RESESARCH ARTICLE

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Food webs supporting fish over subtropical mudflats are based on transported organic matter not in situ microalgae

Abstract We tested the importance of in situ microphytobenthos (MPB) and transported material (seagrass, seagrass epiphytic algae, mangroves, saltmarsh succulents and saltmarsh grass in adjacent habitats) as ultimate sources of carbon to fish caught over mudflats. We measured $\delta^{13}C$ values of these 6 autotrophs and 22 fish species in the subtropical waters of Moreton Bay, Queensland, Australia. All fish $\delta^{13}C$ values lay in the enriched half of the range for autotrophs. We modelled the distribution of feasible contributions of each autotroph to fishes, and then pooled the contributions for autotrophs with similar isotope values. Carbon from the suite of autotrophs having enriched isotope values (seagrass, epiphytes, saltmarsh grass) provided much of the carbon to fishes: 90–100% of carbon for 3 species, 70–90% for 13 species, and 50–70% for 5 species. For the one other species, the contribution of these autotrophs was lower (30–50%), and for this species the contribution of in situ MPB might be as much as about 50%. We could not, however, separate the MPB contribution from that of mangroves and saltmarsh succulents, which was also low for most species. Organic matter from seagrass meadows is clearly important at the base of food webs for fish on adjacent unvegetated mudflats. We are uncertain whether the apparent contribution of saltmarsh grass is real or a spurious result due to the similarity in isotope values of this autotroph and seagrass. This suite of fish caught over mudflats is supported by food webs relying predominantly on carbon from adjacent habitats and not in situ MPB.

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Introduction

Fish that occupy mudflats in estuarine systems must ultimately obtain their energy and nutrients from one of two potential sources, 1) in situ production, or 2) material transported from nearby autotrophs to the mudflats. In situ production occurs on the surface of the mudflats via microalgae and cyanobacteria, collectively known as microphytobenthos (MPB). Organic matter from macrophytes 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 predator–prey interactions (Kneib 2000). We examined the contributions that these sources make to the production of fish over mudflats in the subtropical waters of Moreton Bay, Australia, where several important fisheries species occur over mudflats (Tibbetts and Connolly 1998).

Theories of organic matter transport in coastal waters have been dominated by the outwelling hypothesis, which 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 saltmarshes on the subtropical east coast of Australia, mangroves dominate the mid-intertidal fringes of estuaries there. Forests of mangroves fix approximately 600 g C m^{-2} year^{-1} in Moreton Bay (Dennison and 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 coastal embayments of subtropical Australia and fix approximately 200 g C m^{-2} year^{-1} in Moreton Bay (Dennison and Abal 1999). While some fishes that are common over mudflats directly consume seagrass,

most seagrass is consumed directly by invertebrate grazers or enters the detrital food web (Duarte and Cebrian 1996). Seagrass epiphytes, a mixture of diatoms and fine filamentous algae, have been shown to contribute carbon to many invertebrates that feed in seagrass beds (Moncreiff and Sullivan 2001) and represent a potential source of carbon for fish that occur over mudflats. In-situ production by MPB has been demonstrated to be an important source of carbon for grazing invertebrates on mudflats (Middelburg et al. 2000), and may also be important to fish. MPB is the most productive autotroph in Moreton Bay, fixing about 1,700 g C m^{-2} $year^{-1}$ (Dennison and Abal 1999). Phytoplankton production presumably occurs in the water column over all habitats in Moreton Bay, and could therefore be considered partly in situ.

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 and Shaw 1995) and as such, are preserved at the cost of mudflats. Some fish species occur more often over mudflats than other areas in estuaries (Gray et al. 1998), indicating that mudflats contribute to biodiversity. 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.

Stable isotopes, particularly of carbon, are being widely used to determine which autotrophs supply energy to food webs. Mixing models have been used to assign percent contributions by different autotrophs to the diet of the consumer of interest. Typically, however, these models have been restricted to analysing one more autotroph than elements used. Only recently was a model developed for situations such as the current study where there are far more potential sources than useful elements that can be employed (Phillips and Gregg 2003). Their model calculates all feasible combinations of sources that could explain the consumer isotope value, thereby placing bounds on the dietary contributions of each source.

