conversely, species richness varied negatively with increasing distance from mangroves (Table 17, Fig. 25).

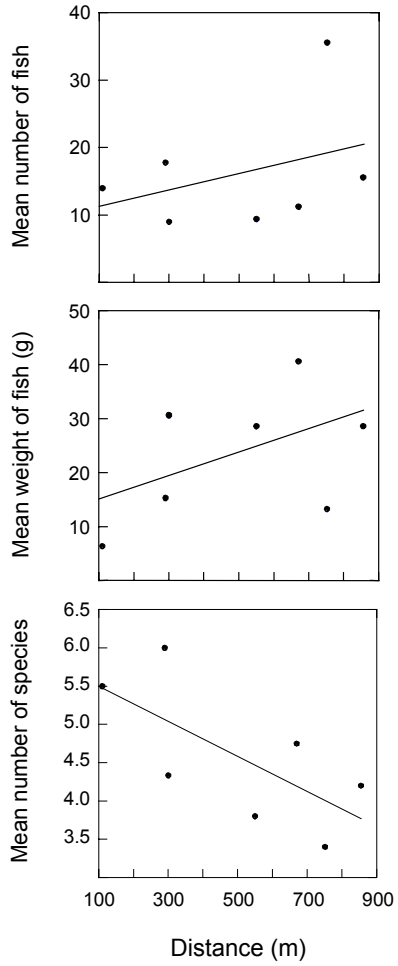

Figure 25. Relationship between each of mean (based on n = 5 net samples) fish abundance, weight of fish and species richness sampled from seagrass in 7 different locations and distance to the nearest stand of mangroves.

Most fish were from the families Syngnathidae and Gobiidae (Table 16). Regression analyses of abundances of these taxa against distance from mangroves showed patterns of fewer pipefish but more gobies as distance to mangroves decreased (Table 17, Fig. 26).

When the four most abundant species were analysed individually some general (but not statistically significant) patterns emerged (Table 17, Fig. 26). There were generally greater abundances of *Stigmatopora nigra* in seagrass beds further from mangroves (Fig 3), although this pattern was influenced strongly by the high abundances of *S. nigra* at one site (site 7), where 102 individuals were caught in one of the five seine shots. Removal of this outlier (to assess how robust the ANOVA was) did not change the overall pattern, but the relationship became slightly more significant statistically ($P = 0.086$). *Idiosepius notoides* were also more abundant in seagrass further from mangroves (Fig. 26). In contrast, *Arenigobius frenatus* were more abundant in seagrass closer to mangroves (Fig. 26), and *Stigmatopora argus* was most abundant at intermediate distances (Fig. 26).

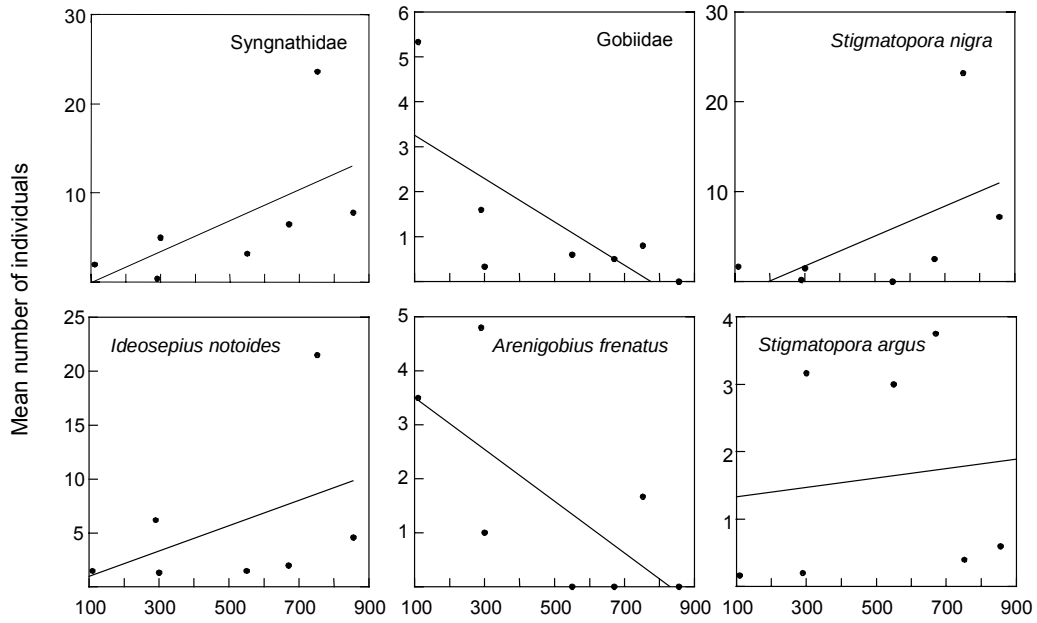

Figure 26. Relationship between mean (based on n = 5 net samples) abundances of the most common 2 families and 4 species of fish sampled from seagrass in 7 different locations and distance to the nearest stand of mangroves.

Finer-scale (10s of meters), within-site patterns in seagrass-associated fish

Some species were only caught in certain shore type × proximity treatments. *Stigmatopora nigra* and *S. argus* were only sampled at the far mangrove position. *Tetractenos glaber* were never caught at either of the far shore positions but were relatively common close to the sandy beach and mangroves. *Aldrichetta forsteri* was only ever caught close to the mangroves.

Significantly more fish were caught in ASUs than mudflat, and there were more fish adjacent to mangroves than sandy beach (Tables 18 & 19, Fig. 27), but there was a strong interaction between shore type, substratum and proximity to shore (Table 19, Fig. 27).

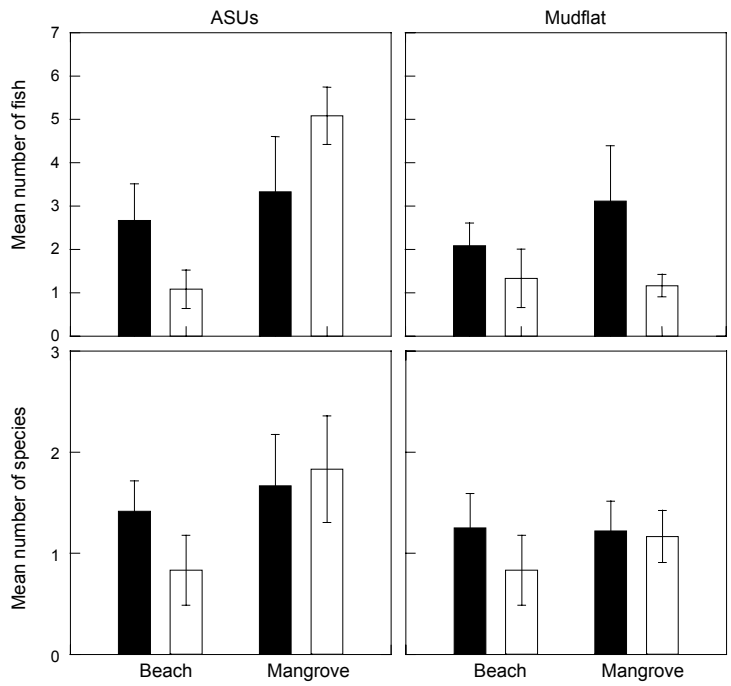

Figure 27. Mean (± se) fish abundance and species richness sampled from ASUs and mudflat placed at 2 distances (near - white, far - black) from sandy beach and mangrove shore-types (n_{total} = 32).

For ASU samples, fish abundances did not differ between shore types at the far location ($df_{1,22}$, MS = 0.761, P = 0.455, Fig. 27) but were greater near mangroves than near sandy beach ($df_{1,22}$, MS = 32.000, P < 0.001, Fig. 27). Mean fish abundances at the far location were greater than those at the near-beach location ($df_{1,22}$, MS = 9.280, P = 0.014, Fig. 27), but lower than the mangrove-near location ($df_{1,22}$, MS = 10.964, P = 0.008, Fig. 27). For the mudflat samples, fish abundances were similar between shore types at the near ($df_{1,22}$, MS = 0.055, P = 0.839, Fig. 27) and far ($df_{1,22}$, MS = 1.810, P = 0.254, Fig. 27) locations, but mean fish abundances were greater at the far than near locations ($df_{1,22}$, MS = 6.701, P = 0.034, Fig. 27).

Species richness showed similar overall patterns to fish abundances (Fig. 27), but did not vary significantly with shore type, proximity or substratum. Nonetheless, we ran the same series of analyses as for fish abundance. Species richness did not vary significantly (P < 0.05) except for ASU samples that were greater in mangrove-near than beach-near locations ($df_{1,22}$, MS = 2.000, P = 0.026, Fig. 27).

Assemblages of fish could not be differentiated between ASUs and mudflat (ANOSIM, R = -0.019, P = 0.61, Table 18, Fig. 28), so these substrata were pooled for comparisons of beach type and proximity to mangroves (near, far). The assemblages of species close to unvegetated beach were significantly different to those in the far-mangrove position (ANOSIM, R = 0.407, P = 0.010, Fig. 28). Similarity percentage analysis showed that *Arenigobius bifrenatus* accounted for 31% of this difference, with few fish sampled from the near-beach position compared to an average of 4 fish from the far-mangrove. Differences were also the result of greater abundances of *Pseudogobius olorum* and *Sillaginodes punctata* at the far-mangrove position and more individuals of *Rhombosolea tapirina* and *Pugnaso curtirostrus* at the near-beach position (Table 18). None of the other beach type × proximity treatments were significantly different from one another (ANSIM, R < 0.253, P > 0.05).

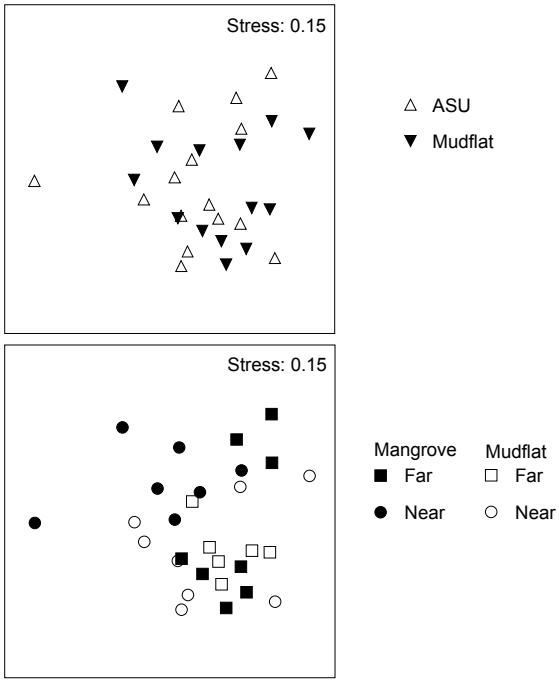

Figure 28. Multidimensional scaling plot, based on Bray Curtis dissimilarity matrix calculated from untransformed fish abundance data showing the degree of similarity in fish assemblages between types of substratum (mudflat, ASUs), proximity to mangroves (near, far) and shore type (mangroves, sandy beach) (n_{total} = 32).

DISCUSSION

Broad-scale survey

Few studies have looked at how the distance to alternative habitats influences faunal assemblages in seagrass. Distance to coral reef habitat has been shown to have a strong effect on the type of fish species found in adjacent seagrass (Nagelkerken et al. 2000b). Experiments by Irlandi and Crawford (1997) showed that there was a greater abundance and movement of pinfish species in seagrass adjacent to saltmarsh compared with seagrass adjacent to unvegetated sand. We could find only one study that has considered how fish assemblages in seagrass vary with the distance from seagrass to mangroves (Poulakis et al 2003). This study is the first to investigate changes in abundance and diversity of temperate seagrass fishes over a variety of distances from mangroves.

In seagrass at sites closer to mangroves we recorded greater species richness. Gobiidae abundance was also positively related to mangrove proximity. Just as other studies have shown that seagrass close to habitats such as coral reefs contains more coral reef species (Nagelkerken et al. 2003, 2004), in our study there were more species that typically utilise mangroves (such as gobies) in seagrass closer to mangroves. Species such as *Pseudogobius olorum*, *Arenigobius frenatus* and *Favonigobius lateralis* occur in relatively high abundances within the mangroves and were almost always only found in seagrass beds within 300m of the mangroves.

Mangroves may benefit these species by providing additional area for foraging. Stable isotope analysis has confirmed that fish feed in the mangroves (Sheaves and Moloney 2000), and this is most common in estuaries with large tidal differences (Nagelkerken and van der Velde, 2004). Sheaves and Moloney (2000) found that a number of species caught in a tropical Australian estuary fed on sesarmid crabs in adjacent

mangroves during high tide. Fish in adjacent habitats may also benefit indirectly from mangroves via outwelling of detrital nutrients, which may be assimilated by adjacent seagrass or invertebrates. Marguiller et al. (1997) found evidence to suggest that mangrove carbon could be used by seagrass consumers up to 1 km away but was assimilated more in seagrass closer to mangroves. Alternatively, seagrass associated fish may gain some benefit in mangroves through the provision of refuge from predation (Laegdsgaard and Johnston 2001).

In contrast to gobiids, syngnathids were more abundant at sites distant from mangroves. This pattern was due to changes in the abundance of the most common fish *Stigmatopora nigra.* Pipefish rarely enter mangroves, so close proximity to mangroves may not be advantageous for these species. In other studies the absence of a species within close proximity to alternative habitats has been linked to predation. The proximity of one habitat to another can effect community dynamics, for instance increasing the abundance of certain predators in otherwise isolated habitats (Micheli & Peterson 1999). Micheli and Peterson (1999) showed that survivorship of clams was lower on reefs connected to seagrass or saltmarsh due to increases in blue crab predation. Variations in depth are known to influence abundances of *S. nigra* which have a strong preference for deeper water (Jenkins et al. 1997, Saunders 1997), but the seagrass beds sampled in this study occurred at similar depths.

Few of the patterns we found were statistically significant. Detecting faunal patterns across seagrass landscapes has proved difficult in many studies (Connolly and Hindell unpublished review). For example, relationships between seagrass patch size and abundance rarely show any consistent difference between small and large patches, or abundances on the edge compared to the middle of the patch (Bell et al. 2001). Some researchers suggest that the impacts of habitat fragmentation are difficult to detect in marine systems because spacing between patches may be insufficient to hinder dispersal. Although a range of seagrass to mangrove distances were assessed, the overall scale of the survey (< 1km) may not have been sufficient to detect subtle effects of distance from mangroves.

Many factors concerning the location of a bed within estuaries may influence assemblage structure. Other studies have correlated water temperature, salinity (Loneragan et al. 1986), water depth, dissolved oxygen levels, local hydrodynamic factors (Hamer & Jenkins 1996), and distance to the mouth of the bay (Bell & Westoby 1986b) with changes in fish abundance. It is also possible that site-to-site variability in the structural complexity of both seagrass and mangroves (e.g. density and length of leaves/pneumatophores) could have contributed to variability in fish associated with seagrass in ways that were completely unrelated to proximity. It is likely these factors contributed to the variability between sites and made it difficult to detect the effect of mangrove proximity to seagrass.

Care was taken in the study design to ensure that some of these factors did not confound our results. Salinity and temperature and dissolved oxygen are relatively uniform across the bay (see earlier chapters), and all samples were collected at similar depths on the edge of the intertidal bank. The distance to the mouth of the bay varied among sites and this probably had some effect on assemblage structure. For example site 2 was located closer to the mouth of the estuary than any other site and consequently marine fish such as seapike (*Sphyraena novaehollandiae*) and anchovy (*Engraulis australis*) were unique to this site. The sites with seagrass close to mangroves occurred at a variety of distances from the mouth of the bay and it is unlikely this factor confounded our results. Future studies should better quantify effects of spatial variability in structure in shaping patterns.

Finer-scale within site patterns

In both the ASU and mudflat plots we found that distance from the shore had a strong effect on the abundance and diversity of fish, and the presence of mangrove had a strong effect on fish abundance and assemblage structure close to shore. Significantly more fish and a greater diversity of species were

recorded in the near-mangrove ASUs than the near-beach ASUs, consisting of both resident intertidal fish and those migrating from the subtidal.

A number of processes may account for the high diversity and abundance of fish immediately adjacent to mangroves. The presence of mangroves may provide a greater area of structure for foraging and protection from predators, for fish that move between the two habitats. A study of a small pinfish (Irlandi and Crawford, 1997) showed that abundance and growth of fish in seagrass was enhanced in areas adjacent to saltmarsh. Irlandi and Crawford (1997) showed that fish moved more between seagrass and saltmarsh than seagrass and the bare sand, thereby utilising a greater are of habitat. Alternatively the productivity of the adjacent seagrass may be enhanced by either outwelling or movement of prey items between mangrove and seagrass. Recent stable isotope analysis has suggested that outwelling may occur at much smaller scales than once imagined. Guest (2004) found that in saltmarsh adjacent to mangroves carbon was assimilated more by invertebrates within meters of mangroves compared to those more than 30m away.

Similar to the pattern observed in the broader scale survey, the presence of mangroves had the strongest effect on small resident gobies of the intertidal. A high diversity of gobies is commonly associated with mangrove habitat across the world (Barletta et al. 2000). Species of this family use their pelvic fins to attach to mangrove roots, seagrass or sediment and are able to breath air by having a highly vascularised bucco-pharyngeal chamber. These adaptations allow for a variety of strategies in a severe and limited environment (Barletta et al. 2000). *P. olorum* was found at significantly higher abundances close to the mangroves and accounted for 54% of the fish caught in this position. *P. olorum* is one of few fish that are capable of remaining in the mangroves at low tide, as they are small enough to shelter in the few very shallow pools and within grapsid crab burrows.

Other fish showed little variation in their abundance across the intertidal or were more abundant in the far-shore treatments. Similar to the results of the broad scale survey, *Stigmatopora sp*. were only caught at the far shore treatments. Post settlement larvae of *Sillaginodes punctata* were generally found in all positions, and were only slightly more abundant in the far shore samples. Although only 2cm in length, studies have shown they *S. punctata* are capable swimmers and are able to selectively choose habitat (Hindell et al. 2003). It has been suggested that the spatial distribution of *S. punctata* is determined by the availability of prey (Jenkins and Hamer 2001), therefore habitat next to mangrove may not provide enhanced food for these larvae.

Even though fish abundances varied little between ASUs and mudflat plots at most locations, those using ASUs 'near' mangroves were much greater than those using ASUs in either of the shoreline 'far' locations or 'near' the non-mangrove beach. This finding is consistent with a model whereby the value of mangroves in seagrass landscapes can be important, but only if there is 'suitable' structure close by. Skilleter et al. (in press) have recently found that dense seagrass close-to (proximal) mangroves supported at least 7 times more prawns (*Metapenaeus bennettae*) than distal-dense, proximal-sparse or distal-sparse seagrass-mangrove combinations. While they cited a need for further work, the differences in community composition between the habitat ◎ proximity treatments were thought to reflect differences in resources (Skilleter et al. in press).

Seagrass landscapes and fisheries

Few of the species sampled here were of economic importance. Those that were, however, such as whiting and mullet, showed patterns that suggest the spatial arrangement of seagrass beds to mangroves may influence fisheries species. Previous work has largely considered habitat units in isolation, i.e. seagrass versus mangroves, but this study suggests that the spatial arrangement of the 2 habitats can be important, and a more holistic view to assessments of habitat use is needed.

Table 16. Summary of the fish abundances sampled in seagrass at each distance from mangroves. M species also sample in mangroves (Hindell and Jenkins 2004, in press). T total fish. % percentage of all fish. μL mean ± standard error length of fish. Mean depth, species richness, abundance and biomass also given below. Standard error shown in parenthesis.

		Distance from seagrass to mangroves									
Species	M	110 m	290 m	300 m	550 m	670 m	752 m	855 m	T	%	μL (± se)
Acanthaluteres spilomelanurus		-	-	4	2	2	1	-	9	1.6	51 (17)
Arcana aurita		-	-	2	-	1	-	-	3	0.5	80 (62)
Arcana ornata		-	-	-	-	2	-	-	2	0.3	37 (6)
Arenigobius frenatus	●	21	24	1	-	-	5	-	51	8.9	25 (8)
Brachaluteres jacksonianus		-	-	-	2	-	-	-	2	0.3	27 (18)
Cristiceps australis		-	-	1	-	-	-	1	2	0.3	92 (53)
Diodon nicthemerus		-	-	-	-	1	-	2	3	0.5	127 (15)
Engraulis australis		-	4	-	-	-	-	-	4	0.7	56 (5)
Favonigobius tamarensis	●	2	3	-	-	-	-	-	5	0.9	33 (10)
Genus C sp 1		-	-	-	-	1	-	1	2	0.3	15 (3)
Gymnapistes marmoratus		3	2	2	9	4	-	4	24	4.1	54 (28)
Haletta semifasciata		-	-	-	5	1	-	2	8	1.4	139 (53)
Heteroclinus adelaide		-	-	2	-	-	-	1	3	0.5	67 (19)
Heteroclinus tristis		-	-	-	5	-	-	-	5	0.9	70 (24)
Idiosepius notoides		6	31	4	3	4	43	23	114	20	13 (4)
Kestratherina brevirostris		-	-	1	-	-	-	-	1	0.2	66
Leptatherina presbyteroides		-	-	-	1	-	-	1	2	0.3	42 (6)
Meuschenia freycineti	●	-	-	-	1	1	-	1	3	0.5	63 (6)
Mitotichthys semistriatus		-	-	1	1	-	-	-	2	0.4	140 (7)
Nesogobius sp 1	●	-	2	2	-	2	3	-	9	1.6	33 (3)
Nesogobius sp. 3		-	-	-	3	-	-	-	3	0.5	41 (6)
Pseudogobius olorum	●	30	3	-	-	-	-	-	33	5.7	13 (2)
Pugnaso curtirostris		5	8	-	-		2	1	16	2.8	55 (4)
Sepioteuthis australis	●	-	-	-	-	1	-	1	2	0.3	64
Sillaginodes punctata		-	1	-	-	-	2	-	3	0.5	88 (51)
Sphyraena novaehollandiae		-	1	-	-	-	-	1	2	0.4	182 (34)

Sprattus novaehollandiae		-	6	-	-	-	-	-	6	1	46 (11)
Stigmatopora argus		1	1	19	15	15	2	3	56	9.7	102 (22)
Stigmatopora nigra		10	1	9	-	10	116	36	182	31.6	80 (22)
Tasmanogobius gloveri		-	-	-	-	-	1	-	1	0.2	50 (0)
Tetractenos glaber	•	5	1	3	-	-	3	1	13	2.3	85 (19)
Trygonorrhina guanerius		-	-	1	-	-	-	-	1	0.2	430
Urocampus carinirostris		1	-	-	-	-	-	-	1	0.2	60
Vincentia conspersa		-	-	1	-	-	-	-	1	0.2	48
Vanacampus phillipi		-	-	1	-	1	-	-	2	0.3	105 (6)
Depth		2.3 (0.1)	2.0 (0.1)	2.3 (0.6)	2.6 (0.58)	2.5 (0.25)	2.6 (0.27)	2.2 (0.1)			
Species richness		5.5 (1.6)	6 (1)	4.3 (2.6)	3.8 (1.8)	4.7 (1.7)	3.4 (1.1)	4.2 (1.5)			
Abundance		14 (6.1)	17.8 (7.1)	9 (7.1)	9.4 (6.6)	11.25 (4.5)	35.6 (64.6)	15.6 (8.8)			
Biomass (g)		6.4 (12.5)	15.3 (10.9)	30.6 (24)	28.6 (36.4)	40.6 (55.4)	13.3 (15.6)	28.6 (40.9)			

Table 17. Regression analyses assessing relationships between each of fish abundance, biomass, species richness, abundances of the 2 most common families and 4 most common species and distance of seagrass from mangroves.

	df	F ratio	*P*	R^2
Abundance	1,5	0.738	0.429	0.129
Biomass	1,5	1.436	0.284	0.223
Species richness	1,5	4.488	0.087	0.472
Syngnathidae	1,5	5.531	0.065	0.522
Gobiidae	1,5	5.433	0.067	0.521
Stigmatopora nigra	1,5	2.281	0.191	0.476
Idiosepius notoides	1,5	1.119	0.338	0.183
Stigmatopora argus	1,5	0.072	0.798	0.014
Arenigobius frenatus	1,5	4.648	0.083	0.482

Table 18. Summary of total fish abundances sampled in each of the shore type (mangrove, sandy beach), proximity (near – N, far – F) and substratum (artificial seagrass units – ASU, mudflat – MF) treatments in the smaller-scale (10s of meters), within-site study.

	Mangrove				Sandy beach			
	N		F		N		F	
Species	ASU	MF	ASU	MF	ASU	MF	ASU	MF
Aldrichetta forsteri	-	1	1	-	-	-	-	-
Arenigobius frenatus	14	1	10	18	-	-	9	9
Diodon nicthemerus	-	1	-	-	-	-	-	-
Favonigobius tamarensis	1	1	-	1	2	-	-	1
Gobiopterus semivestitus	1	-	2	-	2	-	-	-
Idiosepius notoides	-	-	-	-	-	-	3	-
Nesogobius sp 1	-	-	-	-	-	-	1	1
Pseudogobius olorum	34	7	10	6	5	5	6	4
Pugnaso curtirostrus	1	1	-	-	1	3	1	2
Rhombosolea tapirina	4	-	2	-	3	6	-	-
Sillaginodes punctata	2	2	5	4	2	1	8	2
Stigmatopora argus	-	-	-	-	-	-	3	-
Stigmatopora nigra	-	-	-	-	-	-	1	1
Tetractenos glaber	2	2	-	-	-	1	-	-
Total	59	16	30	29	15	16	32	20

Table 19. Results of 3-factor analyses of variance comparing fish abundances and species richness across shore type (mangrove, sandy beach), proximity (near, far) and substratum (ASU, mudflat) treatments in the smaller-scale (10s of meters), within-site study. Data $\log_{10}(x+1)$ transformed.

		Abundance		Species Richness	
Source	df	MS	*P*	MS	*P*
Shore-type (S)	1	14.103	0.004	1.117	0.090
Proximity (P)	1	2.949	0.150	0.365	0.321
Substratum (A)	1	9.231	0.015	0.754	0.159
S x P	1	2.111	0.220	0.570	0.218
S x A	1	6.684	0.035	0.412	0.293
P x A	1	3.778	0.105	0.001	0.950
S x P x A	1	9.462	0.014	0.070	0.662
Error	22	1.323		0.354	

Chapter 6. Effects of proximity to seagrass on patterns of association of fish with mangroves in temperate Australia

INTRODUCTION

Fisheries production is believed to constitute the major value of marketed products from mangrove forests (Ronnback 1999). Economically important fish species contribute markedly to the number and biomass of fish inhabiting mangrove habitat. It has been reported that between 38% to 75% of abundance and 32% to 94% of biomass of fishes in mangroves are of commercial value (Bell et al. 1984, Morton 1990). Estimates of the annual market value of capture fisheries supported by mangroves ranges from US$750/ha to US$16750/ha (Ronnback 1999). The relative contribution of mangrove related species constitutes some 67% of the entire commercial catch in eastern Australia (Hamilton & Snedaker 1984).

The relative significance of mangroves, compared with alternative intertidal (mudflats, seagrass beds) and subtidal (seagrass beds, coral reefs) habitats has been well documented, often showing a greater diversity and abundance of fishes in mangroves than alternative habitats (Robertson & Duke 1987, Thayer et al. 1987, Chong et al. 1990, Morton 1990, Laegdsgaard & Johnson 1995). This evidence has led to mangroves being recognised worldwide as important nursery grounds (an area in which density, survival, growth and consequent movement of juveniles to the adult habitat are enhanced over those in alternative habitat types, Sheridan & Hays 2003) for juvenile fishes (Bell et al. 1984, Robertson & Duke 1987, Parrish 1989, Laegdsgaard & Johnson 1995, Laroche et al. 1997, Nagelkerken et al. 2000, Dorenbosch et al. in press, Mumby et al. 2004).

Although mangroves, seagrass beds and other intertidal and subtidal habitats can exist independently, they commonly form integrated ecosystems of high productivity that are crucial to the productivity and sustainability of fisheries (Ronnback 1999). Few studies, however, have assessed how fauna associated with mangroves might be influenced by the proximity of alternative habitats such as seagrass.

The objectives of this study were to (1) further (to previous chapter) assess artefacts associated with setting pop nets in mangroves (experiment), and (2) assess whether fish assemblages varied among zones within mangroves (edge versus forest) and with proximity to local seagrass beds (survey).

METHODS

Study Site

This study was done in Western Port, Victoria, Australia (Fig. 29), between May and September 2004 (see earlier chapters for description of Western Port).

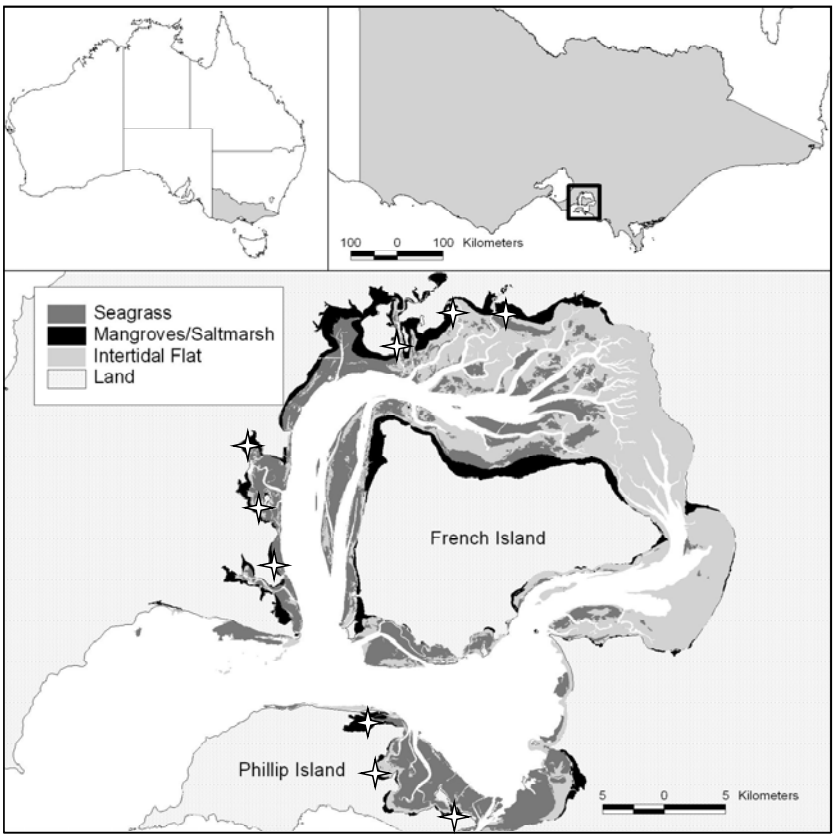

Figure 29. Location of study sites in Western Port, Victoria, Australia. Inset: Location of study region within Victoria and Australia. ✧ denotes study sites, which are, clockwise from left; (1) Woolley's Beach, (2) Jack's Beach, (3) Hastings, (4) Warneet, (5) Blind Bite, (6) Tooradin, (7) Churchill Island, (8) Rhyll, (9) Rhyll Inlet.

Effects of disturbance and presence of artificial structure (pop nets) on fish abundances in mangroves

Pop nets have a better catch efficiency than gears such as seine nets in structurally complex habitats (this report, Connolly 1994b), but results are potentially confounded by the large amount of physical disturbance created while setting these devices in soft, muddy habitats. The effects of physical disturbance in soft sediment environments are often manifested as the partial or complete defaunation of disturbed patches through direct mortality and physical damage, as well as through the displacement of species from their preferred habitats. Although such effects may lead to a long term (weeks to months) shortage of prey species for fishes, in the short term (hours to days) there is likely to be an abundance of prey items for foraging fishes that would otherwise not exist. It is possible that what has previously been perceived to be relatively higher catch efficiency of pop nets may actually be attributable to the active attraction of fishes to experimental plots due to elevated prey availability, foraging efficiency or some other factor related to the effects of disturbance from setting the gear.

This part of the study was done at Woolley's Beach (Fig. 29). This area was chosen because it was representative of the mangrove habitat around the bay and the fish assemblages using the mangrove habitat have been studied more extensively than any other site within the bay (see previous chapters).

Three experimental treatments (the same as those used in the artefacts experiment in Chapter 3; full pop net set in channel, channel only, undisturbed) were set up in each of the two habitat zones (forest interior and pneumatophores) within a site on the same day. Within a zone, treatments were separated by at least 50 m, and care was taken to ensure treatments in the forest were not adjacent to those in the pneumatophore zone.

Each of the treatments were sampled with fyke nets, which are recommended for shallow water and heavily vegetated marsh type habitats (Kelley 1953, Clynick and Chapman 2002). The construction and design of these nets are described in previous chapters. A single net was placed directly seaward of each treatment to sample fish moving out of the 'treatment area' (n = 6 nets in total, 1 for each of the 3 treatments in each of the 2 zones). Fish were removed from the net after the tide had receded. Times of flood and ebb (when the net became submerged and exposed), and depth, were recorded for each fyke net.

All treatments were removed completely after sampling. The whole study was then repeated in previously unmanipulated plots on 3 additional occasions (4 days in total, within a single week).

Where possible fish were identified to species, measured (TL, mm), their weight recorded, and released. Where this was not possible, fish were anaesthetised with clove oil before being preserved in ethanol and identified in the laboratory.

Survey - Influence of zonation and seagrass proximity on mangrove-associated fish assemblages

To assess fish zonation within mangrove habitat, and investigate the effects of seagrass proximity in structuring mangrove associated fish assemblages, fish were sampled in two zones of the mangrove habitat (forest versus edge) at each of 9 sites. Each site was chosen randomly from those available that provided a range of distances to the closest bed of seagrass (they varied in their proximity to the closest seagrass beds by between 100 and 1000 m).

The interior of the mangrove forest (approximately 20 m landward from the seaward margin of the forest), and the pneumatophore zone (edge, immediately seaward of the seaward margin of the mangrove forest) were each sampled with a single pop net at each of the 9 sites. In additional to the requirement of distance from local seagrass (above), these sites also had to meet the following criteria: mangroves must be accessible by land or easily accessible by boat at low tide, substratum must be firm enough to allow traps to be set by foot, and sites must vary in distance to seagrass. Each site was sampled on a separate day with sampling restricted to mid-day high tides to reduce diel variation. On each sampling occasion fish were sampled using pop nets (n = 1 in each zone).

Pop nets are a highly quantitative method of sampling fish communities in intertidal habitats with high levels of vegetative structure (Rozas 1992, Connolly 1994). The construction and setting of pop nets are described in previous chapters. Pop nets were set-off at high tide. Fish were collected from the pop nets as the tide receded (see previous chapters).

Data Analysis

Univariate analysis

Prior to univariate analyses, all data were checked for normality and homogeneity of variances using box plots and plots of residuals (Quinn and Keough 2002). Where diagnostics showed that assumptions were not met, data were transformed using a $Log_{10}(x+1)$ and reassessed. Fish numbers and weights were adjusted for the area fished.

For the experiment, differences in total fish abundance (fish.net^{-1}), total fish biomass (fish weight (g).net^{-1}) and total species richness (spp.net^{-1}) between zones (mangrove forest, pneumatophore) and among treatments (pop net, disturbed, control) were analysed using 3-factor randomised blocks analyses of variance. Zone and treatment were treated as fixed factors. Day of sampling was treated as a random factor. F-ratios and corresponding *P*-values obtained from the simple linear model were adjusted to treat day as a blocking factor as described in Quinn and Keough (2002).

For the survey, differences in total abundances, total biomass, and species richness among sites and between zones were analysed using 2-factor randomised blocks analyses of variance (Quinn & Keough 2002). Zone (mangrove forest, pneumatophores) was treated as a fixed factor, and site (9 levels) was treated as a random factor. The relationships between total abundance, total biomass, species richness, and seagrass proximity were analysed using regression analyses.

Multivariate analysis

Multidimensional scaling (MDS) and analysis of similarity (ANOSIM), based on Bray-Curtis dissimilarities calculated from fish abundances were used to assess variability in fish abundances between zones (mangrove forest, pneumatophore).

RESULTS

Artifact experiment

A total of 622 fish from 5 species and 5 families were sampled over 5 sampling occasions. The smooth toadfish (Tetraodontidae: *Tetractenos glaber*) dominated catches, comprising 96% of all fishes sampled. Sandy sprat (*Hyperlophus vittatus*) comprised 3% of all fishes while the remainder was comprised of greenback flounder (Pleuronectidae: *Rhombosolea tapirina* Gunther), yelloweye mullet (Mugilidae: *Aldrichetta forsteri* Valenciennes), and six spine leatherjacket (Monacanthidae: *Meuschenia Freycineti* Quoy & Gairmard), each of which constituted less than 1% of fish sampled.

Randomised blocks analysis of variance (ANOVA) revealed that there were no significant differences between experimental treatments for total abundances ($P = 0.193$), total biomass ($P = 0.098$), or total species richness ($P = 0.714$) of fishes (Table 23). Similarly, these tests did not reveal any significant variation across zones, or any significant interactions between terms (Table 23).

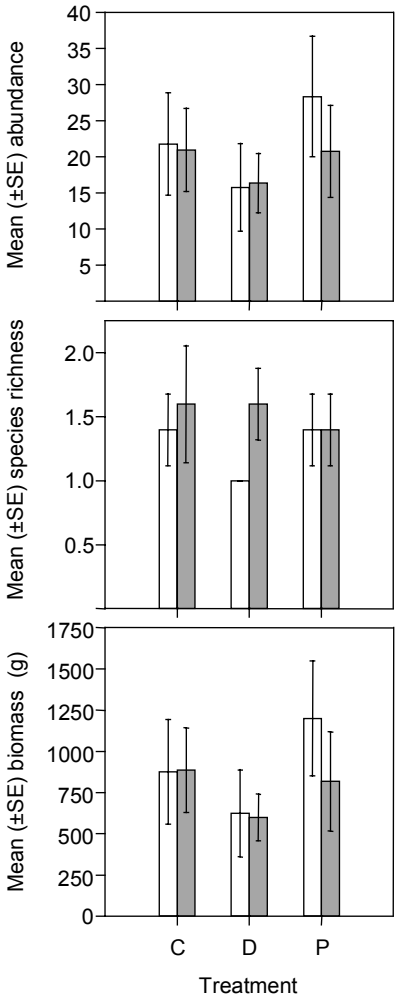

Figure 30. Mean (±se) total fish abundance (fish net $^{-1}$), total fish biomass (weight (g) net $^{-1}$) and species richness (spp. net^{-1}) associated with experimental treatments (C – no net, D – channel only, P – pop net plus channel) in the mangrove forest (open bars) and pneumatophore (shaded bars) zones.

Survey

The fish assemblages were characterised by large numbers of small adult fishes, with few of commercial importance. A total of 493 fish were sampled over nine sampling events. Assemblages were comprised of 11 species from 5 families (Table 20). One species, sandy sprat (Clupeidae: *Hyperlophus vittatus* Castelnau) comprised 55% of all fish caught but were encountered at only one site. Gobiids constituted 41% of all fish caught and were the most diverse family with six species (*Pseudogobius olorum* Sauvage, *Arenigobius bifrenatus* Kner, *Gobiopterus semivestitus* Munro, *Arenigobius frenatus* Gunther, *Favonigobius lateralis* Macleay, *Nesogobius* sp.1) encountered. Tetraodontids (*Tetractenos glaber* Freminville, *Contusus brevicaudus* Hardy) and Atherinids (*Kestratherina esox* Klunzinger) comprised 2.8% and 1.6%, respectively, while one individual southern calamari (Loliginidae: *Sepioteuthis australis*) was encountered.

Although there was considerable variation in patterns of total fish abundance, biomass and species richness across sites, randomised blocks analysis of variance revealed no statistically significant difference among sites (Table 21).

