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Stable isotope evidence for trophic subsidy of coastal benthic fisheries by river discharge plumes off small estuaries

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Abstract

Major rivers produce large plumes which subsidise benthic marine food webs. Because most plumes are smaller, we tested whether these also can link marine food webs with riverine discharges. We used stable isotopes to detect assimilation of terrestrial organic matter by fish, crustaceans and cephalopods harvested from plume areas off two small estuaries in eastern Australia, contrasted with values from marine reference sites. A terrestrial signal was evident in most marine consumers as shifts in carbon and nitrogen isotope ratios. The strongest signal for terrestrial carbon uptake was found in two species harvested commercially, the portunid crab, *Portunus sanguinolentus*, and the flounder, *Pseudorhombus arsius*, demonstrating a link between river discharge and fisheries productivity in coastal seas. Against a backdrop of the general presence of a trophic signal imparted by small plumes, absolute contributions of these subsidies were, however, smaller than in larger systems. Also, for the species occurring in both coastal and estuarine waters (sand whiting, *Sillago ciliata*), isotopic variation was considerably smaller in marine waters than across the estuarine gradient. Overall, small plumes can make contributions to the energy requirements of coastal fisheries species, but their ephemeral nature and small physical dimensions set limits to the degree of land-water ecotonal coupling.

Keywords: crabs, fish, *Penaeus*, stable isotope analysis, trophic subsidy

Introduction

Rivers make substantial contributions of energy (carbon) and nutrients to oceans via estuarine plumes (Ludwig et al. 1996). These contributions are measured in the context of global mass-balance budgets. This is important for our general understanding of carbon transport and for estimating the extent of anthropogenic influence in coastal waters (Cloern 2001). It seems obvious that these inputs could play a role in living components of marine ecosystems, including the benthos, which has been shown to receive organic matter sinking from plumes (Alliot et al. 2003). Although plumes are generally regarded as areas of enhanced biological activity (Devlin et al. 2001; Dagg et al. 2004), this aspect of estuarine plumes is not well known for benthic animals.

One of the key ecosystem processes likely to be affected by estuarine plumes is trophic dynamics. The expectation from detailed studies of sheltered, inshore seas is that outwelled material supports higher secondary production than would otherwise occur (Odum 1968). In aquatic systems, carbon is considered to be more mobile than in terrestrial systems because water acts as a vector for particulate and dissolved organic matter (Carr et al. 2003). There is potential, therefore, for matter exported from estuaries to subsidise food webs elsewhere, especially in coastal waters. Correlations between annual flows in coastal rivers and the size of fish catches (e.g. Lloret et al. 2001; Quinones and Montes 2001) provide indirect evidence for such an effect, but the mechanism underlying such correlations remains mostly unknown (Loneragan and Bunn 1999; Gillanders and Kingsford 2002).

Stable isotope analysis has become the most common method for tracing energy and nutrient transfers over large distances (West et al. 2006). Nitrogen isotopes have been used, for example, to investigate the incorporation of anthropogenic sources of nitrogen from developed catchments into marine food webs (Hansson et al. 1997; Waldron et al. 2001). Stable isotopes also provide an efficacious measure of relative contributions of different food sources, such as terrestrial and marine sources, which often have distinct isotopic ratios (Peterson and Fry 1987). For carbon, this occurs either because plants have different photosynthetic pathways or because they obtain carbon from air rather than water. For nitrogen, the variation in isotopic signatures usually results from the effects of widespread changes in catchment land-uses, in particular urbanisation (McClelland et al. 1997). Since the isotope end-members of the broad source categories, terrestrial and marine, are reasonably well known, stable isotope analysis can detect riverine input to coastal waters (Darnaude et al. 2004b).

Stable isotope studies of large plumes from major rivers discharging into coastal waters have shown that there are food web consequences of plume inputs. For example, a stable isotope study in the Black Sea detected assimilation of riverine organic matter from Europe's second largest river, the Danube, by detritivorous invertebrates and some fish species (Banaru and Harmelin-Vivien 2006). And in the oligotrophic waters of the Mediterranean Sea, isotope signatures of benthic invertebrates reflect a measurable contribution from the Rhone River (Darnaude et al. 2004b). At the higher trophic level of fish themselves, the pattern is less pronounced but nevertheless detectable (Darnaude 2005). For these large rivers, plumes are extensive, and animal isotope values are affected over distances of ten or more kilometres from the river mouth (e.g. Riera and Richard 1997; Lee 2000; Darnaude et al. 2004a). Despite evidence for land-ocean coupling in large river plumes, most rivers discharging to coastal seas worldwide are smaller and generate smaller plumes. In the context of trophic

dynamics of coastal waters, the question thus arises whether such smaller plumes also subsidise marine fisheries food webs.