Many studies have attempted to determine which autotrophs fix carbon used by consumers found in vegetated habitats such as seagrass meadows (Fry et al. 1986; Moncreiff and Sullivan 2001), saltmarshes (Currin et al. 1995) and mangroves (Bouillon et al. 2002). While several studies have examined gut contents of fish caught over mudflats (Connolly 1995), there has been less attention to tracing autotrophic sources. Our own recent work on sillaginid fishes from mudflats in Moreton Bay (Melville and Connolly 2003) and southern Australia (Connolly et al. 2005) has pointed to a greater role for macrophytes than for benthic microalgae. Here, we use carbon stable isotope analysis on a suite of 22 fish species to determine whether carbon transported to mudflats, or in situ MPB production, contributes most to food webs supporting fishes occurring over mudflats in Moreton Bay.

Materials and methods

Sample collection and processing

Moreton Bay in southeast Queensland is characterised by intertidal and shallow subtidal seagrass beds interspersed with extensive mudflats. The coastline is fringed with mangroves, usually backed by saltmarsh. Samples were collected in March 2000 at up to nine locations in southern Moreton Bay (Fig. 1). All samples were frozen immediately upon collection.

Fish were collected from mudflats using seine nets (Table 1). Samples of white muscle were taken for processing. Three species of fish (*Acanthopagrus australis*, *Sillago ciliata* and *S. maculata*) were collected at enough locations to permit a specifically developed spatial analysis of isotope data. Results for those species have been reported previously (Melville and Connolly 2003), but are included again here for completeness. The other 19 species could be collected from only a small number of sites (mostly one or two), preventing conclusive analysis of spatial
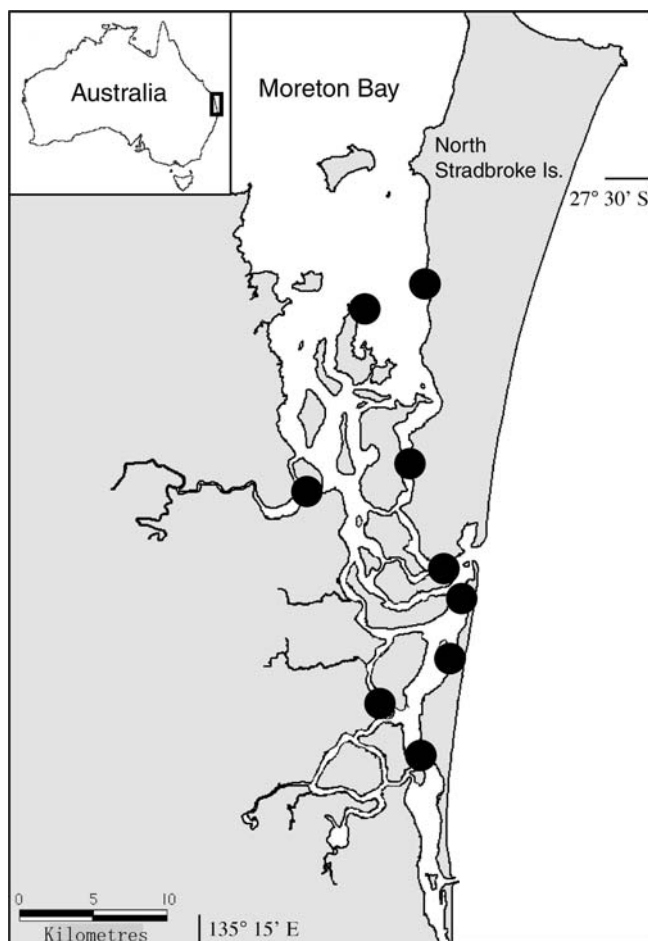

Fig. 1 Map of southern Moreton Bay indicating sampling sites

Table 1 List of fish species, feeding groups, samples sizes, size ranges and their IsoSource category