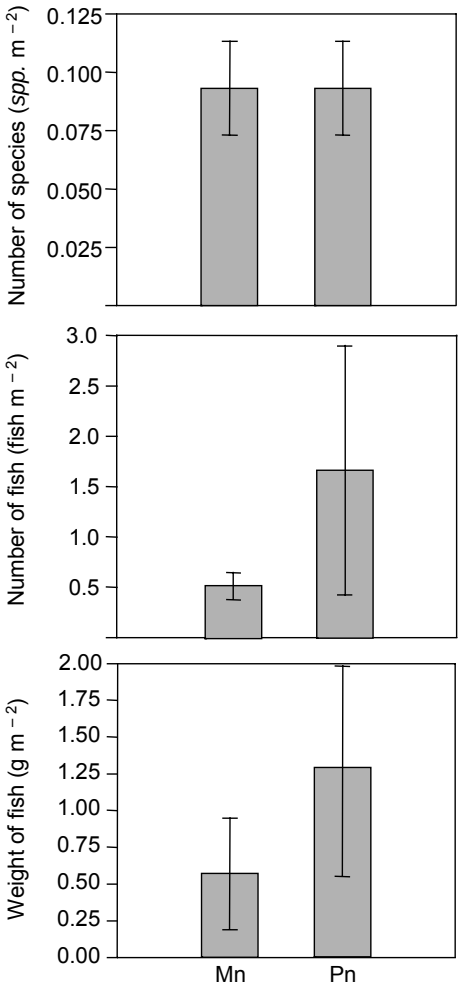

Figure 31. Mean (± se) total abundance, total biomass and total species richness of fish in each zone (mangrove forest - Mn, pneumatophore - Pn).

Randomised blocks analysis of variance revealed no significant variation in total fish abundance, biomass or species richness between the mangrove forest and pneumatophore zones (Table 21, Fig. 31). Number and biomass of the 2 most common taxa, gobiids and tetraodontids also did not vary significantly between zones (Fig. 32).

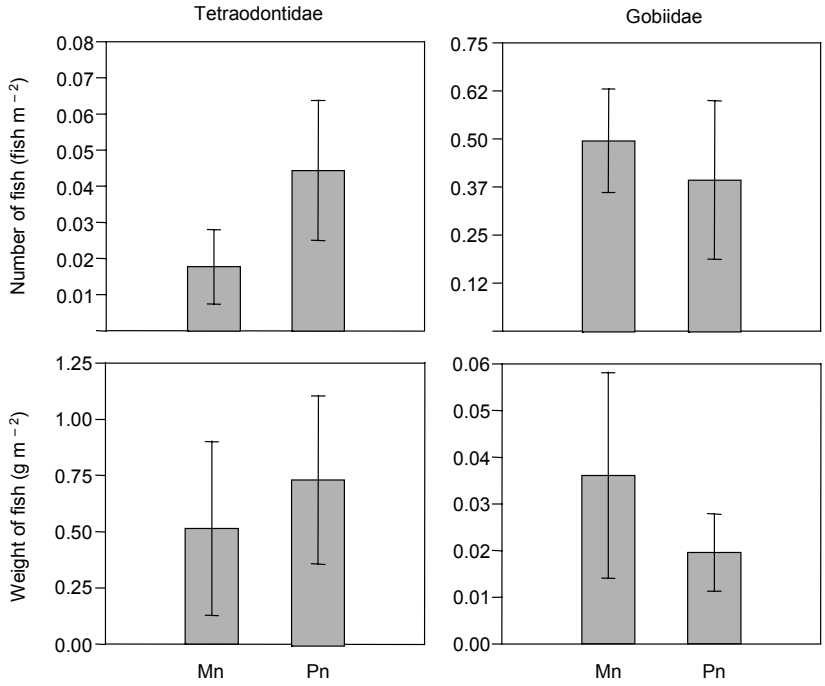

Figure 32. Mean (± se) total abundance, total biomass and total species richness of fish in each zone (mangrove forest - Mn, pneumatophore - Pn).

Analysis of similarity (ANOSIM) revealed that there was no significant difference in total abundance of fishes between the mangrove forest and pneumatophore zones (R = 0.058, *P* = 0.229), and MDS plots did not suggest a difference in fish abundance between the two zones (Fig. 33).

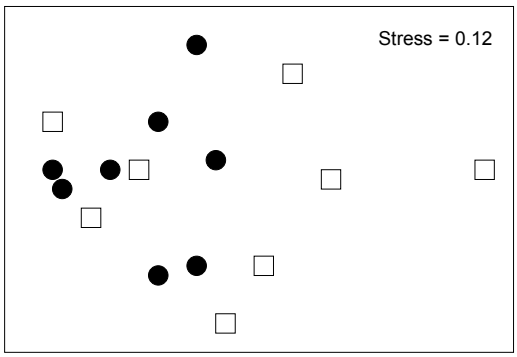

Figure 33. Multidimensional scaling plot based on Bray Curtis dissimilarity measures comparing fish abundance across zones (mangrove forest – shaded squares, pneumatophore – open circles).

The size distribution of all fish species differed between the mangrove forest and pneumatophore zones (Fig. 34). These differences seem to result from the high abundance of *Hyperlophus vittatus* (mean length = 48.68 ± 0.35 mm) in the pneumatophore zone, but this species was only sampled on one occasion at one site, and if omitted there would be little discernible difference in the size distributions between zones.

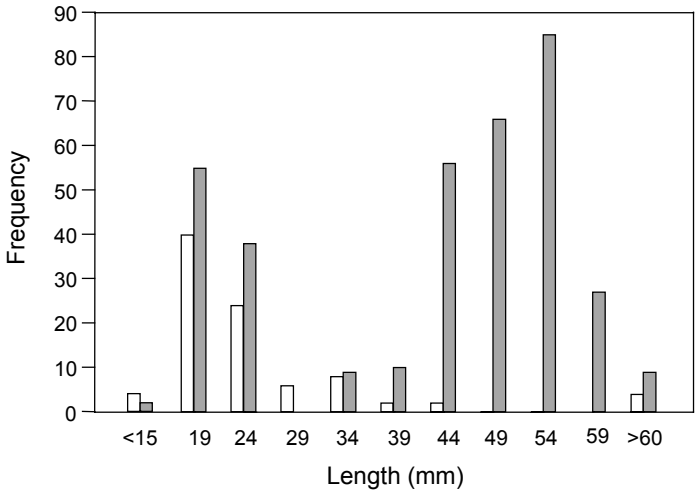

Figure 34. Length-frequency distribution of all fishes sampled with pop nets in the mangrove forest (open bars) and pneumatophore (shaded bars) zone.

Influence of seagrass proximity on mangrove-associated fish assemblages

Regression analysis (Fig. 35) of total biomass against distance to seagrass revealed that as the distance from seagrass increased, the total biomass of fish decreased ($R^2 = 0.443$, $P = 0.050$). Regression analysis of total abundance and total species richness suggested that similar 'positive' relationships existed for these variables with proximity to seagrass (Fig. 35), but these patterns were not statistically significant ($P > 0.05$, Table 22).

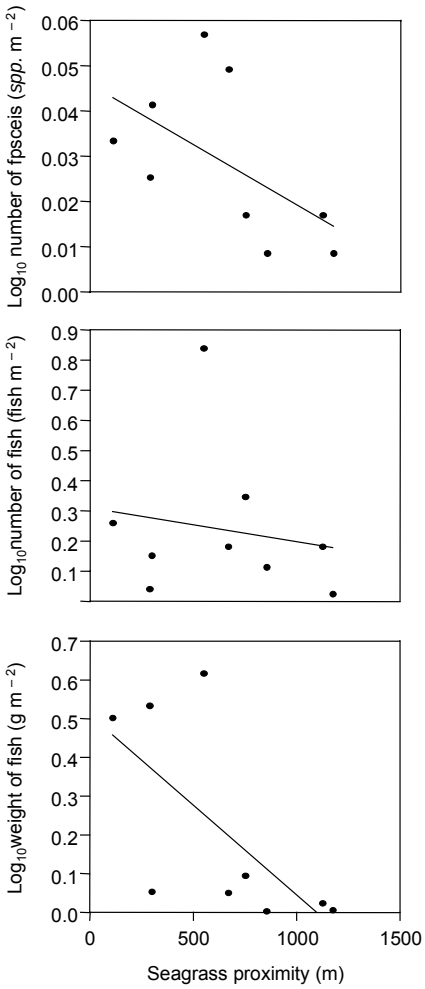

Figure 35 Relationship between each of total abundance, biomass and species richness of fish and seagrass proximity. Data were Log_{10} (x + 1) transformed.

DISCUSSION

Effect of seagrass proximity on mangrove-associated fish assemblages

There were positive (albeit not always statistically significant) relationships between species richness, abundance and biomass, and seagrass proximity. It has been shown that habitat patches that are located nearer to other habitat patches of high productivity are more likely to exhibit high abundances of fauna (Sogard 1989). In our study, most fish could only use mangroves when they were inundated at high tide, and, with the exception of some gobiid species, which can remain in crab burrows or small puddles of water (see previous chapters), must be migrating from subtidal habitats. Toadfish, sprats and yellow-eye mullet are common in seagrass close to our study sites (see previous chapter). It is possible, therefore, that the positive relationship between fish abundance in mangroves and proximity to seagrass beds is due to the increased movement of species from seagrass beds to mangroves.

Alternatively, these patterns could be due to some other (as yet unmeasured) factor related to seagrass proximity. For example, the positive relationship may be due to outwelling (actually inwelling) of nutrients from seagrass to mangroves. Detrital seagrass may be more effectively intercepted in mangrove

habitat than alternative habitats, due to the high structural complexity of mangrove habitat. High inputs of detrital seagrass are likely to provide a rich source of nutrition to higher order consumers such as fishes through a detrital food chain (e.g. Yellow fin whiting in SA – see Hindell, Connolly and Gorman in press, Shaw and Jenkins 1992).

Variability in fish assemblages between zones

Patterns of zonation observed in the present study were not as defined as in previous chapters. Although previous studies often showed a high degree of zonation between the mangrove forest and pneumatophore zone (Vance et al. 1996, Ronnback et al. 1999, Hindell & Jenkins in press), these studies were confounded by inconsistent sampling methods or were done during warmer months (Hindell & Jenkins in press, Smith & Hindell unpublished data). Although no significant patterns of zonation were observed, general patterns were apparent. Abundance and biomass were greater in the pneumatophore zone, though no difference was evident in species richness between the two zones. Tetraodontids were more abundant in the pneumatophore zone, whereas gobiids were more abundant in the mangrove forest. Such trends are not unexpected, as smaller fish are generally associated with more structurally complex habitat, whereas larger species may prefer less structurally complex habitat (Robertson & Duke 1987, Thayer et al. 1987, Parrish 1989, de la Moriniere et al. 2004, Primavera 1997, Laegdsgaard & Johnson 2001, Macia et al. 2003). This idea was supported by the length frequency data, which showed that smaller fishes were distributed across the mangrove and pneumatophore zones, while larger fish were limited to the pneumatophore zone.

Implications of mangrove proximity

This study provides further evidence that mangroves and seagrass beds may form integrated ecosystems, in which patterns of use depend on the spatial scales over which a study is done. It also highlights the ecological consequences of the spatial location of habitat elements, their relative position to other elements, and how these relationships and their consequences affect the characteristics of the surrounding landscape mosaic. A coastal 'seascape' perspective, in which the biophysical interactions among mangroves, seagrass beds and other components are acknowledged, is therefore a prerequisite for the rational management and economic valuation of seafood production (Ronnback 1999). Management schemes should explicitly protect landscapes of connected habitats rather than simply identify representative areas of each habitat in isolation (Nagelkerken et al. 2000a, Mumby et al. 2004).

Table 20. Summary of fishes sampled in each zone pooled across nine sites. N = total number of fishes, W = total weight of fishes (g), L = average length of fishes (±SE) (mm). *n* total = 18.

		Mangrove Forest			Pneumatophore		
Common name	Species name	N	W	L	N	W	L
Bluespot Goby	*Pseudogobius olorum*	40	3.72	23.1 ± 0.84	15	0.35	23.6 ± 1.9
Bridled Goby	*Arenigobius bifrenatus*				1	1.50	77.0
Glass Goby	*Gobiopterus semivestitus*	65	1.3	13.6 ± 1.9	68	1.70	19.0 ± 0.2
Girdled Goby	*Nesogobius* sp 1	4	2.4	44.7 ± 5.2			
Halfbridled Goby	*Arenigobius frenatus*	2	0.6	46.0 ± 3.5	5	1.05	34.3 ± 2.15
Longfin Goby	*Favonigobius lateralis*	1	0.3	39.0			
Pikehead Hardyhead	*Kestratherina esox*	1	0.3	40.0	7	1.83	39.3 ± 0.75
Prickly Toadfish	*Contusus brevicaudus*	1	31.6	110.0			
Sandy Sprat	*Hyperlophus vittatus*				269	116.8	48.7 ± 0.3
Smooth Toadfish	*Tetractenos glaber*	3	84.17	131.5 ± 13.5	10	163.98	84.0 ± 10.2
Southern Calamari	*Sepioteuthis australis*	1	3.61	75.0			
Total		118	128.19	25.41 ± 2.68	375	287.25	40.84 ± 2.11

Table 21. Results of 2-factor randomised blocks analyses of variance (ANOVAs) comparing total biomass, abundance and species richness, as well as the biomass and abundance of the two most common families (Tetraodontidae & Gobiidae) sampled across zones and sites. All data were Log_{10} (x + 1) transformed. *n* = 18. Bold if significant.

	Source	df	MS	*P*
Total abundance	Site	8	0.081	0.24
	Zone	1	0.033	0.43
	Error	8	0.048	
Total biomass	Site	8	<0.001	0.32
	Zone	1	0.001	0.20
	Error	8	<0.001	
Total species richness	Site	8	0.021	0.36
	Zone	1	0.009	0.48
	Error	8	0.016	

Table 22. Regression analyses of the relationship between each of total abundance, biomass and species richness, as well as the abundance and biomass of the two most common families (Tetraodontidae & Gobiidae) and seagrass proximity. *n* = 9. Bold if significant.

		df	MS	*P*	R
Total abundance	Regression	1	0.014	0.66	0.03
	Residual	7	0.067		
Total biomass	Regression	1	0.238	0.050	0.44
	Residual	7	0.043		
Total species richness	Regression	1	0.001	0.11	0.32
	Residual	7	<0.001		

Table 23. Summary of results of 3-factor randomised blocks analyses of variance (ANOVAs) comparing Log_{10} (x + 1) total abundance and Log_{10} (x + 1) total biomass of fishes sampled in each experimental treatment in each zone across five days. *n* = 30. Bold if significant.

	Source	df	MS	*P*
Total abundance	Zone (Z)	1	0.003	0.86
	Treatment (T)	2	0.084	0.33
	Day (D)	4	0.288	0.02
	T x Z	2	0.036	0.53
	Z x D	4	0.101	0.2
	T x D	8	0.065	0.38
	Error	8	0.052	
Total biomass	Zone (Z)	1	0.010	0.78
	Treatment (T)	2	0.121	0.26
	Day (D)	4	0.479	0.01
	T x Z	2	0.061	0.46
	Z x D	4	0.112	0.27
	T x D	8	0.077	0.46
	Error	8	0.071	
Species richness	Zone (Z)	1	0.014	0.18
	Treatment (T)	2	0.002	0.71
	Day (D)	4	0.006	0.53
	T x Z	2	0.008	0.36
	Z x D	4	0.022	0.07
	T x D	8	0.008	0.4
	Error	8	0.006	

Chapter 7. Application of stable isotopes in describing food web structure

GENERAL INTRODUCTION

Marine vegetated habitats are regarded as important in the provision of habitat for fisheries species because they provide shelter and food (Hutchings 1981, Bell & Pollard 1989, Connolly et al. 1999). In the majority of cases, however, the 'value' of vegetated habitats is ambiguous because the work is based largely on abundance data – little is known of the processes driving associations such as nutrition.

Primary production in coastal marine and estuarine ecosystems supports food webs through consumers grazing either directly on live plant material or on detrital material derived from those producers (Higgins and Thiel 1988, Wilson 1988, Kennish 1990). The role of the various types of primary producers in driving the food web in these systems can vary substantially. Macrophytes, including saltmarshes, mangroves, macroalgae and seagrasses can constitute a large biomass in comparison to other aquatic primary production. Saltmarshes, mangroves and seagrasses can supply invertebrates with nutrients, particularly through the detrital route (Zieman et al. 1984, Thresher 1992, Kwak and Zedler 1997, Loneragan et al. 1997, Castellanos and Rozas 2001). However, filamentous algae, benthic micro-algae and phytoplankton can also provide nutrients to many organisms (Haines 1976, Newell et al. 1995, Kwak and Zedler 1997).

Many of the above studies have relied on the natural abundance of stable isotopes of elements, particularly carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$), to trace different sources of primary producers and other food in food webs (Couch 1988, Wada and Mizutani 1991, Bunn and Boon 1993, Riera 1993, Loneragan et al.1997). The relative abundance of one isotope to the other gives each of these elements a stable isotopic ratio, which can vary among different primary producers depending on the mechanisms by which the elements are taken up (Lambers 1998). Consumers subsequently assimilate nutrients from their food and acquire a stable isotope fingerprint close to that of the combined nutrient sources (DeNiro and Epstein 1978, 1981). Thus, by comparing the stable isotope signatures of different potential nutrient sources and consumers, it is possible to estimate the individual contribution of each source to each consumer. It is preferable to use multiple nutrients, as they provide more detailed isotope signatures of sources and consumers (Peterson & Fry 1987, Riera et al. 1996).

The relative abundances of nitrogen and carbon stable isotopes in tissues of animals provide a time-integrated approximation of assimilated diet (Hobson 1999). There is generally limited fractionation of carbon between trophic levels, so ratios of ^{13}C to ^{12}C in predators reflects that of their prey, and ultimately, the base of nutritional support (DeNiro & Epstein 1978). Conversely, the preferential excretion of ^{14}N leads to the enrichment of ^{15}N by 3–5 ‰ with each consecutive trophic level (Minagawa & Wada 1984), which is relatively consistent between food webs (Hansson et al. 1997). Stable isotope analysis is particularly useful in determining the importance of prey items where empty stomachs are common, or where the taxonomic resolution of prey items in the stomach contents is poor (Beaudoin et al. 1999). These situations are common in studies of the trophic ecology of larger predatory fishes, many of which support valuable recreational and commercial industries.

GENERAL METHODS

Sample collection and processing

Only white muscle tissue immediately ventral to the anterior region of the dorsal fin was used for stable isotope analyses of fish because there is less variability in this tissue than others (Pinnegar & Polunin 2000). Only the most recent growth in fronds and leaves of macroproducers were prepared for isotope analysis. These were cleaned of epibionts and other detrital matter with a razor blade. Each sample consisted of several leaves/fronds from shoots pooled from different locations within a site. Epiphytes were scraped from seagrass fronds using a razor blade, being careful not to remove parts of the seagrass frond. Phytoplankton samples were washed through a series of progressively smaller sieves (500, 250, 125, 63 and 30 μm) to remove larger, non-microalgal components (e.g. large zooplankton and detrital matter). Benthic microalgae were separated from mud and inorganic contaminants with the procedures developed by Connolly and Hyndes (see SA, WA and Qld chapters).

All samples were dried to constant weight at 60°C, ground to a powder, placed in tin capsules and analysed on an Isoprime isotope ratio mass spectrometers. Between 1.5 and 2 mg of the fish tissue, and 5 mg of the plant samples were placed in tin capsules for analysis. The ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were expressed as the relative per mil (‰) difference between the sample and conventional standards (air for nitrogen; PeeDee belemnite limestone carbonate for carbon). Carbon was the main element used in analyses but nitrogen results are reported here for completeness.

Stable isotope analyses

Analyses of samples from Victoria and WA were analysed at Edith Cowan University, WA, Australia using an ANCA-NT/20-20 stable isotope ratio mass spectrometer (Europa Scientific, Crewe, UK). Samples from SA and Queensland were analysed at Griffith University using an Isoprime mass spectrometer.

Modelling producer contributions to fish nutrition

Where the number of potential sources is more than the number of elements employed (the case here, with 8 sources and 1 element), no unique mixing solution can be obtained. Therefore, IsoSource (Phillips and Gregg 2003) was used to calculate all possible solutions to mass balance equations and determine the feasible combinations of plants that explain the consumer signature.

Autotrophs were pooled into six taxa: saltmarsh, mangroves, seagrass, epiphytic algae, microphytobenthos and macroalgae. Mean $\delta^{13}C$ values were calculated for each fish species and each autotroph taxon across all locations, separately for the two periods. We used these mean values in the Isosource model of Phillips and Gregg (2003) to calculate feasible combinations of autotrophs that could explain the consumer signature. This method examines all possible combinations of each autotroph potential contribution (0 - 100%) in small increments (here 1%). Combinations that added to within 0. 1‰ of the consumer signature were considered feasible solutions. $\delta^{15}N$ was not used in the modelling because of sensitivity to fractionation corrections (see below). For selected species, as examples, we report results as the distribution of feasible solutions for each autotroph. We also give the median contribution and the 1%ile and 99%ile range (rather than the full range, which is sensitive to small numbers of observations on the tails of the distribution; Phillips & Gregg 2003).

Previous studies have shown that nitrogen isotopes in organisms are enriched relative to their diet (e.g. Peterson & Fry 1987). This fractionation is much larger for ^{15}N than ^{13}C, hence nitrogen isotopes can provide useful information about the trophic level of animals and the food web structure. For modelling of feasible mixtures, however, $\delta^{15}N$ values of consumers must be corrected for fractionation. We initially included $\delta^{15}N$ in our modelling using a fractionation correction based on the most recently reported

average fractionation increase of 2.2‰ per trophic level (McCutchan et al. 2003). However, we could not be confident that this fractionation rate applied to the species we were analysing. The fractionation rate per trophic level is known to vary with animal age, growth rates and food quality (Vander Zanden & Rasmussen 2001), and we had no information about how these factors affected fractionation in the species being analysed here. When we ran the model using C and N data, we found that results varied substantially if we changed our corrected $\delta^{15}N$ value by even a small amount (*Sillago* is shown as an example, see Table 28 in SA isotope study). We decided that using N was unhelpful in feasibility modelling. Nitrogen isotopes can be helpful in determining trophic levels and we therefore report them here for completeness.

Fractionation in $\delta^{13}C$ is relatively minor, typically < 1‰ per trophic level (McCutchan et al. 2003). We therefore used no correction for fractionation for $\delta^{13}C$. Nevertheless, to test the sensitivity of the model to small fractionation shifts in $\delta^{13}C$, as well as running the model using the mean $\delta^{13}C$ value, we re-ran it using adjusted $\delta^{13}C$ values, both adding and subtracting 1‰ to the mean for fish values. The results were less affected by these adjustments than for nitrogen, and the rank order of autotroph contributions was not affected (again, *Sillago* scenarios are shown as an example, see Table 28 in SA isotope study).

Chapter 8. Stable isotope studies in Victoria

INTRODUCTION

Much is known about the association of fish with different marine habitats in Victorian coastal waters. Seagrass for example is an important habitat for early post-settlement fishes such as King George whiting. Conversely, mangroves appear to have very little value to fisheries species. Less is known, however, about the processes through which shallow water habitats support local assemblages of juvenile and adult fisheries species.

Since the early stable isotope work of Klumpp and Nichols et al. (1983), much has been learnt of the role of shallow habitats in supporting the nutrition of fisheries species. Longmore et al. (2002) assessed the ultimate sources of primary production for commercial species such as Australian salmon (*Arripis trutta*), greenback flounder (*Rhombosolea tapirina*), southern sea garfish (*Hyporhamphus melanochir*), grass whiting (*Haletta semifasciata*), King George whiting (*Sillaginodes punctata*), rock flathead (*Platycephalus laevigatus*), sand flathead (*Platycephalus bassensis*) and yellow-eye mullet (*Aldrichetta forsteri*). These fisheries species fell into three groups: (1) pelagic piscivores (e.g. Australian salmon) with mixed algae as the most important ultimate source of primary production; (2) pelagic/benthic feeders (e.g. garfish, yellow-eye mullet and sand flathead) dependent on *Amphibolis*, *Zostera*/*Heterozostera* epiphytes, zooplankton and green algal detrital webs; and (3) primarily benthic feeders (flounder, grass whiting, King George whiting and rock flathead) ultimately dependent on seagrass *Zostera*/*Heterozostera* and *Amphibolis*. Much of this work was done in only Western Port Bay, however, and data on the contribution of primary producers to the nutrition of fisheries species in other systems was needed.

This study had 2 objectives: 1) to assess which primary producers supported fisheries species in large Victorian embayments; 2) determine whether tropic linkages changed among sites within embayments and between embayments.

MATERIALS AND METHODS

Study locations

This study was done at 4 locations in each of 2 embayments (Western Port and Corner Inlet), Australia (Fig. 1) between June 2003 and March 2004. The embayments have been described in detail in previous chapters.

General collection methods

Fish (consumers) and plant (producers) samples were collected from all 8 locations. Where possible, we attempted to collect the same types (taxa) of samples in each location so that we could get an estimate of the spatial variability. Sampling was done at 2 times (of the year); the first sampling time corresponded with winter (between July and August 2003), while the second sampling time corresponded with summer (January and February 2004). We attempted to collect 3 replicates of each sample (1 each from haphazardly chosen positions) in each location at each time of the year. All samples were placed on ice as soon as possible after collection and later frozen to reduce decomposition.

Sampling fish

Fish were sampled at each site with several types of equipment to maximise the likelihood of sampling as many of the commercial species as possible. An experimental otter trawl (2.4 m wide, with a body made from 3.3 cm sq. mesh and bag of 3.1 cm sq. mesh netting) was used to catch demersal species in deeper (> 2 m) channels. The two trawl boards (40 × 23 cm) were attached to tow lines 23 m long. Beach seine nets (one 30 m long × 2 m high with 1 cm mesh, the other 10 m long × 2 m high with 1 mm mesh) were used to catch fish from shallow (< 2 m) off the shore. Gill and fykes nets (see previous chapters) were used to catch fish using intertidal habitats.

Sampling plants

Table 24 lists the plant samples collected. Macroalgae, seagrass and seagrass epiphytes, mangrove and saltmarsh samples were simply collected by picking fronds. Only the most recent growth was collected (i.e. ends of fronds or stems). Phytoplankton samples were collected by towing a 50 cm diameter, 30 μm net in the surface 1 m of water behind a small boat for 15 to 20 minutes. Benthic microalgal samples were collected by scraping the surface 5 mm of substratum from otherwise unvegetated patches of intertidal mudflat to a total volume of approximately 500 ml into a plastic bag.

Sample processing for stable isotope analyses

See chapter on General Methods

Mixing model

The relative contributions of the alternative producers were calculated as in the General Methods. Given the mostly large (> 14 cm) size of fish and the generally slow rates of tissue turnover for fish, we made no attempt to differentiate the base for nutritional support between summer and winter.

RESULTS

We sampled 20 species of fish of commercial and recreational importance over the 2 sampling times of this project (Table 24). Some of these species were only sampled in winter (e.g. pink ling), others only in summer (e.g. estuary perch, mackerel), and several species were only sampled as juveniles (e.g. snapper, garfish, King George whiting) (Table 24).

There was little difference in mean values $\delta^{13}C$ and $\delta^{15}N$ between times of the year (Fig. 36). Regardless of the time of year, the mangrove-saltmarsh complex was most depleted and seagrass (samples dominated by *Heterozostera tasmanica*) was most enriched. There was generally quite good separation of $\delta^{13}C$ between sources (ANOVA $df_{7,351}$, MS = 2377.678, $P << 0.001$). Of the pairwise comparisons (Tukeys tests) brown algae (BA) was not significantly different to benthic microalgae (BMA) or green algae (GA), epiphytes (EPI) could not be separated from BMA, BA, GA or seagrass, neither phytoplankton nor red algae (RA) could be separated from BMA. Values of $\delta^{15}N$ also varied significantly among sources (ANOVA $df_{7,351}$, MS = 32.101, $P << 0.001$), with BMA different to all except RA and SG different to all other sources. Even though there were subtle differences between sources, our real interest was in which sources supported fisheries species, and given the slow rates of turnover in fish tissue, and the similar ranking in sources between seasons, we subsequently pool sources across seasons for isotope modelling.

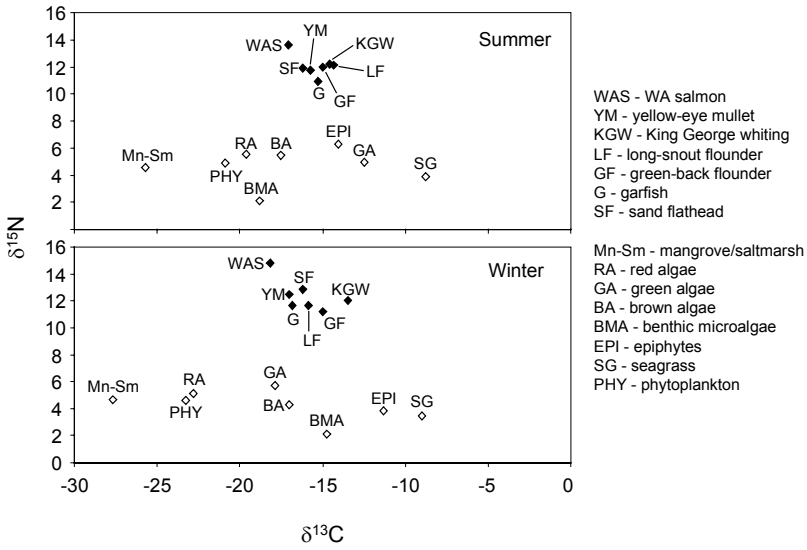

Figure 36. Summary of the values $\delta^{13}C$ and $\delta^{15}N$ for the fisheries species and primary producers (sources) sampled in this study during each season. Estimates of variance are provided in Table 24.

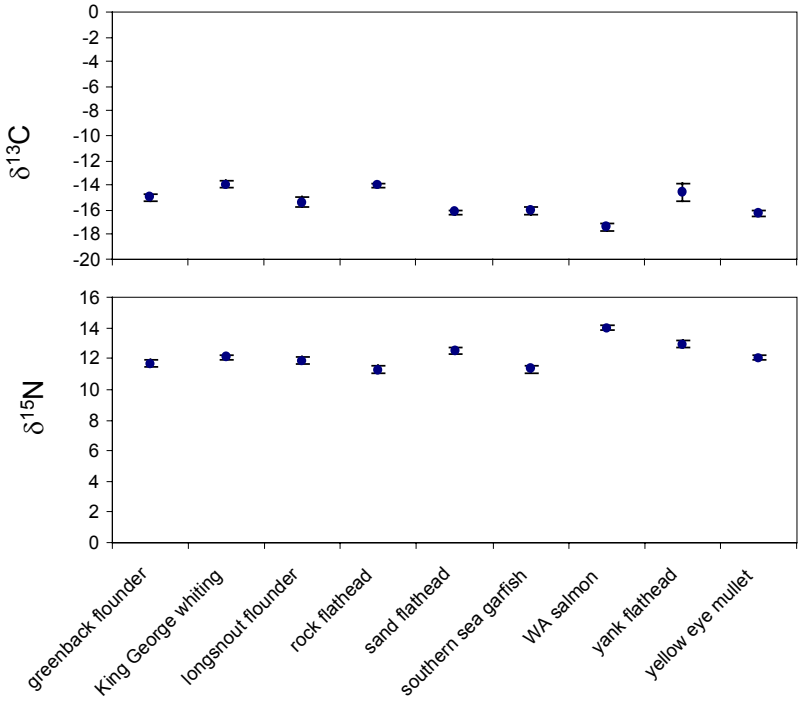

Figure 37. Mean (± se) value of $\delta^{13}C$ and $\delta^{15}N$ for the common fish species sampled in this study. Data pooled across seasons.

Regardless of season, there were significant differences in values of $\delta^{13}C$ (ANOVA $df_{6,357}$, MS = 50.856, $P << 0.001$) and $\delta^{15}N$ among species (ANOVA $df_{6,357}$, MS = 39.728, $P << 0.001$). The values of $\delta^{13}C$ in King George whiting were significantly different from those of WA salmon, sand flathead, garfish and yellow eye mullet, while those of WA salmon were significantly different to greenback flounder, long-snout flounder and garfish (Fig. 37). WA salmon clearly had a higher trophic position compared with all of the other most abundant fish (Fig. 37, Tukeys test < 0.05); sand flathead and yellow eye mullet also had higher trophic position than garfish, which had the lowest values of $\delta^{15}N$.

The modelling failed to show any particularly strong contributions to fisheries species by any one source (Table 25, Figs. 38-46). With the exception of mangrove-saltmarsh, which contributed very low proportions (generally less than 10), sources generally varied in their contributions between 13 and 17 %, and fish showed similar patterns in reliance on sources such as seagrass, algae and epiphytes. Brown algae was the highest contributor to fish nutrition for 7 species, BMA 4 species, epiphytes 4 species, green algae 8 species, red algae 2 species, and seagrass just a single species (rock flathead) (Table 25).

The lack of differentiation among sources to the nutrition of fisheries species shown above also occurred on a site-by-site basis (Table 26). While each of fisheries species ultimately relied on different sources at different locations, the amount of variation in these modelled contributions precluded any strong partitioning of particular sources on a site-by-site basis (Table 26).

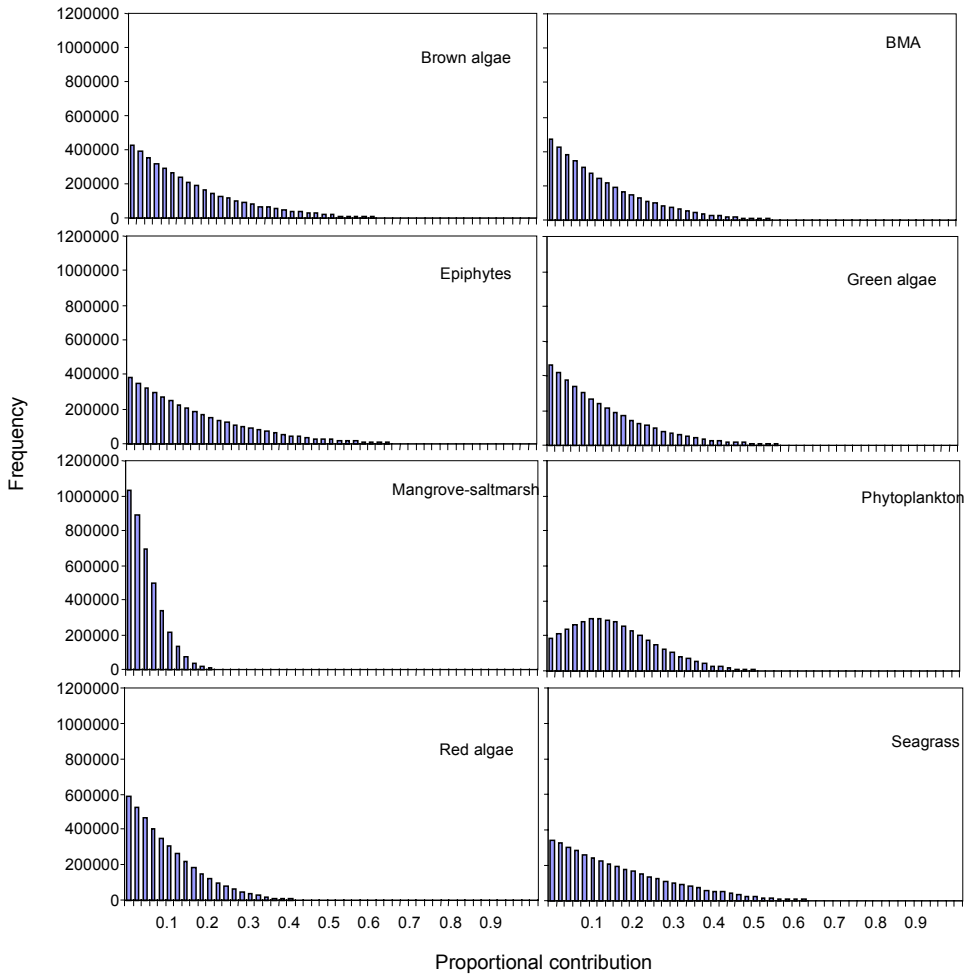

Figure 38. Frequency distributions of the possible proportional contributions of each source to the nutrition of estuary perch.

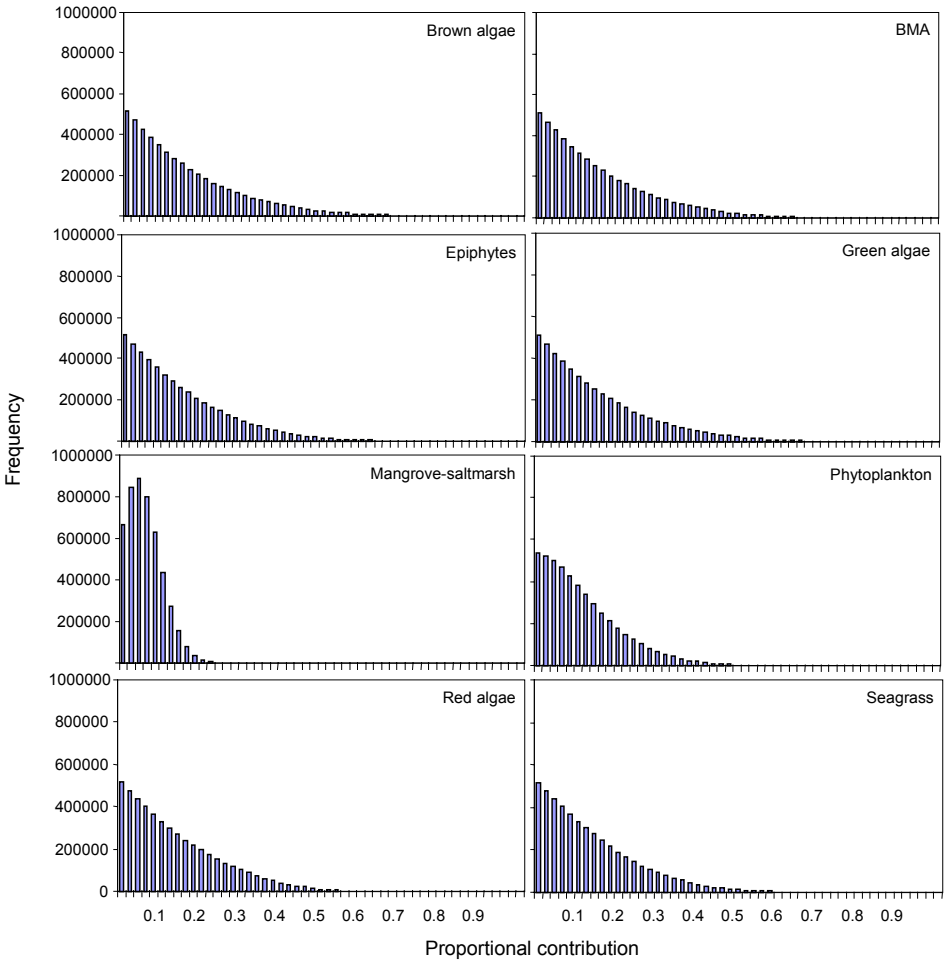

Figure 39. Frequency distributions of the possible proportional contributions of each source to the nutrition of garfish.

