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Critical estuarine habitats for food webs supporting fisheries in Port Curtis, central Queensland, Australia

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Abstract

Port Curtis in central Queensland, Australia, is a large subtropical embayment with very extensive intertidal and shallow subtidal mudflats. Many economically important fish and crustacean species occur over mudflats lacking conspicuous vegetation. The autotrophic source(s) supporting food webs leading to animal production on the mudflats might be either *in situ* microalgae or material transported from adjacent habitats dominated by macrophytes. We measured stable isotopes of C and N values of 9 fish and 4 crustacean species, and 8 autotroph taxa (*Zostera* seagrass, *Halophila* seagrass, mangroves, saltmarsh succulents, saltmarsh grass and algal mats in adjacent habitats, *in situ* microalgae on mudflats, and particulate organic matter in the water column – including phytoplankton) at three locations in Port Curtis. The contribution of each autotroph to fish species was modeled using a Euclidean mixing model. Fish C isotope values lay exclusively in the enriched half of the range for autotrophs, indicating very minor contributions from depleted autotrophs (mangroves, saltmarsh succulents). Seagrass (mainly *Zostera*) was in the top three potential contributors for all fish species. For crustaceans such as mud crabs (*Scylla serrata*) and banana prawns (*Fenneropenaeus merguiensis*), seagrasses (including *Halophila*) had the highest potential contributions. Organic matter from seagrass beds is an important source for animals on adjacent unvegetated mudflats, either through outwelling of particular organic matter or via a series of predator-prey interactions (trophic relay). Saltmarsh grass (*Sporobolus*) also had high putative contributions for many animal species but from work elsewhere we suspect this is a spurious result, reflecting the similarity in isotope values of this autotroph to seagrass. Although macrophyte production in adjacent habitats was the dominant source of nutrition for the suite of animals over unvegetated mudflats, *in situ* microalgae had a high potential contribution to half of the fish species and one of the crustacean species (*Scylla serrata*), and particulate organic matter, including phytoplankton, was a likely contributor to several other species.

Introduction

Animals occurring over unvegetated mudflats in estuaries must ultimately obtain nutrition either from *in situ* autotrophic sources or from organic matter transported (outwelled) from elsewhere. *In situ* sources are microalgae either in the water column (phytoplankton) or on the surface of the mudflats (microphytobenthos). Organic matter can be transported to mudflats either by direct movement of plant material from external sites of production, or in the bodies of animals as a series of trophic interactions (Kneib 2000).

Port Curtis is a marine-dominated estuarine embayment with very extensive areas of estuarine habitat. The outwelling hypothesis 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 1984). While there are substantial areas of saltmarsh (including unvegetated saltpan) in Port Curtis (49 km^2), mangroves dominate the mid-intertidal fringes of estuaries there (56 km^2). 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, and in Port Curtis occur lower in the intertidal and shallow subtidal zone (no area estimate available). Some seagrass is consumed directly by crustaceans but the majority enters the detrital food web (Edgar & Shaw 1995). The most obvious feature of the bay, however, is the enormous areas of shallow mudflats (77 km^2). *In situ* production by microphytobenthos living on and in the mud and phytoplankton in the water column may be an important source of nutrition for fish that occur over mudflats.

High rates of anthropogenic development in the coastal zone mean managers are often faced with choosing which habitats to preserve. Seagrass beds, saltmarshes and mangrove forests are considered to be of high conservation value (Edgar & Shaw 1995) and as such, are preserved at the cost of mudflats. Mudflats in subtropical east Australian bays are occupied by several fish and crustacean species, some of which also occur over vegetated habitats but less frequently (Gray et al. 1998). Although fin-fish are of interest in Port Curtis, important fisheries also exist here for crustacean species. For example, over 40% of mud crabs (*Scylla serrata*) caught in Queensland come from the central Queensland region around Port Curtis (Walker 1997). Banana prawns (*Fenneropenaeus merguiensis*) are another important fisheries species in and around Port Curtis. Clearly mudflats contribute to estuarine biodiversity and should achieve some conservation status from this aspect alone. If *in situ* production supplies a substantial proportion of the nutrition to fish that occur over mudflats, managers should also be preserving this habitat for its trophic contribution to fisheries production.

Recent developments in isotope analysis have led to mixing models that use variances about autotroph and consumer mean isotope values to calculate variances about mean contributions by autotrophs (Phillips & Gregg 2001). However, mixing models used in previous studies (e.g. Phillips & Gregg 2001) have been restricted to analysing one more autotroph than elements used. For example, a study using isotopes of carbon and nitrogen could only analyse the contribution of three autotrophs. However, in the current study there are eight taxa of autotrophs, and so isotope ratios of seven elements would be needed. To overcome this problem Melville (2005) developed a Euclidean mixing model that determines, for any consumer, the mean putative contribution, and variance about this contribution, for multiple autotrophs. We use "putative contribution" to describe results from the Euclidean mixing model because, as with all modeling in this situation, there are multiple solutions for each analysis.