Species	Common name	Family	Feeding group	n	Size range (mm)	IsoSource category
Acanthopagrus australis	Yellowfin bream	Sparidae	Benthic carnivore	30	45–263	2
Ambassis jacksoniensis	Yellow perchlet	Ambassidae	Pelagic carnivore	13	26–30	4
Arrhamphus sclerolepis	Snub-nosed garfish	Hemiramphidae	Omnivore	4	32–124	2
Girella tricuspidata	Luderick	Girellidae	Omnivore	6	263–342	3
Herklotsichthys castelnaui	Southern herring	Clupeidae	Pelagic carnivore	35	59–115	3
Hyporhamphus australis	Sea garfish	Hemiramphidae	Omnivore	6	192–235	1
Hyporhamphus quoyi	Short-nosed garfish	Hemiramphidae	Omnivore	18	44–130	3
Liza argentea	Tiger mullet	Mugilidae	Detritivore	8	73–250	3
Lutjanus russelli	Moses perch	Lutjanidae	Piscivore	2	56–62	2
Mugil cephalus	Sea mullet	Mugilidae	Detritivore	13	246–303	2
Myxus elongatus	Silver mullet	Mugilidae	Detritivore	12	99–124	1
Platycephalus arenarius	Sand flathead	Platycephalidae	Piscivore	2	66–112	2
Platycephalus fuscus	Dusky flathead	Platycephalidae	Piscivore	9	289–532	2
Pomatomus saltatrix	Tailor	Pomatomidae	Piscivore	8	290–373	3
Pseudorhombus arsius	Large-toothed flounder	Bothidae	Benthic carnivore	18	31–110	2
Pseudorhombus jenynsii	Small-toothed flounder	Bothidae	Benthic carnivore	4	34–54	2
Rhabdosargus sarba	Tarwhine	Sparidae	Omnivore	8	108–288	2
Scomberoides lysan	Double-spotted queenfish	Carangidae	Piscivore	13	50–115	2
Sillago ciliata	Sand whiting	Sillaginidae	Benthic carnivore	136	15–337	2
Sillago maculata	Winter whiting	Sillaginidae	Benthic carnivore	26	19–103	2
Tylosurus gavialoides	Stout longtom	Belonidae	Piscivore	6	248–630	2
Valamugil georgii	Fantail mullet	Mugilidae	Detritivore	8	123–280	1

Feeding groups listed as: benthic carnivores, detritivores, omnivores with a strongly herbivorous bent (labelled "Omnivores"), pelagic carnivores and piscivores. Feeding group is correct for ontogenetic stage used. IsoSource category is defined in Table 2

variability. Data from different locations were therefore pooled. The suite of 22 species is broadly representative of fishes occurring on mudflats in Moreton Bay, with particular emphasis on species of economic importance. The suite includes piscivores (e.g. *Pomatomus saltatrix*), benthic carnivores (*S. ciliata*), pelagic carnivores (*Herklotsichthys castelnaui*), omnivores with a strongly herbivorous bent (*Hyporhamphus australis*), and detritivores (*Mugil cephalus*).

Autotrophs were collected from as many of the locations as possible. Mangrove leaves were collected from three species (*Aegiceras corniculatum*, *Avicennia marina* and *Rhizophora stylosa*). Isotope values of these three species were pooled because they were similar. Three species of seagrass (*Zostera capricorni*, *Halophila ovalis* and *H. spinulosa)* were also collected, and again the isotope values were pooled because they were similar. Seagrass epiphytes were separated from seagrass in the laboratory by scraping them off with a scalpel (Guest et al. 2004a). Saltmarsh plants were collected, and values were pooled into two groups, saltmarsh succulents (*Sarcocornia quinqueflora* and *Suaeda australis*) and saltmarsh grass (*Sporobolus virginicus*). MPB was separated from superficial sediments on mudflats by sieving and centrifuging as described by Connolly et al. (2005).

Phytoplankton densities were very low relative to the high load of sediment and 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), although this was not considered further as a potential source in itself.

All samples were dried to constant weight at 60°C, placed in tin capsules and analysed on an Isoprime isotope ratio mass spectrometer. Ratios of $^{13}C/^{12}C$ were expressed as the relative difference (‰) between the sample and the conventional standard, Pee Dee belemnite limestone carbonate. Precision of the mass spectrometer, calculated as the 90% confidence interval of differences between paired values from duplicate samples, was 0.2‰.

Modelling feasible source mixtures to explain fish nutrition

Autotrophs were pooled into six taxa: mangroves (MAN), microphytobenthos (MPB), seagrass (SG), seagrass epiphytes (EPI), the C_3 saltmarsh succulents (SMS) and the C_4 saltmarsh grass (SMG). Mean $\delta^{13}C$ values were calculated for each fish species and each autotroph taxon across all locations. These mean values were used in the IsoSource model of Phillips and Gregg (2003) to calculate feasible combinations of autotrophs that could explain the consumer signatures. 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. IsoSource reports results as the distribution of feasible solutions for each autotroph. For most fishes, the breadth of distributions for different autotrophs prevented rigourous conclusions about the relative contributions. We therefore combined the contributions for autotrophs with similar isotope values (Newsome et al. 2004), to give sharper estimates of contributions

from three groups of autotrophs (enriched: SG, EPI, SMG; depleted: MAN, SMS; intermediate: MPB).