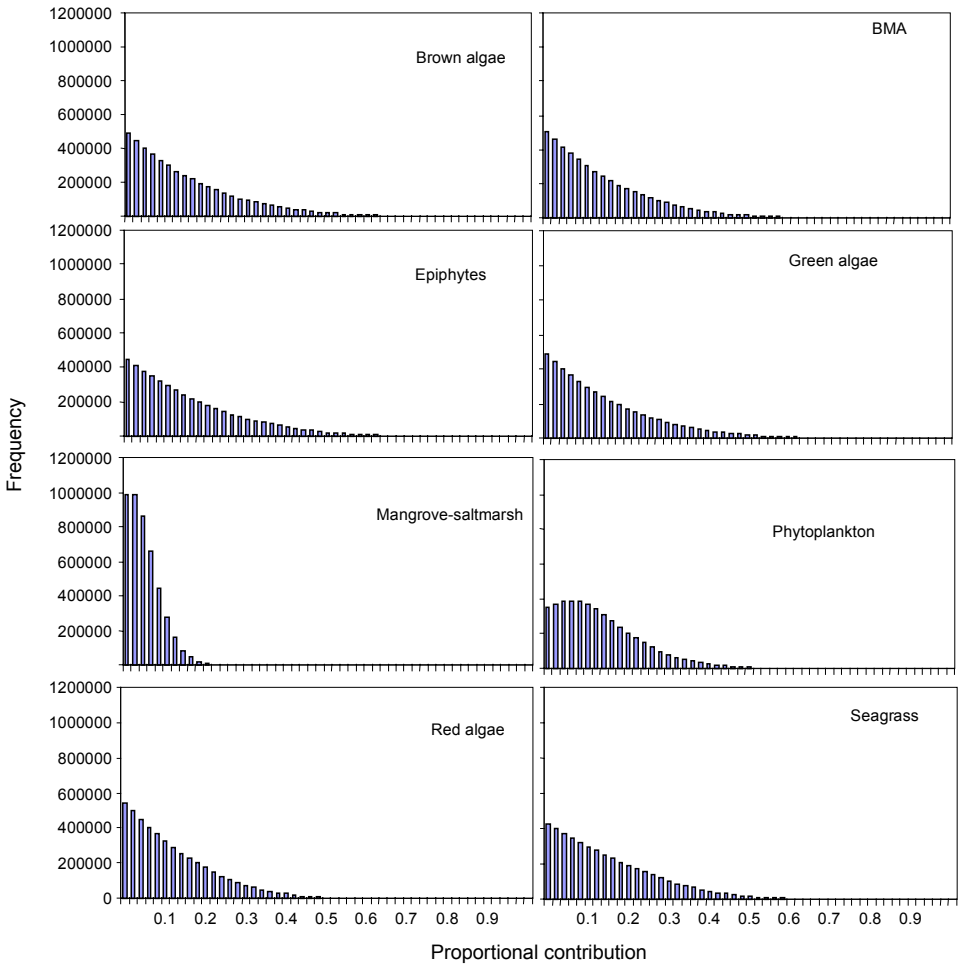

Figure 40. Frequency distributions of the possible proportional contributions of each source to the nutrition of greenback flounder.

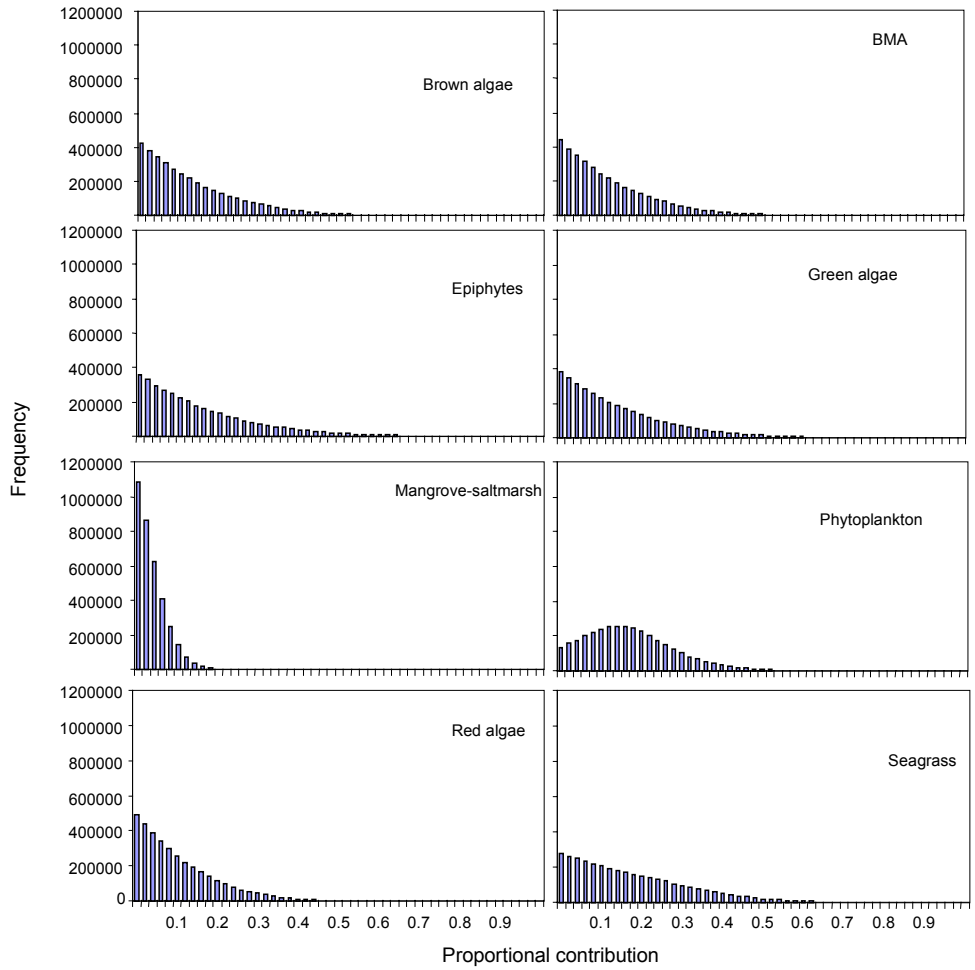

Figure 41. Frequency distributions of the possible proportional contributions of each source to the nutrition of King George whiting.

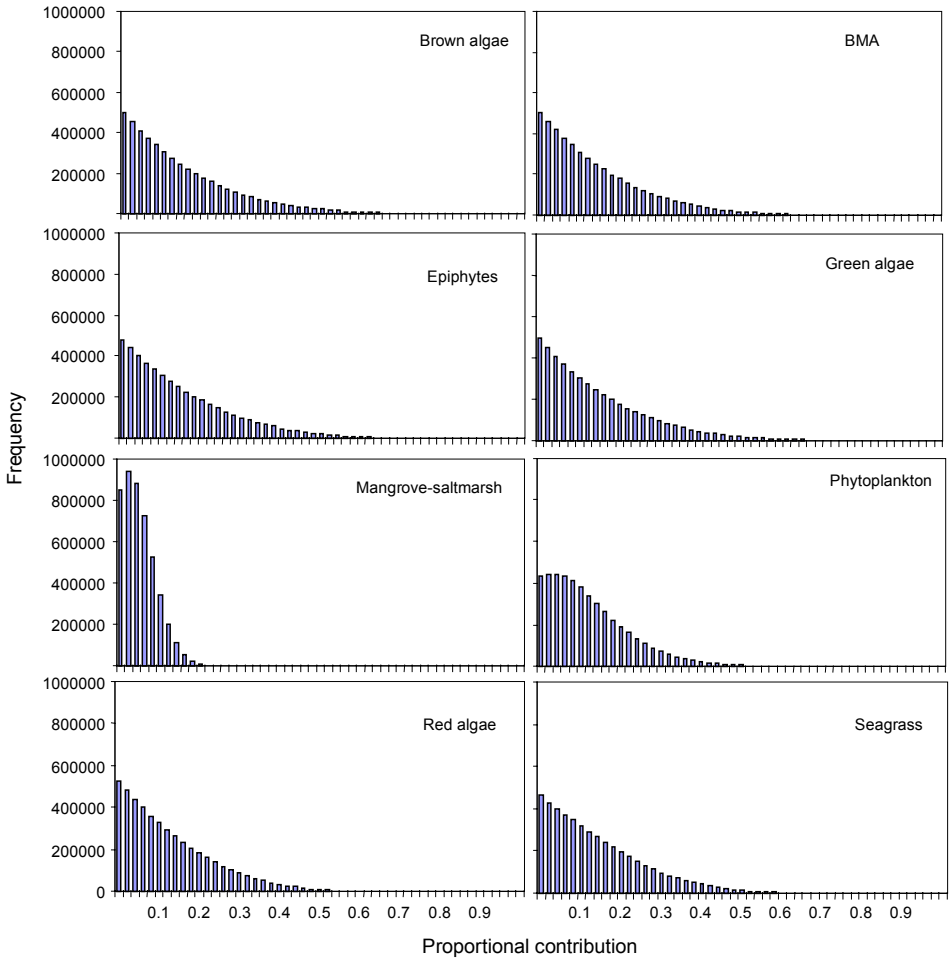

Figure 42. Frequency distributions of the possible proportional contributions of each source to the nutrition of longsnout flounder.

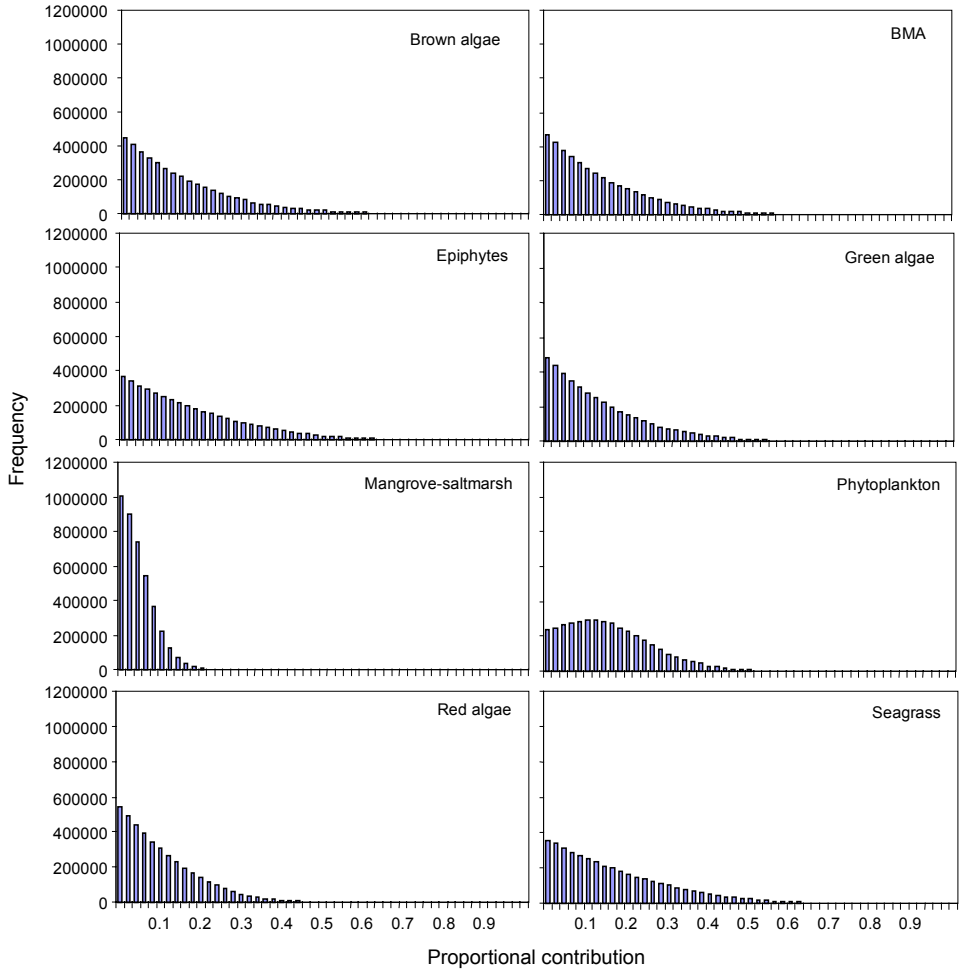

Figure 43. Frequency distributions of the possible proportional contributions of each source to the nutrition of rock flathead.

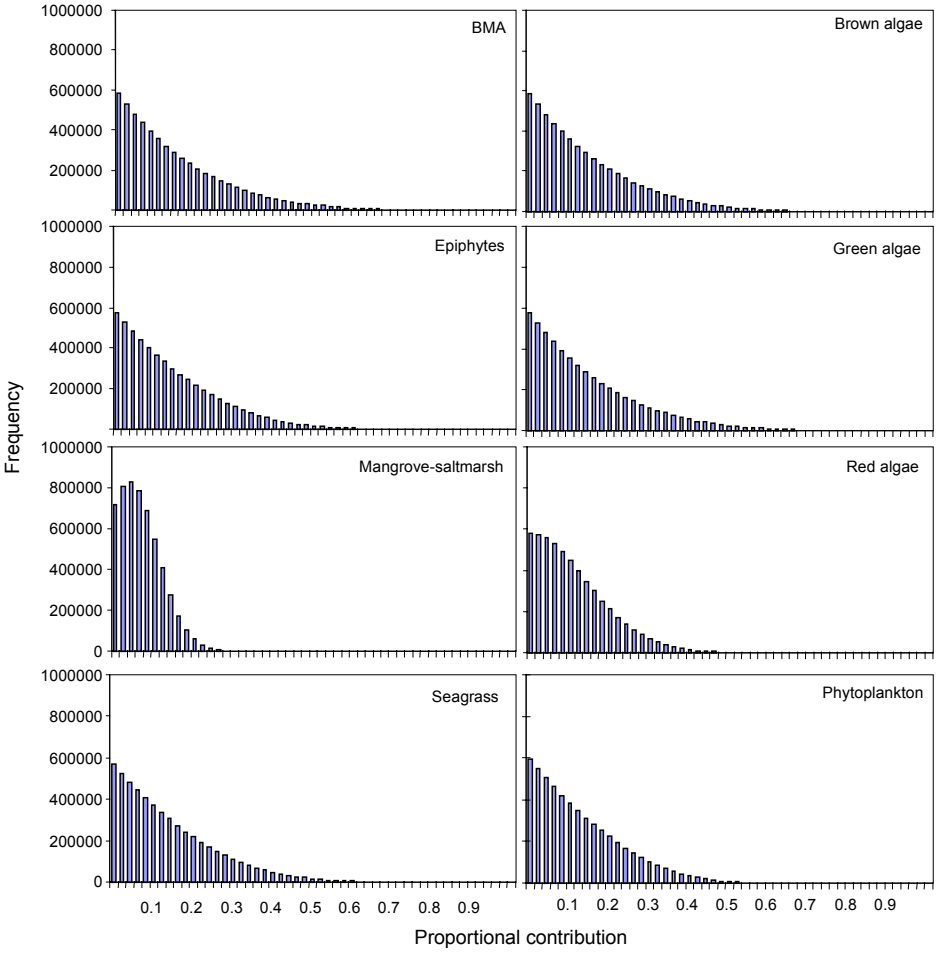

Figure 44. Frequency distributions of the possible proportional contributions of each source to the nutrition of sand flathead.

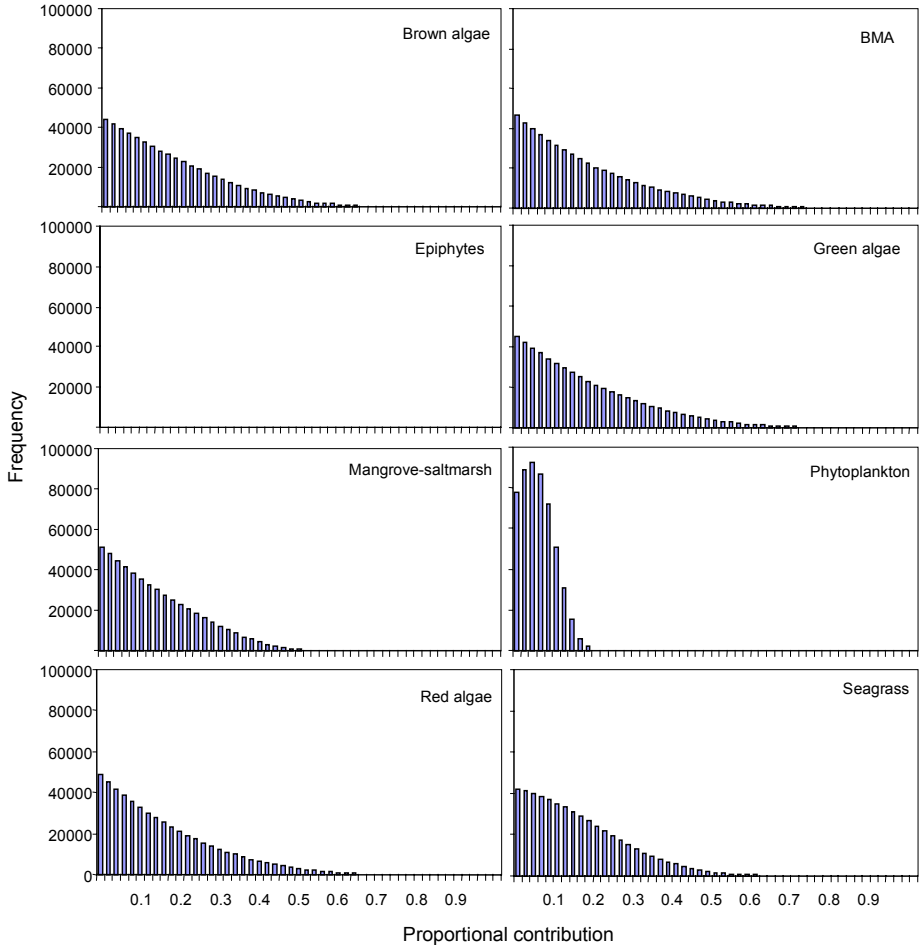

Figure 45. Frequency distributions of the possible proportional contributions of each source to the nutrition of sandy sprats.

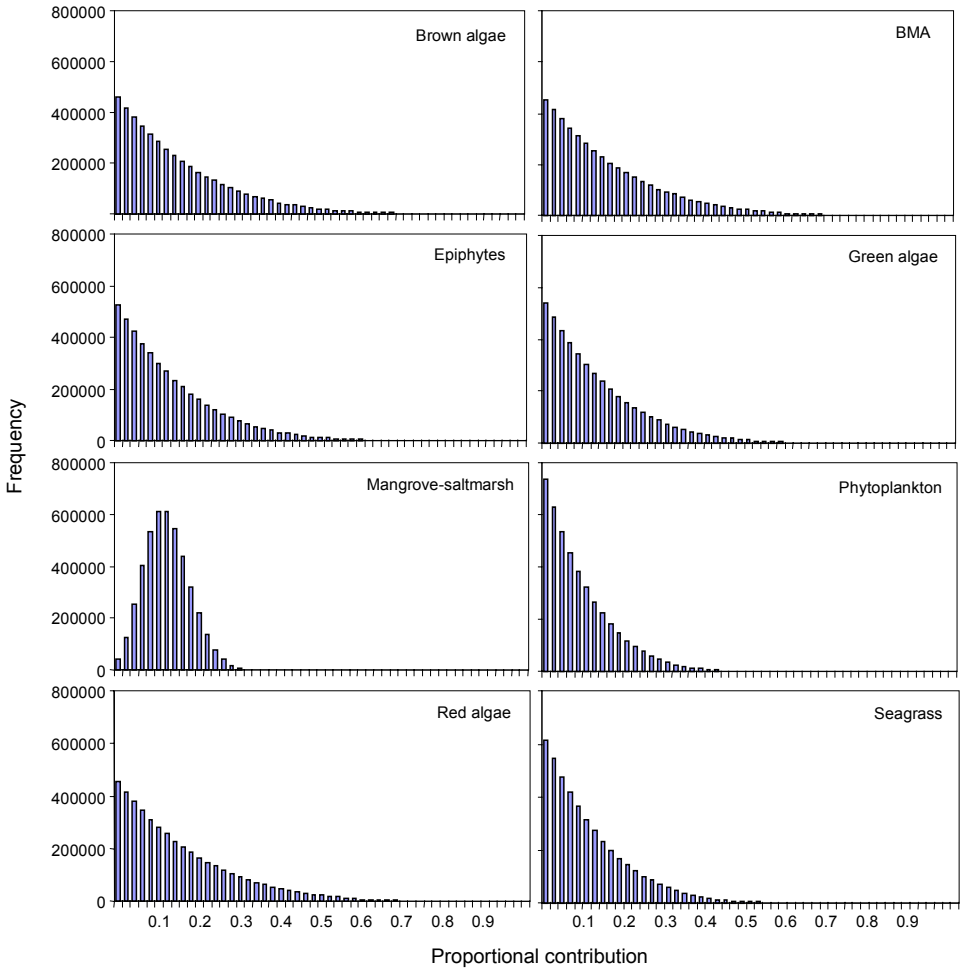

Figure 46. Frequency distributions of the possible proportional contributions of each source to the nutrition of snapper.

DISCUSSION

The application of stable isotopes in assessing the base for nutritional support of fisheries species has received much attention in Victoria (see Longmore et al. 2002, Hindell et al. FRDC 1999/215). The primary finding from this work is that fisheries species in temperate Victorian embayments are supported by a combination of producers including brown, red and green algae, seagrass and seagrass epiphytes, phytoplankton and benthic microalgae.

Macro-producers such as macroalgae, seagrass and mangroves and easily collected and almost always included in stable isotope studies. Micro-producers such as benthic microalgae and epiphytes are generally harder to collect and are not always included in trophic modelling. This study suggests that sources such as benthic microalgae, phytoplankton and epiphytes can be important contributors to fisheries nutrition (sometimes the most important contributors), and must be measured to best assess the base/s of nutritional support.

The spatial variability in source contribution has been used to infer patterns of animal movement. This study showed that the nutrition of a species of fish is not ultimately supported by the same suite of sources among locations. King George whiting, for example, depended on one or a combination of epiphytes, seagrass and brown algae, depending on where they were sampled. Whether these patterns reflect the overall biomass of alternative sources within an area (location) or differential feeding regimes among sites is unknown. The data suggest, however, that patterns in nutrition break down over larger spatial scales, and predictions of the consequences to fisheries productivity in one area based on changes to a base for nutritional support may not be supported in alternative areas separated by as little as 10 km.

The biggest impediment to using stable isotopes to trace the ultimate sources of nutrition to fisheries species is the lack of clear separation of stable isotope signatures of producers. Many of the sources in this study could be separated, but this did not necessarily improve the ability to separate source contributions. All of the fisheries species in this study fell in the middle of the sources which, when modelled, meant that several sources had similar (and low) relative contributions to the nutrition of fish. The principal implication of these 'generalist' patterns is that even the complete loss of one habitat, for examples seagrass, will cause of loss of nutritional support of no more than 20%. It is unlikely that the alternative producers are fully exploited and this loss will be compensated for by increasing reliance on one of several alternatives.

Mangroves, and to a lesser extent saltmarshes, are thought to be important sources of nutrients, sometimes supporting fisheries species offshore through outwelling (Lee 1995). Recent studies using biological tracers are suggesting, however, that mangroves and saltmarshes are much les important than subtidal sources such as seagrass and algae in the nutrition of fisheries species (Connolly et al. in press). This is consistent with earlier findings in this study that mangroves support few fisheries species directly through the provision of habitat, and further suggests that temperate mangroves and saltmarshes may not be that important to fisheries species

This work presents compelling evidence that the use of carbon and nitrogen stable isotopes to infer trophic dynamics is only of benefit where there is good separation of source signatures, *and* the signatures of fish do not fall in the middle of the sources. Stable isotopes are simply one of many alternative methods, which should be used along with diet analyses and other tracer techniques (e.g. fatty acids) to better describe the course and flow of nutrients through fisheries.

Table 24. Summary of the number of samples (No.), mean length (μL) and mean stable isotope values for nitrogen and carbon ($\delta^{15}N$ $\delta^{13}C$, respectively). Standard error given in parenthesis. [J] only juveniles sampled

Common name	Species name	No.	μL	$\delta^{15}N$	$\delta^{13}C$
Blue sprat	*Spratelloides robustus*	13	42.8 (3.1)	12.8 (0.1)	-22.1 (0.2)
Estuary perch	*Macquaria colonorum*	29	279.0 (4.9)	17.2 (0.2)	-16.4 (0.3)
Greenback flounder	*Rhombosolea tapirina*	39	158.8 (13.7)	11.7 (0.2)	-15.0 (0.3)
King George whiting[J]	*Sillaginodes punctata*	35	139.1 (8.1)	12.1 (0.2)	-13.9 (0.3)
Longsnout flounder	*Ammotretis rostratus*	19	126.1 (14.8)	11.8 (0.2)	-15.4 (0.4)
Mackerel	*Trachurus novaezelandiae*	1	145.0	13.9	-20.4
Pink ling	*Genypterus tigerinus*	1	510.0	12.0	-12.9
Rock flathead	*Platycephalus laevigatus*	15	279.3 (11.3)	11.3 (0.2)	-14.0 (0.2)
Sand flathead	*Platycephalus bassensis*	35	176.6 (7.7)	12.5 (0.2)	-16.2 (0.2)
Sandy sprats[J]	*Hyperlophus vittatus*	8	54.5 (7.7)	12.8 (0.1)	-20.2 (0.1)
Sea mullet	*Mugil cephalus*	3	163.0 (39.2)	10.1 (1.2)	-18.8 (5.8)
Shortfin pike	*Sphyraena novaehollandiae*	1	340.0	14.6	-17.9
Skipjack trevally[J]	*Pseudocaranx wrightii*	3	60.0 (10)	11.6 (1.3)	-17.0 (1.6)
Snapper[J]	*Pagrus auratus*	5	101.4 (22.1)	13.5 (0.5)	-17.9 (0.7)
Southern sea garfish[J]	*Hyporhamphus melanochir*	67	178.3 (7.6)	11.3 (0.2)	-16.1 (0.3)
Tailor[J]	*Pomatomus saltatrix*	4	172.0 (32)	15.3 (0.7)	-18.4 (0.6)
Tommy ruff[J]	*Arripis georgiana*	6	79.8 (7.4)	14.0 (0.2)	-18.7 (0.4)
WA salmon[J]	*Arripis truttacea*	51	109.8 (4.5)	14.0 (0.2)	-17.4 (0.3)
Yank flathead	*Platycephalus speculator*	9	352.8 (53.3)	12.9 (0.2)	-14.6 (0.7)
Yellow eye mullet	*Aldrichetta forsteri*	121	175.1 (8.4)	12.0 (0.1)	-16.3 (0.3)

Table 25. Summary of the mean proportional contribution of each source to the nutrition of the most abundant fisheries species. Standard error given in parenthesis. BA – brown algae, BMA – benthic microalgae, EPI – epiphytes, GA – green algae, MN-SM – mangrove/saltmarsh, PHYTO – phytoplankton, RA – red algae, SG – seagrass.

	Sand flathead		Rock flathead		Long snout flounder		King George whiting		Green back flounder		Garfish		Estuary perch	
Source	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %
BA	14 (13)	56	14 (13)	52	14 (13)	56	12 (11)	48	14 (13)	56	14 (13)	56	14 (13)	54
BMA	14 (13)	54	13 (12)	50	14 (13)	52	12 (11)	46	13 (12)	50	14 (13)	54	13 (12)	48
EPI	14 (12)	50	16 (14)	56	14 (13)	54	15 (14)	58	15 (13)	56	14 (12)	52	16 (14)	58
GA	14 (13)	56	12 (11)	46	14 (13)	56	14 (13)	54	14 (13)	56	14 (13)	56	13 (12)	50
MN-SM	7 (5)	22	4 (4)	16	5 (4)	16	3 (3)	14	4 (4)	16	6 (4)	18	4 (4)	16
PHYTO	11 (9)	38	15 (11)	44	12 (10)	42	17 (11)	46	13 (10)	44	11 (10)	40	16 (10)	44
RA	14 (12)	50	10 (9)	38	13 (11)	46	10 (9)	38	12 (10)	42	13 (11)	46	9 (8)	34
SG	13 (11)	44	16 (14)	56	14 (12)	50	17 (14)	56	15 (13)	52	13 (12)	48	16 (14)	56

	Yellow-eye mullet		Yank flathead		WA salmon		Trevally		Tommy ruff		Tailor		Snapper		Sandy sprats	
Source	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %	mean	99th %
BA	14 (13)	56	14 (13)	54	14 (13)	56	16 (14)	56	15 (14)	58	14 (13)	56	15 (13)	58	16 (14)	56
BMA	14 (13)	56	13 (12)	50	15 (13)	56	17 (15)	62	14 (13)	54	14 (13)	56	15 (14)	58	17 (15)	64
EPI	14 (12)	52	15 (13)	54	13 (12)	50	0	0	11 (11)	44	12 (11)	46	13 (12)	50	0	0
GA	15 (13)	56	14 (13)	56	14 (13)	56	14 (11)	46	14 (12)	52	15 (13)	58	12 (11)	48	17 (15)	60
MN-SM	6 (4)	18	4 (4)	14	7 (4)	18	11 (8)	34	11 (6)	26	9 (5)	22	12 (6)	26	14 (11)	44
PHYTO	11 (10)	40	13 (10)	44	11 (9)	40	16 (14)	56	9 (8)	36	10 (9)	38	9 (8)	34	6 (4)	16
RA	13 (12)	48	13 (11)	46	14 (12)	50	17 (15)	64	15 (13)	54	15 (13)	54	15 (14)	58	16 (14)	56
SG	13 (12)	48	14 (12)	52	13 (11)	48	10 (8)	34	12 (11)	44	12 (11)	46	11 (10)	42	15 (12)	50

Table 26. Summary of the mean and 99th percentile proportional contribution of each source to the nutrition of the most abundant fisheries species at the various sampling locations. Standard error given in parenthesis. See Table 25 for explanation of source abbreviations.

	Hastings		Newhaven		Port Albert		Port Welshpool		Toora		Warneet		Yanakie	
source	mean	99th%	mean	99th%	mean	99th%	mean	99th%	mean	99th%	mean	99th%	mean	99th%
Garfish														
BMA	14 (13)	54	14 (13)	54	13 (12)	48	15 (13)	56	13 (12)	50	15 (13)	56	14 (13)	56
BA	12 (11)	46	13 (11)	46	14 (13)	56	14 (12)	50	15 (14)	58	15 (14)	58	14 (13)	56
EPI	12 (11)	46	14 (12)	50	14 (13)	56	14 (12)	52	15 (13)	56	12 (11)	46	13 (11)	48
GA	14 (13)	54	14 (13)	56	14 (13)	54	14 (13)	52	14 (13)	56	14 (13)	52	14 (13)	52
MN-SM	14 (5)	26	6 (5)	18	7 (5)	20	7 (5)	22	5 (5)	18	9 (6)	24	8 (6)	24
RA	9 (9)	36	12 (10)	40	11 (9)	38	10 (9)	38	14 (11)	46	9 (9)	36	11 (9)	38
SG	11 (10)	44	14 (12)	50	13 (11)	46	12 (11)	48	15 (13)	54	12 (11)	46	13 (11)	46
PHYTO	15 (14)	58	14 (13)	54	14 (12)	50	15 (13)	56	8 (6)	26	15 (12)	50	12 (10)	40
King George whiting														
BMA	14 (13)	52	12 (11)	46	10 (10)	40	14 (12)	52	nd	nd	14 (13)	56	11 (10)	42
BA	14 (13)	54	10 (9)	38	12 (11)	48	12 (11)	46	nd	nd	14 (13)	54	12 (11)	46
EPI	14 (13)	54	17 (15)	58	15 (13)	58	15 (13)	56	nd	nd	14 (12)	50	18 (15)	62
GA	14 (13)	54	12 (11)	46	15 (14)	58	15 (13)	56	nd	nd	15 (13)	56	9 (9)	36
MN-SM	6 (4)	18	4 (4)	14	4 (4)	18	5 (5)	18	nd	nd	7 (5)	20	4 (4)	14
RA	12 (10)	42	18 (11)	48	16 (10)	44	12 (9)	40	nd	nd	11 (9)	38	21 (13)	52
SG	14 (12)	50	17 (14)	58	17 (13)	54	14 (12)	50	nd	nd	14 (12)	50	19 (15)	60
PHYTO	13 (12)	48	12 (11)	44	11 (10)	42	14 (13)	52	nd	nd	12 (11)	42	7 (6)	26
Greenback flounder														
BMA	15 (13)	58	13 (11)	48	14 (13)	52	14 (12)	52	14 (12)	52	14 (12)	52	nd	nd
BA	12 (12)	50	11 (10)	40	15 (13)	56	12 (11)	46	15 (14)	56	13 (12)	50	nd	nd
EPI	12 (12)	48	16 (14)	56	14 (13)	52	15 (13)	56	15 (13)	54	15 (13)	52	nd	nd
GA	15 (13)	56	13 (12)	48	13 (12)	52	15 (13)	56	14 (13)	56	15 (13)	58	nd	nd
MN-SM	10 (5)	22	4 (4)	16	8 (6)	22	5 (5)	18	6 (5)	18	5 (5)	20	nd	nd
RA	9 (9)	38	16 (11)	46	10 (9)	36	12 (9)	40	14 (11)	44	13 (10)	40	nd	nd
SG	12 (11)	46	16 (14)	56	12 (11)	44	14 (12)	50	15 (13)	54	15 (13)	52	nd	nd
PHYTO	15 (14)	58	12 (11)	46	15 (13)	54	14 (13)	52	8 (7)	26	11 (10)	40	nd	nd

Table 26. cont.

	Hastings		Newhaven		Port Albert		Port Welshpool		Toora		Warneet		Yanakie	
source	mean	99th%	mean	99th%	mean	99th%	mean	99th%	mean	99th%	mean	99th%	mean	99th%
Sand flathead														
BMA	14 (13)	56	14 (12)	52	14 (13)	52	15 (14)	58	14 (13)	52	14 (13)	56	nd	nd
BA	12 (11)	48	12 (11)	44	15 (13)	58	15 (13)	54	15 (13)	56	15 (14)	58	nd	nd
EPI	12 (11)	48	15 (13)	52	14 (13)	52	13 (12)	50	15 (13)	54	12 (11)	46	nd	nd
GA	14 (13)	56	14 (13)	52	13 (12)	52	13 (12)	52	14 (13)	56	14 (13)	52	nd	nd
MN-SM	12 (5)	24	5 (4)	16	8 (6)	22	9 (5)	22	6 (5)	20	9 (6)	24	nd	nd
RA	9 (9)	36	13 (10)	42	10 (9)	36	9 (9)	36	14 (11)	44	9 (8)	36	nd	nd
SG	11 (11)	46	15 (13)	52	12 (11)	44	12 (11)	46	15 (13)	52	12 (11)	46	nd	nd
PHYTO	15 (14)	60	13 (12)	52	15 (13)	54	15 (13)	58	8 (7)	26	15 (12)	50	nd	nd
Yellow eye mullet														
BMA	15 (14)	58	14 (13)	54	nd	nd	15 (13)	56	14 (13)	54	13 (12)	52	14 (13)	56
BA	13 (12)	50	13 (11)	46	nd	nd	14 (12)	50	15 (13)	56	14 (13)	54	15 (13)	56
EPI	13 (12)	50	14 (12)	52	nd	nd	14 (12)	52	15 (13)	54	11 (10)	42	14 (12)	48
GA	15 (13)	58	14 (13)	54	nd	nd	14 (13)	54	14 (13)	56	12 (11)	48	14 (12)	50
MN-SM	9 (5)	22	5 (4)	18	nd	nd	7 (5)	22	6 (5)	20	16 (6)	30	7 (6)	22
RA	10 (9)	38	12 (10)	42	nd	nd	10 (9)	38	13 (11)	44	8 (8)	32	12 (10)	40
SG	12 (11)	46	14 (12)	50	nd	nd	13 (11)	48	14 (13)	52	11 (10)	42	14 (12)	48
PHYTO	15 (14)	56	14 (13)	54	nd	nd	15 (13)	56	9 (7)	28	16 (15)	60	11 (9)	38

Chapter 9. Stable isotope studies in South Australia

INTRODUCTION

Many of South Australia's important fisheries species, including several whiting species and blue swimmer crabs, spend a major portion of their lives in shallow, inshore waters. South Australian inshore fisheries can essentially be divided into three regions: Gulf St Vincent, Spencer Gulf and the West Coast. The focus of this chapter is on the two gulfs, which contribute the majority of inshore finfish and blue swimmer crab catches in the state (Knight et al. 2003). The upper sections of these gulfs, in particular, have very extensive areas of inshore fisheries habitat, which are subject to continually increasing pressure from anthropogenic activities.

In the upper parts of the South Australian gulfs, several autotrophs (primary producers, either higher plants or algae) potentially provide organic material to food webs that support valuable fisheries. The most conspicuous sources are seagrasses and their associated algal epiphytes, mangroves, and saltmarsh plants. The intertidal mudflats also contain microalgae.

For several years, government bodies in Australia have been planning a series of marine protected areas to conserve habitat capable of supporting marine animal resources (Stevens 2002). South Australia has been going through a drawn-out planning phase (Edyvane 1999), and implementation of MPAs is less advanced than in some other states. The timing of the implementation therefore provides an opportunity for reporting scientific evidence useful in the design of MPAs. Managers are aware that they need to protect not only the habitat in which animals occur, but also separate habitats from which autotrophic production contributes to food webs. Unfortunately, there is no evidence of the autotrophic sources of nutrition for fisheries species in South Australia, including for inshore fishery species.

The aim of the work in South Australia was to determine the autotrophic source(s) contributing to the base of food webs providing nutritional support for key fishery species.

METHODS

Sample collection and processing

The upper sections of the gulfs of South Australia are fringed by substantial stands of mangrove. Saltmarsh is common on the landward side of the mangroves. Mudflats without conspicuous vegetation extend up to 200 m seaward of the mangroves to a narrow band of intertidal seagrass and extensive subtidal seagrass meadows. Autotrophs and fish were collected twice, once in winter (June 2002) and once in summer (January 2003), at eight locations along approximately 200 km of coastline (Fig. 47). These two periods were not used as an attempt to represent seasons *per se* but to obtain data at more than one time. All samples were frozen immediately upon collection.

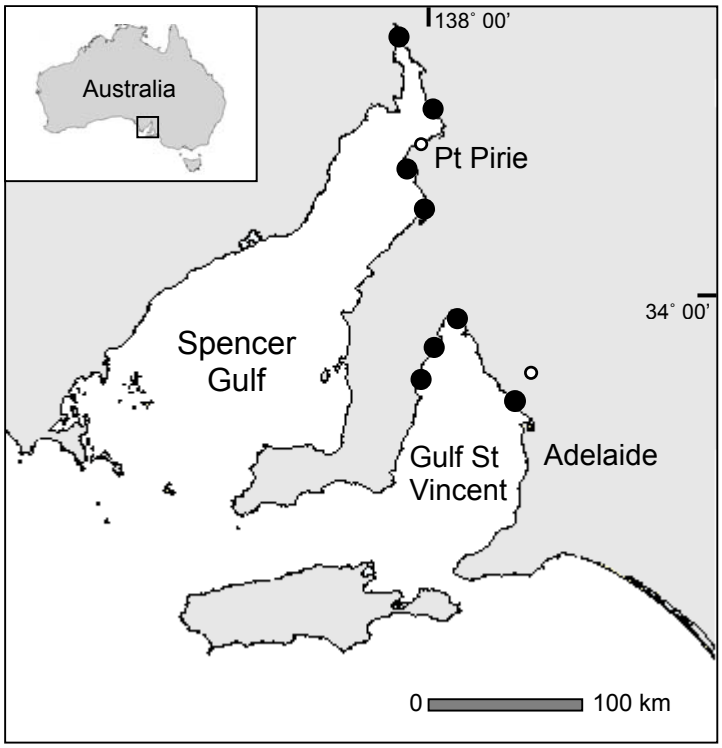

Figure 47. Map of the South Australian gulfs indicating the eight sampling locations. Inset: Location of study region in Australia.