Although there have been studies that examine gut contents of fish found over unvegetated mudflats (e.g. Connolly 1995, Edgar & Shaw 1995), there have been no studies that attempt to determine which autotrophs fix carbon for these fish. Here, we use stable isotope analysis of carbon and nitrogen to determine whether outwelling of carbon to mudflats, or *in situ* production, contributes most nutrition to fish and crustaceans that occur over mudflats in the large estuarine embayment of Port Curtis. The Euclidean mixing model is used to assess the putative contribution of autotrophs to estuarine fish and crustaceans.

Methods

Sample collection and processing

Port Curtis in central Queensland is characterised by intertidal and shallow subtidal seagrass beds interspersed with extensive mudflats. The coastline comprises islands and the mainland, fringed by very extensive mangrove forests backed by saltmarsh, including unvegetated saltpans. Autotrophs and fish were collected in May 2000 at three locations in Port Curtis (Fig. 1). All samples were frozen immediately upon collection. Most fish and crustacean species and autotroph taxa could be found only at one or two of the locations, and data from the different locations were therefore pooled prior to analysis.

Fish and crustaceans were collected from mudflats using seine nets. Nine fish species and four crustacean species were collected. Samples of muscle tissue were taken for processing.

Mangrove leaves (MAN) were collected from 3 species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora stylosa*), where present, at each location. All samples of mangrove leaves were green, as the stable isotope ratios of green and yellow mangrove leaves do not differ (Connolly et al. 2003), and green mangrove leaves are more easily and efficiently collected. Values from the three species were pooled as their isotopic signatures were similar.

Where present, two species of seagrass (SG; *Zostera capricorni*, *Halophila ovalis)* were collected from each location. The mean δ^{13}C signatures of these two species were > 5 ‰ apart, so they were not pooled, and were treated as separate taxa when modelling. Not enough seagrass epiphyte material could be obtained to do isotope analysis.

Saltmarsh plants used for stable isotope analysis comprised three species; the C_3 saltmarsh succulents (SMU; *Sarcocornia quinqueflora* and *Suaeda australis*) and the C_4 saltmarsh grass (SMG; *Sporobolus virginicus*).

Microphytobenthos (MPB) was 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 (density = 1.21) and centrifuged at 10,000 rpm for 10 minutes. A band of diatoms 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.

Dense algal mats (AM) consisting predominantly of cyanobacteria covered quite large areas of unvegetated pans on saltmarshes. These were scraped from the sediment surface and washed clean in the laboratory prior to processing.

Particulate organic matter (POM) was defined as that fraction retained after filtering 100-800 litres of water through 37 µm mesh. Note that this is a coarser sample than the POM collected on filter paper in some other studies, and is more a collection of seston.