The extent of plumes from small estuaries has been determined from maps of the distribution of conservative tracers in sediments. In southeast Queensland, Australia, for example, where small estuarine plumes punctuate long stretches of sandy coastline, plumes off the Mooloolah River after heavy rain cover an area of 1- 2 km² (Gaston et al. 2006). The background information about physico-chemical and organic matter properties available for this river led us to use it, and the nearby Maroochy River (Schlacher et al. 2005), as representative examples of small estuarine plumes. Conceptually, the nutrition of fish in coastal waters will be some mixture of marine and terrestrial/estuarine sources. For smaller estuaries such as the Mooloolah and Maroochy, we expect any subsidy of animal nutrition from estuaries to be most easily detected against background isotope ratios of the same fish species at reference sites far (> 10 km) from potential plume influences. Our strategy, therefore, was to compare carbon and nitrogen isotope values for a suite of species occurring at plume and non-plume sites. We focussed on benthic species with relatively restricted movements, since these are more likely than pelagic species to be part of food webs affected by plumes (Darnaude et al. 2004a). As stable isotope ratios of fish are known to vary strongly among different reaches of estuaries (Deegan and Garritt 1997), we also sought to provide a wider context for changes in isotope values (and thus nutrition) by sampling one common species from sites along the estuarine gradient as well as in coastal waters.

Material and methods

Animal collections

We designed a purpose-specific sampling program using trawl collections of benthic assemblages of fish, crustaceans and cephalopods. The spatial component of our design was a contrast between replicate plume areas and multiple ($n = 4$) marine reference sites in non-plume areas (Figure 1). Thus, benthic consumers were collected from two sites within the known area of the combined influence of plumes from two adjacent estuaries, whereas reference sites were located well outside the influence of any estuaries, a minimum of 10 km offshore and from areas further north where no river influence exists (Figure 1). We knew the extent of plumes from multiple aerial surveys of conspicuous turbidity fronts, and mapping of copper concentrations and isotope signatures of organic matter in sediments (Gaston et al. 2006).

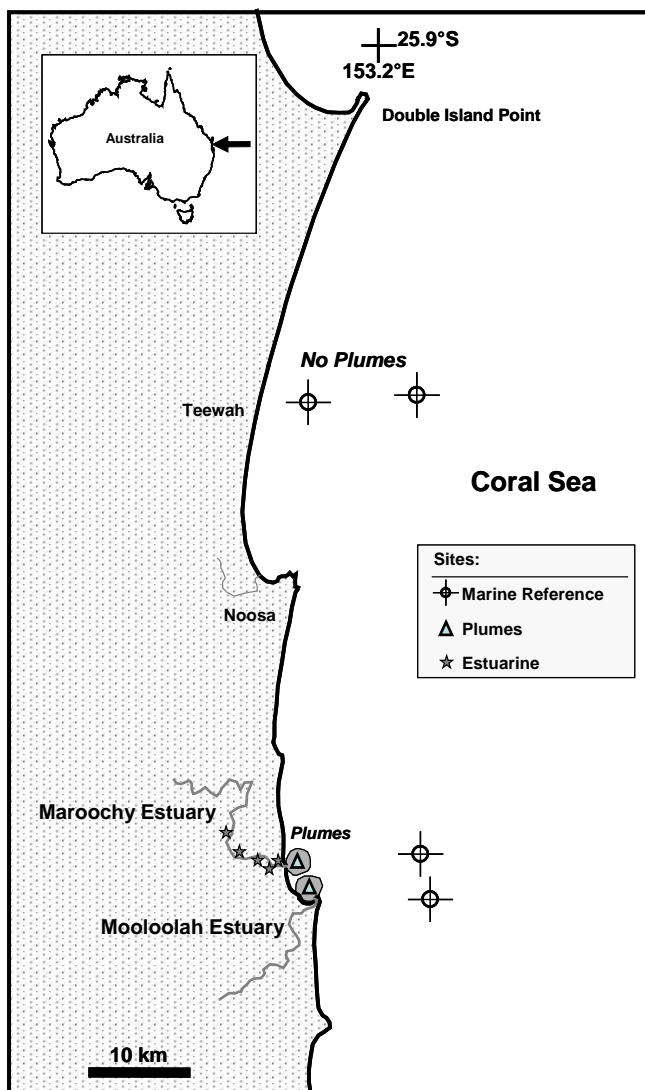


Figure 1 Map showing sampling sites for animals in areas under plumes caused by discharges from the Maroochy and Mooloolah estuaries, contrasted with sites offshore and to the north well outside the influence of plumes.