We collected fish from a range of inshore habitats using gill, seine and trawl nets (see Victorian chapter) at different tidal stages. Generally we collected three individuals of each species at both periods from every location, although at some locations we could not collect all species (Table 27). Where more than the required number of fish was caught, we selected fish of a length most commonly found at that period (lengths shown in Table 27). Nine species were caught frequently enough at both periods to be able to analyse (Table 27). The emphasis was on finfish species of recreational and/or commercial importance (*Aldrichetta forsteri, Arripis georgianus, Hyporhamphus melanochir, Liza argentea, Sillaginodes punctata, Sillago schomburgkii*) and blue swimmer crabs (*Portunus pelagicus*). Two common species of no direct economic importance (*Gymnapistes marmoratus, Pelates octolineatus*) were also included in the study to better represent the whole suite of shallow-water fish in the South Australian gulfs.

Three samples of the following autotrophs were collected from every location at both times, except where otherwise noted. On the saltmarsh, leaves were collected from the two most abundant species, bearded glasswort (*Sarcocornia quinqueflora*) and grey samphire (*Halosarcia halocnemoides*). Isotope values from the two species were similar to each other at both times (< 1.2‰ difference for C and N at each site) and were therefore pooled. Green leaves were collected from the single species of mangrove that occurs in South Australia, the grey mangrove (*Avicennia marina*). Two types of seagrass were collected: eelgrass (*Zostera capricorni*) at the bottom of the intertidal zone and strapweeds (*Posidonia australis* or *P. sinuosa*) subtidally. Isotope values from the two types were similar to each other at both times (< 1.5‰ difference for C and N at each site) and were therefore pooled. Seagrass epiphytes consisting of diatoms and fine, filamentous algae were separated from seagrass in the laboratory by scraping with a scalpel (Guest et al. 2004).

Enough epiphyte material for isotope analysis was obtained from every location in the summer but from only five locations in winter. Macroalgae were never common at any location, probably because of the lack of hard substratum in the upper parts of the gulfs, but at some locations macroalgae were found attached to shells and small rocks in sufficient quantity to collect a sample. Macroalgal samples consisted of red algae (predominantly *Laurencia* spp.) in winter and brown algae (*Cystophora* spp.) in summer.

Microalgal and cyanobacterial cells, collectively known as microphytobenthos, were collected by scraping the surface 1 cm of sediment from mudflats near where collections of fish were made. Sediment was washed through 53 μm mesh to remove infauna. Material passing through the mesh was then washed through 5 μm mesh. Material retained on this mesh was added to a centrifuge tube containing colloidal silica (LUDOX ™, density = 1.21) and centrifuged at 10 000 rpm for 10 minutes. A band of diatoms, some organic matter and silica particles formed at the top of the centrifuge tube. This band was removed and again washed through a 5 μm mesh to remove the silica and any remaining microbes. Inspection of samples showed that they consisted predominantly of microalgae (mainly diatoms) with occasional contamination by very fine detrital fragments.

Phytoplankton densities were very low relative to the high load of particulate detrital material in the water at our locations. We were therefore unable to process samples of suspended particulate matter to obtain a phytoplankton sample pure enough to represent this autotroph. Instead we filtered seawater to obtain a measure of the isotope signature of suspended particulate matter (seston).

Modelling feasible source mixtures to explain fish nutrition

For each fish/crab species, we tabulated the top three ranked autotrophs. There was a strikingly consistent pattern in the rankings for most animal species, and we highlighted this by summarising the rankings for each autotroph. This summary demonstrates the overall importance of different autotrophs to fishery food webs.

RESULTS

Carbon isotope values of autotrophs were well spread and were similar over winter and summer. Autotrophs fell into three predictable groups (Fig. 48): mangroves and saltmarsh with depleted values (-26 to -27‰), seagrass and epiphytes with enriched values (-8 to -13‰), and macroalgae and MPB with intermediate values (-19 to -20‰). Mean nitrogen isotope values were typical for marine/estuarine autotrophs, ranging between 3 and 6 ‰.

Carbon isotope values of fishes and crabs fell in a narrow band between approximately -13 and -17‰, consistent over winter and summer. Animal values therefore lay in the enriched half of the range for autotrophs (Fig. 48). Nitrogen isotope values of animals were all more enriched than autotroph values, lying between about 7 and 11‰.

Isosource modelling of feasible contributions from the different autotrophs showed similar results for all of the animal species, principally because of the narrow range of carbon isotope values for animals. Contributions were slightly different between winter and summer, and even this difference was consistent for the various fish and crab species (examples are shown for *Sillago schomburgkii, Sillaginodes punctata* and *Portunus pelagicus*, Figs. 49, 50, 51 respectively). Median and upper 99%ile values demonstrate the likely importance of organic material from seagrass meadows, with the top contributors being either seagrass or algae epiphytic on seagrass, for both seasons.

The striking similarity in Isosource results among the different fish and crab species is borne out when the contributions from different autotrophs are ranked for each animal species (Table 29). In winter,

seagrass is the top ranked and epiphytes the second ranked autotroph for every one of the nine species (range of median contributions 27-64% and 19-27%, respectively), with algae commonly ranked third but having much lower contributions (4-13%). In summer, epiphytes were ranked top and seagrass second for all nine species (range of median contributions 23-42% and 22-28%, respectively), and algae and MPB were ranked joint third for all species (again with low contributions, between 8-19%). Mangroves and saltmarsh did not occur in the top three rankings for any species in either winter or summer.

A summary of the contributions of the different autotrophs clearly highlights the major contribution of seagrass and epiphytes over both sampling periods (Table 30). Macroalgae seem also to have been involved in a minor way at both periods, as was MPB in summer. These tables are all based on median contributions. Since Phillips and Gregg (2003) caution against the use of only a single parameter in deciding on the importance of different sources, we re-analysed all species based on the 75%ile. In all cases, the rank order contribution of autotrophs was the same as for the tables based on medians, supporting the results presented above (tables based on 75%ile values are not shown).

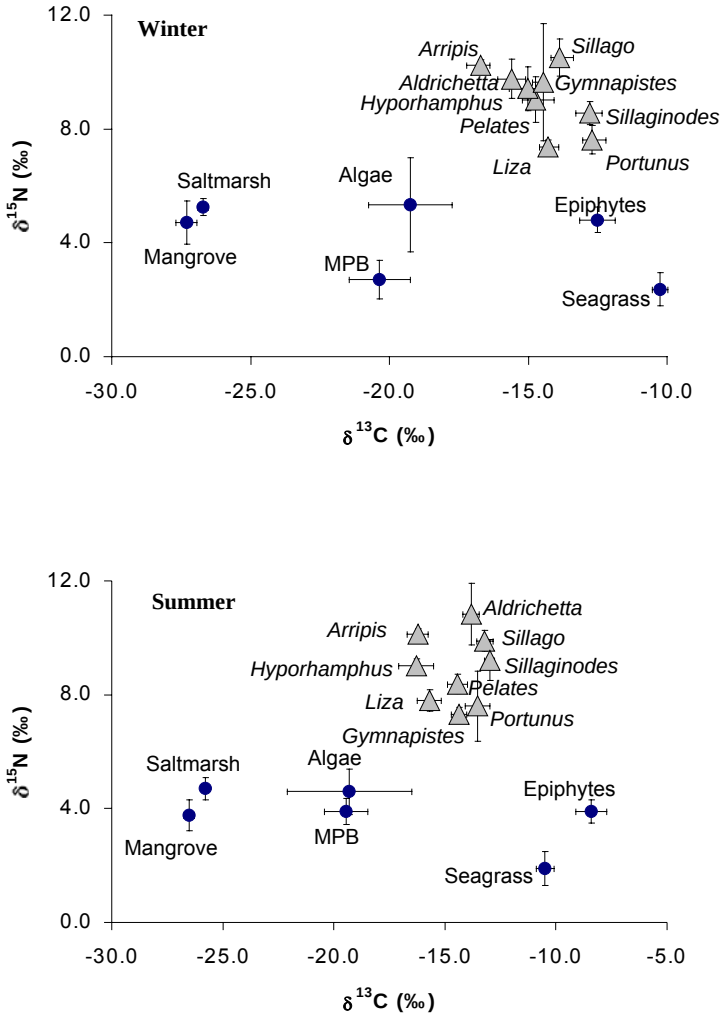

Figure 48. Plots of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) for the nine fish and crab species and the six autotroph sources in winter and summer. MPB = microphytobenthos.

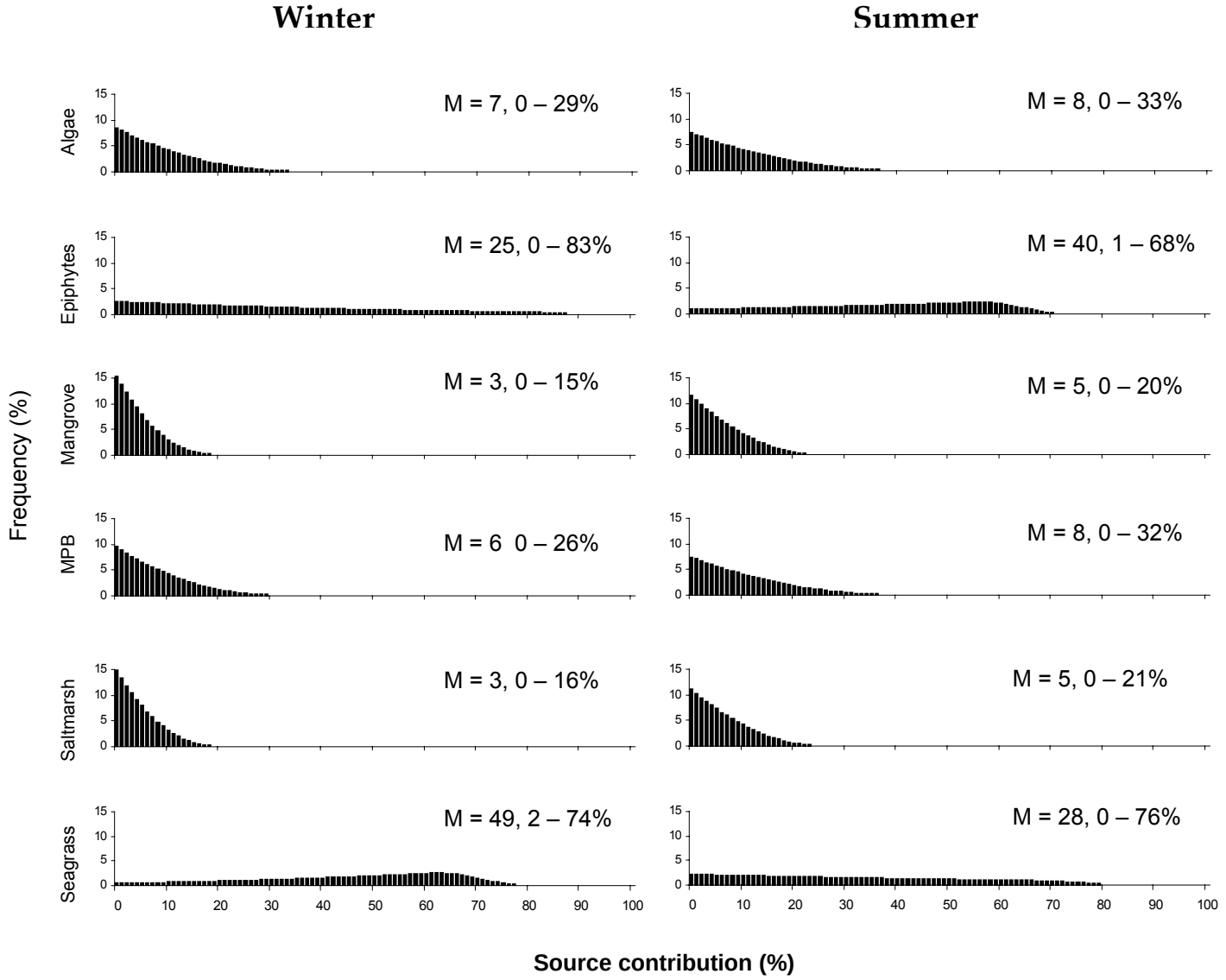

Figure 49. Distributions of feasible contributions of the 6 autotrophs to *Sillago schomburgkii* based on $\delta^{13}C$ values only. M = median, the ranges are 1%ile and 99%ile values.

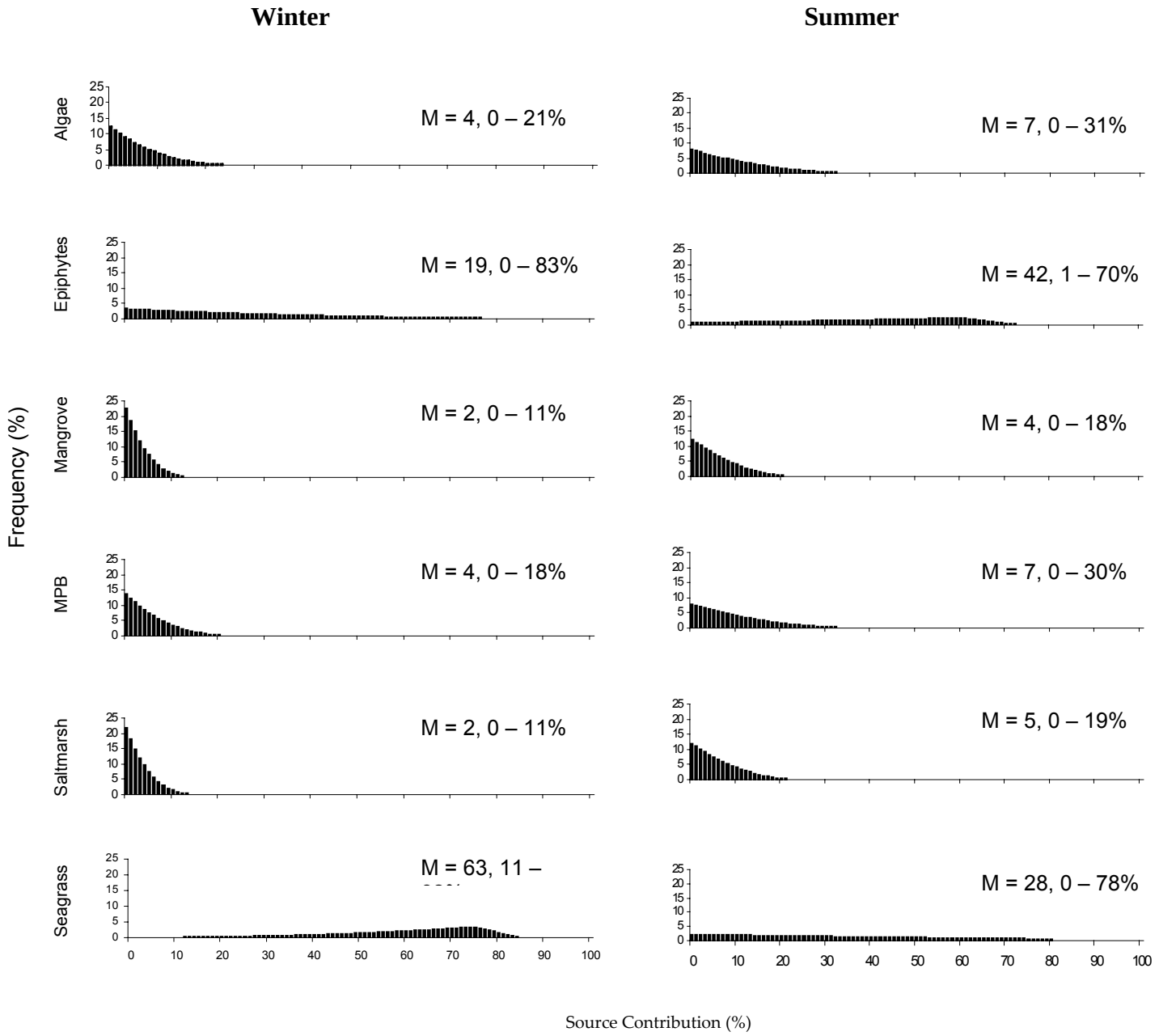

Figure 50. Distributions of feasible contributions of the 6 autotrophs to *Sillaginodes punctata* based on $\delta^{13}C$ values only. M = median, the ranges are 1%ile and 99%ile values.

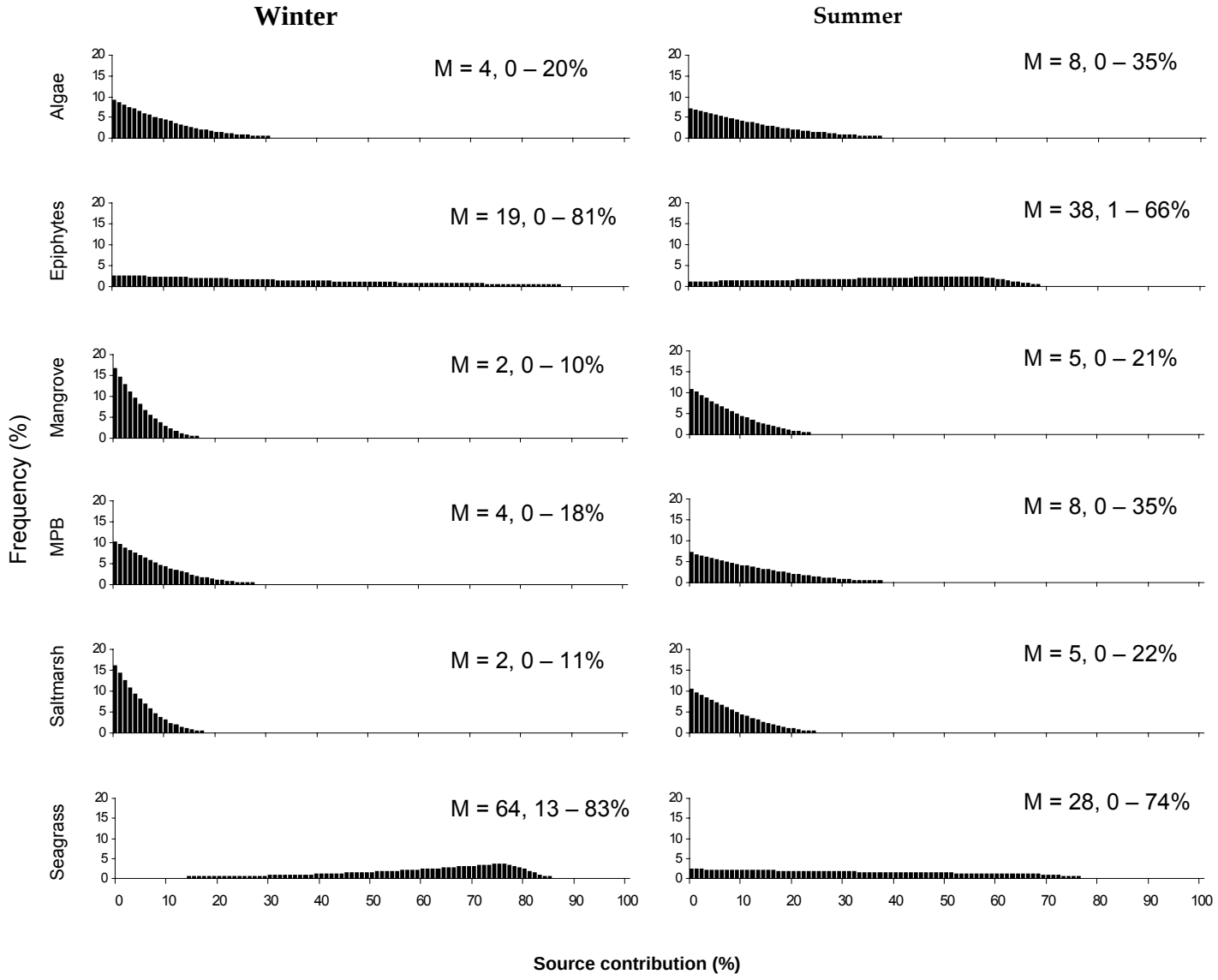

Figure 51. Distributions of feasible contributions of the 6 autotrophs to *Portunus pelagicus* based on $\delta^{13}C$ values only. M = median, the ranges are 1%ile and 99%ile values.

DISCUSSION

Contribution of different autotrophs to fish and crab nutrition

The ultimate sources of nutrition for all fish and crab species analysed were predominantly seagrass and epiphytic algae on seagrass. This overwhelming contribution of organic material originating from seagrass meadows was consistent across the two periods examined. The relative contributions of seagrass and epiphytic algae varied through time, with seagrass dominant in the winter period and epiphytes in the summer. We did not test whether this is a seasonal phenomenon; that test would require data from the two seasons over a number of years. Previous studies examining the contribution of seagrass and epiphytes to animals living in seagrass meadows report that seagrass and/or epiphytes are ultimately the main source of nutrition (e.g. Moncreiff & Sullivan 2001). It has also been shown that seagrass meadows produce more organic matter than can be utilised by consumers living in the meadows (Duarte & Cebrian 1996), therefore excess production is potentially available for use in detrital food webs in adjacent habitats.

Feasibility modelling of source mixtures was able to detect a third ranked contribution from macroalgae (with or without MPB, depending on the sampling period), although this contribution was relatively minor. The contributions from mangroves and saltmarsh were minor at all times for all animal species. The most likely scenario in winter is that seagrass was the dominant source followed by epiphytes, together contributing in the order of 80% of nutrition, with algae the largest component of the remainder (perhaps 10%) and trivial contributions from the other autotrophs. In summer, epiphytes exceeded seagrass in importance, and MPB along with macroalgae were the largest contributors of the alternative autotrophs.

A review of studies of mangrove contributions to food webs in other habitats found little evidence of mangroves being important, despite conspicuous production of mangrove leaf material and the widely-held view that outwelled mangrove detritus supports species in subtidal habitats (Lee 1995). The present study provides the first test of the role of mangroves in food webs in temperate waters in Australia or elsewhere, and shows that mangroves contribute little to the nutrition of inshore finfish and crabs. This conclusion is particularly important for *Sillago schomburgkii*. We were able to catch this species only alongside mangroves in this study, and their highest densities in South Australia have been recorded from mangrove-lined creeks (Connolly & Jones 1996), so we consider this species to be more likely than most to show a reliance on mangrove material. It did not, however, and this suggests that any importance of mangroves in food webs is limited to consumers actually resident in the mangrove forests rather than to consumers having merely a loose association with the forests. Furthermore, the significant contribution of material from adjacent seagrass systems (seagrass and epiphytes) is consistent with the movement of subtidal material into intertidal regions.

Separating the contributions of seagrass and epiphytes

The relative contribution of macrophytes versus epiphytic algae has been the subject of long-standing debate in freshwater (Boon & Bunn 1994) and estuarine systems (Moncreiff & Sullivan 2001). In studies of the contribution of seagrass and epiphytic algae to animals living in seagrass meadows, results have either been inconclusive, or have shown that epiphytes are important (Moncreiff & Sullivan 2001). Our study is exceptional in that it provides evidence of some contribution of seagrass itself. Similarity of carbon isotope values of seagrass and epiphytes, as found in the current study, frequently prevents studies from distinguishing between these two sources. We make an attempt in a subsequent chapter using sulfur isotope analysis on *Sillaginodes punctata* across Victoria, South Australia and Western Australia to achieve higher resolution of the relative contributions of seagrass and epiphytes to the nutrition of fisheries species.

Comparison with existing isotope data on finfish from Moreton Bay, Queensland

The most comprehensive study of the contributions of different habitats to the nutrition of inshore finfish in Australia was in a previous FRDC study (Connolly et al. 2003) in Moreton Bay, Queensland. We have summarised results for the 22 species studied in Moreton Bay in the same format as used in the current study (Tables 31 & 32), to highlight one major similarity and one striking contrast with the South Australian results. As in South Australia, for the suite of species studied in Queensland the major autotroph contributors to fish nutrition were seagrass and epiphytic algae. However, results from Queensland hint that saltmarsh grass (*Sporobolus virginicus*) was another major contributor. This grass does not occur in South Australia, where the saltmarshes are dominated by succulent herbs and bushes from the family Chenopodiaceae. Connolly et al. (2003) could not properly separate the contributions from seagrass meadows and saltmarsh grass because of the similarity in carbon isotope values of seagrass and saltmarsh grass. This issue is raised again in the analysis of crab nutrition in Queensland in the current report (see Queensland isotope study), where a novel sampling design is used to separate the contributions of the sources.

Table 27. Species of fish and crabs analysed in South Australian food web study, showing numbers of specimens analysed in winter and summer, and fish lengths. * *Portunus* measurement is carapace width.

Species	Common Name	Winter		Summer	
		n	mean length (mm)	n	mean length (mm)
Aldrichetta forsteri	Yellow-eye mullet	28	185	26	189
Arripis georgianus	Tommy ruff	12	96	12	188
Gymnapistes marmoratus	Cobbler	25	50	25	54
Hyporhamphus melanochir	Southern garfish	13	169	20	194
Liza argentea	Flat-tailed mullet	13	180	9	271
Pelates octolineatus	Western striped trumpeter	27	107	32	64
*Portunus pelagicus**	Blue swimmer crab	25	82	28	84
Sillaginodes punctata	King George whiting	25	104	31	133
Sillago schomburgkii	Yellowfin whiting	28	229	23	198

Table 28. Sensitivity of Isosource modelling to changed assumptions about fractionation of isotope values across trophic levels. Figures are median contributions of each autotroph to *Sillago schomburgkii* nutrition. Assumed fractionation is either our estimate of the most likely actual rate (labelled as "target", being 0 for C, 2.2‰ per trophic level for N) or +/- 1‰ from the target value. C modelling used only this element. N modelling used both elements, and the target value for C was used. Where no value is given, the corrected value for *S. schomburgkii* lay outside the polygon of autotrophs and no feasible solutions were possible. MPB = microphytobenthos.

Element	Season	Assumed fractionation	Autotroph contribution (%)					
			Epiphytes	Macroalgae	Mangroves	MPB	Saltmarsh	Seagrass
C	Winter	- 1	20	5	2	4	2	62
		target	25	7	3	6	3	49
		+ 1	27	9	5	8	5	40
	Summer	- 1	48	6	3	6	4	27
		target	40	8	5	8	5	28
		+ 1	33	10	6	10	6	27
N	Winter	- 1	-	-	-	-	-	-
		target	81	6	2	2	2	4
		+ 1	33	8	3	5	3	44
	Summer	- 1	-	-	-	-	-	-
		target	61	18	3	5	8	2
		+ 1	26	7	4	8	4	45

Table 29. Results of Isosource modelling, summarised for fish/crab species, for summer and winter. For each fish/crab species, autotrophs are ranked by median contribution (1, 2 and 3). Where more than one autotroph is shown for a rank, this indicates a tied ranking. ALG – macroalgae, EPI – seagrass epiphytes, MPB – microphytobenthos, SG – seagrass.

Species	Median contribution – rank			Median contribution (%)		
	1	2	3			
Winter						
Aldrichetta forsteri	SG	EPI	ALG	35	26	10
Arripis georgianus	SG	EPI	ALG	27	24	13
Gymnapistes marmoratus	SG	EPI	ALG	43	26	8
Hyporhamphus melanochir	SG	EPI	ALG	39	27	9
Liza argentea	SG	EPI	ALG	45	26	8
Pelates octolineatus	SG	EPI	ALG	41	27	9
Portunus pelagicus	SG	EPI	ALG, MPB	64	19	4
Sillaginodes punctata	SG	EPI	ALG, MPB	63	19	4
Sillago schomburgkii	SG	EPI	ALG	49	25	7
Summer						
Aldrichetta forsteri	EPI	SG	ALG, MPB	36	27	9
Arripis georgianus	EPI	SG	ALG, MPB	23	22	13
Gymnapistes marmoratus	EPI	SG	ALG, MPB	33	27	10
Hyporhamphus melanochir	EPI	SG	ALG, MPB	23	22	19
Liza argentea	EPI	SG	ALG, MPB	26	24	12
Pelates octolineatus	EPI	SG	ALG, MPB	33	27	10
Portunus pelagicus	EPI	SG	ALG, MPB	38	28	8
Sillaginodes punctata	EPI	SG	ALG, MPB	42	28	7
Sillago schomburgkii	EPI	SG	ALG, MPB	40	28	8

Table 30. Results of Isosource modelling, summarised by autotroph taxa, for summer and winter. Values represent the number of fish species out of 9 in total for which the contribution of a particular autotroph is important, ranked by median contribution (1, 2 or 3).

Season	Autotroph	Rank 1	Rank 2	Rank 3	Total	%*
Winter	Algae	0	0	9	9	100
	Epiphytes	0	9	0	9	100
	Mangrove	0	0	0	0	0
	MPB	0	0	2	2	22
	Saltmarsh	0	0	0	0	0
	Seagrass	9	0	0	9	100
Summer	Algae	0	0	9	9	100
	Epiphytes	9	0	0	9	100
	Mangrove	0	0	0	0	0
	MPB	0	0	9	9	100
	Saltmarsh	0	0	0	0	0
	Seagrass	0	9	0	9	100

*** percentage (%) values are representative of the rankings combined**

Table 31. Results of Isosource modelling for fish in Moreton Bay, Queensland (after Connolly et al. 2003). All methods and information is the same as in Table 29. SMG – saltmarsh grass, EPI – seagrass epiphytes, MPB – microphytobenthos, SG – seagrass.

Species	Median contribution – rank			Median contribution (%)		
	1	2	3			
Acanthopagrus australis	SG	SMG	EPI	25	21	20
Ambassis jacksoniensis	MAN, MPB, SMU			16		
Arrhamphus sclerolepis	SG, EPI, SMG			18		
Girella tricuspidata	EPI, SMG		SG, MPB	16		15
Herklotsichthys castelnaui	SG, EPI, SMG			17		
Hyporhamphus australis	SG			99		
Hyporhamphus quoyi	SG	SMG	EPI	23	21	20
Liza argentea	SG, EPI, SMG			17		
Lutjanus russelli	SG	SMG	EPI	27	22	21
Mugil cephalus	SG	SMG	EPI	25	21	20
Myxus elongatus	SG	SMG	EPI	45	21	17
Platycephalus arenarius	SMG	SMG	EPI	45	21	17
Platycephalus fuscus	SG	SMG	EPI	25	21	20
Pomatomus saltatrix	SG, EPI, SMG			18		
Pseudorhombus arsius	SG	SMG	EPI	30	22	20
Pseudorhombus jenynsii	SG	SMG	EPI	24	21	20
Rhabdosargus sarba	SG	SMG	EPI	28	22	21
Scomberoides lysan	SG	SMG	EPI	33	22	20
Sillago ciliata	SG	SMG	EPI	30	22	21
Sillago maculata	SG	SMG	EPI	25	21	20
Tylosurus gavialoides	SG	SMG	EPI	29	22	21
Valamugil georgii	SG	SMG	EPI	68	13	10

Table 32. Results of Isosource modelling for fish in Moreton Bay, Queensland (after Connolly et al. 2003), summarised by autotroph taxa. Values represent the number of fish species out of 22 in total for which the contribution of a particular autotroph is important, ranked by median contribution (1, 2 or 3).

Autotroph	Rank 1	Rank 2	Rank 3	Total	%*
Epiphytes	5	0	15	20	91
Saltmarsh succulents	1	0	0	1	5
Saltmarsh grass	6	15	0	19	86
Seagrass	19	0	1	20	91
Mangroves	1	0	0	1	5
MPB	1	0	1	2	9

*** percentage (%) values are representative of the rankings combined**

Chapter 10. Stable isotope studies in Western Australia

INTRODUCTION

Stable isotopes provide a useful alternative to standard dietary approaches, as they reflect the material that has been assimilated rather than material that has merely been ingested. In addition, since higher-order consumers (e.g. fish) typically consume lower-order consumers (e.g. grazing invertebrates), dietary studies rarely provide information on direct links to primary producers. This is clearly apparent in south-western Australia, where the vast majority of fish in coastal systems feed predominantly on invertebrates or small fish (Thomson 1957; Ayvazian & Hyndes 1995; Hyndes et al. 1997; Potter and Hyndes 1999; Schafer et al. 2002). Furthermore, at best, there is very little information available on the dietary preferences of those invertebrates that constitute major prey for fish species in these systems. Any evaluation of the link between primary producers and fish therefore relies on approaches such as those offered by stable isotopes.

The aim of this study was to identify the possible contribution of the major primary producers to the food web in coastal systems on the southern coast of Western Australia using dual stable isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$). Particular emphasis has been placed on determining which primary consumers have a greater role in driving the productivity of economically important species in those systems. Prior to achieving this, preliminary work was carried out to develop methods to collect inconspicuous primary producers (benthic micro-algae and phytoplankton) to include in the stable isotope analyses.

MATERIALS AND METHODS

Sampling inconspicuous primary producers

Pilot work to refine the sampling and laboratory procedures for the collection of inconspicuous primary producers concentrated mainly on refining the use of traps to collect benthic microalgae (BMA) and developing the collection and laboratory procedures for purifying the phytoplankton from the seston. Benthic microalgae traps (Fig. 52) that had been developed prior to this study were further tested in the field to determine whether this approach was feasible. The traps were developed to allow BMA both on and within the surface layer of sediment to migrate through 63µm mesh and attach to furnaced sediment within the trap. Work during the current study focused on decreasing the amount of detritus accumulating in the samples, by placing the traps in various coastal areas in the Perth metropolitan region and Princess Royal Harbour, Albany, in 2002.

To refine techniques for the collection of phytoplankton samples, seston (phytoplankton and detritus) was collected from several locations within the Swan River Estuary and Princess Royal Harbour by pumping 1000 litres (0.5 hours of pumping) of seawater through a series of 500 and 100µm mesh sieves and into a 20µm mesh plankton net. Each sample retained in the plankton net was placed into a sample jar and placed on ice in a dark container for transport to the laboratory.

In the laboratory, seston samples were centrifuged in a 50ml Falcon tube to concentrate the sample at the bottom of the tube. Samples were centrifuged for 10 minutes at a speed of 3400 rpm. Excess water was decanted off and the tube filled with Ludox and shaken to resuspend the pellet. It was spun again for 30min at 3400 rpm, at which time there was separation of the sample. Each of the top and bottom portion was removed using a pipette and placed in an epindorf tube for drying. Sub-samples of the top portion,

which contained the algal cells, were examined under a microscope to estimate the relative proportion of phytoplankton and small particulate detritus.

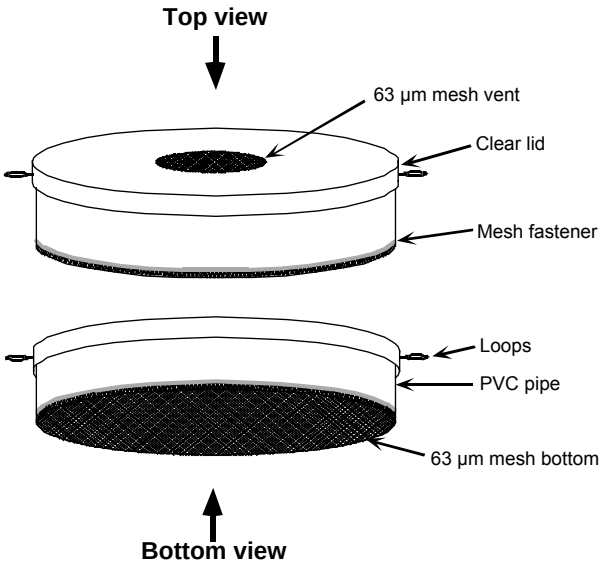

Figure 52. Schematic diagram of 15cm diameter benthic microalgae collector.

Field locations and sample collection

This part of the study was conducted in Oyster Harbour and Princess Royal Harbour, near Albany, on the south coast of Western Australia (Fig. 52). The distance between the two systems examined in Western Australia was small compared to Victoria and South Australia. However, these were the only relatively sheltered coastal systems that had permanent exchange with the ocean and that comprised a large suite of primary producers, including seagrass, saltmarshes and algae.

Princess Royal Harbour is a sheltered marine embayment with limited exchange to the ocean. There are no tributaries entering the embayment, thus the only freshwater input is derived from groundwater, direct runoff or precipitation. Princess Royal Harbour has an area of 29km^2 and a maximum depth of 5m. Oyster Harbour is a marine-dominated estuarine system, with two main tributaries, the King River and Kalgan River, entering the estuary at its north-western and north-eastern shores, respectively. Oyster Harbour has an area of 16km^2 and a maximum depth of 5m. Both systems have large areas of seagrass meadows, dominated by *Posidonia australis*, and contain fringing areas of saltmarsh vegetation dominated by *Juncus* and *Halosarcia* species. Unlike the systems examined in South Australia and Victoria, these two systems did not contain mangroves, as is the case for all coastal systems along the south coast of Western Australia.

Sampling of primary producers and consumers was conducted at three sites in each system (Fig. 53), which represented the spatial variability in each system, taking into account distance from the entrance channels and differing levels of salinity. Sampling was conducted in July 2002 and January 2003 to collect the range of primary producers, as well as consumers, including meiofauna, macro-invertebrates and fish.

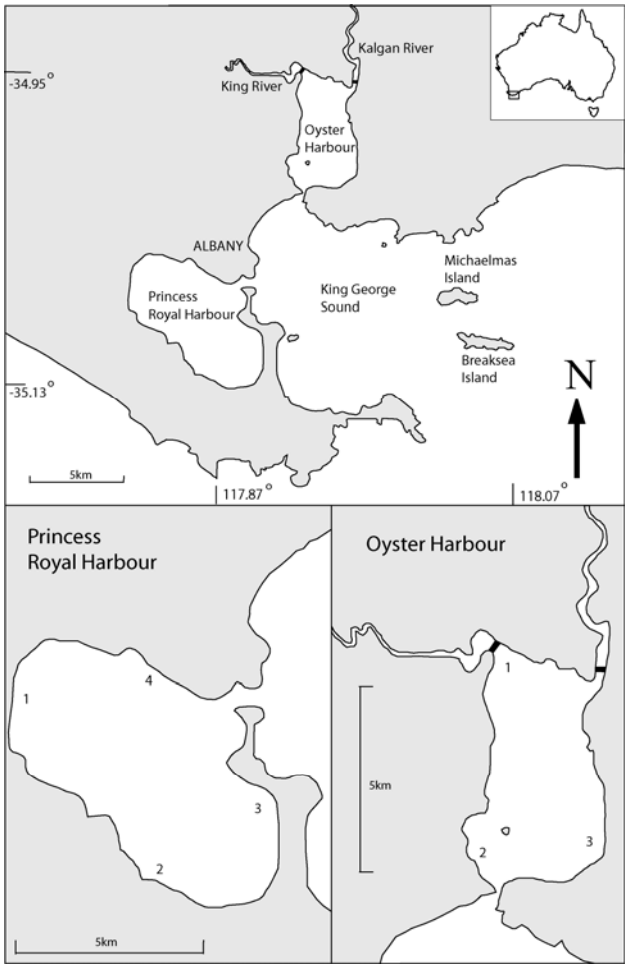

Figure 53. Map showing study region, systems and sites within systems

Small and less mobile fish, shrimp and large decapods were collected using a 21m seine net (2 m deep with 3 and 9mm mesh in the wings and pocket, respectively) in seagrass meadows and unvegetated, nearshore areas during daylight hours, while larger, more mobile fish were collected using gill nets (5 to 10 cm mesh size) that were set prior to dusk and collected after dawn. Where possible, 3-5 individuals of each species were collected at each site. Fish were placed in an ice slurry and returned to the laboratory for processing. Additional economically important species were collected from commercial fishers in the two systems, both during and up to two weeks before and after the sampling trip.

A range of techniques was used to collect potential prey of fish species. Amphipods and shrimp were collected at each site using a 250μm mesh dip net. Dip netting was carried out over a broad area (>1000 m^2) within each site. Samples of amphipods and shrimp, which also contained filamentous algae and detritus, were placed in bags and put into a cool esky for their return to the laboratory. Polychaetes and bivalve and gastropod molluscs were collected using either a sediment core or a shovel. These macro-invertebrates were extracted from the sediment using 1 mm sieves, and subsequently placed in containers of seawater and placed in a cool esky for return to the laboratory.