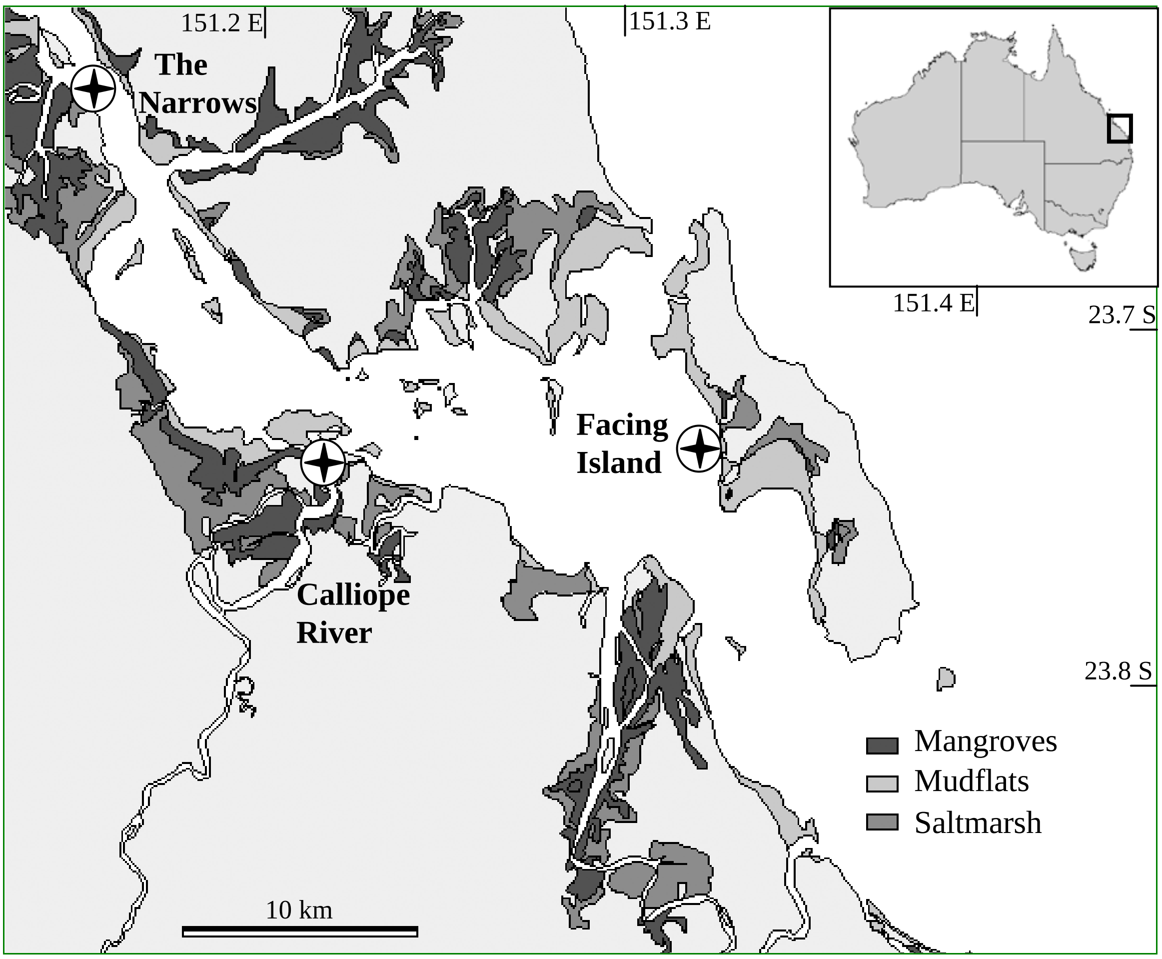

Figure 1. Map of Port Curtis indicating the 3 sampling sites.

All samples were dried to constant weight at 60° C. After processing, samples were placed in tin capsules and analysed on an Isoprime isotope ratio mass spectrometer. 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).

Fractionation and trophic level

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. To account for fractionation of nitrogen we subtracted the assumed 3 ‰ per trophic level increase from the nitrogen isotope signature of the animals (De Niro & Epstein, 1981). The number of trophic levels above autotrophs for each animal species was assigned using published dietary information for each species (Table 1). $\delta^{13}C$ fractionation is close to zero (Peterson & Fry 1987), so no adjustment was made for this element.

Euclidean mixing model

Autotrophs were pooled into eight taxa: mangroves, *Zostera* seagrass, *Halophila* seagrass, POM, MPB, algal mats, the C_3 saltmarsh succulents and the C_4 saltmarsh grass. Mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated for each animal and autotroph taxon. Only animal species for which more than one specimen was obtained were modelled (six fish and three crustacean species). Using the $\delta^{13}C$ and $\delta^{15}N$ values as Cartesian coordinates, Euclidean distances (E) between fish values and each of the autotroph categories were calculated according to:
$E = [(\delta^{13}C_{autotroph} - \delta^{13}C_{fish})^2 + (\delta^{15}N_{autotroph} - \delta^{15}N_{fish})^2]^{0.5}$

Variances were calculated about these Euclidean distances as follows:
$s^2 = a \times s^2 (\delta^{13}C_{autotroph}) + a \times s^2 (\delta^{13}C_{fish}) + b \times s^2 (\delta^{15}N_{autotroph}) + b \times s^2 (\delta^{15}N_{fish})$
where s^2 = variance, $a = ((\delta^{13}C_{autotroph} - \delta^{13}C_{fish}) / distance)^2$ and $b = ((\delta^{15}N_{autotroph} - \delta^{15}N_{fish}) / distance)^2$

Table 1. List of fish and crustacean species analysed and trophic levels used for correction of fractionation for each species.

Species	Common name	Trophic level(s) above autotrophs	References
Fish			
Acanthopagrus australis	Yellowfin bream	2	Blaber & Blaber 1980
Arrhamphus sclerolepis	Snub-nosed garfish	1.5	Blaber & Blaber 1980
Drepane punctata	Sicklefish	2.5	Kuiter 1996
Gerres subfasciatus	Common silverbiddy	2	Kuiter 1996
Herklotsichthys castelnaui	Southern herring	2	Kuiter 1996
Hyporhamphus quoyi	Short-nosed garfish	1.5	Robertson & Klumpp 1983
Leiognathus equulus	Common pony fish	2	Amesbury & Myers 1982
Sillago ciliata	Sand whiting	2	Burchmore et al. 1988
Valamugil georgii	Fantail mullet	1	Morton et al. 1987
Crustaceans			
Fenneropenaeus merguiensis	Banana prawn	1.5	This study
Oratosquilla stephensoni	Stephenson’s Mantis Prawn	2.5	This study.
Penaeus esculentus	Tiger Prawn	1.5	Wassenberg & Hill 1987
Scylla serrata	Mud Crab	2	This study

A small Euclidean distance between a fish and an autotroph indicates a large putative dietary contribution, so distances were inverted to make the measure more intuitive. The inverted distance for each autotroph was then calculated as a percentage of the total of the inverted distances for all autotrophs for a particular fish species.