Samples were also analysed for nitrogen stable isotopes, and we attempted to use this element in the modelling. Previous studies have shown that trophic fractionation is much larger for $\delta^{15}N$ than $\delta^{13}C$ (e.g. Peterson and Fry 1987), hence nitrogen isotopes can provide useful information about the trophic level of animals and 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 any or all of the fishes analysed. The fractionation rate per trophic level is known to vary considerably with animal age, growth rates and food quality (Vander Zanden and Rasmussen 2001), and we had no information about how these factors affected fractionation in any of the species. 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. We decided that using N was unhelpful in feasibility modelling and therefore in tracing autotrophic sources.

Fractionation in $\delta^{13}C$ is relatively minor, typically < 1‰ per trophic level (McCutchan et al. 2003). Previous IsoSource modelling has shown that, where autotrophs are well separated, variations in consumer $\delta^{13}C$ values of 1‰ have little effect on the reported distributions and do not affect the rank order of autotroph contributions (Connolly et al. 2005). We therefore used no correction for fractionation for $\delta^{13}C$ in the current study.

Results

Autotroph and fish isotope values

Carbon isotope values of the six autotroph taxa were generally well separated (Fig. 2). Mangroves and saltmarsh succulents had the most depleted $\delta^{13}C$ values while seagrass, seagrass epiphytes and saltmarsh grass had the most enriched values. MPB values were intermediate. The mean $\delta^{13}C$ value for seston was −19.8‰ (SE 0.4).

Isotope values of fish varied, but less so than for autotrophs (Fig. 2). All fish species had $\delta^{13}C$ values lying within the enriched half of the range of autotroph values, between approximately −12 and −21‰.

Modelling results

The range of feasible contributions for each autotroph was very broad for most fishes. Median and maximum contributions were higher for the enriched sources (seagrass, epiphytes and saltmarsh grass) than for either

MPB or the depleted macrophytes (mangroves and saltmarsh succulents), but the breadth of the distributions limited the conclusions we could make directly from the IsoSource results for most species (see *Pomatomus* result as an example, Fig. 3). The combined contributions of the autotrophs in the three groups, however, defined contributions much more sharply (one fish species shown as an example for each of four categories, Fig. 4). Fishes fell into four categories (Table 2), defined by the range of possible contributions from the enriched groups of autotrophs (seagrass, epiphytes, saltmarsh grass). The enriched autotrophs contributed 90–100% of the carbon for 3 species, 70–90% for 13 species, 50–70% for 5 species and 30–50% for 1 species (Table 1). *Hyporhamphus australis*, an omnivore with a major herbivorous component to its diet, had a very enriched $\delta^{13}C$ value, slightly more enriched even than the value of the most enriched autotroph (seagrass). IsoSource modelling could not be used for this species, since it lay just outside the range of autotroph values. We therefore ascribed this species a value of 100% seagrass contribution, and it was thus included in category 1. A clear result was also obtained for *Valamugil georgii*, for which the seagrass contribution was demonstrated even prior to the combining with the other enriched autotrophs (Fig. 3).

The remainder of the carbon is derived from MPB or the depleted macrophytes (mangroves and saltmarsh succulents). For most species, however, the range of possible contributions for these two groups are not easily separated and their relative contributions remain unresolved.

Discussion

Autotroph and fish isotope values

Most of the autotroph $\delta^{13}C$ values have been presented and discussed previously (Melville and Connolly 2003). Given the current focus on mudflats, it is important to substantiate the $\delta^{13}C$ determination for MPB. The mean $\delta^{13}C$ value of MBP was at the depleted limit of values reported from mudflats (Middelburg et al. 2000; Wainright et al. 2000), similar to values determined for MPB on the sediments of mangrove forests (Guest et al. 2004b), where the entire carbon pool is thought to be depleted via photosynthesis of the mangroves (Bouillon et al. 2002). Many methods have been used to collect and extract algal cells from sediment for isotope analysis, but our method is considered the most reliable (Hamilton et al. 2005).