In the laboratory, dip net samples were washed through a series of 2000, 1000 and 500μm sieves using filtered seawater. Amphipods and shrimp were removed from the samples and placed in large containers of filtered seawater that were aerated. Similarly, copepods were extracted from the >500μm fraction and placed in aerated containers. Larger macro-invertebrates were placed in separate containers of filtered

and aerated seawater. All invertebrates were kept in these containers overnight to clear their guts of any food that may contaminate stable isotope analyses. In the case of the larger macro-invertebrates, such as polychaetes and shrimp, at least three individuals of each species or higher taxonomic group were placed in vials and frozen for processing. Due to the small size of copepods and amphipods, all individuals within each sample were pooled to provide enough material for analyses.

Fresh seagrass leaves (with epiphytes), macroalgae and saltmarsh leaves were collected from each site. At least three samples of each species were collected and placed in plastic bags and put on ice. A sample of seston (phytoplankton and detritus) was collected from each site by pumping over a 1000 litres of water sequentially through a 100 μm mesh and 20 μm plankton net. Each sample retained in the plankton net was placed into a sample jar and placed on ice in a dark container. Samples of benthic microalgae (plus sediment and detritus) were collected over a wide area by skimming the upper 1cm layer of sediment using a shovel. Each sample was placed in a plastic bag and frozen for their return to the laboratory.

Sample preparation

Samples were prepared as in General Methods. Benthic microalgae was separated from the sediment using the technique of Connolly (see SA isotope chapter). Processing of seston samples for phytoplankton followed the procedures described in Section 2 (above).

Stable isotope analyses

Samples from WA were analysed as in General Methods.

Data analyses

The mixing model Isosource (Phillips & Greg 2003) was used to estimate the potential bounds of contribution of 10 primary producer groups to the first order consumers. For each primary consumer, the frequency and range of the possible contribution (0-100%) of each possible source (primary producer) at increments of 5% were determined. Solutions were considered feasible where combinations summed to within 0.1‰. As recommended by Phillips and Greg (2003), the range between 1-99% are given, as the tails of the distributions are sensitive to small numbers.

Mixing model analyses have been restricted to detritus and the primary consumers, copepods, amphipods, shrimp and sedentary polychaetes, as they graze on plant and detrital material and represent the product of one trophic step. The enrichment of $\delta^{15}N$ between trophic levels can be highly variable for marine invertebrates (Rolff 2000, Vanderklift & Ponsard, 2003). Furthermore, $\delta^{15}N$ can increase linearly with the logarithmic size of organisms (Rolff 2000), rather than in the step-wise increase per trophic level that is often assumed. For this reason, we have not used $\delta^{15}N$ values in the mixing model. Since $\delta^{13}C$ exhibits minimal or no enrichment between trophic groups (Rolff 2000, Staddon 2004), we have restricted the mixing model analyses to this isotope and not adjusted $\delta^{13}C$ values of consumers.

RESULTS

Development of procedures to sample inconspicuous primary producers

The placement of benthic micro-algae (BMA) traps at various locations and times during 2002 yielded inconsistent proportions of detritus (30-80% detritus) in the BMA samples. This meant that the amount of BMA collected was highly variable and the placement of traps for 5-7 days rarely provided the minimum of 2mg of dried material required for isotope analyses. This method was therefore considered

impractical, and the study adopted the approach of Connolly (see SA isotope chapter) to collect BMA samples.

After the centrifuging of seston samples (described earlier) was complete, a band of detritus material settled on the bottom of most tubes, while a band of phytoplankton cells remained suspended in the column of Ludox. Examination of the phytoplankton sample under a microscope revealed that the samples had a purity of between 85 and 100% phytoplankton. Between 8.2 and 180.1mg dry weight of phytoplankton was collected from the samples, which was separated from between 8.3 and 32.3mg dry weight of detritus. The above procedure provides adequate amounts of relatively pure phytoplankton material for stable isotope analyses, thereby providing the basis for phytoplankton sampling in subsequent field trips of the current study.

Stable isotopes

Primary producers

During winter 2002 in Oyster Harbour, the mean $\delta^{13}C$ values of saltmarsh vegetation ranged between –30 and –24‰, whereas those for seagrasses were far greater ranging between –10 and –7‰ (Fig. 54). The values for most other primary producers were located between these two extremes. The brown alga *Sargassum* and green alga *Cladophora* had mean values of –16 and -11‰, respectively. The mean $\delta^{13}C$ value for *Hormosira* was similar to seagrass (-13‰), while epiphytes on *Posidonia australis* and *P. sinuosa* had values of –8 and -12‰, respectively.

The $\delta^{13}C$ values for the broad primary producer groups collected in summer 2002/03 were similar to those for winter. The $\delta^{13}C$ values for saltmarsh vegetation ranged from –28 to -23‰, while those for seagrasses ranged from –11 to -6‰ (Fig. 54). *Hormosira* had a similar mean $\delta^{13}C$ value to the previous season, whereas *Sargassum* had a higher value of –13 ‰. Epiphytic algae had values of approximately -9‰.

The $\delta^{15}N$ values for those groups of primary producers were similar in both seasons. Saltmarsh vegetation had mean values ranging between 2 and 6‰, while seagrasses and epiphytic algae had values between 0 and 5‰ (Fig. 54). The ^{15}N values for macroalgae ranged between 3 and 5‰.

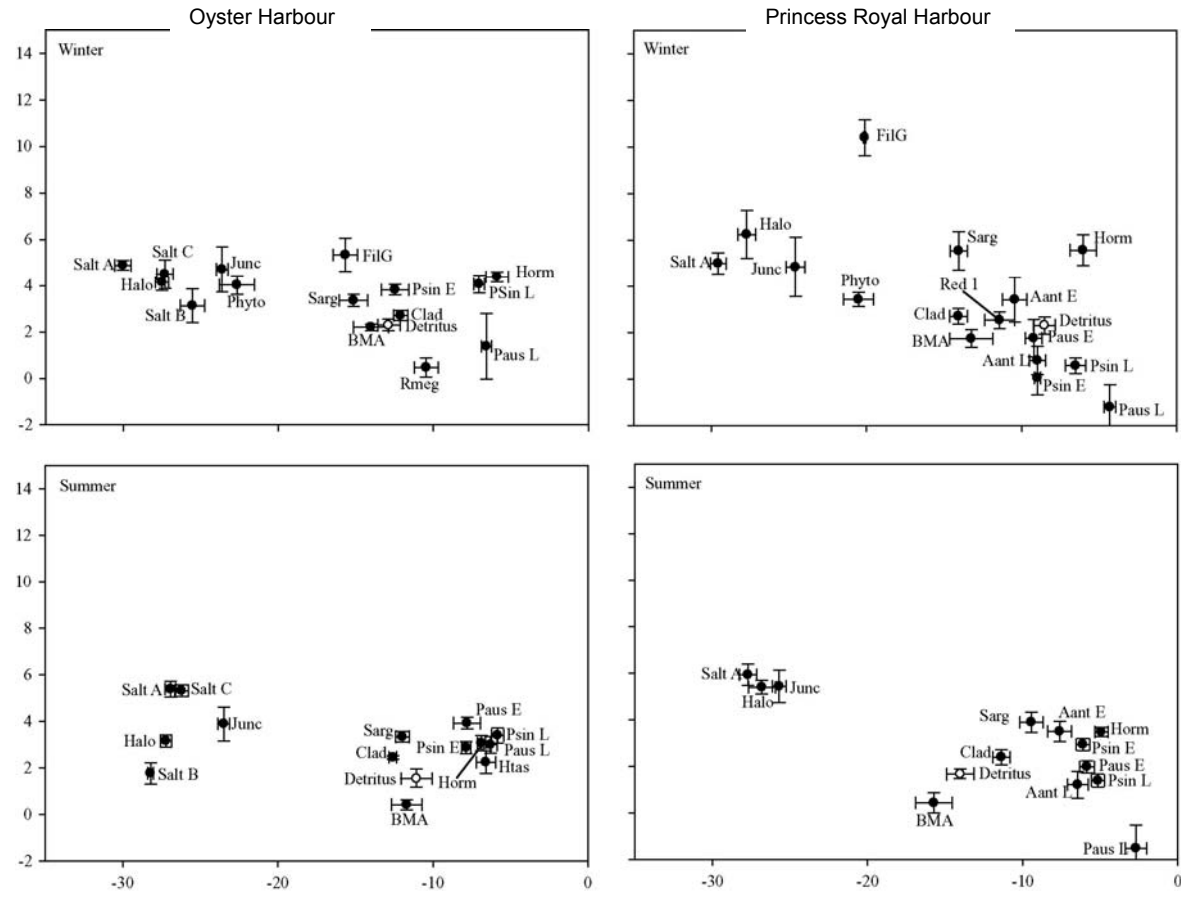

Figure 54. Mean values of $\delta^{15}N$ and $\delta^{13}C$ of potential primary food sources (closed circles) and detritus (open circles) in Oyster Harbour and Princess Royal Harbour on the south coast of Western Australia.

Compared to Oyster Harbour, saltmarsh vegetation was less prevalent at Princess Royal Harbour. However, the $\delta^{13}C$ values for the broad groups of producers in Princess Royal Harbour were similar to those in Oyster Harbour. The $\delta^{13}C$ values for saltmarshes ranged between –31 and -24‰, compared to between –10 and –4‰ for seagrasses (Fig. 54). Macroalgae typically ranged between -15 and –9‰, except for *Hormosira* which had mean values of approximately –7‰. Epiphytic material had $\delta^{13}C$ values from –11 to –7‰.

Benthic micro-algae had mean $\delta^{13}C$ values between –15 and -12‰ in both systems and seasons (Fig. 54). Due to the inability to remove all of the detritus from the BMA samples, samples contained varying amounts of detritus. In winter, the samples comprised only 7 and 8% BMA in Oyster Harbour and Princess Royal Harbour, respectively, compared to 39 and 41% for the respective systems in summer. The $\delta^{13}C$ values for BMA were higher than those of phytoplankton (-22 and –20‰) in both systems during winter. In comparison, the $\delta^{13}C$ values for detritus ranged from -15‰ in Oyster Harbour during winter to -9‰ in Princess Royal Harbour during the same season (Fig. 54). Detritus therefore fell within similar values to algae, with the exception of Princess Royal harbour in winter, when values were similar and in both seasons (Fig. 54).

Invertebrates

The $\delta^{13}C$ values for invertebrates ranged from –20.5 to –8.7‰, which typically lay within the boundaries of most algae (Table 33, Figs. 55 & 56). For crustaceans, the values for amphipods and copepods tended to be lower (–20.5 to –13.6‰ and –19.0 and –13.6‰, respectively) compared to *Majidae* spp (-9.9 to –8.7‰).

Graspidae spp had values that ranged between –13.8 and –11.4‰, which were similar to those of the shrimp *Palaemonetes australis* (-13.1 to –11.1‰). With the exception of shrimp, which had $\delta^{15}N$ values of approximately 8-9‰, the values of crustaceans generally ranged between 4 and 6‰.

All gastropods had $\delta^{13}C$ values that ranged from approximately –18 to -11‰ (Table 33, Figs 55 & 56). With the exception of Oyster Harbour in summer, the gastropods *Lepsiella vinosa* and *Nassarius albinus* had higher $\delta^{15}N$ values than *Astele multigranum*, Gastropod sp. 4 and *Clanculus atopurpureus* (6.2-8.9‰ vs ~5‰). The *Paphia crassisulca* had $\delta^{13}C$ values that ranged between –18.0 and –13.7‰, and $\delta^{15}N$ values of 4.6-6.6‰.

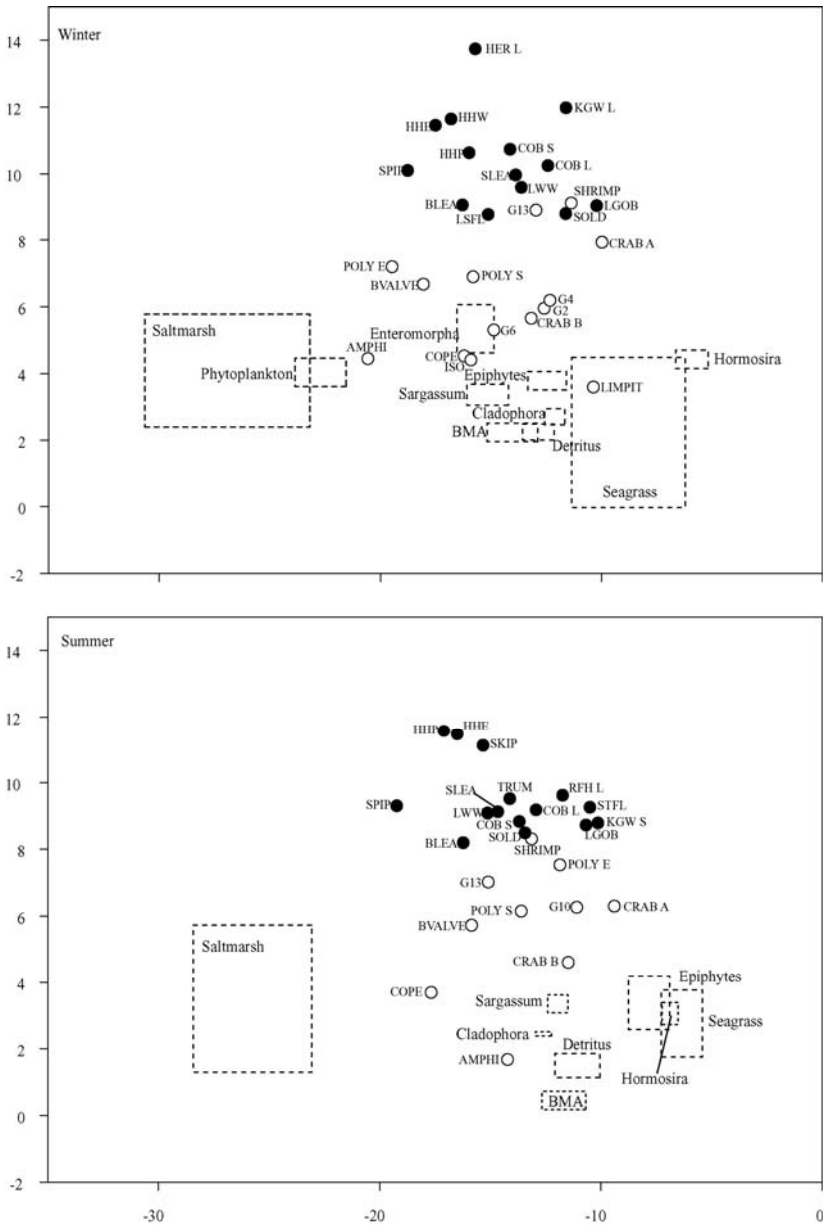

Figure 55. Mean values of $\delta^{15}N$ and $\delta^{13}C$ of invertebrates (open circles) and fish (closed circles) in Oyster Harbour on the south coast of Western Australia. Boxes in dashed lines encapsulate the range of values for different groups of primary producers. Standard error values are located in Table 33.

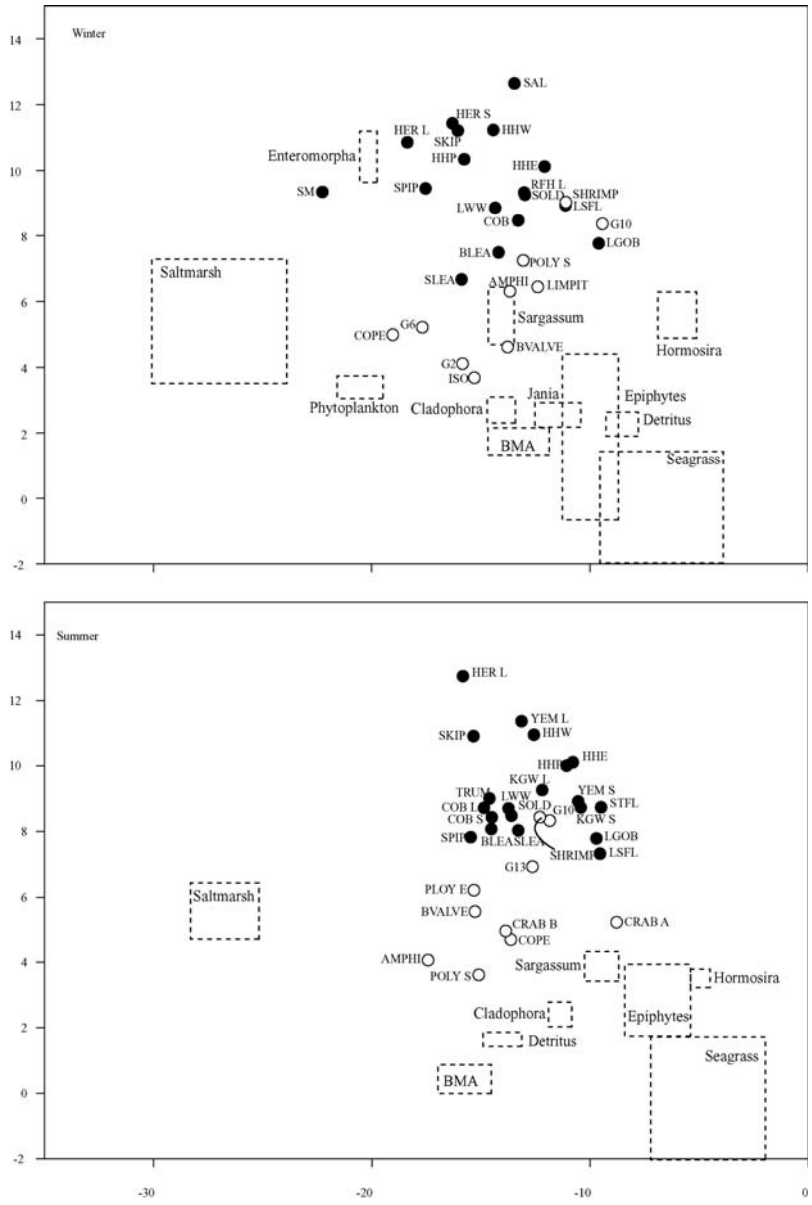

Figure 56. Mean values of $\delta^{15}N$ and $\delta^{13}C$ of invertebrates (open circles) and fish (closed circles) in Princess Royal Harbour on the south coast of Western Australia. Boxes in dashed lines encapsulate the range of values for different groups of primary producers. Standard error values are located in Table3.

Similar to a number of other invertebrate groups, $\delta^{13}C$ values for polychaetes ranged from –19.4 to –11.8‰, while the $\delta^{15}N$ values ranged from 3.6 to 9.1‰ (Figs 55 & 56). There were no clear patterns associated with Order (Errantia or Sedentaria) for either isotope.

Fish

In terms of economically important species, King George whiting (*Sillaginodes punctata*), cobbler (*Cnidoglanis macrocephalus*), Skipjack Trevally (*Pseudocaranx dentex*), Long-snouted flounder (*Ammotretis*

rostratus) and Australian herring (*Arripis georgiana*) were caught in both systems, and in at least one season for each system. A range of sizes of fish was collected in both seasons (Table 34). There was no clear separation of small and large cobbler based on $\delta^{13}C$ values, which ranged between –14.8 and –12.4‰ (Table 33, Figs. 55 & 56). The $\delta^{13}C$ values for *S. punctata* were similar to those of *C. macrocephalus*, and where small and large fish were caught in the same system and season, there was likewise no clear difference in their $\delta^{13}C$ values. *Pseudocaranx dentex* had similar values of –16.0 to –15.3‰, while Long-snouted flounder had slightly elevated values (-15.1 to –9.5‰). Relative to the above species, *A. georgiana* had lower $\delta^{13}C$ values, ranging between –18.3 and -15.8‰. Rock flathead (*Leviprora laevigatus*) was caught in Oyster Harbour in summer and Princess Royal Harbour in winter, when the mean $\delta^{13}C$ values were –13.0 and –11.7‰, respectively.

Fish species that have no direct economic value, but are likely to be important forage fish for a number of those economically important species, had similar $\delta^{13}C$ values (Table 34, Figs 55 & 56). Hardyhead species (*Leptatherina presbyteroides*, *L. wallacei* and *Atherinasoma elongatus*) had values ranging between –17.5 and –10.7‰, which were typically lower than those values for the Long-finned goby *Favonigobius lateralis* (-10.6 to –9.6‰). The spotted pipefish *Stigmatopora argus* tended to have the lowest $\delta^{13}C$ values of this group of fish (-19.2 to –15.4‰).

Not surprisingly, the $\delta^{15}N$ values for fish were elevated relative to many of the invertebrates, which in turn were elevated compared to most primary producers (Table 34, Figs 55 & 56). The $\delta^{15}N$ values for fish typically ranged between 8 and 14‰. *Arripis georgiana*, *Pseudocaranx dentex* and the Australian salmon *Arripis truttaceus* often had the highest values, exceeding 11‰.

Mixing Model

The contribution of primary producers to detritus was variable between systems and seasons. According to the results of Isosource using dual isotopes, benthic microalgae made the greatest contribution to detritus (0-85%) in Oyster Harbour in winter, followed by *Cladopora*, *Sargassum*, *P. australis* and *R. megacarpa* (Fig. 57). Benthic microalgae still made a substantial contribution in summer, but other primary producers (*Cladophora* and *H. tasmanica*) also made a substantial contribution. While the contribution of benthic microalgae was particularly high in Princess Royal Harbour during summer, it was much less in winter, when seagrasses and epiphytic algae made substantial contributions to the detritus. *Cladophora* and *P. australis* were also important sources in summer.

The contribution of sources to copepods and amphipods varied considerably between system and season (Fig. 58). For copepods, the Isosource mixing model indicated that the saltmarsh vegetation (Saltmarsh A and *Juncus*) had a high probability of contributing to their carbon in Oyster Harbour during summer and Princess Royal Harbour during winter (Fig 58a). Benthic microalgae, *Cladophora* and Sargassum made substantial contributions to these crustaceans, particularly in Oyster Harbour during winter and Princess Royal Harbour during summer. For amphipods, saltmarsh vegetation had a relatively high contribution in Oyster Harbour during winter and Princess Royal Harbour during summer (Fig 58b). The contribution of phytoplankton was also high in Oyster Harbour in winter, while benthic microalgae was high in Princess Royal Harbour during summer. The importance of benthic microalgae, *Cladophora* and *Sargassum* was high in Oyster Harbour during summer and Princess Royal Harbour during winter. Epiphytic algae and seagrasses also made relatively high contributions to amphipods in these systems at these times.

The contribution of sources to the shrimp *Palaemonetes australis* also varied between system and season. However, unlike copepods and amphipods, the probability of saltmarsh vegetation contributing to the carbon of shrimp was low. Instead, the seagrasses *Posidonia australis* and/or *A. antarctica* made considerable contributions in both systems during both seasons (Fig. 59a). Furthermore, the seagrass *Ruppia megacarpa* also potentially contributed to shrimp in Oyster Harbour during winter. *Cladophora*,

benthic microalgae and to a lesser extent epiphytes and *Sargassum* were important in both systems during both seasons.

Results of the mixing model indicate that benthic microalgae, epiphytes, *Sargassum* and *Cladophora* consistently contributed to the carbon for sedentary polychaetes across both systems and seasons (Fig. 59b). *Amphibolis antarctica* was also important in Princess Royal Harbour during winter.

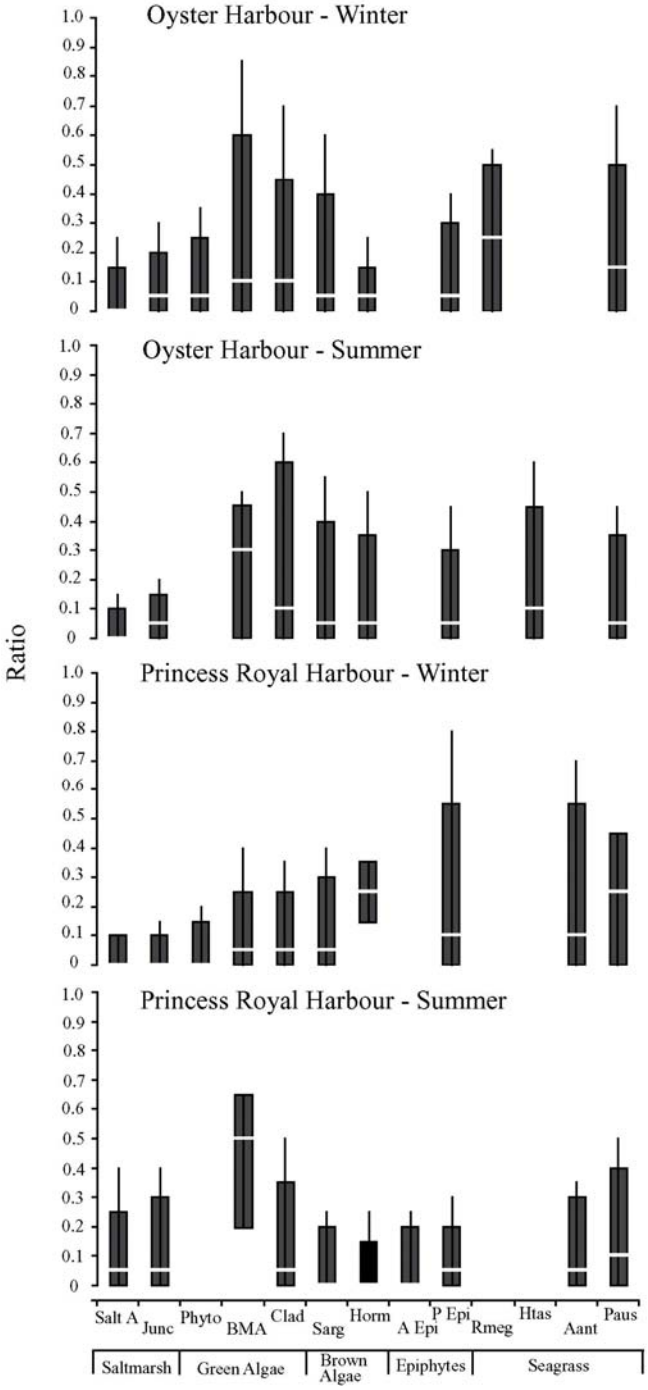

Figure 57. Box-whisker plots representing the distribution of the feasible contributions of 10 representative primary producers to detritus based on $\delta^{13}C$ and $\delta^{15}N$ values. Plots show minimum, 1st, 50th and 99th percentiles and maximum values of the distributions.

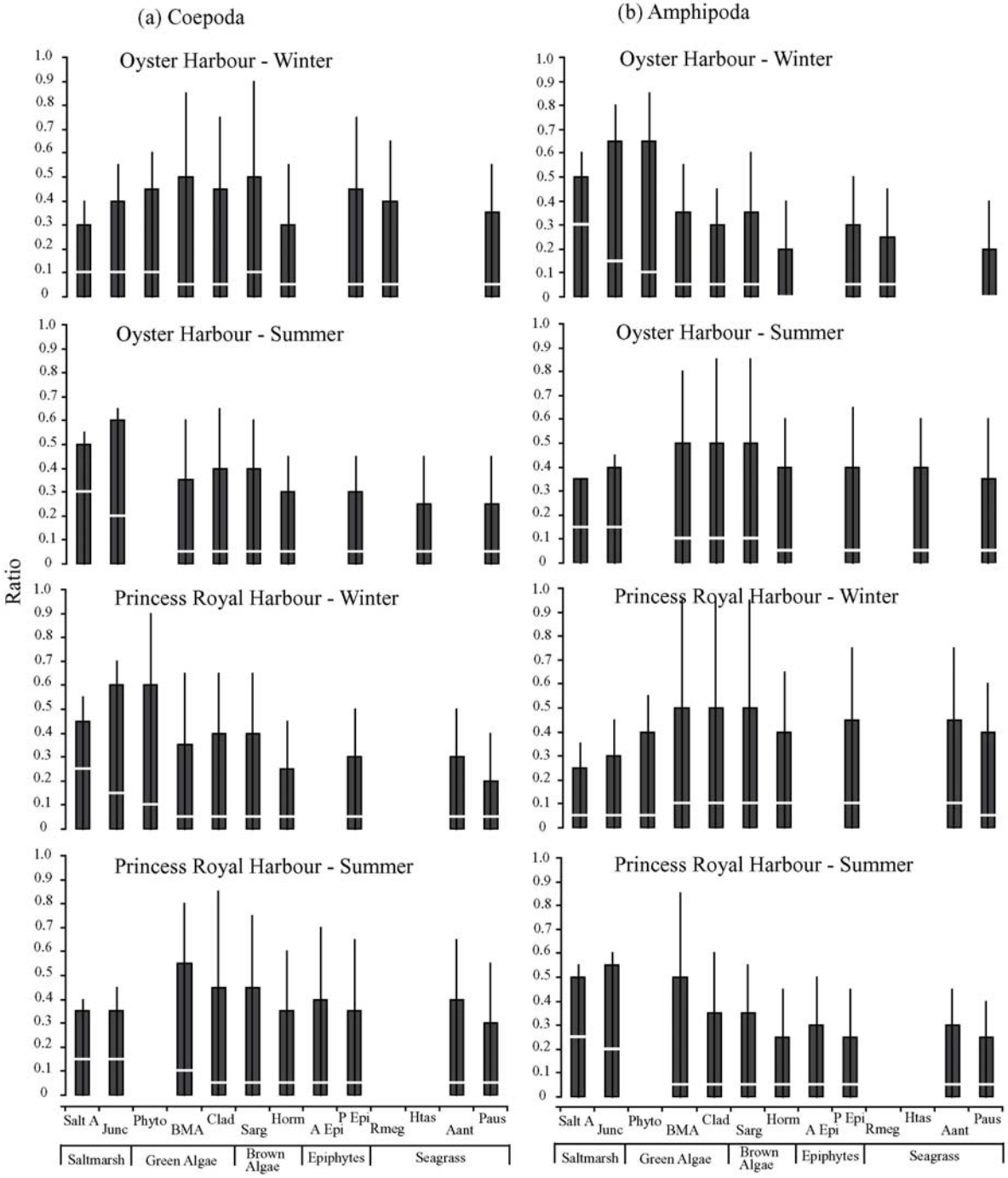

Figure 58. Box-whisker plots representing the distribution of the feasible contributions of 10 representative primary producers to (a) copepods and (b) amphipods based on $\delta^{13}C$ values. Plots show minimum, 1st, 50th and 99th percentiles and maximum values of the distributions.

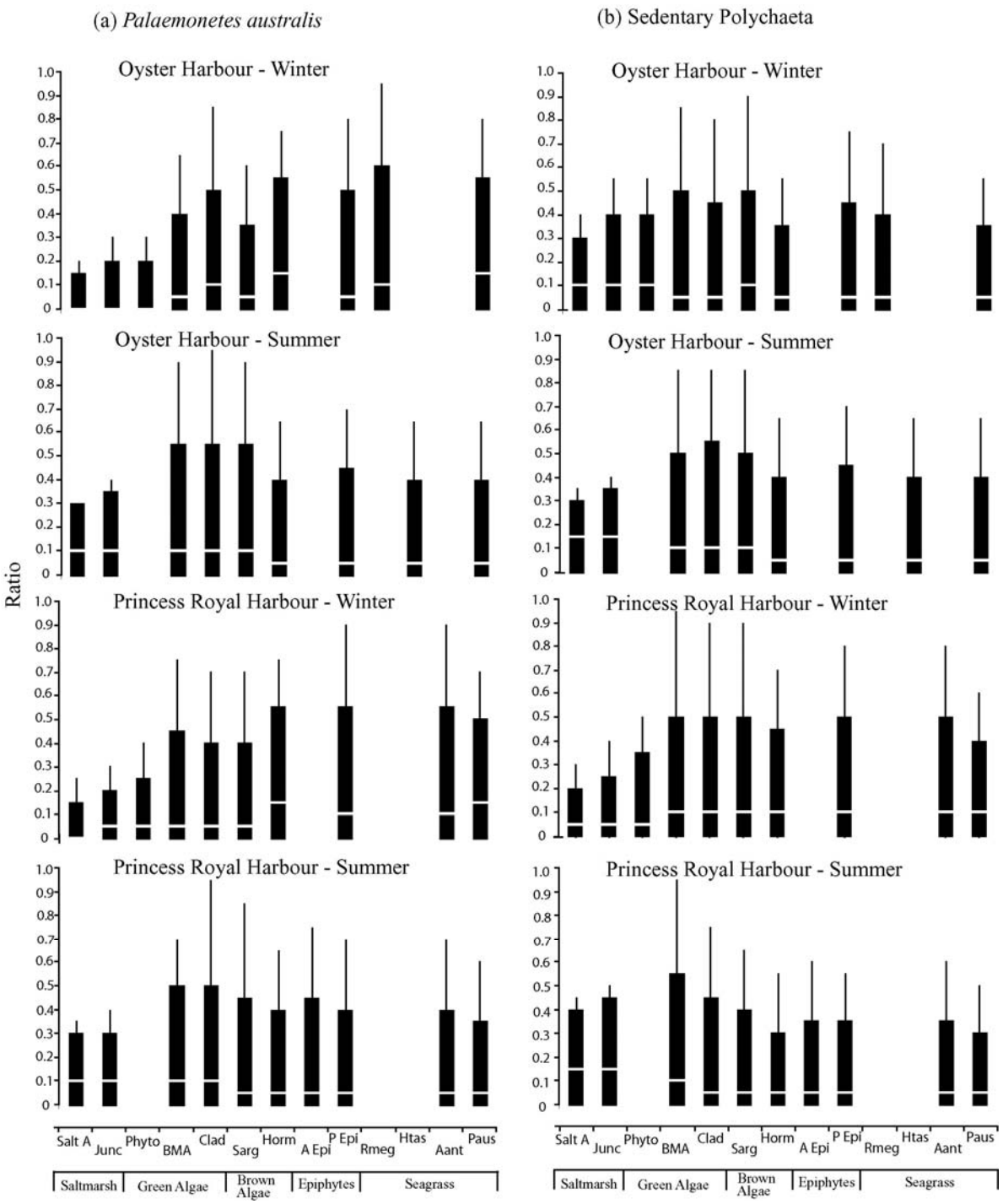

Figure 59. Box-whisker plots representing the distribution of the feasible contributions of 10 representative primary producers to (a) *Palaemonetes australis* and (b) sedentary polychaetes based on $\delta^{13}C$ values. Plots show minimum, 1st, 50th and 99th percentiles and maximum values of the distributions.

DISCUSSION

The results of the present study indicate that in Oyster Harbour and Princess Royal Harbour, on the south coast of Western Australia, a range of primary producers contribute to the production of benthic invertebrates, such as amphipods, shrimp, copepods, gastropods, bivalve molluscs and polychaetes. Since these invertebrates constitute major prey for the numerous coastal fish species (Thomson 1957; Prince et al. 1982; Gill & Potter 1993; Humphries & Potter 1993; Hyndes et al. 1997), a range of primary producers are likely to sustain fish production in those systems. This is supported by the similar range of $\delta^{13}C$ values exhibited by fish and invertebrates. However, the contribution of primary producers varied among invertebrate groups. Thus, the dependence of certain fish species on particular primary producers will depend on their main prey, as well as the location and time in which they occur.

Plant material in coastal ecosystems can enter the food web through invertebrates grazing either directly on plant material or indirectly through grazing on detritus. However, food webs in these ecosystems are often considered to be detrital based (Benner et al. 1984; Cebrián et al. 1997; Vizzini et al. 2002). Interpretation of the detrital composition through isotopes can help our understanding of the movement of plant material through the food web. These interpretations do not consider any possible fractionation for both ^{15}N and ^{13}C during microbial breakdown. Since such processes are poorly investigated (Turner et al. 1983; Benner et al. 1984; Zieman et al. 1984, Focken & Becker 1998), it has to be assumed that there is zero fractionation.

The mixing model indicated that detritus in both systems comprised mainly benthic microalgae (BMA), as well as the brown algae *Sargassum* and *Hormosira*, the green alga *Cladophora* and the seagrasses *Posidonia australis* and *Amphibolis antarctica*. It must be noted, however, that the results indicating the high contribution of BMA to detritus is likely to be misleading, as the BMA samples often contained relatively large proportions of detritus that could not be removed using the Ludox procedure. This was particularly apparent for samples in Princess Royal Harbour during winter, when the BMA samples comprised >90% detritus. In addition, the similar stable isotope values of different groups of macrophytes make it difficult to differentiate between groups. This was particularly apparent for *Hormosira* vs seagrasses and *Sargassum* vs *Cladophora*. Compared to *Hormosira* and *Sargassum*, *Posidonia australis* and *Cladophora* were present in far greater biomass in Oyster Harbour or Princess Royal Harbour (pers. obs.). It is therefore highly likely that these two groups of macrophytes contribute substantially to the detritus, whereas *Hormosira* and *Sargassum* are likely to have low contributions.

Saltmarsh vegetation appears to make only a minor contribution to detritus in both systems, with a maximum contribution ranging between 10 and 40%. This contribution was lower than that shown for Walpole-Nornalup Estuary approximately 100kms to the west, where detritus was shown to comprise up to 60% saltmarsh or riverine vegetation (Svensson et al. submitted). The contribution of saltmarsh to detritus varied spatially in Walpole-Nornalup Estuary, with areas closest to river mouths showing the greatest contributions.

Results of the mixing model indicate that both copepods and amphipods derive a substantial amount of their carbon from saltmarsh vegetation, but this varies spatially and temporally. Since the saltmarsh areas in Oyster and Princess Royal harbours are only occasionally inundated with water (pers. obs.), it is unlikely that these crustaceans would graze directly on saltmarshes, but rather rely on the detrital material being transported from those fringing areas. The higher contribution of saltmarsh, compared to detritus, to copepods and amphipods , suggests that they can selectively feed on particles of saltmarsh in the detrital pool or selectively assimilate essential elements from their food (Zieman et al. 1984; Couch 1989; Riera et al. 1996; Coull 1999).

In contrast to amphipods, the shrimp *Palaemonetes australis* appears to derive its nutrients mainly from seagrass, *Cladophora* and epiphytic algae. The relatively high contribution of seagrass to the production of

this shrimp has also been shown in Wilson Inlet and Wellstead Estuary, where the seagrass *Ruppia megacarpa* is abundant (Forbes & Walker in press). The high $\delta^{15}N$ value of shrimp relative to the seagrass and *Cladophora* (4-8‰) exceeds the expected 3.4‰ enrichment expected for one trophic level (Minagawa & Wada 1984). This suggests that shrimp are deriving their nitrogen from an unidentified source, possibly through the consumption of microbes, which colonise detrital material and can strongly influence the $\delta^{15}N$ composition of the consumer (Zieman et al. 1984). The consumption of seagrass by the shrimp *P. australis* has also been shown for other shrimp or prawn species (Loneragan et al. 1997; Schwamborn & Criales 2000; Schwamborn et al. 2002). Since a number of gastropod species (*Astele multigranum* and Gastropod sp 4), as well decapod crabs (Majidae spp) had similar $\delta^{13}C$ values to *Posidonia australis*, seagrass is also likely to contribute substantially to the production of these species.

Unlike the above crustaceans, seagrass and saltmarsh rarely made major contributions to sedentary polychaetes. Instead, this group of organisms appeared to derive its carbon mostly from algae, particularly *Cladophora*, BMA, *Sargassum* and epiphytic algae. Since *Cladophora* is present in high biomass in both systems, this green alga is likely to contribute significantly to the food web through these benthic invertebrates. Algae has also been shown to contribute substantially to the production of polychaetes in unvegetated areas on the lower west coast of Western Australia (Hyndes & Lavery in press).