Results

Autotroph isotope signatures

Isotope signatures of the eight taxa of autotrophs were generally well separated using both carbon and nitrogen (Fig. 2 & 3). Autotrophs fell into 3 groups based on $\delta^{13}C$ signatures: 1) enriched sources of *Zostera*, saltmarsh grass and MPB, 2) sources with middle values, consisting of *Halophila*, algal mats, and POM, and 3) depleted sources of mangroves and saltmarsh succulents. MPB had the most depleted $\delta^{15}N$ signatures and algal mats, POM and seagrass (both species) had the most enriched signatures.

Fish and crustacean isotope signatures

Isotope signatures varied among fish and crustacean species (Table 2). The variability among fish and crustacean species is less than that for autotrophs for $\delta^{13}C$ signatures yet similar for $\delta^{15}N$ signatures (Fig. 2 and 3, respectively). All fish species had $\delta^{13}C$ signatures lying within the enriched half of the range of autotroph values (Fig. 2). Crustacean $\delta^{13}C$ signatures were very closely grouped, all lying in the centre of the range of autotroph values, with means between -18 and -20 ‰. Crustacean values were depleted relative to all but one fish species (*Herklotsichthys castelnaui*). Carnivores (e.g. *Acanthopagrus australis* and *Sillago ciliata*) had the most enriched $\delta^{15}N$ signatures whereas detritivores (e.g. *Valamugil georgii*) and omnivores (e.g. *Hyporhamphus quoyi* and *Arrhamphus sclerolepis*) had the most depleted $\delta^{15}N$ signatures (Table 2). After correction for fractionation the $\delta^{15}N$ signatures of all species lay within the range of autotroph $\delta^{15}N$ signatures (Fig. 3).

Table 2: Size range and $\delta^{13}C$ and $\delta^{15}N$ values for all fish and crustacean species.

Species	n	Size Range (mm)	$\delta^{13}C$		$\delta^{15}N$	
			Mean	SE	Mean	SE
Fish						
Acanthopagrus australis	2	70 - 140	-18.04	0.26	11.79	0.80
Arrhamphus sclerolepis	1	150	-13.32		6.74	
Drepane punctata	1	420	-16.17		11.40	
Gerres subfasciatus	5	65 – 90	-16.57	0.52	10.56	0.49
Herklotsichthys castelnaui	3	70 – 125	-19.55	1.12	9.04	0.28
Hyporhamphus quoyi	2	90-95	-15.51	0.67	7.47	0.51
Leiognathus equulus	9	30 – 75	-16.27	0.59	9.51	0.59
Sillago ciliata	1	70	-16.58		11.63	
Valamugil georgii	11	110 - 300	-14.57	0.31	7.94	0.46
Crustaceans						
Fenneropenaeus merguiensis	4	15 – 35	-19.97	0.53	7.76	0.27
Oratosquilla stephensoni	3	-	-19.33	0.21	10.61	0.09
Penaeus esculentus	1		-18.73		8.40	
Scylla serrata	2	130 - 150	-19.17	1.71	6.54	1.20

Euclidean mixing model

Detailed results of the mixing models show that putative contributions of autotrophs vary among animal species (Table 3). When these results are summarised into just the top three contributing autotrophs for each animal species (Table 4), it becomes clear that only a subset of autotrophs are making substantial contributions. For fish, very high putative contributions were recorded for *Zostera* for *Valamugil georgii* and for saltmarsh grass for *Hyporhamphus quoyi*. Mangroves and saltmarsh succulents were not in the top three contributors for any fish species. For crustaceans, putative contributions of the top three autotrophs were very even (i.e. little difference between first and third ranked autotrophs), with *Halophila* the top contributor for *Oratosquilla stephensoni* and *Fenneropenaeus merguiensis*, and MPB for *Scylla serrata*. Mangroves and saltmarsh succulents were not in the top three contributors for crustaceans either.

Relative importance of in situ *production versus outwelled carbon*

In situ autotroph sources, MPB and part of POM, both ranked in the top three putative contributors to fish species (Table 5), with MPB occurring most frequently (three out of six species). Five out of the six fish species had an *in situ* autotroph in the top three contributors (Table 4). Of the outwelled sources, *Zostera* and saltmarsh grass were in the top three autotrophs most often, being involved in four of the six fish species (Table 5). For crustaceans, MPB and POM both occurred in the top three frequently (Table 5), and each of the three crustacean species had *in situ* sources in the top three (Table 4). Of the outwelled sources, *Halophila* was the most prominent for crustaceans (Table 5).

Table 5. Summary of Euclidean mixing model results for each autotroph. Values represent the number of fish species out of six and the number of crustacean species out of three in total for which the putative contribution of a particular autotroph is important, ranked by putative contribution (1, 2 or 3). % values in final column are representative of combined rankings.