Isotope values of fish were about where they could be expected from our own previously published analyses (Melville and Connolly 2003) and studies in estuarine habitats elsewhere (e.g. Peterson and Fry 1987). We analysed a more comprehensive suite of species than most other studies, and provided the first focussed attempt at determining fishery food webs over unvegetated
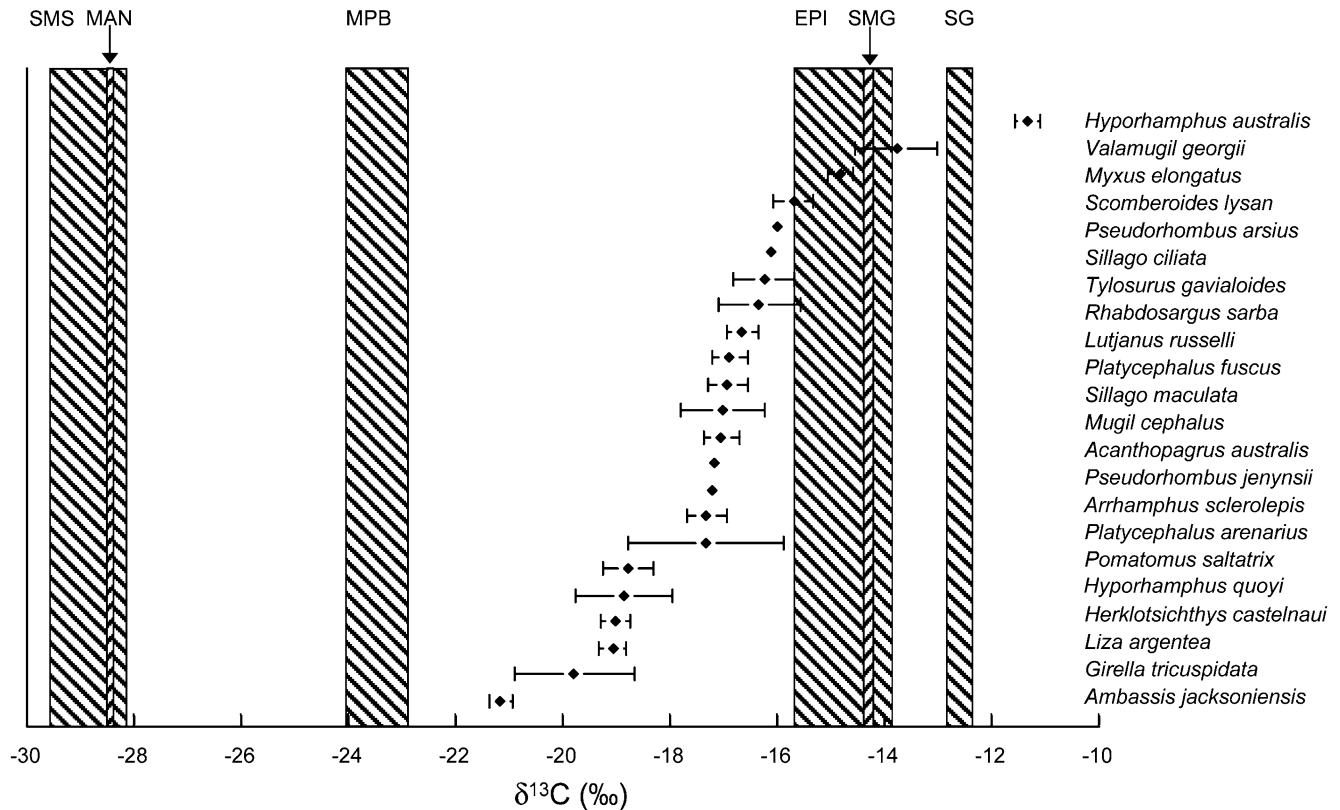
Fig. 2 Mean δ^{13}C values of fish overlaid on autotroph values. Values are mean $\pm$ SE for fish and autotrophs

mudflats. The most striking feature of our results is the narrow range of isotope values for the majority of fish, with 17 of the 22 species lying between approximately -16 and -19‰.

Modelling results

IsoSource modelling successfully highlighted autotrophs likely to make major contributions to the nutrition of fish. The combination of raw IsoSource results for groups of autotrophs having similar isotope values greatly improved the interpretation. Nevertheless, results from any mixing model used to analyse many more sources than elements should be interpreted with caution (Phillips and Gregg 2003).