The strength of the terrestrial signal in isotope studies of food webs in plume areas has been shown to increase after periods of high river flow (Banaru and Harmelin-Vivien 2005). In the study region, strongly seasonal rainfall implies that the maximum trophic subsidy of coastal waters is expected to occur at the end of the wet season (austral summer), after most of the annual river discharge has entered coastal seas in the form of multiple plume events. Thus, samples were taken over 2 days of trawling in May 2003, at the end of the (austral) summer.

For estuarine sampling, we required species that occurred in marine waters and also along the estuarine gradient. Just one species fulfilled this requirement, the sand whiting (*Sillago ciliata*). Sand whiting were collected at five sites spaced along the middle and lower reaches, covering the final 10 km of the estuary (Figure 1). This is an important fisheries species known to feed on benthic invertebrates, that has previously been part of stable isotope studies in the Maroochy estuary (Schlacher et al. 2007) and nearby waters (Melville and Connolly 2003). The Maroochy estuary, like the Mooloolah (Gaston et al. 2006), is narrow (width 100–300 m) and shallow (generally < 3 m). The Maroochy catchment is a mixture of natural forest and rural lands, with urbanised lower reaches. The forests of the catchment and mangrove-lined banks of the middle reaches provide organic matter inputs with carbon isotope ratios distinctly depleted in ^{13}C (around -30 ‰), but small patches of seagrass in the lowest estuarine reach (the last 2 km) have distinctly enriched ratios (around -12 ‰). Nitrogen isotope ratios are enriched in upper and middle estuarine reaches by treated sewage entering through multiple outfalls (Schlacher et al. 2007). Overall, the overwhelming river plume signal to the sea is suspended particulate organic matter (SPOM) with depleted carbon and enriched nitrogen isotope ratios relative to marine reference values: namely, for $\delta^{13}\text{C}$: -26 river versus -21 ‰ marine; and for $\delta^{15}\text{N}$: +8 river versus +3 ‰ marine (Schlacher et al. 2005, Gaston et al. 2006).

Stable isotope analysis

Muscle tissue was dissected from animals and dried to constant weight at 60°C, before being placed in tin capsules and analysed in the Isotope Analytical Facility of Griffith University on an automated Isoprime Isotope-Ratio Mass Spectrometer. Stable isotope ratios are expressed in ‰ using the conventional delta (δ) notation: $\delta X (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$; where X is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, and R is the $^{15}\text{N}/^{14}\text{N}$ (nitrogen) or $^{13}\text{C}/^{12}\text{C}$ (carbon) ratio in the sample and standards (Vienna PDB equivalent for carbon and the IAEA international standard of atmospheric N_2 for nitrogen). Precision of this mass spectrometer for fish and invertebrate samples is 0.2 ‰, calculated as the 90% confidence interval of differences between paired values from duplicate samples.

Results

Carbon

Uptake of terrestrial and estuarine carbon was predicted to lower the carbon isotope ratios of marine consumers under plumes. Two-thirds of species did, indeed, have more depleted carbon isotope ratios in plume than in non-plume areas, indicating a trophic subsidy of material outwelled from estuaries (Table 1). Over the whole assemblage, there was a clear pattern of small but measurable depletion of carbon ratios in plume areas (Figure 2). Carbon isotope depletion in individual species ranged up to 1.5 ‰, and was strongest for a portunid crab (*Portunus sanguinolentus*) and a flatfish (*Pseudorhombus arsius*). Significantly, both of these species are caught in regional fisheries, indicating the presence of a terrestrial carbon subsidy in marine fishery production. Of the remaining species, *Sillago ciliata* showed no distinct spatial contrast in carbon signatures, while two others showed small and non-significant differences (Table 1).