The majority of the fish species collected during the study feed on a range of invertebrates (Thomson 1957; Humphries and Potter 1993; Gill and Potter 1993; Hyndes et al. 1997; Potter and Hyndes 1999), although the leatherjacket *Acanthuleteres spilomelanurus* and the weed whiting *Neoodax balteatus* can consume algae (Hyndes *et al*. 1998). The wide range in feeding at least partly explains the high degree of variability in $\delta^{13}C$ and $\delta^{15}N$ values. Furthermore, the $\delta^{13}C$ values for fish generally exhibited a similar range and degree of variability to those of invertebrates, again reflecting their consumption of those prey. The high $\delta^{15}N$ values of fish, relative to invertebrate groups, indicate that there is at least one trophic step between fish and those invertebrates. Interestingly, the $\delta^{15}N$ values for *A. spilomelanurus* and *N. balteatus*, which can consume plant material, had similar values to those species that are solely carnivorous (e.g. the soldierfish *Gymnapistes marmoratus* and the cobbler *Cnidoglanis macrocephalus*), suggesting that if plant material was consumed, it formed only a small component of their diets.

The $\delta^{13}C$ values of fish are likely to reflect those of their main prey groups. For example, the $\delta^{13}C$ values of *C. macrocephalus* were often similar to those of bivalve molluscs and polychaetes, which form major components of this species' diet (Potter and Hyndes 1999). Also, the $\delta^{13}C$ values of *S. punctata* were similar to those of a mixture of polychaetes, shrimp and crabs, which can form a substantial part of the diets of fish greater than 175mm TL (Hyndes et al. 1997). The higher $\delta^{15}N$ values for species such as the Australian herring and salmon, *Arripis georgiana* and *A. truttaceus*, suggest that they are feeding on other fish in addition to invertebrates.

Table 33. Mean and standard error values of $\delta^{15}N$ and $\delta^{13}C$ of primary producers, detritus, invertebrates and fish in Princess Royal Harbour on the south coast of Western Australia.

Type	Code	Species Name	Oyster Harbour								Princess Royal Harbour							
			Winter				Summer				Winter				Summer			
			δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N
Plants	AANT – E	*Amphibolis antarctica* – epiphytes									-10.4	0.8	3.4	1.0	-7.6	0.8	3.5	0.4
	AANT – L	*Amphibolis antarctica* – leaves									-9.0	0.5	0.8	0.6	-6.4	0.7	1.2	0.6
	CLAD	Cladophora	-12.1	0.5	2.7	0.2	-12.6	0.2	2.4	0.1	-14.1	0.6	2.7	0.3	-11.4	0.5	2.4	0.3
	Detritus	Detritus	-12.9	0.7	2.3	0.2	-11.0	1.0	1.5	0.4	-8.5	0.7	2.3	0.3	-14.0	0.9	1.6	0.2
	FILG	Enteromorpha	-15.7	0.8	2.3	0.7					-20.1	0.1	10.4	0.8				
	HALO	Halosarcia	-27.5	0.4	4.1	0.4	-27.2	0.4	3.2	0.3	-27.7	0.6	6.2	1.0	-26.8	0.9	5.4	0.3
	HORM	Hormosira	-5.9	0.7	4.4	0.2	-6.9	0.3	3.1	0.3	-6.0	0.9	5.6	0.7	-4.9	0.4	3.5	0.2
	HTAS	*Heterozostera tasmanica*					-6.58	0.6	2.2	0.5								
	JUNC	Junus	-23.6	0.4	4.7	1.0	-23.5	0.4	3.9	0.7	-24.6	0.6	4.8	1.3	-25.7	0.4	5.4	0.7
	BMA	Benthic Micro Algae	-14.0	1.1	2.2	0.1	-11.7	1.0	0.4	0.2	-13.2	1.4	1.7	0.4	-15.7	1.2	0.4	0.4
	PAUS – E	*Posidonia australis* – epiphytes					-7.8	0.9	3.9	0.3	-9.2	0.5	1.8	0.8	-5.9	0.5	2.0	0.3
	PAUS – L	*Posidonia australis* – leaves	-6.6	0.3	1.4	1.4	-6.3	0.4	3.0	0.4	-4.3	0.4	-1.2	1.0	-2.7	0.7	-1.5	1.0
	PHYTO	Phytoplankton	-22.7	1.1	4.0	0.4					-20.5	1.0	3.4	0.3				
	PSIN – E	*Posidonia sinuosa* – epiphytes	-12.5	0.9	3.8	0.2	-7.8	0.3	2.9	0.3	-9.0	0.2	0.1	0.7	-6.1	0.4	2.9	0.3
	PSIN – L	*Posidonia sinuosa* – leaves	-7.1	0.3	4.1	0.4	-5.8	0.4	3.4	0.3	-6.5	0.6	0.6	0.3	-5.1	0.4	1.4	0.3
	JANIA	Jania									-11.4	1.0	2.5	0.4				
	RMEG	*Ruppia megacarpa*	-10.5	0.8	0.5	0.4												
	SALT A	Saltmarsh sp a	-30.0	0.5	4.9	0.2	-26.9	0.3	5.4	0.3	-29.6	0.5	5.0	0.5	-27.7	0.6	5.9	0.5
	SALT B	Saltmarsh sp b	-25.5	0.8	3.1	0.7	-28.2	0.2	1.8	0.5								
	SALT C	Saltmarsh sp c	-27.3	0.5	4.5	0.6	-26.2	0.4	5.3	0.2								
	SARG	Sargassum	-15.1	0.9	3.3	0.3	-12.0	0.5	3.3	0.2	-14.1	0.	5.6	0.8	-9.4	0.7	3.9	0.4
Invertebrates	AMPHI	Gamarid Amphipod	-20.5	3.6	4.4	0.3	-14.2		1.7		-13.6		6.3		-17.3	2.3	4.0	1.3
	BVALVE	*Paphia crassisulca*	-18.0	0.4	6.6	0.2	-15.8	0.5	5.7	0.2	-13.7	1.0	4.6	0.2	-15.2	0.7	5.5	0.3
	COPE	Copepoda	-16.2	3.3	4.5	0.8	-17.6	3.6	3.7	1.4	-19.0	1.5	5.0	1.0	-13.6	1.6	4.7	0.2
	CRAB A	Majidae spp	-9.9	0.6	7.9	0.3	-9.3	0.8	6.3	0.6					-8.7	0.4	5.2	0.3
	CRAB B	Graspidae spp	-13.1	4.0	5.6	1.0	-11.4	2.8	4.6	0.8					-13.8	1.4	4.9	0.3
	G10	*Lepsiella vinosa*					-11.0	1.6	6.2	0.5	-9.4	0.5	8.3	0.6	-11.8	0.4	8.3	0.3
	G13	*Nassarius albinos*	-12.9	0.1	8.9	0.6	-15.0	0.5	7.0	0.4					-12.6	0.7	6.9	0.2
	G2	*Astele multigranum*	-12.6	2.4	5.9	0.8					-15.8	0.7	4.1	0.1				

	G4	Gastropod sp4	-12.3	1.1	6.1	0.6												
	G6	*Clanculus atropurpureus*	-14.8	0.7	5.3	0.3					-17.6	1.2	5.2	0.2				
	ISO	Isopoda	-15.9	0.9	4.4	0.2					-15.3	0.6	3.7	0.3				
	LIMPIT	*Hipponix conicus*	-10.3	0.3	3.6	0.1					-12.4	0.6	6.4	0.9				
	POLY E	Errant Polychaeta	-19.4	3.1	7.2	0.0	-11.8		7.5						-15.2	1.7	6.2	0.5
	POLY S	Sedentary Polychaeta	-15.8	1.4	6.9	0.1	-13.6	0.9	6.1	0.5	-13.0	0.6	7.2	0.7	-15.0	0.2	3.6	0.6
	SHRIMP	*Palaemonetes australis*	-11.3	3.1	9.1	1.2	-13.1	2.2	8.3	5.7	-11.1	1.2	9.0	1.7	-12.2	1.4	8.4	0.8
Economic Fish Species	COB L	*Cnidoglanis macrocephalus* -Large	-12.4	0.7	10.2	1.7	-12.9	0.5	9.2	0.3	-13.2	0.5	8.4	0.2	-14.8	0.3	8.7	0.1
	COB S	*Cnidoglanis macrocephalus* -Small	-14.1	0.4	10.7	0.4	-13.6	1.0	8.8	0.3					-14.4	0.9	8.4	0.4
	HER L	*Arripis georgiana* -Large	-15.7	0.2	13.7	0.8					-18.3	0.1	10.8	0.9	-15.8	0.2	12.7	1.7
	HER S	*Arripis georgiana* -Small									-16.3	2.5	11.4	0.5				
	KGW L	*Sillaginodes punctata* -Large	-11.6	0.4	11.9	0.4									-12.1	0.4	9.2	0.3
	KGW S	*Sillaginodes punctata* -Small					-10.1	0.8	8.8	0.3					-10.3	0.7	8.7	0.2
	LSFL	*Ammotretis rostratus*	-15.1	0.3	8.7	0.5					-11.1	0.4	8.9	0.6	-9.4	0.7	7.3	0.1
	RFH L	*Leviprora laevigatus* -Large					-11.7	0.5	9.6	0.7	-13.0	1.2	9.3	0.2				
	SAL	*Arripis truttaceus*									-13.4	0.6	12.6	0.2				
	SKIP	*Pseudocaranx dentex*					-15.3	0.4	11.1	0.1	-16.0	0.2	11.2	0.2	-15.3	1.2	10.9	0.2
	SM	*Mugil cephalus*									-22.2	0.1	9.3	0.1				
	STFL	*Psuedorhombus jenynsii*					-10.4	0.7	9.2	0.1					-9.4	0.3	8.7	0.6
	TRUM	*Pelates sexlineatus*					-14.1	0.7	9.5	0.3					-14.5	0.4	9.0	0.3
	YEM L	*Aldrichetta forsteri* -Large													-13.1	1.8	11.3	0.5
	YEM S	*Aldrichetta forsteri* -Small													-10.5	0.1	8.9	0.9
Non-Economic Fish Species	BLEA	*Ancanthaluteres spilomelanurus*	-16.3	0.4	9.0	0.3	-16.2	0.1	8.2	0.1	-14.1	0.9	7.5	0.2	-14.4	0.5	8.0	0.1
	HHE	*Atherinasoma elongata*	-17.5	0.4	11.4	0.2	-16.5	0.4	11.4	0.1	-12.0	0.9	10.1	0.3	-10.7	0.4	10.1	0.2
	HHP	*Leptatherina presbyteroides*	-16.0	1.0	10.6	0.3	-17.1	0.3	11.6	0.1	-15.7	1.1	10.3	0.3	-11.0	0.3	10.0	0.2
	HHW	*Leptatherina wallacei*	-16.8	0.3	11.6	0.2					-14.4	0.5	11.2	0.2	-12.5	0.3	10.9	0.2
	LGOB	*Favonigobius lateralis*	-10.2	0.7	9.0	0.3	-10.6	0.7	8.7	0.3	-9.6	0.4	7.7	0.2	-9.6	0.3	7.8	0.2
	LWW	*Neoodax balteatus*	-13.6	0.3	9.6	0.2	-15.1	0.3	9.1	0.1	-14.3	0.5	8.8	0.2	-13.7	0.4	8.7	0.1
	SLEA	*Meuschenia freycineti*	-13.8	0.7	9.9	0.2	-14.6	0.3	9.1	0.1	-15.8	0.5	6.6	0.2	-13.2	0.4	8.0	0.4
	SOLD	*Gymnapistes marmoratus*	-11.6	0.3	8.8	0.2	-13.4	0.4	8.5	0.2	-12.9	0.4	9.2	0.3	-13.5	0.2	8.4	0.2
	SPIP	*Stigmatopora argus*	-18.7	0.4	10.1	0.1	-19.2	0.1	9.3	0.2	-17.5	1.1	9.4	0.3	-15.4	1.3	7.8	0.3

Table 34. Mean length and range of lengths for species of fish collected from Oyster Harbour and Princess Royal Harbour on the south coast of Western Australia.

Species Name	Group	2002 Mean	Range	2003 Mean	Range
Commercial Species					
Aldrichetta forsteri	large	273	235 - 310	243	224 - 260
	small			96	53 - 139
Ammotretis rostratus		90	17 - 186	71	57 - 90
Arripis georgiana	large	233	200 - 270	231	226 - 240
	small	43	35 - 52	89	86 - 91
Arripis truttaceus		282	273 - 292	192	192 - 192
Cnidoglanis macrocephalus	large	361	267 - 650	354	262 - 565
	small	126	91 - 154	49	40 - 67
Leviprora laevigatus		419	387 - 451	375	340 - 400
Meuschenia freycineti		194	66 - 328	99	45 - 238
Mugil cephalus		29	27 - 30		
Pelates sexlineatus				176	27 - 225
Pseudocaranx dentex		250	244 - 256	250	195 - 292
Psuedorhombus jenynsii		0	0 - 0	177	141 - 265
Silaginodes punctata	large	313	309 - 318	267	231 - 335
	small			70	37 - 92
Non Commercial Species					
Ancanthaluteres spilomelanurus		71	52 - 104	59	20 - 126
Atherinasoma elongata		62	31 - 85	68	50 - 90
Favonigobius lateralis		48	30 - 70	60	45 - 81
Gymnapistes marmoratus		92	46 - 170	87	34 - 150
Leptatherina presbyteroides		58	37 - 79	65	51 - 86
Leptatherina wallacei		52	38 - 71	52	44 - 64
Neoodax balteatus		80	46 - 114	75	36 - 105
Stigmatopora argus		178	104 - 224	145	93 - 190

Table 35. Mean and standard error values of $\delta^{15}N$ and $\delta^{13}C$ of primary producers, detritus, invertebrates and fish at three sampling sites in Oyster Harbour on the south coast of Western Australia.

Species Name	Winter 1				2				3				Summer 1				2				3			
	$\delta^{13}C$	SE C	$\delta^{15}N$	SE N	$\delta^{13}C$	SE C	$\delta^{15}N$	SE N	$\delta^{13}C$	SE C	$\delta^{15}N$	SE N	$\delta^{13}C$	SE C	$\delta^{15}N$	SE N	$\delta^{13}C$	SE C	$\delta^{15}N$	SE N	$\delta^{13}C$	SE C	$\delta^{15}N$	SE N
Sources																								
Amphibolis antartica – epiphytes																								
Amphibolis antartica – leaves																								
Benthic Micro Algae	-11.8	1.0	2.4	0.8	-12.1	0.3	1.5	0.0	-18.2	0.5	2.4	0.2	-13.6		1.1		-13.2	1.4	0.4	0.5	-9.5	0.9	0.3	0.2
Cladophora					-12.1	0.5	2.7	0.2													-12.6	0.2	2.4	0.1
Detritus	-12.1	0.3	2.4	0.2	-10.6	0.4	1.5	0.0	-15.4	0.6	2.6	0.2	-16.3		3.0		-11.3	0.6	1.7	0.5	-9.0	0.7	0.8	0.1
Enteromporha	-14.8	1.4	3.7	0.0					-16.5	0.7	6.9	0.1												
Halosarcia	-27.4	0.4	3.4	0.5	-26.3	0.5	4.4	0.6	-28.7	0.5	4.6	0.7	-26.8	0.3	2.3	0.3	-27.2	0.6	3.7	0.3	-27.6	1.0	3.5	0.2
Heterozostera tasmanica					-7.9	0.5	2.6	0.8													-6.6	0.6	2.2	0.5
Hormosira	-5.3	0.9	4.0	0.1	-7.2	1.6	4.3	0.3	-4.9	0.3	5.2	0.3	-5.9	0.1	3.4	0.1	-7.3	0.0	3.9	0.3	-7.4	0.4	1.8	0.1
Jania																								
Junus	-24.2	0.2	3.3	0.3	-22.3	0.1	8.1	1.6	-24.3	0.5	2.8	0.5	-23.2	0.6	2.4	0.4	-22.7	0.6	3.3	1.5	-24.5	0.4	6.0	0.6
Phytoplankton	-24.8		3.3		-21.0		4.1		-22.2.		4.7													
Posidonia australis – epiphytes	-9.3		2.6										-4.9	1.2	4.7	0.3	-10.3	0.7	3.5	0.3	-8.9	0.7	3.4	0.4
Posidonia australis – leaves	-6.9	0.6	0.5	3.0	-6.2	0.4	2.2	0.5					-7.0	0.4	2.2	0.8	-7.1	0.7	4.2	0.1	-5.2	0.6	2.7	0.1
Posidonia sinuosa – epiphytes									-12.5	0.9	3.8	0.2					-7.85	0.3	2.9	0.3				
Posidonia sinuosa – leaves									-7.1	0.3	4.1	0.4					-5.8	0.4	3.4	0.3				
Ruppia megacarpa					-10.5	1.7	-0.3	0.4	-10.4	0.1	1.2	0.3									-7.3	0.2	-0.6	0.9
Saltmarsh sp a	-30.1		4.8		-31.3	0.1	4.5	0.3	-28.6	0.4	5.3	0.3	-27.6	0.2	5.6	0.5	-25.9	0.3	5.6	0.7	-27.2	0.7	4.9	0.7
Saltmarsh sp b	-26.3	1.5	2.4	1.4	-24.0	1.0	4.5	1.2	-26.7	1.3	2.2	0.2	-28.2	0.3	0.5	0.5	-28.3	0.5	1.5	0.6	-28.0	0.2	3.2	0.4
Saltmarsh sp c	-27.3	1.4	3.0	1.1	-27.4	0.8	5.6	0.5	-27.2	0.1	5.0	0.8	-26.8	1.1	5.8	0.3	-26.4	0.3	5.3	0.3	-25.3	0.5	4.8	0.5
Sargassum					-15.1	0.9	3.4	0.3					-11.0	0.5	3.8	0.1	-12.3	0.5	3.1	0.5	-12.6	1.0	3.1	0.5
Invertebrates																								
Gamarid Amphipod	-16.9		3.8						-24.2		4.42										-14.2		1.4	
Paphia crassiculca	-16.7	0.1	6.3	0.1	-17.1		5.9		-19.3	0.2	6.8	0.1	-15.1	0.1	5.7	0.1	-17.5	1.1	6.6	0.4	-14.8	0.4	4.8	0.2
Copepoda	-9.61		3.8		-20.51		3.09		-18.4		5.74		-24.4		1.4		-16.4		6.0		-12.1		2.8	
Majidae spp	-9.4	0.3	7.9	0.1	-11.72		6.6						-13.0		3.5						-8.6	0.4	6.5	0.4
Graspidae spp					-13.15	4	5.3	1.0					-14.3		3.5						-8.6		5.1	
Lepsiella vinosa																					-11.1	1.6	6.2	0.5
Nassarius albinos	-12.9	0.1	8.9	0.8									-14.4	1.9	6.6	0.8	-15.4	0.2	8.0	1.1	-15.3	0.4	6.6	0.5
Astel multigranum					-10.1		5.2		-15.0		6.7													
Gastropod sp 4	-11.4	0.7	7.2	0.7	-5.4		3.7		-16.8	0.4	4.6	0.2												
Clanculus atropurureus	-12.0		5.51		-13.6	0.1	4.4	0.2	-16.7	0.8	6.0	0.4												
Isopoda					-15.9	0.9	4.1	0.2																
Hipponix conicus					-10.3	0.3	3.6	0.1																
Palaemonetes australis	-12.2	0.3	10.3	0.2	-8.0	0.2	7.6	0.1	-14.5	1.4	9.4	0.4					-14.3	0.8	8.7	0.2	-12.6	1.1	8.1	0.3
Polychaeta – Errant	-16.3		7.2		-22.5		7.2										-11.8		7.5					
Polychaeta – Sedentary	-13.6	0.3	6.8	0.2	-19.1	0.2	7.0	0.4									-12.2	0.8	6.9	0.1	-15.6	0.2	5.0	0.0
Economic Species																								
Aldrichetta forsteri – Large																								
Aldrichetta forsteri – Small																								
Ammotretis rostratus	-15.1	0.3	8.8	0.5																				
Arripis georgiana – Large																								
Arripis georgiana – Small																								
Arripis truttaceus													-14.9		12.8									
Cnidoglanis macrocephalus – Large	-13.1		11.9		-11.7		8.5										-12.6	0.7	8.9	0.4	-13.7	0.0	9.8	0.1
Cnidoglanis macrocephalus – Small	-13.6		11.7						-14.3	0.4	10.4	0.4					-17.5		8.6		-12.9	0.7	8.8	0.4
Leviprora laevigatus													-12.4		10.1		-12.3		12.0		-11.2	0.8	8.6	0.1
Meuschenia freycineti	-14.1	0.1	10.5	0.2					-13.6	1.8	9.2	0.2	-13.5		9.5		-15.1	0.1	9.3	0.2	-14.3	0.5	8.9	0.2

Mugil cephalus																						
Pelates sexlineatus												-14.8	1.1	10.4	0.9	-18.6		8.9		-13.1	0.5	9.3	0.4
Portunus pelagicus												-12.7		7.5						-14.0	0.6	8.3	0.4
Pseudocaranx dentex												-15.3	0.4	11.1	0.1								
Psuedorhombus jenynsii																				-10.5	0.7	9.2	0.1
Sillaginodes punctata – Large																							
Sillaginodes punctata – Small																-11.9	0.5	9.3	0.2	-7.9	0.7	8.1	0.2
Non Economic Fish Species																							
Ancanthaluteres spilomelanurus	-15.4	.3	9.4	0.3	-15.6	0.3	9.3	0.1	-17.8	0.5	8.4	0.9	-16.0	0.2	8.7	0.2	-16.9	0.1	8.0	0.1	-15.9	0.2	8.1	0.1
Atherinasoma elongata	-17.5	0.9	11.4	0.2	-18.2	0.3	11.4	0.5	-16.5	0.1	11.5	0.2					-17.4	0.2	11.4	0.2	-15.6	0.4	11.4	0.2
Favonigobius lateralis	-10.3	0.1	10.0	0.2	-7.1	0.5	7.8	0.2	-13.2	0.6	9.3	0.5					-12.2	0.5	9.5	0.1	-9.1	0.7	7.9	0.2
Gymnapistes marmoratus	-12.5	0.1	9.3	0.3	-11.6	0.7	8.9	0.4	-10.7	0.5	8.2	0.2					-13.9	0.2	7.9	0.2	-13.0	0.6	8.8	0.2
Leptatherina presbyteroides	-17.8	0.7	11.1	0.2	-14.2	1.5	10.1	0.5									-18.0	0.1	11.6	0.1	-16.1	0.3	11.5	0.1
Leptatherina wallacei	-16.5	0.4	11.3	0.2	-16.5		12.4		-17.5	0.0	12.0	0.2									-16.7		11.2	
Neoodax balteatus	-14.5	0.2	10.4	0.2	-12.9	0.3	8.8	0.3	-13.4	0.5	9.5	0.2					-15.6	0.6	8.8	0.1	-14.5	0.1	9.4	0.2
Stigmatopora argus	-19.3	0.2	10.1	0.2	-16.8	2.1			-19.0	0.2	10.1	0.2					-19.4	0.1	8.8	0.1	-19.0	0.2	9.7	0.2

Table 36. Mean and standard error values of $\delta^{15}N$ and $\delta^{13}C$ of primary producers, detritus, invertebrates and fish at three sampling sites at three sampling sites in Princess Royal Harbour on the south coast of Western Australia.

Species Name	Winter												Summer											
	1				2				3				1				2				3			
	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N	δ^{13} C	SE C	δ^{15} N	SE N
Primary Sources																								
Amphibolis antartica – epiphytes	-10.4	0.9	6.5	0.5	-12.4	0.6	2.2	0.3	-7.6	0.9	0.5	0.5	-6.7	0.8	4.4	0.2					-8.5	1.2	2.6	0.1
Amphibolis antartica – leaves	-8.1	0.5	2.7	0.4	-10.1	1.1	-0.9	0.9	-8.8	0.8	0.6	0.3	-6.4	0.8	1.5	0.4					-6.5	1.2	0.9	1.2
Benthic Micro Algae	-10.1	0.4	3.2	0.3	-12.9	1.0	1.2	0.2	-15.8	2.5	0.9	0.2	-12.3	0.3	1.2	0.2	-16.7	2.1	-0.9	0.9	-18.1	1.7	1.0	0.2
Detritus	-10.0	0.4	3.6	0.4	-10.3	1.8	1.7	0.0	-6.5	0.5	1.6	0.1	-11.5	0.5	2.2	0.1	-16.3	1.6	1.4	0.4	-14.2	0.8	1.3	0.3
Cladophora	-12.6	0.4	3.9	0.3	-16.1	0.5	2.1	0.2	-13.6	0.2	2.0	0.4	-11.0	0.6	2.8	0.5	-11.8	1.0	2.0	0.4				
Enteromorpha	-20.1	0.1	10.4	0.8																				
Halosarcia	-27.7	0.6	6.2	1.0									-26.8	0.9	5.4	0.3								
Heterozostera tasmanica																								
Hormosira	-4.7	1.0	6.8	0.9	-7.4	0.9	4.3	0.1					-4.3	0.8	3.3	0.2	-4.6	0.9	3.8	0.6	-5.8	0.3	3.4	0.2
Jania					-13.6	0.3	3.0	0.5	-9.2	0.1	2.1	0.4												
Junus	-23.9	0.9	7.1	1.4	-25.2	0.7	2.6	1.0					-25.7	0.4	6.8	0.7	-25.7	0.9	4.1	0.4				
Phytoplankton	-18.6		2.9		-21.7		3.4		-21.2		4.0													
Posidonia austalis – epiphytes	-8.5	0.6	4.3	0.4	-10.2	1.4	-0.4	1.1	-8.9	0.7	1.4	0.8	-5.1	0.9	2.1	0.6	-5.8	0.8	1.5	0.4	-6.7	0.7	2.4	0.3
Posidonia australis – leaves	-4.8	0.1	0.6	0.5	-3.4	0.9	-4.8	0.8	-4.7	0.4	0.6	1.0	-2.7	1.2	-2.7	1.0	-0.9	0.4	-3.9	0.9	-4.5	0.9	2.1	0.3
Posidonia sinuosa – epiphytes					-9.0	0.2	0.1	0.7					-5.7	0.4	3.5	0.3					-6.4	0.7	5.6	0.1
Posidonia sinuosa – leaves					-6.5	0.6	0.6	0.3					-5.0	0.8	1.0	0.5					-5.3	0.5	1.8	0.2
Ruppia megacarpa																								
Saltmarsh sp a	-29.6	0.5	5.0	0.5									-27.7	0.6	5.9	0.5								
Saltmarsh sp b																								
Saltmarsh sp c																								
Sargassum	-14.6	0.2	7.4	0.0	-13.5	1.1	3.7	0.2					-8.1	0.5	4.8	0.4	-10.8	0.8	3.0	0.2				
Invertebrates																								
Gamarid Amphipod									-13.6		6.0		-15.1		2.4						-19.6		5.1	
Paphia crassiculca	-13.7	0.2	5.7	0.2	-12.7	0.2	4.3	0.1	-13.9	0.7	5.0	0.1	-14.2	0.1	6.8	0.1	-12.4	0.2	4.8	0.1	-18.5	0.2	4.9	0.1
Copepoda	-17.4		6.6		-17.6		3.4		-22.0		3.9		-14.5		4.8		-12.6		4.1		-16.6		4.3	
Majidae spp													-10.0		4.5						-8.4	0.2	5.0	0.4
Graspidae spp																	-11.2	0.6	5.2	0.2	-16.4	1.7	4.1	0.1
Lepsiella vinosa	-10.7	0.2	10.1	0.2	-8.4	0.1	7.0	0.1					-11.0	0.2	9.3	0.4	-10.6	0.5	7.3	0.1	-13.5	0.2	8.1	0.1
Nassarius albinos																	-12.6	0.7	6.9	0.2				
Astel multigranum					-17.6	0.4	4.1	0.2	-14.0	0.8	4.0	0.2												
Gastropod sp 4	-5.06		5.73																					
Clanculus atropurureus					-17.6	1.2	5.2	0.3																
Isopoda					-15.3	0.6	3.4	0.3																
Hipponix conicus	-11.9	0.4	7.9	0.2					-12.8	1.2	4.9	0.3												
Palaemonetes australis	-10.4	0.3	10.7	0.3	-11.1	0.4	7.4	0.1	-14.1		8.6		-11.4	0.5	9.2	0.3	-11.6	0.5	7.9	0.3	-14.0	0.2	8.5	0.3
Polychaeta – Errant													-20.1		4.9		-9.5		5.7		-15.5	0.8	6.8	0.7
Polychaeta – Sedentary	-13.7	0.6	7.9	0.8					-11.3	0.2	5.4	0.4	-14.4	0.3	2.6	1.3	-14.9	0.5	2.0	0.5	-15.6	0.4	5.6	0.2
Economic Species																								
Aldrichetta forsteri – Large													-11.0	0.2	11.2	0.7	-15.1	3.5	11.4	1.0				
Aldrichetta forsteri – Small													-10.6	0.2	9.0	0.1					-10.3	0.2	8.8	0.1
Ammotretis rostratus	-10.7		10.1		-11.3	0.6	8.3	0.0									-11.5		7.2		-8.8	0.3	7.3	0.1
Arripis georgiana – Large													-15.7	0.3	12.9	1.3					-15.8		11.9	
Arripis georgiana – Small	-20.4		11.7		-16.6		12.0		-11.8		10.5										-17.0	0.4	11.4	0.2
Arripis truttaceus																								
Cnidoglanis macrocephalus – Large									-13.8		8.4		-14.9	0.2	8.6	0.1	-14.7		8.6		-14.7	0.7	8.7	0.1
Cnidoglanis macrocephalus – Small													-13.5	1.0	8.1	0.6					-15.4	1.4	8.7	0.6
Leviprora laevigatus																					-13.6		8.4	
Meuschenia freycineti									-14.4		7.1										-13.2	0.4	8.0	0.4
Mugil cephalus	-22.2	0.1	9.3	0.1																				
Pelates sexlineatus													-12.5		9.5						-15.0	0.1	8.9	0.3
Portunus pelagicus													-11.5	0.3	8.7	0.6								

Pseudocaranx dentex													-15.3	1.2	10.9	0.2							
Psuedorhombus jenynsii													-9.4	0.5	9.5	0.9	-9.5	0.2	7.7	0.1			
Sillaginodes punctata – Large													-11.6	0.6	8.4	0.6	-13.2	0.6	9.7	0.4	-10.2		8.1	
Sillaginodes punctata – Small													-8.3	0.3	8.6	0.2	-9.7	2.2	7.4	0.3				
Non Economic Fish																								
Ancanthaluteres spilomelanurus					-13.9	1.7	7.6	0.2	-14.4	0.6	7.4	0.3									-14.5	0.5	8.0	0.1
Atherinasoma elongata	-11.4	0.7	11.0	0.6	-11.3	2.5	9.4	0.1	-14.1	1.6	10.0	0.2	-11.1	0.3	10.9	0.2	-10.1	0.7	9.3	0.3	-10.9	0.8	10.0	0.2
Favonigobius lateralis	-9.4	0.4	8.5	0.3	-9.8	0.8	7.3	0.1	-9.5	0.9	7.4	0.2	-10.3	0.2	8.2	0.5	-10.0	0.3	7.6	0.1	-8.6	0.5	7.4	0.1
Gymnapistes marmoratus	-12.2	0.3	10.3	0.4	-13.0	1.0	8.5	0.3	-13.6	0.2	8.8	0.1	-13.8	0.1	9.0	0.3	-12.5	0.2	7.9	0.1	-14.2	0.2	8.4	0.1
Leptatherina presbyteroides	-13.2	2.0	10.7	0.5	-17.3	1.8	9.6	0.1	-17.5	0.1	10.5	0.2	-11.7	0.2	11.1	0.2	-10.3	0.6	9.2	0.2	-10.9	0.3	9.7	0.2
Leptatherina wallacei	-14.6	0.4	11.3	0.1	-12.9		10.5						-12.3	0.3	11.1	0.1	-13.7		10.1					
Neoodax balteatus	-13.9	0.1	9.7	0.1	-13.7	0.8	8.4	0.1	-15.1	0.9	8.9	0.3	-14.1	0.7	8.9	0.6	-12.4	0.4	8.2	0.1	-14.8	0.2	9.1	0.1
Stigmatopora argus					-15.8	3.1	9.4	0.1	-18.5	0.4	9.3	0.5					-11.6	1.0	6.8	0.2	-18.5	0.1	8.6	0.1

Chapter 11. Stable isotope studies in Queensland

INTRODUCTION

The role of autotrophs from inshore habitats in fisheries food webs in Moreton Bay, Queensland, has previously been the subject of another FRDC study (Connolly et al. 2003). That study analysed the nutrition of a suite of 22 species of finfish collected over unvegetated mudflats, showing that organic material from seagrass meadows and possibly saltmarsh was at the base of food webs that ultimately supported fisheries production in the bay (Connolly et al. 2003, Melville & Connolly 2003).

The present study afforded an opportunity to further the work in Moreton Bay by expanding the knowledge of food webs to the two economically important inshore crab species in southeast Queensland, blue swimmer crabs (known as sand crabs in Queensland), *Portunus pelagicus*, and mud crabs, *Scylla serrata*. This was achieved with minimal additional resources from the current project because of synergies with the large number of isotope analyses being done in southern states. Both crab species are omnivorous scavengers, but the intention here is not to examine diet *per se*, but the ultimate autotrophic source(s) at the base of the food web.

Theories of animal nutrition in estuaries and marine embayments are typically derived from the northern hemisphere, where the model of outwelling of organic material dominates. The outwelling model was developed to explain high secondary productivity near the extensive areas of the saltmarsh plant *Spartina alterniflora* on the east coast of the USA (Odum, 2000). While there are substantial saltmarshes on the subtropical east coast of Australia, mangroves dominate the mid-intertidal fringes of estuaries here. Forests of mangroves fix approximately 600 g carbon m^{-2} y^{-1} in Moreton Bay (Dennison & Abal, 1999). As yet, however, there is little evidence that carbon fixed by mangroves moves far out of these forests (Lee, 1995). Seagrasses represent another potential source of carbon in subtropical estuarine systems. Seagrasses form large beds in the estuaries of subtropical Australia and fix approximately 200 g carbon m^{-2} y^{-1} in Moreton Bay (Dennison & Abal, 1999). Seagrass epiphytes, a mixture of diatoms and fine filamentous algae, may fix as much carbon as the seagrass they grow on (Keough & Jenkins, 1995). Seagrass epiphytes have been shown to contribute carbon to many invertebrates that feed in seagrass beds (Moncrieff & Sullivan, 2001) and represent a potential source of carbon for crabs that occur in other habitats in Moreton Bay. Production by microphytobenthos (MPB) and phytoplankton may also be an important source of carbon for crabs in Moreton Bay. Microphytobenthos, the most productive autotroph in Moreton Bay, fixes approximately 1700 g carbon m^{-2} y^{-1} (Dennison & Abal, 1999). Phytoplankton, which is ubiquitous in estuarine systems, fixes approximately 175 g carbon m^{-2} y^{-1} in Moreton Bay (Dennison & Abal, 1999).

In addition to the survey of crab nutrition, a methodological component to the Queensland work matched an objective of the overall study to further isotope methodology for inshore food web studies. Carbon and nitrogen isotopes are analysed routinely in marine food web studies. Where these elements are unable to separate the contributions of different sources to the nutrition of animals, sulfur isotopes are considered likely to be useful. Sulfur isotopes, however, are expensive and more difficult to analyse. It was considered valuable, therefore, to test the usefulness of sulfur isotopes in separating potential sources.

The aims of the work in Queensland were to:

1. demonstrate the usefulness of sulfur isotopes in separating autotrophic sources, and
2. determine the autotrophic source(s) contributing to the base of food webs providing nutritional support for blue swimmer crabs and mud crabs.

METHODS

Separation of sources using sulfur isotopes

To determine the likely usefulness of sulfur isotopes in separating contributions to food webs of microalgae and macrophytes (e.g. seagrass), we isolated microscopic and fine filamentous algae from the leaves of seagrass and processed them ready for isotope analysis as described in previous chapters. Sulfur stable isotope analysis was done by Iso-Analytical in the United Kingdom. Stable isotope signatures were reported in standard delta notation (units per mil, ‰), calculated as follows:

$$\delta^{34}S = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is $^{34}S/^{32}S$.

Sample collection and processing for crab study

Moreton Bay, southeast Queensland, is characterised by intertidal and shallow subtidal seagrass beds interspersed with extensive mudflats. The coastline comprises islands and the mainland, both fringed with mangroves, which are often backed by saltmarsh. Autotrophs and crabs were collected twice, once in summer (March 2003) and once in winter (August 2003), at six locations spread throughout the bay (Fig. 60). All samples were frozen immediately upon collection.

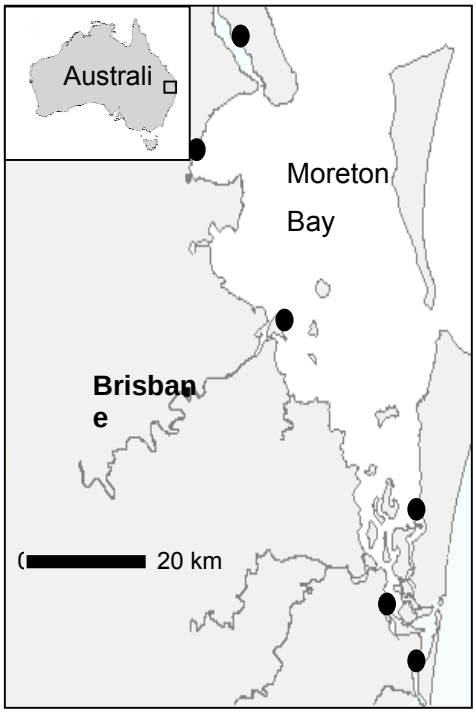

Figure 60. Map of Moreton Bay, indicating the six sampling locations. Inset: Location of study region in Australia.

Three individuals of both crab species were collected from every location using baited traps and nets. Consumption of bait immediately prior to collection does not measurably affect the isotope values of crabs, since the isotope values of tissue reflect a longer term diet of up to several weeks. Samples of muscle were taken from claws for processing, after demonstrating that muscle tissue from legs and claws had similar isotope values. All crabs were male. Carapace widths of *Portunus* ranged between 106 and 175 mm in summer and 69 and 1725 in winter. Carapace widths of *Scylla* ranged between 134 and 185 mm in summer and 56 and 160 in winter.

At each location, autotroph material was collected from the following six taxa:

1. Mangroves, the dominant species in the bay (*Avicennia marina*).
2. Seagrass (combined values for the two most common species, *Zostera capricorni* and *Halophila ovalis*), which had very similar values at all sites and were therefore pooled.
3. Seagrass epiphytes, separated from seagrass as described in previous chapters.
4. Saltmarsh succulents, comprising a pooled value for the two common species having a C_3 photosynthetic pathway (*Sarcocornia quinqueflora* and *Suaeda australis*, which had similar values).
5. Saltmarsh grass (*Sporobolus virginicus*), a C_4 plant that therefore has a different carbon isotope signature to the other saltmarsh plants.
6. Microphytobenthos (MPB), collected using the scrape of superficial sediment and processing described in previous chapters.

Macroalgae is not a major component of the flora of Moreton Bay and was excluded from this study. Phytoplankton is present in the water column in Moreton Bay, but we found that it was at low densities relative to sediment and detrital particulate matter and we could not isolate enough material to obtain an isotope value.

All samples were processed using procedures described in previous chapters.

Modelling feasible source mixtures to explain crab nutrition

Modelling procedures were identical to those described in for South Australian work (Chapter 9). Since only two species were analysed, distributions of feasible contributions are able to be reported in full for both sampling periods for both species.