Autotroph	Source	Rank 1	Rank 2	Rank 3	Total	%
Fish (6 species)						
Saltmarsh Grass	outwelled	3	1	-	4	67
Zostera capricorni	outwelled	2	1	1	4	67
Halophila ovalis	outwelled	2	1	-	3	50
MPB	*in situ*	-	1	2	3	50
Algal mat	outwelled	-	2	-	2	33
POM	*in situ*, outwelled	-	1	1	2	33
Mangrove	outwelled	-	-	-	-	-
Saltmarsh Succulent	outwelled	-	-	-	-	-
Crustaceans (3 species)						
Halophila ovalis	outwelled	2	-	1	3	100
Algal mat	outwelled	-	1	1	2	67
POM	*in situ*, outwelled	-	1	1	2	67
MPB	*in situ*	1	-	-	1	33
Saltmarsh Grass	outwelled	-	1	-	1	33
Mangrove	outwelled	-	-	-	-	-
Saltmarsh Succulent	outwelled	-	-	-	-	-
Zostera capricorni	outwelled	-	-	-	-	-

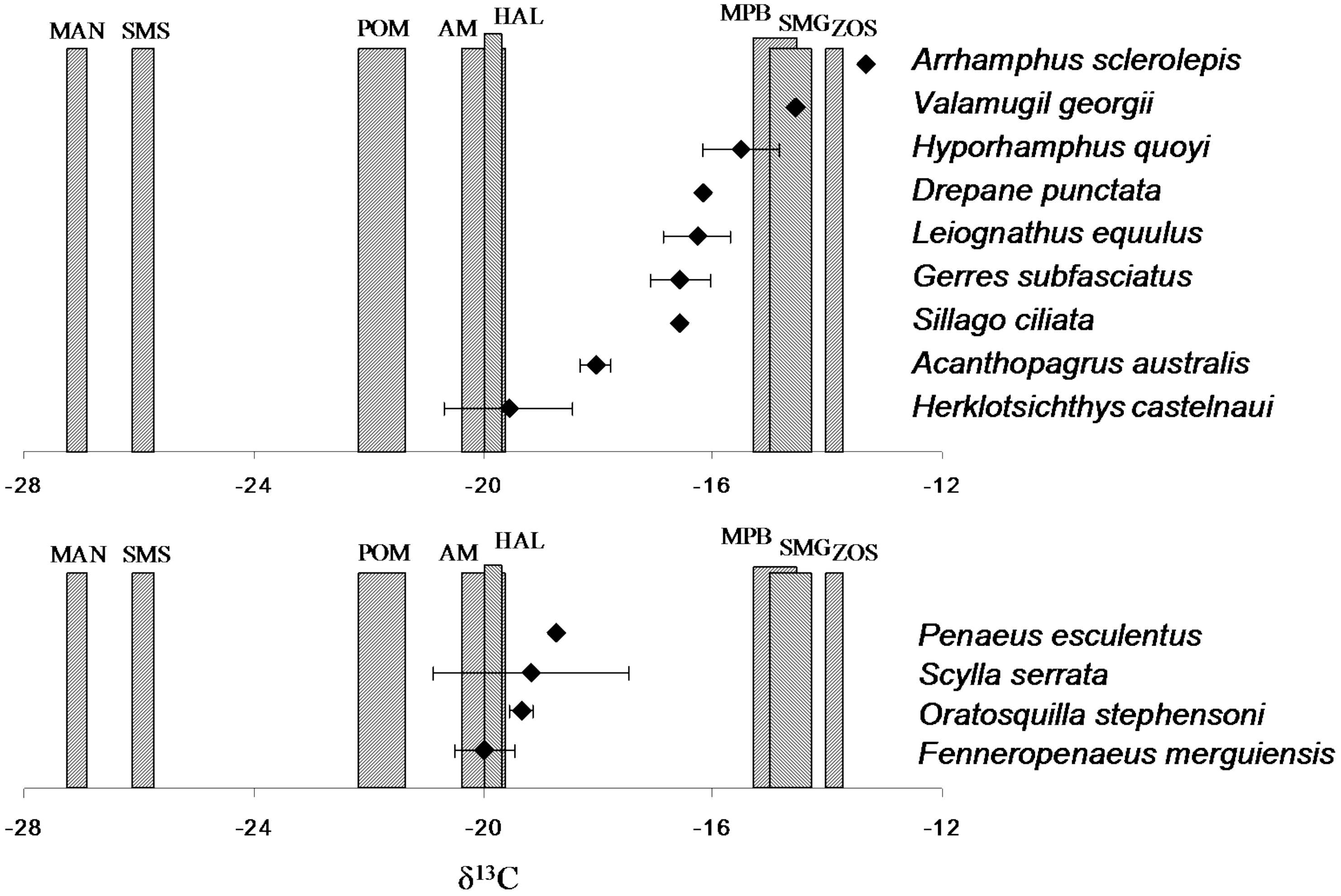

Figure 2: Mean $\delta^{13}C$ (‰) values of fish and crustaceans overlaid on autotroph values. Values are mean ± SE for animals and autotrophs. (Algal mat – AM; Zostera – ZOS; mangroves – MAN; microphytobenthos – MPB; particulate organic matter – POM; saltmarsh grass – SMG; saltmarsh succulents – SMS; Halophila - HAL)