The main issue with the current results is whether all three of the enriched autotrophs contribute to the nutrition of fish. Any autotroph with an isotope value similar to that of another autotroph making a major contribution to fish nutrition will necessarily appear to be making a contribution, whether or not it is. There is a distinct possibility, in particular, that saltmarsh grass merely appears to be an important contributor because it has a similar δ^{13}C value to seagrass and its epiphytes. Although saltmarsh grass is a C$_4$ plant and is likely to be highly productive, the total areal cover of saltmarsh (7 km^2) is only 17% of that of seagrass in the study area (Sinclair Knight Mertz 2000). Saltmarsh consists of areas of both

succulents and grass, therefore the areal cover of saltmarsh grass will be less than this. Also, it is situated higher on the shore than mangroves and is only inundated on spring tides. It has been shown that infrequent inundation prevents material produced by upper intertidal autotrophs entering the main waterways of an estuary (Lee 1995). This query over the relevance of saltmarsh grass does not reduce the effectiveness of our test of in situ versus transported carbon, but we recommend further tests using alternative elements such as sulfur (Connolly et al. 2004) to separate the contributions of organic material from seagrass meadows and saltmarshes.

A smaller issue with the feasibility modelling is that the δ^{13}C value of one species, *Hyporhamphus australis*, was slightly more enriched than the value of even the most enriched autotroph. Confamilial hemirhamphids are known to ingest seagrass directly (Connolly 2003). The slight enrichment of *H. australis* values relative to even the most enriched autotroph is probably due to either selective assimilation of seagrass cellular components, or enrichment by fractionation between source and consumer. In any case, this species shows no reliance on in situ MPB production.

Relative importance of in situ production versus transported carbon

The majority of carbon in fish caught over mudflats is clearly derived from adjacent habitats. Not all adjacent habitats play an important role, however. Foremost among the transported carbon was organic material
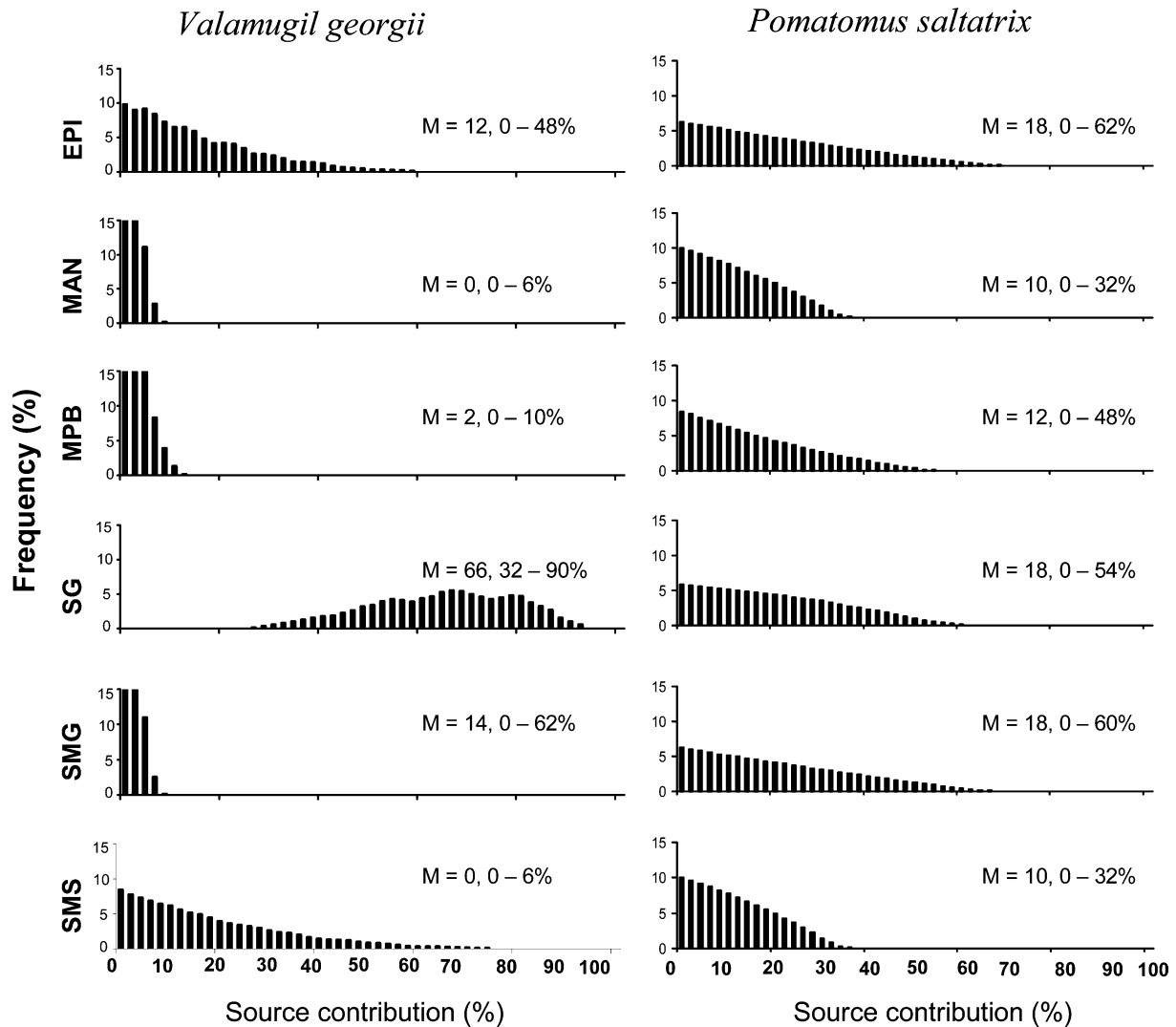
Fig. 3 Distributions of feasible contributions of the 6 autotrophs to *Valamugil georgii* and *Pomatomus saltatrix* based on δ^{13}C values only. *M* median, the ranges are 1 and 99 percentile values. Autotroph codes as for Fig. 2