Separating the contribution of seagrass and saltmarsh grass to mud crabs

As in a previous study of food webs supporting fish in Moreton Bay (Connolly et al. 2003), the present study found that for crabs, both seagrass and saltmarsh grass were likely to be major contributors. Connolly et al. (2003) have previously argued that the contribution of saltmarsh grass might be erroneously overestimated because of the similarity in carbon isotope values of seagrass and saltmarsh grass. We attempted to separate the contributions of the two sources in a survey of mud crabs in a third sampling period (November 2004). During the initial surveys, it was noted that variation in mud crab isotope values could be explained by the distance crabs were from the nearest seagrass meadow. Crabs collected from very close to seagrass (within a kilometre or so) had more enriched values than those further away. However, further examination of the habitat at each location showed that where locations were close to seagrass, they were also close to saltmarsh grass. Existing data could not, therefore, be used to separate the importance of the two sources. However, in this additional survey we were able to deliberately select 12 locations so that some were close to seagrass but far from saltmarsh grass, and vice

versa. All collections and processing of autotrophs and crabs were in other ways identical to the initial surveys described above. Carbon isotope data were analysed by examining whether curved lines describing depletion in isotope values of crabs at increasing distance from the habitat were best fitted to seagrass or saltmarsh grass distances, using a comparison of R^2 values.

RESULTS

Separation of sources using sulfur isotopes

We predicted that the sulfur isotope ratio of seagrass (which uptakes sulfur largely as depleted sulfides in sediments) would be depleted relative to that of the attached microalgae (which are thought to use more enriched sulfates from the water column). The mean sulfur isotope ratio of seagrass was in fact more *enriched* than that of epiphytic algae (Fig. 61). We suspected that the microalgae value resulted from contamination by small amounts of calcareous encrusting red algae, so we submitted further samples for analysis after removing potential contaminants using acid digestion. Acid-digested samples had even more depleted signatures (i.e. were even more different to predicted values). Macroalgae was shown to have enriched values (as predicted) with relatively little variability. Taken overall, sulfur isotopes show potential for separating certain groups of producers. Sulfur analysis is expensive and far from routine, and should be used in selected situations where carbon and nitrogen fail to determine the importance of particular sources. A full review of the use of sulfur isotopes in marine and estuarine food web studies has been published separately as part of this study (see Connolly et al. 2004, Appendix 3). A detailed examination of the causes behind variability in sulfur isotope values of seagrass in Moreton Bay was also undertaken, and has also been published separately (see Oakes & Connolly 2004, Appendix 3). The analysis of isotopes of epiphytic algae remains problematic, and is dealt with further in the later chapter on examining the nutrition of *Sillaginodes punctata* across the three southern Australian states.

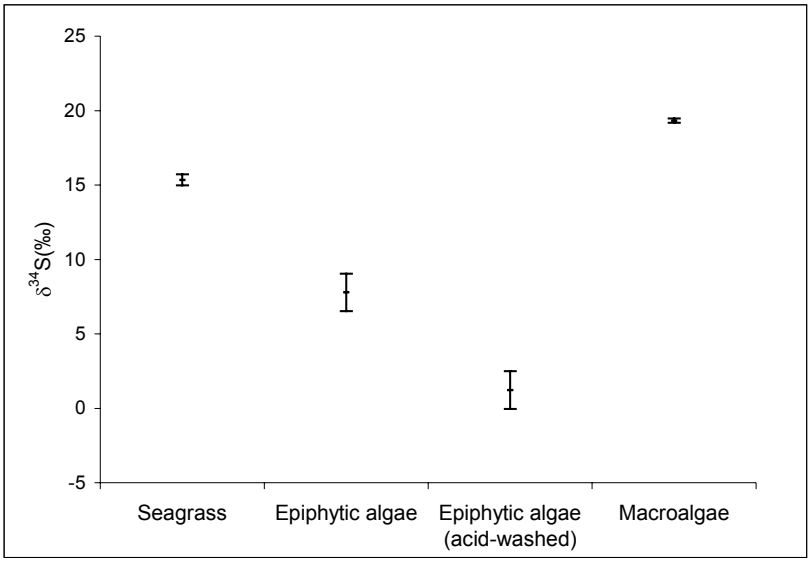

Figure 61. Mean (+/- SE) $\delta^{34}S$ values for seagrass, epiphytic algae (both acid-washed and non-acid washed) and macroalgae from Moreton Bay, Queensland (n = 5 for each species).

Contribution of different autotrophs to crab nutrition

Carbon isotope values of most autotrophs fell into two predictable groups in both winter and summer (Fig. 62): mangroves and saltmarsh succulents with depleted values (-27 to -28‰), and seagrass, epiphytes and saltmarsh grass with enriched values (-10 to -18‰). The values for MPB varied substantially between sampling periods (-20 in winter, -25‰ in summer), but at both periods remained intermediate between the other two groups. Mean nitrogen isotope values were typical for marine/estuarine autotrophs, ranging between 3 and 6‰ for all taxa except saltmarsh grass, which was below 2‰ at both periods.

The mean carbon isotope value of *Portunus* was -16‰ in both summer and winter, and for *Scylla* was -18‰ in both summer and winter (Fig. 62). The mean nitrogen isotope values of *Portunus* were 9‰ in summer and 11‰ in winter, and those for *Scylla* were 9 and 10‰, respectively (Fig. 62).

Isosource modelling of feasible contributions highlighted certain autotrophs as most likely to be contributing to food webs supporting crabs. However, modelling did not quantify those contributions particularly well because the ranges of feasible contributions for each autotroph were wide. We can therefore distinguish important autotrophs but cannot be so confident about their percentage contribution. At both periods, the top contributor to *Portunus* (Fig. 63) was seagrass, followed by saltmarsh grass and then epiphytic algae. *Scylla* had the same rank order of important contributors, although in winter MPB also apparently made a substantial contribution (Fig. 64).

Separating the contribution of seagrass and saltmarsh grass to mud crabs

The apparent role of saltmarsh grass in crab nutrition described above is intriguing. Isosource modelling cannot distinguish whether this: 1) represents a real contribution of saltmarsh grass, or 2) merely reflects an artefact of the situation of saltmarsh grass having a similar carbon isotope value to seagrass (and its epiphytes). Results from the additional survey of mud crabs point strongly to the latter. A plot of carbon isotope values of mud crabs against the distance mud crabs were from seagrass meadows when caught shows clear enrichment within about a kilometre of seagrass, declining at greater distances (Fig. 65, excellent fit of decay line, $R^2 = 0.88$). The pattern is less clear when crab isotope values are plotted against distance from saltmarsh grass (no clear fit to decay line, $R^2 = 0.08$).

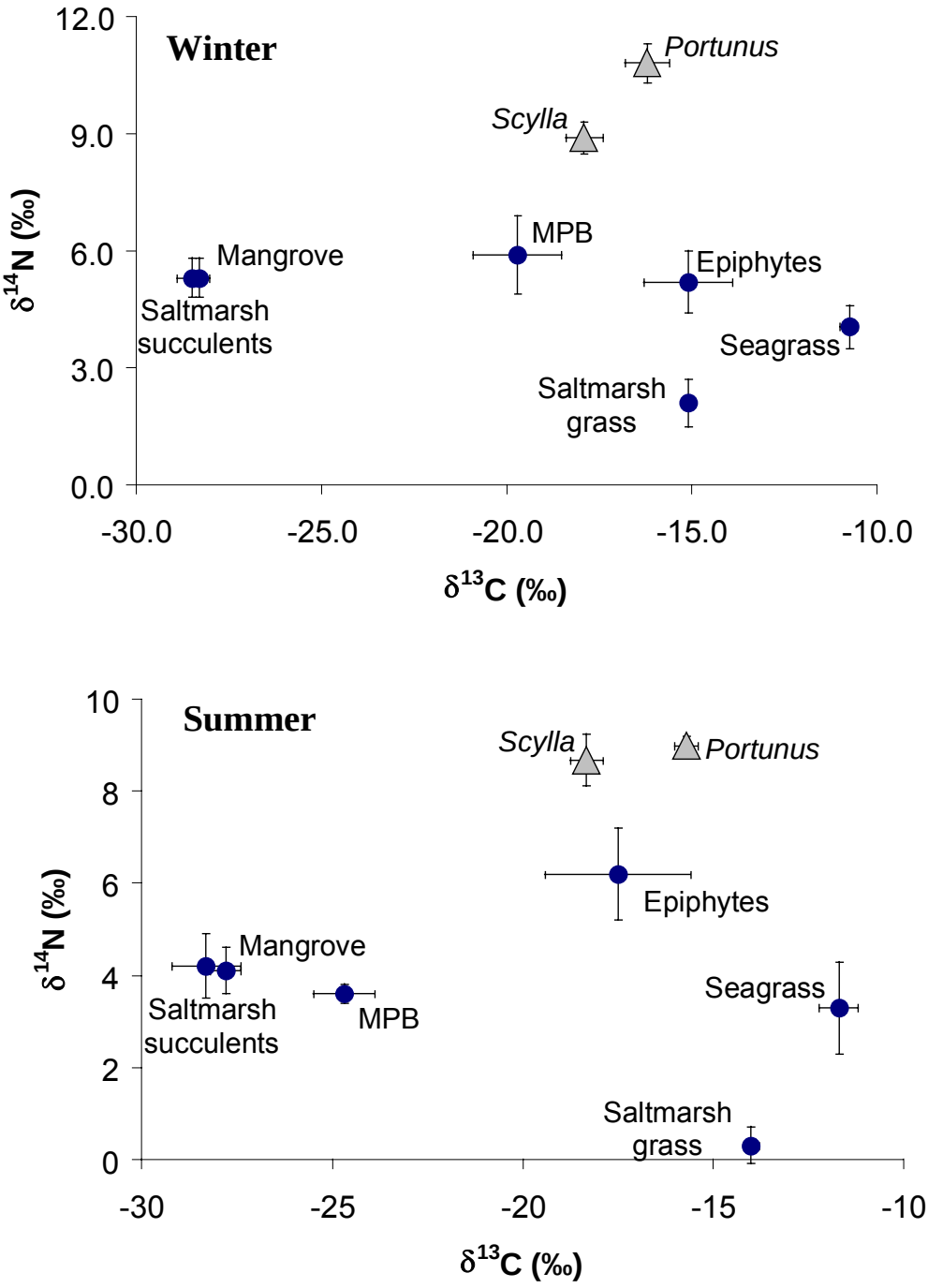

Figure 62. Plots of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) for the two crab species (triangle) and the six autotroph (circles) sources in winter and summer. MPB = microphytobenthos.

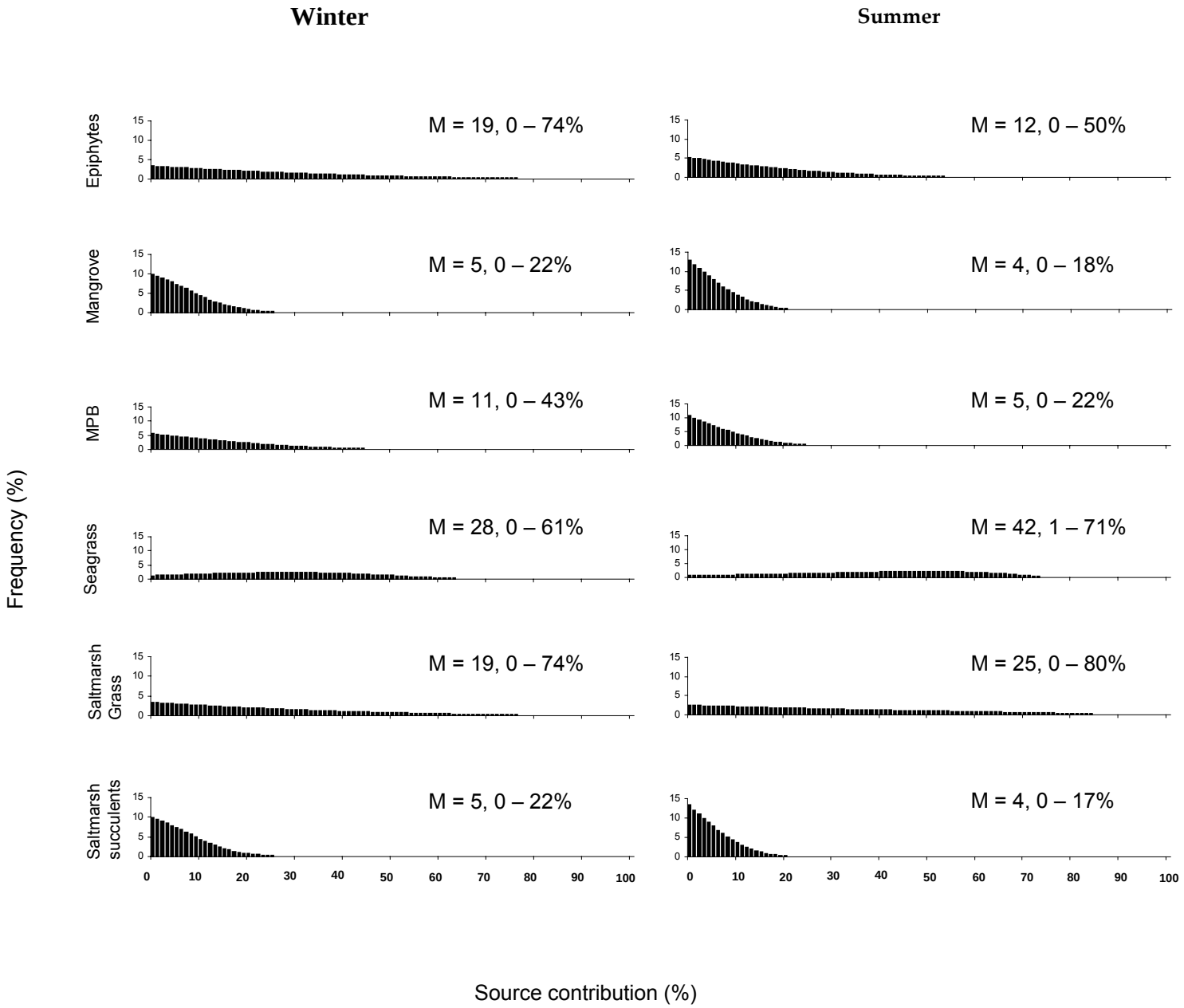

Figure 63.. Distributions of feasible contributions of the 6 autotrophs to *Portunus pelagicus* based on $\delta^{13}C$ values only. M = median, the ranges are 1%ile and 99%ile values

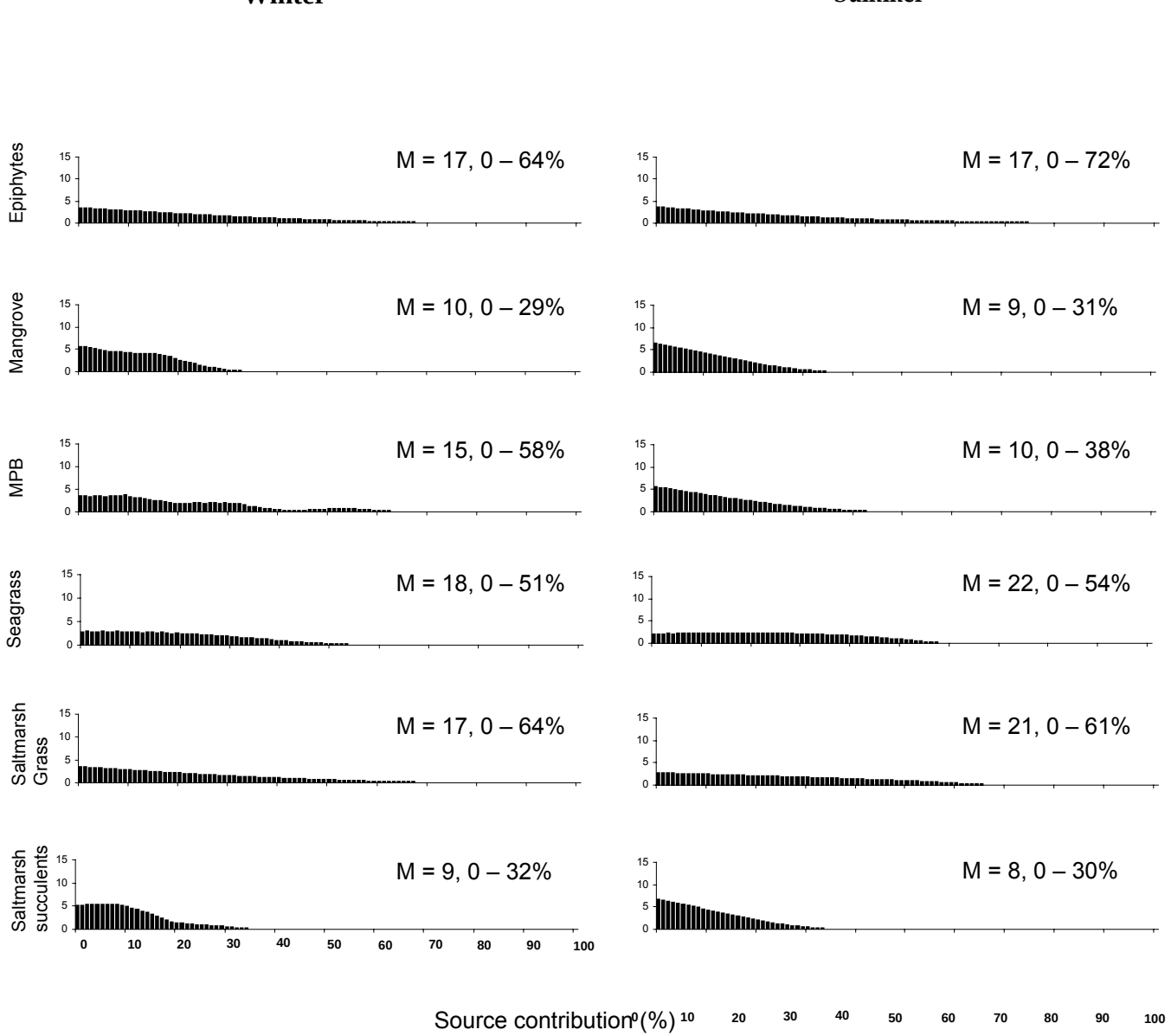

Figure 64. Distributions of feasible contributions of the 6 autotrophs to *Scylla serrata* based on $\delta^{13}C$ values only. M = median, the ranges are 1%ile and 99%ile values.

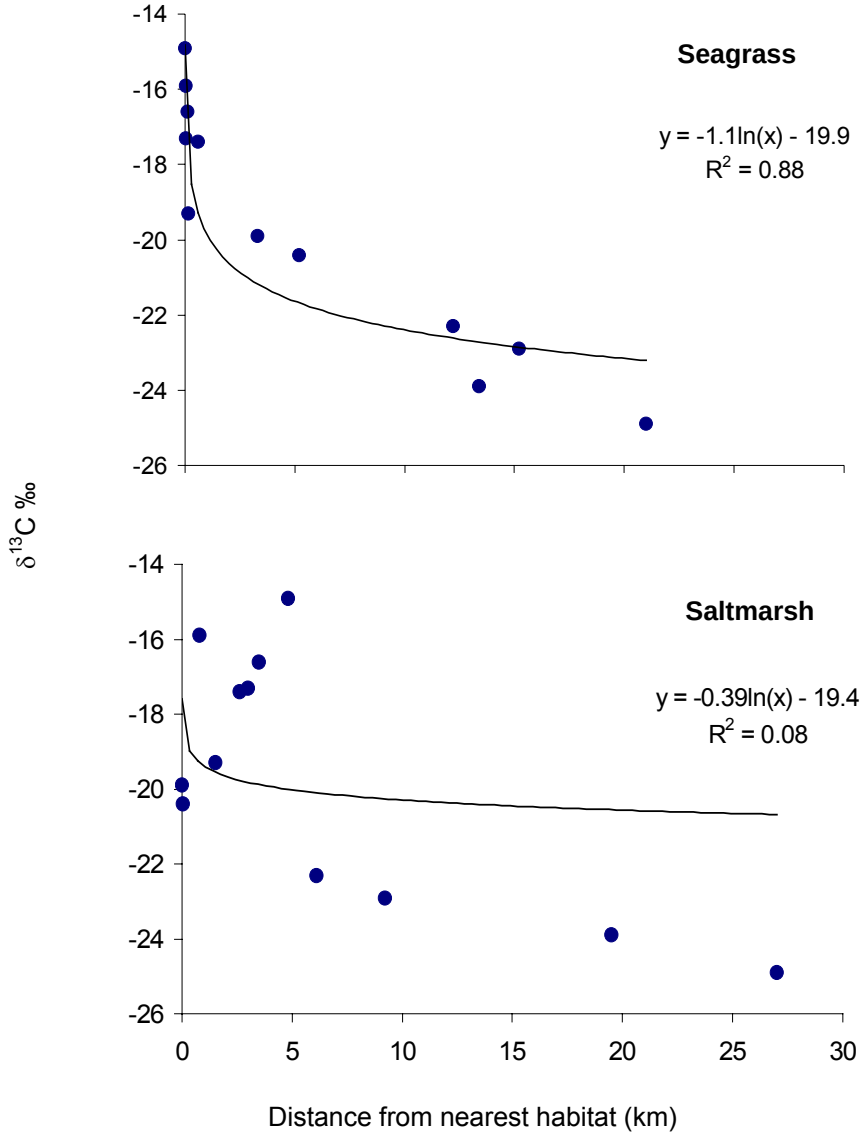

Figure 65. Relationships between carbon isotope values of *Scylla serrata* and the distance crabs were caught from the nearest patch of two habitats, seagrass and saltmarsh. Curved decay lines of best fit are shown, along with their equation and R^2 value.

DISCUSSION

Contribution of different autotrophs to crab nutrition

The main sources of organic material supporting food webs leading to crab production in Moreton Bay come from seagrass meadows. Modelling also pointed to a substantial contribution from saltmarsh grass, but this appears to be merely an artefact of the similarity in isotope values of saltmarsh grass and seagrass (see below). The predominance of seagrass and its epiphytic algae as ultimate sources of support for crab food webs is almost identical with the results for 22 species of finfish from Moreton Bay analysed in a previous FRDC project (Connolly et al. 2003). Together, the work on finfish and crabs demonstrates that material from seagrass meadows plays a major role in food webs for animals with a range of life-history characteristics and habitat preferences. Among the two crab species, for example, *Scylla* typically has a closer association with mangroves than *Portunus*, inhabiting more truly estuarine reaches of the bay

(Tibbetts & Connolly 1998). Despite this, and the broad diets of these omnivorous crabs, ultimately they are both reliant to a large extent on organic matter from seagrass meadows. This important role of seagrass is also similar to that described for *Portunus* and several finfish species in South Australian waters (see chapter 9).

The difficulty in distinguishing the relative contributions of seagrass and their epiphytic algae has been described previously (see Chapter 9). One avenue for separating the contribution of macrophyte and algal contributions in future studies would be experimental isotope enrichment methods, pioneered in marine waters in Moreton Bay by Winning et al. (1999). Natural abundance sulfur isotope analysis is also likely to be useful. Our results demonstrated that epiphytes can be separated from seagrass based on their sulfur isotope ratio. We follow this further in a subsequent chapter (Chapter 12) for King George whiting in South Australia, but sulfur work would also prove useful in the future in Queensland waters.

The issue of whether saltmarsh grass truly makes a major contribution to fishery food webs in Moreton Bay has been difficult to resolve because of the similarity in isotope values between saltmarsh grass and seagrass. The very strong patterns in mud crab isotope values with distance from seagrass but not with distance from saltmarsh grass points to saltmarsh having only a minor role. Its apparent importance in Isosource modelling results, for crabs in the present study and for fish in previous a previous study (Connolly et al. 2003), is merely an artefact of it having a similar carbon isotope value to seagrass. This leaves material derived from seagrass meadows as easily the single most important source of organic matter at the base of food webs supporting production of *Portunus* and *Scylla*.

Our work demonstrates that for food webs sustaining fisheries production in Moreton Bay, seagrass meadows are critical. The importance of seagrass and its epiphytic algae to production of fisheries species in Moreton Bay reinforces the need to conserve and protect seagrass meadows from adverse anthropogenic influences.

Chapter 12. Continental-scale assessment of the base for nutritional support of a fisheries species using stable isotopes

INTRODUCTION

King George whiting (*Sillaginodes punctata*) is a valuable recreational and commercial species along the southern Australian Coastline. In Victoria, the commercial catch for King George whiting was around 111 tonnes in 2002/03, with a market value of approximately $1,289,000 (Fisheries Victoria 2003). The recreational catch in Victoria's bays and inlets is thought to be more valuable, and is certainly greater in weight, which is estimated at around 214 tonnes/annum (Henry and Lyle FRDC 99/158).

In South Australia, *S. punctata* is the most valuable finfish species commercially, and the most sought after recreationally. It is taken commercially by gill nets, seine nets and line, and recreationally mainly by line. Catches are made in shallow waters across three regions, Gulf St Vincent, Spencer Gulf and the west coast, with small numbers also taken in deeper, offshore waters. Commercial landings are currently about 400 t p/a (Knight et al. 2003). The recreational catch is very high near human population centres, where it is equal to or possibly greater than the commercial catch (McGlennon & Branden 1994).

In Western Australia, *S. punctata* is caught predominantly in estuaries and marine embayments by both commercial and recreational fishers. The fishery is based mainly in the Blackwood River estuary, Leschenault Estuary, Oyster Harbour, Wilson Inlet, Irwin Inlet, Broke Inlet, and Cockburn Sound, in the south-western region of the State, but the recreational fishery also extends into more offshore areas particularly in the Perth metropolitan region. The commercial fishery uses mainly beach seine nets along the south coast, compared to set and haul nets along the lower west coast (Lenanton 1984). The recreational fishery is based mainly on hand-line catches.

Work on the early juvenile stages suggests that seagrass is critical habitat. In Victoria, larval whiting, which are thought to be spawned in SA, settle into seagrass after between 80-150 days in the plankton (Jenkins et al. 1997ab, 1998). A few months after settlement, however, juvenile fish move out of seagrass and begin to school and forage over unvegetated (or sparsely vegetated) sand and mud. Less is known of the habitat preferences of these older individuals, although dietary studies suggest that animals living within seagrasses are likely to be important.

In south-western Australia *Sillaginodes punctata* settle into a benthic habit in the shallow, nearshore waters in sheltered regions of the coastline (Hyndes et al. 1996a 1998). In contrast to south-eastern Australia, *S. punctata* in south-western Australia recruit into shallow, unvegetated areas, and with increasing length, move into deeper areas where they can occupy seagrass meadows as well as unvegetated areas (Hyndes et al. 1996). Settlement occurs at 14-24 mm SL between September and November (Hyndes et al. 1998), which is similar to the settlement period of this species in Victoria (Jenkins and Black 1994, Jenkins and May 1994), but three months later than that in South Australia (Fowler and Short 1996). Spawning also begins three months later in south-western Australia compared to South Australian waters, *i.e.* June *vs* March (Hyndes et al. 1998). Fish migrate from shallow, nearshore waters (<1.5 m) to deeper and more offshore waters of marine embayments and estuaries (2-6 m) before migrating to depths of six to at least 50 m in marine waters near or around reefs after they attain maturity at approximately 4 years of age and 370 mm in length (Hyndes et al. 1998).

The life history of *S. punctata* in South Australia begins with mid-winter recruitment of post-larvae into shallow embayments and the limited estuaries available in South Australian waters. During the first two years *S. punctata* has a close association with seagrass habitats (Connolly 1994). This is the life-history period on which the current work focuses in South Australia. Towards maturity (2-3 yr old), whiting migrate to deeper waters, making periodic movements offshore to spawn (Fowler et al. 2000).

The base for nutritional support of King George whiting has previously been assessed using stable isotopes in Port Phillip Bay, Western Port and the Gippsland lakes. Hindell et al. (2001) found that whiting juveniles assumed a seagrass-related isotope signal (mean $\delta^{13}C \approx -12$) within a few months of settlement, and this signature remained as fish grew. Longmore et al. (2002) assessed the contribution of alternative sources to the nutrition of King George whiting in Western Port with stable isotopes modelled with Isosource. They showed that seagrass (range 21 – 66%, median 42%) was the dominant contributor to the nutrition of larger (> 12 cm) whiting. The present study is the first to take a more holistic approach to fisheries nutrition by assessing the nutritional base of whiting across their whole range, from southeastern Victoria, through South Australia to the southwest coast of Western Australia.

Earlier chapters suggest that the nutrition of King George whiting is based on a mixture of green and brown alga, seagrass and seagrass epiphytes, and benthic microalgae. The stable isotopic signatures of whiting generally fell directly in the middles of the these sources, and their possible contributions to the diets of whiting could not be differentiated with any confidence. For this reason, we took a more focussed approach to teasing apart the relative contributions of sources with similar carbon stable isotope signatures in several ways. First we restricted our collection of sources to only those that were likely to contribute (based on previous chapters). Second, we made a greater effort to separate the epiphytes from the seagrass, and for some States, to separate the various components of epiphytes (e.g. diatoms, green and red microalga). Third, we also analysed some samples for sulphur stable isotopes, the merit of which has been explained in a previous chapter.

This study had several objectives: 1) Identify which sources were the base for nutritional support of King George whiting; 2) Assess whether the base for nutritional support varied among States; and, 3) Determine the utility of sulphur and carbon stable isotopes in assessing the trophic structure of fisheries species.

MATERIALS AND METHODS

Study Regions

Samples for our study were collected from 2 randomly chosen locations in each of 2 different embayments in Western Australia, South Australia and Victoria. In WA there are no site names but samples were collected from 2 locations in each of Princess Royal Harbour and Oyster Harbour. In South Australia, samples were collected from 2 locations in Gulf St Vincent (Middle Beach, Port Arthur) and Spencer Gulf (Fishermans Bay, Weroona Island). In Victoria, samples were collected from 2 locations in Corner Inlet (Yanakie and Port Welshpool) and Western Port (Hastings and Rhyll). These sites are described in the earlier chapters for each State.

Collection of samples

Based on studies in Victoria, King George whiting appear to reach a 'stable' base for nutritional support at a length of approximately 80 mm (Hindell et al. 2000c). We therefore focussed on fish ranging in length between 100 and 200 mm. This size range is common in each of the 3 states.

Dietary studies by Jenkins (unpublished data), Connolly (unpublished data) and Edgar and Shaw (1995b) suggest that benthic invertebrates such as polychaetes and amphipods are the primary prey for King George whiting greater than 80 mm, although other decapod crustaceans and molluscs are also be eaten. We therefore sampled polychaetes, amphipods, copepods, some molluscs, and various decapod crustacea from each site.

Seagrass is thought to be one of the most important sources of nutrition in shallow coastal waters, but earlier chapters (Stable isotope studies in SA, Victoria and WA) suggest that red, brown and green alga, as well as seagrass epiphytes can be (more) important. We therefore sampled red, brown and green alga, benthic microalgae, seston, and all species of seagrass within each site. The epiphytes on the seagrass leaves were removed to provide better resolution of the relative importance of seagrass leaves versus epiphytes.

All samples were collected and processed following the methods outlined in previous chapters. Table 37 provides a summary of the samples collected from each state.

Isotope analyses

Carbon and nitrogen stable isotope analyses were run on each of the samples. We do not present the results from N isotope analyses here because they are not considered to be a strong method of assessing base for nutritional support due to the difficulty in determining trophic fractionation (see General Methods). Because carbon isotopes are not always successful in separating some sources, we also analysed some of the samples for sulphur isotopes (see Stable isotope studies in Queensland). The potential value of sulphur isotopes in helping to tease apart sources not 'split' by carbon isotopes is well described by Connolly et al. (2004) and in the Stable isotope studies in chapter 11. All Sulphur stable isotope analyses were done by IsoAnalytical, United Kingdom.

Modelling

IsoSource was used to model the relative contributions of sources to the nutrition of fish. The lack of consistency in the availability of particular species of sources and potential prey among sites precluded a comparison across southern Australia on a site by site basis. Instead, we averaged sources, prey and whiting values within a State and modelled results for each State separately. In addition to modelling the contribution of different sources to whiting nutrition, we also modelled the possible contributions of different prey to the diets of whiting to better understand the pathways through which the sources are incorporated.

We did the modelling of sources for whiting in 2 stages. We first ran the model using only data for carbon stable isotopes. We then re-ran the modelling with carbon and sulphur to assess whether incorporating this element changed our results. In some cases we had to reduce the overall number of sources in the combined element run because there was not enough sample to run both analyses for some sources.

RESULTS

Western Australia

The King George whiting sampled from WA ranged average size between 72 and 296 mm. Seven potential prey and 7 sources were collected and processed (Table 38).

IsoSource modelling showed that the nutrition of whiting in Western Australia was supported most by benthic microalgae (mean % of 24 ± standard deviation of 16) and green algae (24 ± 16) (Fig. 66). Brown

algae (19 ± 17) also contributed a substantial amount, but the seagrasses and seagrass epiphytes (*Posidonia* – 7 ± 6, *Amphibolis* – 9 ± 8, *Zostera* – 10 ± 8, *Posidonia* epiphytes – 8 ± 7) contributed much less (Fig. 66).

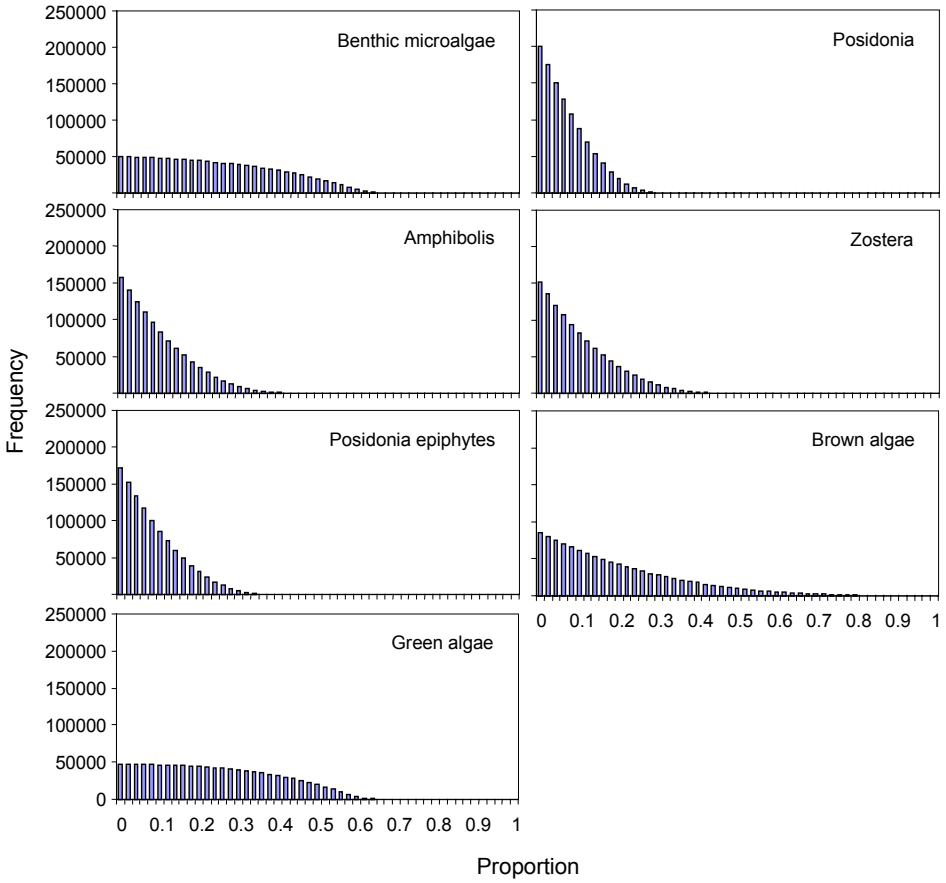

Figure 66. Frequency distribution of the proportional contributions of alternative sources to the nutrition of King George whiting in Western Australia. Estimates based on carbon isotope only.

The IsoSource modelling with carbon and sulphur failed to give any estimates because all of the values of sulphur in the sources measured were greater than that for the whiting.

Modelling of the prey contributions to whiting diets showed that copepods and shrimp (*Macrobrachium*) were similarly important, and on average potentially represented 45 and 31 %, respectively, of the diet (Table 39). Amphipods, gastropods, bivalves and polychaetes were low contributors to the nutrition of whiting in Western Australia.

South Australia

The King George whiting sampled in South Australia ranged in average size (mean ± se) between 96 ± 4 mm at Port Arthur and 130 ± 8 mm at Fishermans Bay, while fish from Middle Beach and Weroona Island were 110 ± 2 and 110 ± 3, respectively. Six prey taxa and 8 different sources were sampled (Table 40).

IsoSource modelling based on only carbon showed that the nutrition of King George whiting in South Australia was based on a much broader range of sources than fish in Western Australia (Fig. 67). With the exception of green algae (mean % of 5 ± standard deviation of 5), the other sources contributed more than

10% but less than 20% to the nutrition of whiting in SA (benthic microalgae – 11 ± 10, brown algae – 12 ± 11, red algae – 14 ± 10, *Heterozostera* – 16 ± 14, *Heterozostera* epiphytes – 14 ± 13, Posidonia – 16 ± 14, Posidonia epiphytes – 13 ± 12) (Fig. 67).

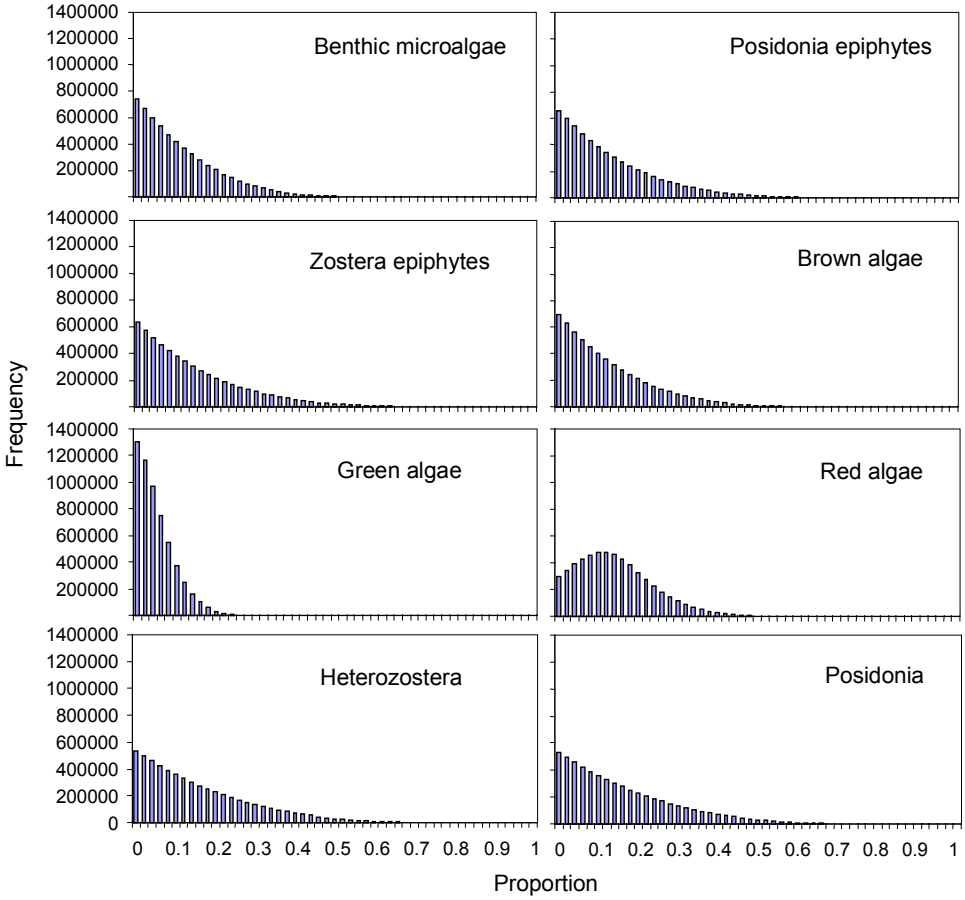

Figure 67. Frequency distribution of the proportional contributions of alternative sources to the nutrition of King George whiting in South Australia. Estimates based on carbon isotope only.