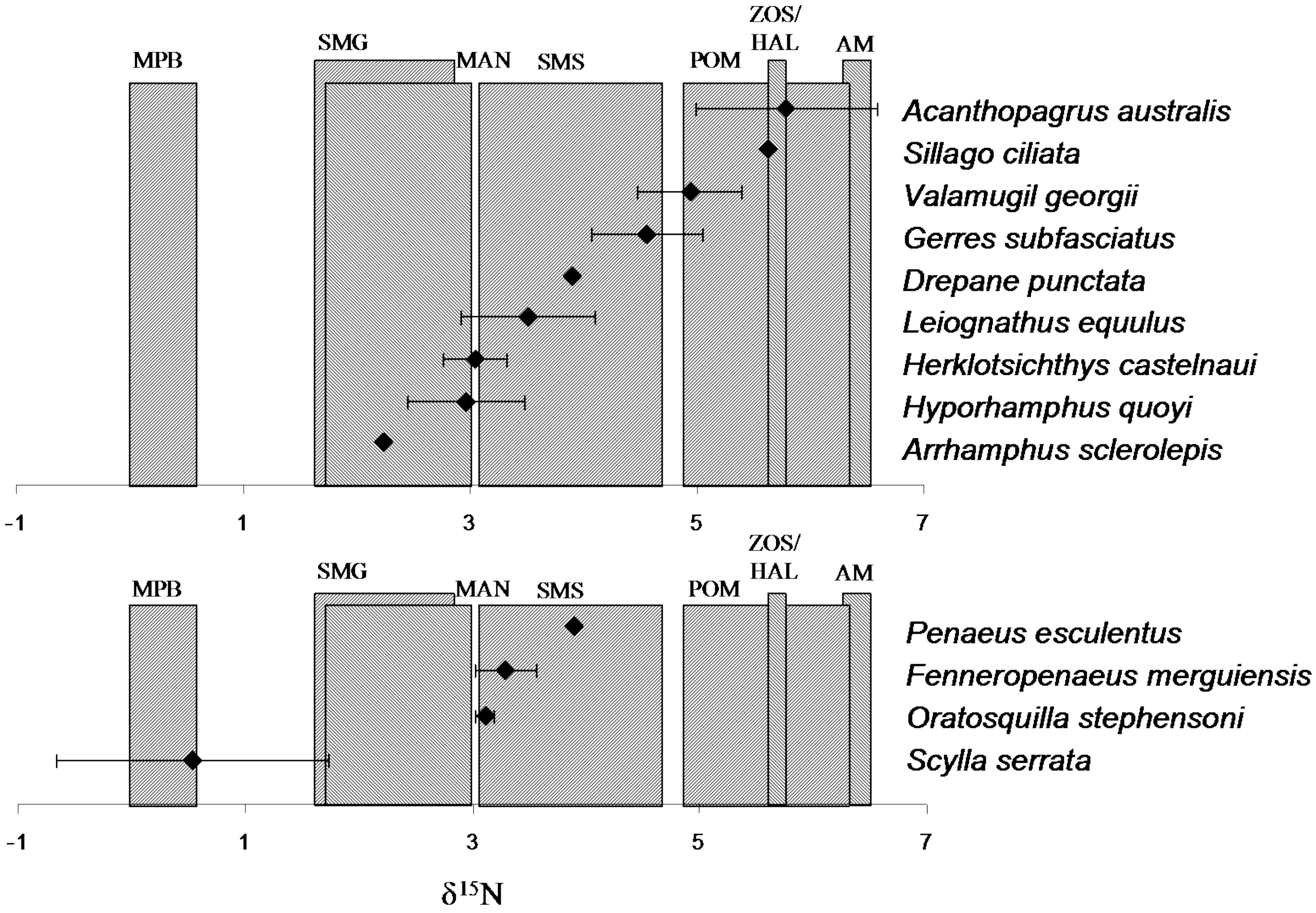

Figure 3: Mean δ^{15}N (‰) values of fish and crustaceans (adjusted for fractionation) overlaid on autotroph values. Values are mean ± SE for animals and autotrophs. Abbreviations as for Fig. 2.

Table 3: Detailed results of Euclidean mixing model for fish and crustacean species. All values are putative contributions (%). Top three contributors in bold.