from seagrass meadows. Seagrass meadows cover a substantial amount of the study area (estimated at 41 km², Sinclair Knight Mertz 2000). Some of the species caught over mudflats are also caught over seagrass meadows. These species might have obtained some of their carbon directly from seagrass meadows. All but the piscivorous species might obtain seagrass carbon by consuming invertebrates that feed in seagrass beds but move to mudflats. Piscivorous fish might then consume seagrass carbon via the fish that feed on invertebrates. As such, the suite of fish may be part of a trophic relay from seagrass beds to mudflats (Kneib 2000). Algae epiphytic on seagrass also seems likely to make a large contribution to fish nutrition.

Several studies have shown that animals living within seagrass meadows rely on organic matter produced there (Moncreiff and Sullivan 2001), but fewer have detected a role for seagrass material in adjacent habitats. More organic material is produced in seagrass meadows than can be consumed there (Duarte and Cebrian 1996), and occasionally this material has been shown to underpin food webs in adjacent habitats, either offshore (Thresher et al. 1992) or on sandy beaches (Robertson and Lenanton 1984). Organic material from seagrass meadows was shown recently to play an important role in food webs on mudflats in the shallow waters of southern Australian embayments (Connolly et al. 2005).

It is difficult to separately assess the contribution of mangrove carbon to fish from that of saltmarsh succulents and MPB, but for the majority of fishes the maximum contribution that could have been made by mangrove carbon was small (<30%). Although the extent of mangroves in the study area is large (70 km², Sinclair Knight Mertz 2000), their minor contribution is not unexpected. While early studies used the high productivity of mangrove forests to argue that they must be important contributors to food webs, evidence is accumulating that they contribute little (Lee 1995). Contributions of mangrove carbon may be more substantial for other species. For the five species in category 3,