When sulphur stable isotopes were included in the modelling, however, the relative importance of *Heterozostera* and *Heterozostera* epiphytes increased considerably to 38 ± 16 and 22 ± 18, respectively, while, with the exception of benthic microalgae (17 ± 12), the importance of the other sources dropped below 10% (*Posidonia* – 3 ± 3, *Posidonia* epiphytes – 8 ± 7, brown algae – 3 ± 3, green algae – 2 ± 2, red algae – 6 ± 5)(Fig. 68).

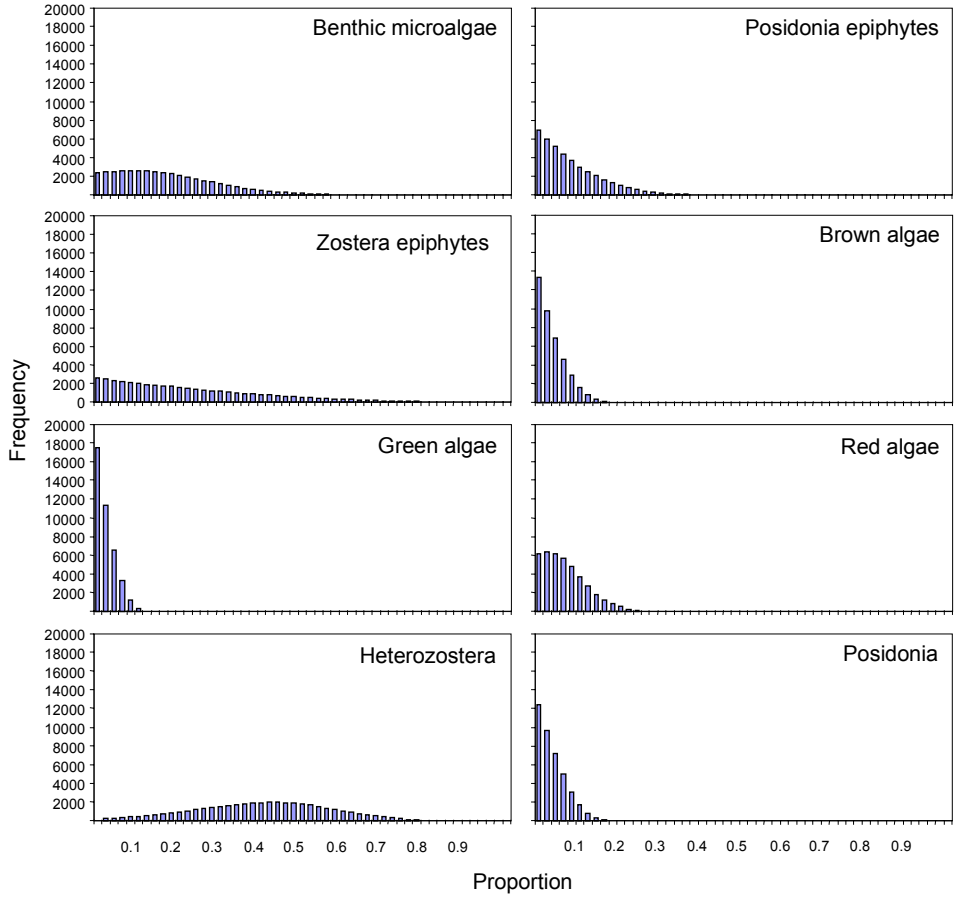

Figure 68. Frequency distribution of the proportional contributions of alternative sources to the nutrition of King George whiting in South Australia. Estimates based on carbon and sulphur isotopes.

The diets of King George whiting in South Australia were dominated by shrimps (*Macrobrachium*) and to a lesser extent polychaetes, which contributed as much as 82 and 74%, respectively (Table 41). Copepods, amphipods, bivalves and isopods contributed very low amounts to the diets of whiting in South Australia.

Victoria

The fish sampled in Victoria ranged in size 6.1 - 17.4 cm, with an average length (± standard deviation) of 9.5 ± 2.9. Five potential prey taxa and 8 potential sources were also sampled (Table 42).

IsoSource modelling based on only carbon showed that the nutrition of King George whiting sampled from Victorian coastal waters is clearly supported most by seagrass (*Heterozostera tasmanica*, mean % of 45 ± standard deviation of 5)(Fig. 69). The contribution by the other sources did not exceed 12% and many were below 10% (*Heterozostera* epiphytes – 9 ± 8, brown algae – 10 ± 9, green algae – 10 ± 9, red algae – 5 ± 5, phytoplankton – 11 ± 10, benthic microalgae – 12 ± 11)(Fig. 69).

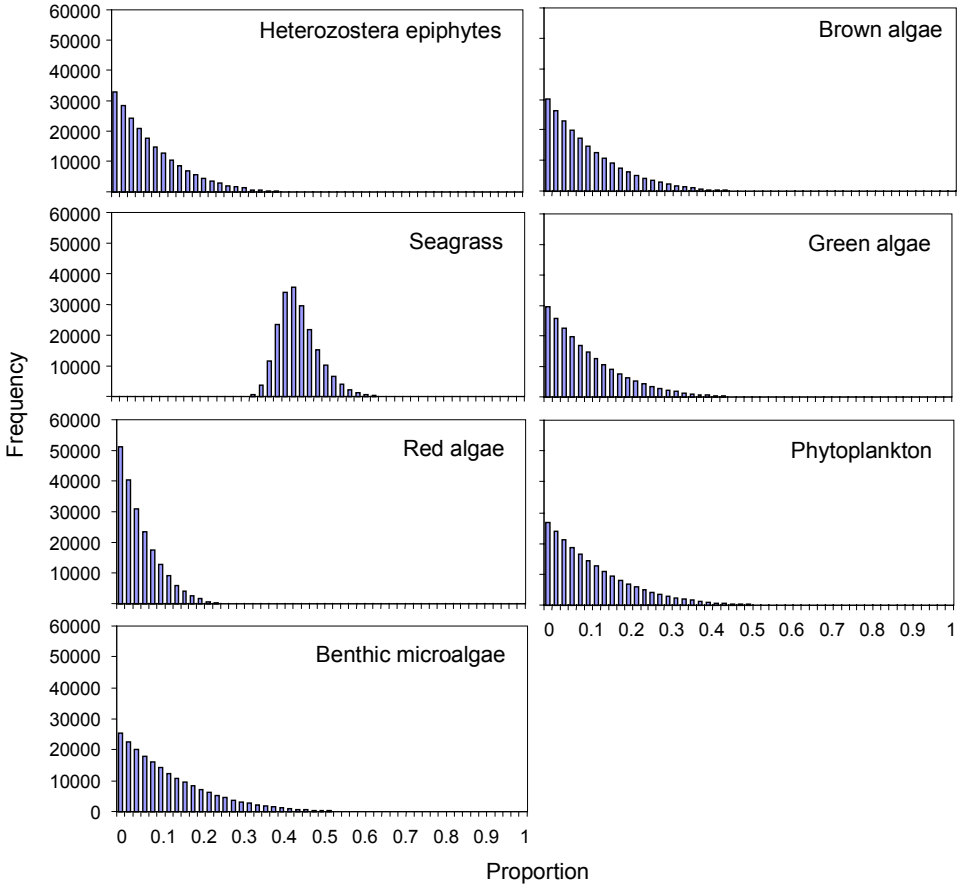

Figure 69. Frequency distribution of the proportional contributions of alternative sources to the nutrition of King George whiting in Victoria. Estimates based on carbon isotopes only.

The addition of sulphur in the isotope modelling did not change the results from carbon isotope modelling that showed seagrass to be the most important source in the nutrition of King George whiting in Victoria (Fig. 70). *Heterozostera tasmanica* (mean % of 47 ± standard deviation of 4) greatly exceeded the contribution by *Heterozostera* epiphytes (10 ± 8), brown algae (10 ± 8), green algae (11 ± 9), red algae (6 ± 5), phytoplankton (6 ± 4), benthic microalgae (9 ± 7)(Fig. 70).

The diets of King George whiting in Victoria appeared to be dominated by decapods (small crabs and grass shrimp) and polychaetes. Amphipods, copepods and a burrowing decapod (*Callianassidae*) contributed less that 10% to the nutrition of whiting (Table 43).

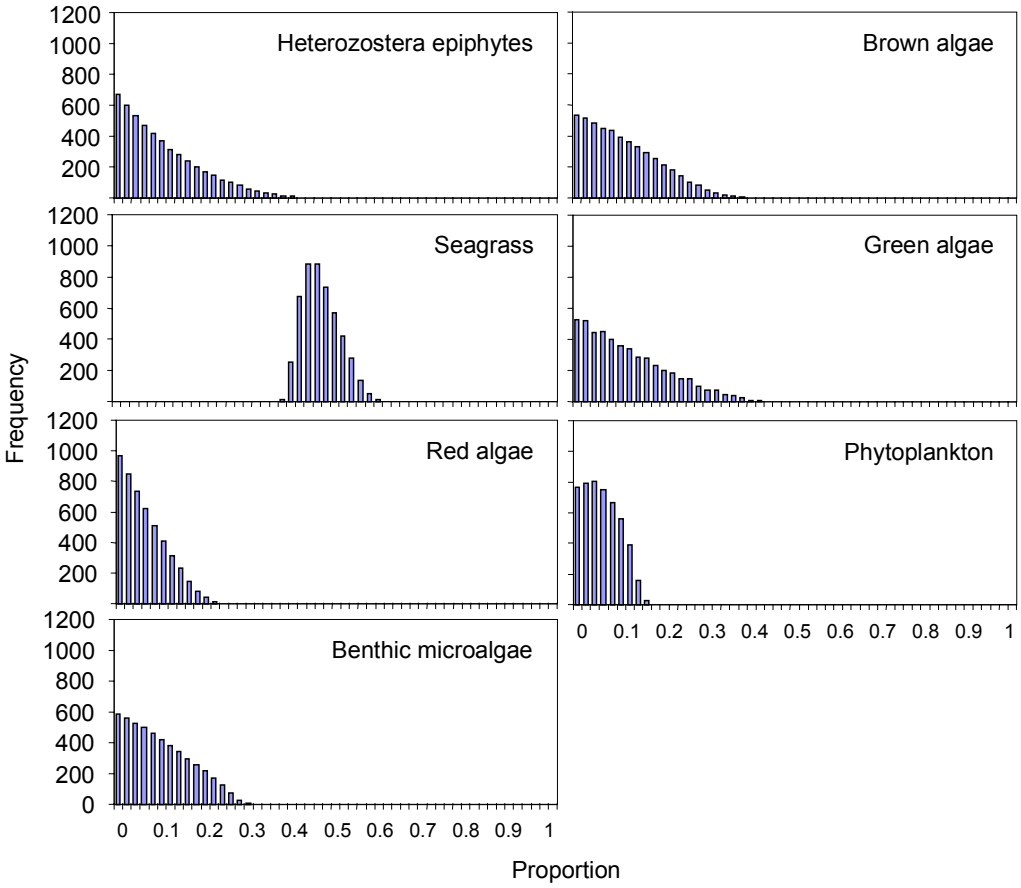

Figure 70. Frequency distribution of the proportional contributions of alternative sources to the nutrition of King George whiting in Victoria. Estimates based on carbon and sulphur isotopes.

DISCUSSION

The nutrition of King George whiting varies across southern Australia. The base for nutritional support of Western Australian King George whiting appears to be primarily algae (especially green, brown and microalgae), while those in Victoria and South Australia are based strongly on seagrasses from the family Zosteraceae. The choice of stable isotopes to model impacted greatly on the relative importance of alternative primary producers, but only in some States. The contribution of prey to the diets of whiting varied less among states, with carid shrimp and polychaetes important contributors to the diets of fish.

Seagrass habitat is critical for early post-settlement whiting (Connolly 1994a, Jenkins et al. 1997ab, 1998). King George whiting larvae begin settling into seagrass beds at around 15mm in length (although this size varies among States). On settling into seagrass, the diets of these small fish are composed almost exclusively of seagrass associated copepods (Jenkins et al. 1996). Over the next few months fish grow rapidly, reaching 50mm by the end of summer. In Victoria, Hindell et al. (FRDC 1999/215) have shown that by the time fish are 30 to 50 mm in length, their carbon stable isotope signatures have changed from one similar to phytoplankton (≈- 20) to one more similar to seagrass (≈ - 12). Also, at around this time fish begin to move off seagrass and forage almost exclusively over patches of unvegetated sand and mud, often on intertidal banks. The fish sampled in the present study are slightly larger than those analysed by Hindell et al. (FRDC 1999/215), but, at least in Victoria and South Australia, the signatures of King George

whiting foraging over predominantly sparsely vegetated and unvegetated mudflat are still consistent with seagrass as the primary base for nutritional support.

In Western Australia the nutrition of fish was based on algae rather than seagrass. The reduced influence of seagrass is likely to be associated with the reduced dependence of post-settlement King George whiting on Seagrass meadows. Compared to south-eastern Australia, King George whiting larvae settle out into shallow, unvegetated areas in Western Australia (Hyndes et al. 1996, 1998). Post-settlement fish are therefore likely to consume invertebrates that graze on primary producers other than seagrasses. Furthermore, in comparison to the systems examined in south-eastern Australia, Posidonia spp. dominated the seagrass assemblages rather than Zostera tasmanica, which may be a more palatable seagrass for grazers. Since King George whiting exhibit a greater association with seagrass patches at larger sizes (Hyndes et al. 1996), their reliance on invertebrates grazing on seagrass as a primary food source is likely to increase ontogenetically.

Carbon stable isotopes have been the isotope of choice for most researchers assessing food web structure. Recently, however, sulphur has been shown to be useful in separating sources which could not previously have been separated based on their carbon stable isotope signatures (Melville and Connolly 2003). The present study suggests that the utility of sulphur stable isotopes in improving our understanding of trophic linkages can vary over large spatial scales. In Western Australia, the inclusion of sulphur isotopes in source modelling failed to provide estimates because the sulphur values of producers were all greater than those of the fish. In South Australia the inclusion of sulphur isotopes greatly improved our ability to separate different sources as the algae and a species of seagrass were removed as probable contributors leaving a single species of seagrass (*Heterozostera*) and its epiphytes. In Victoria, the use of sulphur isotopes did not improve assessments of nutrition for whiting over carbon isotopes.

Dietary studies on King George whiting generally conclude that amphipods and polychaetes are common prey items (Edgar and Shaw 1995b). This study confirms the importance of polychaetes using stable isotope analyses rather than observations of stomach contents. Interestingly, however, it also identifies small decapods (particularly grass shrimp, *Macrobrachium*) as important in the diets of fish. Previous dietary studies have not shown this group to be important in the diets of whiting, and the size of the fish sampled here are unlikely to be large enough to be consuming the size of the decapods sampled. Instead, it is more likely that these invertebrates are integrating similar sources in their nutrition. *Macrobrachium* in particular are very closely associated with seagrass and are thought to feed on seagrass detritus and epiphytic material.

Table 37. Summary of samples collected from each state.

		State					
		WA		SA		VIC	
	Sample	$\delta^{13}C$	$\delta^{34}S$	$\delta^{13}C$	$\delta^{34}S$	$\delta^{13}C$	$\delta^{34}S$
Fish	King George whiting	✓	✓	✓	✓	✓	✓
Invertebrate prey	Copepods	✓		✓	✓	✓	
	Amphipods	✓		✓	✓	✓	
	Gastropods	✓					
	Bivalves	✓		✓	✓		
	Shrimp	✓		✓	✓	✓	
	Polychaetes	✓		✓	✓	✓	✓
	Isopods			✓	✓		
	Decapods					✓	
Seagrass	*Posidonia*	✓	✓	✓	✓		
	Amphibolis	✓					
	Zostera	✓		✓	✓	✓	✓
	Heterozostera			✓	✓	✓	✓
	Seagrass epiphytes	✓	✓			✓	✓
Algae	Brown Algae	✓	✓	✓	✓	✓	✓
	Green Algae	✓	✓	✓	✓	✓	✓
	Red Algae			✓	✓	✓	✓
Other sources	Seston			✓	✓	✓	✓
	BMA	✓		✓	✓	✓	✓

Table 38. Summary of the carbon and sulphur stable isotope values for the fish, invertebrates and sources collected at each site in Western Australia.

Species	Site PRH1	PRH4	OH2	OH3	$\mu\delta^{13}C$	Site PRH1	PRH4	OH2	OH3	OH3	$\mu\delta^{34}S$
KGW - Small	-7.3	-12.4	-12.6	-7.2	-9.9	12.7	10.8	13.8	14.2	12.9	12.9
Copepods	-12.8	-18.2	-16.8	15.8	-8.0						
Amphipods	-20.5	-27.0		-21.5	-23.0						
Gastropods 13	-12.8		-14.7	-14.2	-13.9						
Bivalves	-13.0	-18.4	-18.8	-14.1	-16.1						
Paleomonaetes	-6.1		-11.9	-9.4	-9.1						
Polychaetes Errant	-9.1		-10.8	-16.1	-12.0						
Polychaetes Sedentary	-13.0			-12.9	-13.0						
BMA	-10.7	-15.2	-10.5	-12.4	-12.2						
Posidonia	-2.2	-5.7		-5.9	-4.6	16.8	17.3	19.6	18.5	18.1	18.1
Amphibolis	-6.5	-7.1			-6.8						
Zostera			-6.9	-7.3	-7.1						
Epiphytes (*Posidonia*)	-4.9	-7.4		-6.1	-6.1	18.2	17.9	17.6	20.0	18.4	18.4
Sargassum	-10.9	-11.3		-9.1	-10.4	19.9	18.7		20.8	19.8	19.8
Cladophora	-12.0	-12.3		-12.6	-12.3	19.3	18.0		19.4	18.9	18.9

Table 39. Summary of the relative contributions (%) by invertebrate prey to the diets of juvenile King George whiting in Western Australia. Estimate based only on carbon isotopes.

	copepods	amphipods	gastropods	bivalves	shrimp	polychaetes
MEAN	45	2	7	5	31	9
MINIMUM	0	0	0	0	0	0
MAXIMUM	88	12	32	24	94	44
1 %ile	0	0	0	0	0	0
50 %ile	48	2	6	4	26	8
99 %ile	78	10	26	18	84	34
Stand. Dev.	20	2	6	5	23	8

Table 40. Summary of the carbon and sulphur stable isotope values for the fish, invertebrates and sources collected at each site in South Australia.

Species	Site MB	PA	FB	WI	$\mu\delta^{13}C$	Site MB	PA	FB	WI	$\mu\delta^{34}S$
Fish										
King George whiting	-13.1	-13.1	-12.0	-13.8	-13.0	9.1	9.0	6.4	6.1	7.6
Prey										
Amphipods	-16.5	-15.6	-13.5	-13.4	-14.8		5.1	6.1		5.6
Copepods	-16.4	-14.4	-13.3	-15.4	-14.9		9.3	6.4	1.1	5.6
Macrobrachium	-12.4	-9.2	-12.4	-15.1	-12.3	11.7	10.7	10.5	10.4	10.8
Polychaetes	-12.8	-13.2	-14.3	-13.2	-13.4	3.2			3.8	3.5
Bivalve	-18.0	-12.9	-14.8		-15.2	13.0	13.7	10.5		12.4
Isopods	-15.3	-16.1	-13.8	-18.9	-16.0	16.9	12.4	13.5	15.1	14.5
Sources										
Benthic microalgae	-20.5	-18.0	-17.6	-17.5	-18.4	10.7	5.6	12.4	14.7	10.8
Posidonia epiphytes	-13.8	-14.8	-13.6	-18.6	-15.2	11.4	13.4	11.2	15.1	12.4
Zostera epiphytes	-16.7	-12.3	-13.5	-13.7	-14.0	11.4	12.3	3.9	3.8	7.9
Brown Algae	-18.5		-13.2	-18.2	-16.6		19.5			19.5
Green Algae	-17.1		-16.1	-7.5	-13.6				20.0	20.0
Red Algae	-23.9	-31.5		-19.9	-25.1		20.0			20.0
Heterozostera-Zostera	-12.3	-9.2	-8.2	-11.4	-10.3	0.6	8.0	1.8	2.4	3.2
Posidonia	-12.1	-7.2	-9.4	-12.0	-10.2	12.1	14.8	13.4	13.8	13.6
Seston		-18.3			-18.3		5.5			5.5

Table 41. Summary of the relative contributions (%) by invertebrate prey to the diets of juvenile King George whiting in South Australia. Estimates based only on carbon isotopes.

	copepods	amphipods	shrimps	polychaetes	bivalve	isopods
MEAN	6	6	64	15	5	4
MINIMUM	0	0	26	0	0	0
MAXIMUM	32	34	82	74	28	22
1 %ile	0	0	40	0	0	0
50 %ile	4	4	66	12	4	2
99 %ile	22	24	78	54	20	16
SD	6	6	9	13	5	4

Table 42. Summary of the carbon and sulphur stable isotope values for the fish, invertebrates and sources collected at each site in Victoria.

Species	Vic H	R	W	Y	$\mu\delta^{13}C$	Vic H	R	W	Y	$\mu\delta^{13}C$
Fish										
King George whiting	-14.5	-13.3	-12.6	-10.5	-12.7	10.8	12.0	10.3	9.1	10.5
Prey										
Amphipods	-21.3	-16.3	-19.5	-13.1	-17.5					
Copepods	-18.1			-12.1	-15.1					
crab	-13.2	-10.4	-14.6	-7.6	-11.4					
grass shrimp	-12.9	-12.5	-13.6	-9.8	-12.2					
Polychaetes	-11.7	-17.5	-13.9	-11.9	-13.7					
snapping shrimp	-17.9	-13.3	-15.4		-15.5					
Sources										
Benthic microalgae	-15.5	-18.6	-15.6	-10.7	-15.1	-0.3	-0.1	-0.1	-3.1	-0.9
Epiphytic Green Algae	-17.0	-16.2	-17.1	-16.8	-16.8	11.3	10.4	15.8	14.3	12.9
Epiphytic diatoms	-18.1	-17.3	-16.8	-12.9	-16.3	3.0	7.5	3.6	10.8	6.2
Epiphytic Red Algae	-19.6	-18.5	-16.9	-23.2	-19.5	12.6	16.4	17.0	19.3	16.3
Brown Algae	-14.0	-19.6	-15.8	-16.7	-16.6	21.0	20.2	19.7	17.7	19.7
Heterozostera	-8.4	-8.9	-8.1	-5.5	-7.7	12.2	15.8	13.9	7.6	12.4
Green Algae	-18.1	-16.5	-16.8	-14.3	-16.4	19.0	7.8	16.7	19.1	15.7
Red Algae	-23.0	-22.4	-16.9	-32.6	-23.7	16.3	18.4	21.0	23.9	19.9
Seston	-14.3	-16.8	-13.6	-17.8	-15.6	-18.1	-10.9	-16.7		-15.2

Table 43. Summary of the relative contributions (%) by invertebrate prey to the diets of juvenile King George whiting in Victoria.

	Amphipods	Copepods	crab	grass shrimp	polychaetes	snapping shrimp
MEAN	4	7	41	29	12	7
MINIMUM	0	0	0	0	0	0
MAXIMUM	22	36	80	92	60	34
1 %ile	0	0	0	0	0	0
50 %ile	4	6	44	24	10	6
99 %ile	16	26	70	80	44	24
SD	4	7	18	22	11	6

Benefits

FISH-HABITAT ASSOCIATIONS IN VICTORIA

The first part of this study provides much needed information on fish use of temperate intertidal habitats and fish use of seagrass-mangrove landscapes. We know have a much more balanced understanding of the roles of alternative habitats in supporting fisheries species.

This work suggests that mangroves and saltmarshes are much less important as fish habitat in Victorian waters than seagrass and rocky reef. While many juvenile and adult stages use these habitats, they are only available on high tides (saltmarshes are only available during particular weather patterns) and few of the species are of commercial/recreational value. Only yellow-eye mullet (*Aldrichetta forsteri*) could be considered an economic species that use mangroves and other intertidal habitats on a regular basis.

The role of seagrass-mangrove landscapes suggested that the fish assemblages using each were influenced by the proximity of the other. None of the species sampled, however, were of commercial interest. Nonetheless, the arrangement of seagrass and mangroves habitats to one another affect the ecology of shallow temperate embayments.

These results have implications in marine planning, especially in calculating the risks to fisheries sustainability of changes in the area of intertidal habitat and their arrangement to one another. The recognised importance of seagrass habitats in supporting fisheries species is arguably even greater now that we know how few species use adjacent shallow water areas. Greater efforts must therefore be made to protect these habitats.

BASE FOR NUTRITIONAL SUPPORT OF FISHERIES SPECIES ACROSS SOUTHERN AUSTRALIA

Victoria

The preliminary results from this study provided nothing new to understanding trophic structure of fisheries species. Like the survey work above, the stable isotope studies clearly demonstrated that mangroves and saltmarshes contributed little to the nutrition of fisheries species. Unfortunately, this was the only unambiguous result. With the exception of King George whiting, which showed a strong reliance on seagrass as a base of nutritional support, other fisheries species had stable carbon isotope signatures consistent with a mixture of several sources, including brown, red and green alga, seston, benthic microalgae and seagrass. This research demonstrates the need to incorporate more stable isotope signatures to better elucidate which sources are most important.

South Australia

This study provides empirical evidence of the importance of organic material from seagrass meadows as the basis for nutrition of fisheries species of commercial and recreational importance in South Australia. This is the case even where there is segregation between the habitats in which species tends to occur and those from which they obtain the majority of their ultimate nutrition source (e.g. *Sillago schomburgkii*). The usual assumption is of movement of organic material from shallower to deeper waters, but the opposite appears to apply for *Sillago schomburgkii*. Organic material from subtidal seagrass meadows is important to this species, which spends much of its time, and consumes much of its prey (see specialised analysis in Connolly et al. in press, Appendix 3), over intertidal habitats inshore of the seagrass.

In considering a system of marine protected areas in South Australia (Edyvane 1999), the trophic link between seagrass and the fisheries species occurring in seagrass as well as in adjacent coastal habitats must be taken into account. Organic material from seagrass meadows plays a more important role in the nutrition of fish and crabs than expected based on existing food web theory. The SA chapter therefore provides an example of the need to understand and account for trophic links between nearshore habitats in designing marine protected areas.

Western Australia

The present study has provided evidence of links between secondary production and the major sources of primary production in the two systems on the south coast of Western Australia. The study has shown through stable isotope analyses that the dependence of main invertebrate prey of fish species on the sources of primary production differed among the invertebrate taxa. For example, amphipods had a greater reliance on detritus from saltmarshes, while shrimp relied on a combination of seagrass and the green alga *Cladaphora* and polycheates had a dependence on *Cladaphora*. The transfer of this material further up the food chain will depend on the feeding preference of the fish species. Any impact on the ecosystem through the loss of major primary producers will depend on the plasticity of the feeding of invertebrates. The results of this study suggest that coastal managers need to conserve the mosaic of habitats available in coastal systems. Urbanisation of coastal areas has placed pressure on saltmarsh vegetation and led to losses, which is a concern given the present study indicates that this source of primary production is important for certain prey species. Both Princess Royal Harbour and Oyster Harbour have experienced seagrass losses during the 1970s. This loss coincided with an increase in the biomass of *Cladaphora*, which was considered a nuisance, and led to attempts to mechanically remove this green alga. The current study suggests that both seagrass and *Cladaphora* play key roles in the food web of both systems.

Continental-scale isotope study of King George whiting nutrition.

This study showed that the base for nutritional support of King George whiting varies considerably between regions across southern Australia. This is important to regional coastal planning and the protection of specific habitat types to ensure the sustainability of particular fisheries species.

Sulphur isotope were valuable in better separating the sources identified through carbon isotopes as contributing to the nutrition of fisheries species in some areas (e.g. Victoria). We can therefore better separate the relative importance of similar sources such as seagrass and seagrass epiphytes, which until now has been difficult. The future use of single isotopes will continue to be problematic and multiple isotopes need to be encouraged.

Further Development

FISH-HABITAT ASSOCIATIONS IN VICTORIA

The assessment of fish associated with mangroves, saltmarshes and mudflat complements previous work on seagrasses, rocky reefs and deeper channels. We now have a strong understanding of which fish use the major nearshore habitats in Victoria. This study has raised the need, however, for further research into how the spatial arrangement of habitats influences fish use. There are two parts to this that require further attention. First, we need a better understanding of how fish use changes across the edge of habitat patches. Shallow vegetated habitats are under threat from fragmentation and unless we understand how the use of patch edges compare to the interior, then we will not be able to predict the consequences of habitat fragmentation on fisheries sustainability. Second, the effects of habitat proximity requires further research. This study showed strong trends in fish use of mangroves and seagrass as the distance between the habitats changed. To best manage particular habitat arrangements, we need to understand more about what processes are causing these patterns.

BASE FOR NUTRITIONAL SUPPORT OF FISHERIES SPECIES ACROSS SOUTHERN AUSTRALIA

Victoria

Stable isotope analyses have been used extensively in Victoria. Much of the information from these studies has been ambiguous, with a wide variety of sources contributing variable amounts to the nutrition of fisheries species. The one exception, it seems, is King George whiting, which appears to rely on seagrass for at least 50% of its nutrition. Future studies of trophic structure should use more than one stable isotope as well as other tools such as diet composition. Fatty acid research has also shown some merit in advancing our understanding of which sources are most important in supporting fisheries species.

South Australia

In South Australia, stable isotope analysis has been successful at demonstrating which habitats provide nutrition for key fisheries species. Where good dietary information was available (e.g. yellowfin and King George whiting), the isotope data has been complementary, and has better defined the relationships of these fishes with the various habitats in South Australian gulfs. For other species analysed, we recommend further work to better define diets by direct stomach content analysis, and to extend isotope analysis to use sulfur in addition to carbon and nitrogen (as was done successfully for King George whiting here). Two heavily exploited inshore species, snapper and western king prawns, were unable to be properly sampled in the current study, but warrant inclusion in future fisheries habitat work. The overwhelming importance of organic material from seagrass meadows in nearshore foodwebs should also form the basis of the conceptual understanding for any proposed work on the sustainability of aquaculture of bivalves in coastal waters.

Queensland

In Queensland, this project has added to the solid state of knowledge about fisheries habitat in southern Queensland waters (at least for Moreton Bay). Despite a very helpful result from our survey of stable

isotopes of mudcrabs, the main trophic (feeding) issue remaining for inshore species in southern Queensland waters is the role of saltmarsh grass in foodwebs. Saltmarshes are the habitat under most threat in southeast Queensland, and are being lost and reclaimed at a greater rate than any other marine habitat. We recommend further attempts at establishing the trophic role of saltmarshes for fisheries species using alternative biomarkers, in particular through lipid (fatty acids, sterols) analysis.

Western Australia

The $\delta^{13}C$ and $\delta^{15}N$ values allowed saltmarshes to be distinguished from seagrasses and algae. Furthermore, with the exception of the brown alga *Hormosira*, seagrasses could be distinguished from algae groups. However, there was no clear separation of stable isotope signatures among the algal groups, which limited the ability to determine the relative importance of the different algal groups as sources of production to consumers. Although the isotope $\delta^{34}S$ can help remove any such ambiguity in the results, this isotope did not appear to help consistently differentiate among these groups in Western Australia (see WA isotope study chapter). However, the use of other biomarkers, such as fatty acid composition, is proving to be a useful tool in a similar study by Crawford and Hyndes. Thus, further work needs to be carried out to examine the usefulness of this approach. The transfer of material from primary producers through the food web could also be clarified using manipulative experiments, where targeted primary producers are spiked with elevated levels of ^{13}C or ^{15}N.

Planned Outcomes

Victoria

Victoria has recently legislated a series of marine parks, some of which are in protected bays and inlets and incorporate many of the shallow vegetated habitats studied here. The results from this study will improve understanding of the benefits to fisheries of protecting particular habitat types, particularly seagrass and mangroves. The Victorian State Government is currently debating the role of channel dredging in Port Phillip Bay, and the results from this study will also help to understand the ecological consequences of increased disturbance on fisheries via altering particular habitat types. The data from this study will be incorporated into a preliminary study by the CSIRO and Marine and Freshwater Systems (PIRVic) that is testing the potential for predictive modelling to help understand the ecological functioning of Western Port.

South Australia

South Australian work has provided clear scientific results about the trophic (feeding) links between the different inshore habitats and key fisheries species. There is currently a major emphasis on habitat protection in South Australia, via the development of a representative system of Marine Protected Areas and through Natural Resources Management planning more generally. Our results feed neatly into that process, by highlighting the very strong dependency of fisheries species on seagrass meadows, whether or not the animals themselves are typically caught over seagrass. The important role of both subtidal *Posidonia* and intertidal *Zostera* beds has been identified. The first published manuscript from South Australia (on yellowfin whiting) has been sent to PIRSA (habitat mapping project) and our collaborating scientist, Dr Sue Murray-Jones, at the Dept Environment and Heritage. Further discussion with both groups are planned once this final report is available.

Queensland

In Queensland, confirmation of the role of seagrass at the base of foodwebs leading to production of the two most important crab species, blue swimmer crab and mud crab, has built on the finfish work of previous FRDC projects. There is already considerable focus on the health and distribution of seagrasses in southern Queensland waters, where this habitat is vulnerable to increasing sediment and nutrient loads generated by the rapidly increasing human population. The current results add urgency to the issue of managing coastal waters for fisheries productivity as well as for water quality *per se*. The main communication channels are through the Marine Permit section of Dept Primary Industries and Fisheries, and the Moreton Bay Catchment and Waterways Partnership.

Western Australia

Systems such as Princess Royal Harbour and Oyster Harbour make a significant contribution to the commercial and recreational fisheries along the south coast of Western Australia. The planned outcome for this study was to provide an increased understanding of the importance of different habitats to different species of fish in coastal systems. This study has provided evidence that a suite of primary producers, e.g. seagrasses, saltmarsh and macroalgae, that constitute major habitats in those systems contribute to the food web, and ultimately to the production of important commercial and recreational fisheries, e.g. King George whiting and flathead. The study provides evidence that managers need to conserve or improve the mosaic of habitats that are present in these systems to ensure the sustainability of catches in the future.

Conclusions

Victoria

The work in Victoria represents the most comprehensive assessment of fish use of intertidal habitats in southern Australia, including mangroves, mudflat and saltmarshes. Few species of economic importance were found to use these habitats, but many non-commercial species, including some that are commonly found in the diets of economic species (such as gobiids and atherinids) were common. Experimental studies showed that the use of these habitats may not be driven by predation-related processes, but their role in the provision of food or shelter from other forms of disturbance could not be discounted.

The application of landscape ideas to seagrass-mangrove systems has great potential given advances in remote sensing and mapping, and the links shown here between seagrass-mangrove landscape structure and fish assemblages. Fish assemblages were completely different along the edges of mangroves, where several species of economic importance, such as King George whiting and Australian salmon, were common, compared to areas inside the forest where non-commercial species such as gobiids dominated. This pattern has implications for the effects of mangrove forest fragmentation, suggesting that increasing the amount of edge to area could actually benefit species of economic importance.

The proximity of mangroves to seagrass and seagrass to mangroves strongly influences the assemblage structure of fishes using each habitat. Like the earlier work (above), while few of the species caught were of direct economic importance, many contribute to food chains of economic species. Indirectly, therefore, the structure of seagrass-mangrove landscapes may strongly influence the local value of coastal areas to fisheries species.

The application of stable isotopes in better understanding which primary producers are most important to fisheries species gave mixed results. King George whiting were one of the few species for which stable isotopes gave a strong indication of base for nutritional support. Based on carbon isotopes, whiting appeared to rely most heavily on seagrass, and the use of an additional isotope (sulphur) did not change this result. Conversely, the other fisheries species had stable carbon signatures that fell in the middle of several sources, and subsequent isotope modelling failed to differentiate among them. In Victoria, therefore, stable isotopes may be of limited value in determining the ultimate source of nutrition for many of the fisheries species, and future work using these methods should be augmented with traditional dietary studies and novel fatty acid methods to best delineate alternative sources.

South Australia

In South Australia, we found that organic material from seagrass meadows provided the basis for nutrition of fisheries species of commercial and recreational importance. This was the case even where there was segregation between the habitats in which species tended to occur and those from which they obtain the majority of their ultimate nutrition source. Organic material from seagrass meadows plays a more important role in the nutrition of fish and crabs in South Australian waters than would be expected based on existing food web theory. The trophic link between seagrass meadows and the fisheries species occurring both in seagrass and in adjacent habitats must be taken into account in the planning of protection measures for coastal habitats.

Queensland

In Queensland, our work has demonstrated that for food webs sustaining crab production in Moreton Bay, seagrass meadows are critical. Both seagrass and its epiphytic algae are important in the production of fisheries species in Moreton Bay. This finding is consistent with previous results for finfish, and reinforces the need to conserve and protect seagrass meadows from adverse anthropogenic influences.

Western Australia

Most of the fish species collected in Oyster and Princess Royal harbours feed on invertebrates, or in the case of larger fish, a combination of invertebrates and smaller fish, which in turn feed on invertebrates. Since the source of production varied considerably among invertebrate-prey groups, the flow-on of those sources is also likely to be variable. Those fish that eat mainly on amphipods will have a greater reliance on saltmarsh vegetation, whereas those consuming shrimp and crabs will have a greater reliance on seagrasses and *Cladophora* which are present in high biomass in both systems. Fish exhibit a degree of plasticity in their feeding as the diet of species can differ considerably among size classes and also among habitats and seasons (e.g. Hyndes et al. 1996; Connolly 2003). However, the ability of a system to cope with losses of particular types of vegetation (e.g. seagrasses or saltmarshes) will depend on the feeding plasticity of invertebrates, the potential prey of fish. Although this study has provided further information on the trophic interactions in coastal systems in temperate Australia, there is a level of ambiguity in the results, which relates to the similar $\delta^{13}C$ and $\delta^{15}N$ values of some primary producer groups, making it difficult to establish the true source of production. The use of other biomarkers, such as the isotope $\delta^{34}S$, may help to differential between those groups of plants, as is suggested by Connolly et al. (2004).

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Appendix 1: Intellectual Property

The FRDC's share of project income, based on the relative value of financial contributions to this project, is 55.79%.

Appendix 2: Staff

PRINCIPAL INVESTIGATOR

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Appendix 3: Papers published in international journals

VICTORIA

1. Hindell J, Jenkins GP (2004) Spatial and temporal variability in the assemblage structure of fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate Australian embayments. Marine Biology 144:385-395
2. Crinall S, Hindell J (2004) Assessing the use of saltmarsh flats by fish in a temperate Australian estuary. Estuaries 27:731-742
3. Hindell J, Jenkins G (in press) Assessing patterns of fish zonation in temperate mangroves, with emphasis on evaluating sampling artifacts. Mar Ecol Prog Ser
4. Smith T, Hindell J (in press) Assessing effects of diel period, gear selectivity and predation on patterns of microhabitat use by fish in a mangrove dominated system in southeastern Australia. Mar Ecol Prog Ser

SOUTH AUSTRALIA

1. Connolly, R.M., Hindell, J.S. & Gorman, D. in press. Seagrass and epiphytic algae support the nutrition of a fisheries species, Sillago schomburgkii, in adjacent intertidal habitats. Mar Ecol Prog Ser

WESTERN AUSTRALIA

QUEENSLAND

1..Connolly RM, Guest MA, Melville AJ, Oakes JM (2004) Sulfur stable isotopes separate producers in marine food web analysis. Oecologia 138, 161-167.

2. Oakes JM, Connolly RM (2004) Causes of sulphur isotope variability in seagrass, *Zostera Capricorni*. J Exp Mar Biol Ecol 302: 153-164