	Fish						Crustaceans		
	Acanthopagrus australis	*Gerres subfasciatus*	*Herklotsichthys castelnaui*	*Hyporhamphus quoyi*	*Leiognathus equulus*	*Valamugil georgii*	*Oratosquilla stephensoni*	*Fenneropenaeus merguiensis*	*Scylla serrata*
Algal mat	**17**	14	**17**	8	11	8	**17**	**17**	13
Halophila ovalis	**21**	**17**	**22**	9	13	8	**22**	**22**	**14**
Mangroves	5	5	7	4	5	3	7	7	9
MPB	12	12	10	**17**	**15**	**10**	10	9	**16**
Saltmarsh grass	12	**18**	11	**37**	**25**	**16**	11	9	**15**
Saltmarsh succulents	7	6	8	4	5	4	8	9	10
POM	**15**	10	**17**	7	9	6	**16**	**18**	13
Zostera capricorni	11	**18**	9	**14**	**16**	**44**	9	8	10

Table 4: Summary results of the Euclidean mixing model showing top 3 autotrophs for each animal species. Autotrophs are ranked by putative contribution (1, 2 and 3). SMG – saltmarsh grass, POM – particulate organic matter, MPB – microphytobenthos, SG – seagrass.

Species	Autotrophs that contributed most energy			Putative contribution (%)			Standard Deviation about putative contribution		
Fish									
Acanthopagrus australis	Halophila	Algal mat	POM	21	17	15	1.12	0.35	2.03
Gerres subfasciatus	Zostera	SM grass	Halophila	18	18	17	1.14	1.88	1.15
Herklotsichthys castelnaui	Halophila	Algal mat	POM	22	17	17	0.50	0.85	2.14
Hyporhamphus quoyi	SM grass	MPB	Zostera	37	17	14	1.63	1.35	0.79
Leiognathus stephensoni	SM grass	Zostera	MPB	25	16	15	2.24	1.79	2.13
Valamugil georgii	Zostera	SM grass	MPB	44	16	10	1.24	2.31	1.86
Crustaceans									
Oratosquilla stephensoni	Halophila	Algal mat	POM	22	17	16	0.19	0.22	1.64
Fenneropenaeus merguiensis	Halophila	POM	Algal mat	22	18	17	0.55	1.88	0.73
Scylla serrata	MPB	SM grass	Halophila	16	15	14	2.84	2.65	1.70

Discussion

Autotroph isotope signatures

Stable isotope signatures for mangroves (Loneragan et al. 1997) and *Zostera* seagrass (Boyce et al. 2001, Davenport & Bax, 2002), and the carbon isotope signature of one of the saltmarsh succulents, *Sarcocornia quinqueflora* (Boon et al. 1997), are similar to those reported in previous studies. We could find no previous reports of stable isotope signatures for *Suaeda australis* or *Sporobolus virginicus*, however, *S. virginicus* is a C_4 plant (King et al. 1990) and has a $\delta^{13}C$ signature characteristic of C_4 plants. Carbon isotope signatures of POM, which includes phytoplankton, were also within the range of previously reported values (Bouillon et al. 2002) and were central in the spread of the autotroph carbon isotope signatures. This is consistent with POM being derived from a variety of plant sources, including phytoplankton and decomposing components of the other autotrophs (Bouillon et al. 2002). The mean carbon isotope signature of MBP was very enriched compared with values in southern Queensland (Guest et al. 2004a, Guest & Connolly 2004) and elsewhere in the world (Middelburg et al. 2000).

One autotroph taxon had quite different values to those expected from work elsewhere. *Halophila ovalis* had more depleted $\delta^{13}C$ than in Moreton Bay (by > 5 ‰), and could not be pooled with *Zostera capricorni*. Seagrass $\delta^{13}C$ signatures are affected by the amount of light reaching them (related to water depth and turbidity) and probably also exposure to water currents (Grice et al. 1996, Guest et al. 2004b). *Halophila* tends to occur in deeper water than *Zostera* in Port Curtis. Although this depth differential potentially explains the different $\delta^{13}C$ signatures, *Halophila* is also deeper in Moreton Bay where no difference in $\delta^{13}C$ signatures was found. Some factor other than water depth is presumably involved. Where autotroph species have different signatures in different bays it provides an opportunity to distinguish the importance of the sources to animals, and this is the case with the two seagrass species in Port Curtis and Moreton Bay.

Isotope variability

The variability in isotope values among animal species and autotroph groups differed between elements. The variability of $\delta^{13}C$ signatures among fish species was less than that among autotrophs, with values for fish species lying exclusively in the enriched half of the range of autotroph values, and values for crustacean species lying together in the centre of the range for autotrophs. For all fish species this demonstrates that the contribution from the two depleted autotroph sources, mangroves and saltmarsh succulents, is minor.

Mixing models

Results from two element mixing models that have more than three sources should be interpreted with caution. If material from one or more sources contributes nothing to the foodweb, values for other sources will be higher than those reported here. If the non-contributing endmember(s) have a stable isotope signature similar to that of the heterotroph being analysed, the remaining endmembers contribute significantly more than is reported by the model (Phillips & Gregg 2001). The rank order of contributions from remaining sources will not, however, be altered. Various other models have recently been employed to cope with too many sources (e.g. Phillips & Gregg 2003), and a comparison of these with the model employed here would be helpful. Another newly developed analytical technique tracking spatial variability in autotroph and animal isotope values might also prove useful (Melville & Connolly 2003).