Fig. 4 Combined contributions from three autotroph groups to four fish species, representing one species from each of the four IsoSource categories
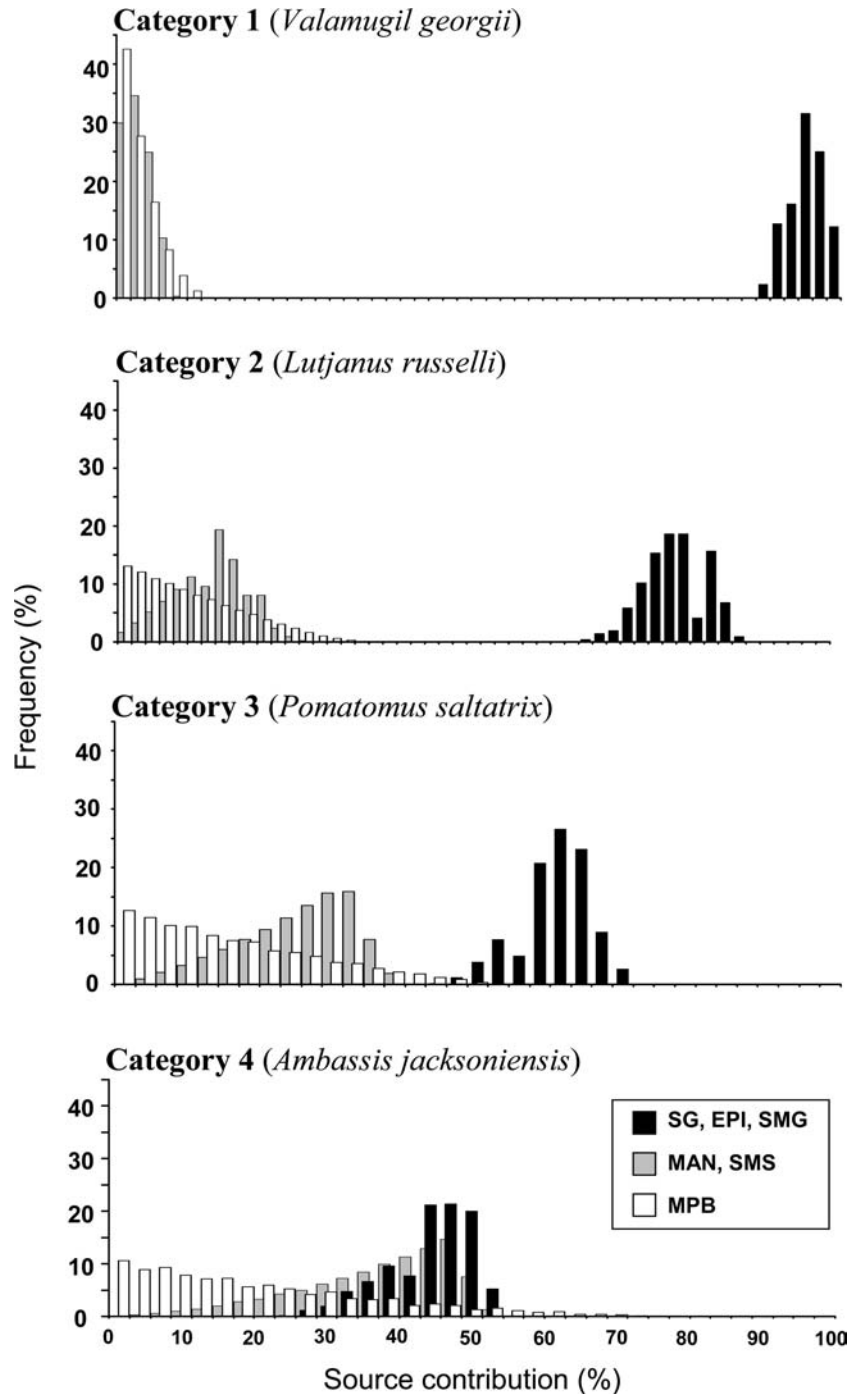
mangrove carbon might have contributed as much as 50%, and for *Ambassis jacksoniensis* in category 4 perhaps even more.

The lack of assimilation of carbon from MPB by the animals occurring on mudflats is unexpected. After being overlooked in food web studies for many years, the importance of MPB in estuarine food webs has emerged recently as a recurrent theme. MPB on mudflats is assimilated by meiofauna (Middelburg et al. 2000), and macroinvertebrates in mangrove forests (Bouillon et al. 2002) and saltmarsh (Wainright et al. 2000) also

assimilate carbon from MPB in intertidal sediments. We have previously argued that the importance of MPB in food webs may depend on algal productivity (Connolly et al. 2005), but in Moreton Bay, productivity is high (Dennison and Abal 1999), yet their role is minor. Perhaps the strong tides in the study area move particulate organic matter so effectively that material from adjacent habitats is freely available on mudflats.

The isotope survey of detritivorous fishes is particularly helpful in determining their dietary sources. Traditional methods such as stomach contents analysis

Table 2 Descriptions of the four IsoSource categories (ranges of contributions)

IsoSource category	Range of contributions (%)	
	Seagrass, epiphytes, saltmarsh grass	Mangrove, saltmarsh succulents and/or microphytobenthos (MPB)
1	90–100	0–10
2	70–90	10–30
3	50–70	30–50
4	30–50	50–70

cannot separate the roles of the many different components of the sediment ingested during feeding. Isotope analysis of these species has proven effective and useful. Prior to this study we considered that detritivores were particularly likely to be relying on MPB, yet instead we found that they obtain their carbon from transported macrophyte and/or epiphytic algae material. They possibly also ingest interstitial microfauna but, if these are important, then they too are relying on transported material. A heavy reliance on organic material from seagrass meadows has previously been shown for detritivorous invertebrates on mudflats in southern Australia (Connolly et al. 2005).

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