A further problem with mixing models (of all types) is the quality of the data used to correct for fractionation. In studies such as these, trophic level must be assigned based on independent information, such as gut content analysis. We used a correction factor of 3 ‰ per trophic level; however, this is a mean (De Niro & Epstein 1981, Peterson & Fry 1987), around which fractionation levels have been shown to vary considerably (e.g. Vander Zanden & Rasmussen 2001). We recommend experimental work to demonstrate how factors such as food quality and growth rates influence fractionation levels for any one species, in combination with the collection of local data on fish and crustacean gut contents. Such experiments will be necessary for key species, since mixing model results would be sensitive to incorrect trophic fractionation adjustments.

Importance of autotrophs to fish

The Euclidean mixing model indicates that across all fish species, *Zostera* and saltmarsh grass are likely to play a substantial role in their nutrition. Several studies have shown how organic matter from seagrass meadows (either the seagrass itself or algae epiphytic on seagrass) contributes to the nutrition of animals living inside the meadows (Lepoint et al. 2000, Moncreiff & Sullivan 2001). The importance of seagrass material to fish occurring elsewhere, however, has been shown only in temperate waters (Thresher et al. 1992, Connolly et al. 2005), so the current study provides important new data regarding the trophic role of seagrass in subtropical waters.

The high putative contributions of saltmarsh grass could simply be a result of this autotroph having a signature similar to *Zostera*. Although the area of saltmarsh in Port Curtis is very large, much of this is unvegetated, and a lot of the vegetated areas consist of saltmarsh succulents. There are no estimates of actual area of saltmarsh grass, but it would be a very small fraction (perhaps as little as 5%) of the saltmarsh area. Given the small area of saltmarsh grass in Port Curtis, and that plants high in the intertidal zone and infrequently inundated are considered to have limited scope for supplying nutrients to deeper waters (Lee 1995), the high putative contribution for this autotroph should be treated with caution. Future work would benefit from using additional elements such as sulfur (Connolly et al. 2004, Oakes & Connolly 2004) or experimental enrichment of C and N isotopes (Winning et al. 1999).

The potentially quite important role of cyanobacterial mats on high intertidal salt flats is the first evidence of this kind, despite previous studies of the extent to which fish utilise the high marsh flats (Thomas & Connolly 2001). Given the degree of developmental pressure salt flats currently face in Pt Curtis, further studies of their trophic importance are recommended.

The mudflats from which fish were sampled are fringed or in one case surrounded by mangrove forests. It is surprising therefore that so little mangrove material is being utilised by fish in Port Curtis. While early studies used the high productivity of mangrove forests to argue that they must be important contributors to food webs (Rodelli et al. 1984), more evidence is accumulating that indicates they contribute little (Lee 2000, Bouillon et al. 2002). Much of the carbon from mangroves is consumed by invertebrates *in situ* (Boto & Bunt 1981, Bouillon et al. 2002) and may be predominantly recycled within the mangrove forest.

Mangroves may nevertheless play other important roles in the ecological structure and function of the coastal zone in Pt Curtis.

In situ production (MPB and part of POM) appears likely to make a substantial contribution to at least some of the fish species occurring over mudflats. Industrial and water transport developments in Port Curtis that require dredging of mudflats may not only affect the amount of habitat available for fish to occupy, but by removing MPB might also reduce autotrophic production sustaining fish production.

Importance of autotrophs to crustaceans

Crustaceans caught over mudflats in Port Curtis were relying on different sources to most fish species. *In situ* production from MPB and phytoplankton (in POM) are important to crustaceans too, but the autotroph material from elsewhere is likely to consist of *Halophila* seagrass rather than *Zostera* (or saltmarsh grass). The contribution from mangroves may be higher to crustaceans than fish, but even species such as *Fenneropenaeus merguiensis* and *Scylla serrata* that are known to have close associations with mangroves obtain no more than about half of their nutrition from mangrove production. These two species occur in mangrove forests as well as on adjacent mudflats, and it would be worth examining in the future whether individuals collected from inside and outside mangroves have different levels of utilisation of mangrove material.

Conclusion

The Euclidean mixing model provided a platform to assess the relative importance of outwelling and *in situ* carbon production to estuarine fish and crustaceans in unvegetated areas of Port Curtis. Outwelled carbon from *Zostera* seagrass beds is a major contributor to many fish species. Mangroves and saltmarsh succulents do not make substantial contributions to the species studied, and saltmarsh grass has a high putative contribution but needs to be considered cautiously because its contribution is unable to be separated from that of seagrass. *In situ* production of MPB and possibly phytoplankton also appears to make a substantial contribution to the nutrition of the fish occurring over unvegetated mudflats in Port Curtis. Seagrass has a high putative contribution to crustaceans, but it is predominantly *Halophila* rather than *Zostera*. The putative contribution to crustaceans of mangroves is higher than for fish, but is still lower than for seagrass or *in situ* sources.

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