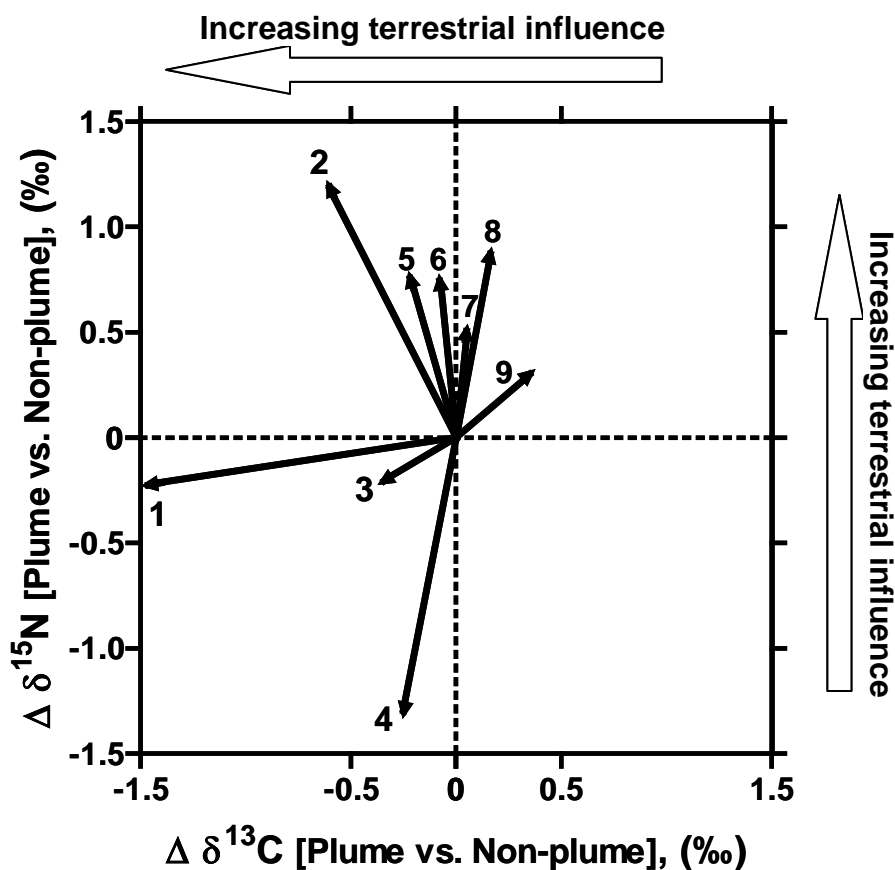


Figure 2 Contrasts in carbon and nitrogen isotope ratios in animals from plume and non-plume areas. For each species, the vector shows the mean difference in isotope ratios inside the plume area against the reference non-plume mean (zero). Species Numbers: 1-*Portunus sanguinolentus* (Three spot crab); 2-*Pseudorhombus arsius* (Large-toothed flounder); 3-*Paramonocanthus choirocephalus* (Hair-finned leatherjacket); 4-*Saurida undosquamis* (Large-scaled grinner); 5-*Penaeus esculentus* (Tiger prawn); 6-*Penaeus plebejus* (Eastern king prawn); 7-*Sillago ciliata* (Sand whiting); 8-*Sepioteuthis* spp. (Squid); 9-*Platycephalus arenarius* (Sand flathead).

Table 1 Contrasts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of animals from plume and non-plume areas. Significant differences between plume and non-plume means using one-way ANOVA are marked * ($p < 0.05$).

$\delta^{13}\text{C}$ (‰)						
	Plume			Non-plume		
	n	mean	(SE)	n	mean	(SE)
Crustaceans						
<i>Penaeus esculentus</i> (Tiger prawn)	13	-16.31	(0.20)	5	-16.10	(0.18)
<i>Penaeus plebejus</i> (Eastern king prawn)	20	-17.18	(0.13)	3	-17.11	(0.16)
<i>Portunus sanguinolentus</i> (Three spot crab)*	16	-17.47	(0.16)	9	-16.02	(0.08)
Cephalopods						
<i>Sepioteuthis</i> sp. (Squid)	7	-18.63	(0.11)	4	-18.78	(0.40)
Fishes						
<i>Paramonocanthus choirocephalus</i> (Hair-finned leatherjacket)	5	-17.76	(0.08)	4	-17.44	(0.13)
<i>Platycephalus arenarius</i> (Sand flathead)	6	-16.62	(0.25)	3	-16.96	(0.40)
<i>Pseudorhombus arsius</i> (Large-toothed flounder)*	10	-17.63	(0.16)	6	-17.03	(0.27)
<i>Saurida undosquamis</i> (Large-scaled grinner)	9	-17.73	(0.12)	14	-17.48	(0.24)
<i>Sillago ciliata</i> (Sand whiting)	12	-17.35	(0.10)	15	-17.40	(0.12)
$\delta^{15}\text{N}$ (‰)						
	Plume			Non-plume		
	n	mean	(SE)	n	mean	(SE)
Crustaceans						
<i>Penaeus esculentus</i> (Tiger prawn) *	13	9.58	(0.32)	5	8.84	(0.28)
<i>Penaeus plebejus</i> (Eastern king prawn) *	20	9.80	(0.31)	3	9.08	(0.03)
<i>Portunus sanguinolentus</i> (Three spot crab)	16	10.00	(0.20)	9	10.22	(0.28)
Cephalopods						
<i>Sepioteuthis</i> sp. (Squid) *	7	10.86	(0.21)	4	10.01	(0.25)
Fishes						
<i>Paramonocanthus choirocephalus</i> (Hair-finned leatherjacket)	5	9.16	(0.56)	4	9.35	(0.35)
<i>Platycephalus arenarius</i> (Sand flathead)	6	12.86	(0.25)	3	12.59	(0.08)
<i>Pseudorhombus arsius</i> (Large-toothed flounder)*	10	12.28	(0.48)	6	11.10	(0.42)
<i>Saurida undosquamis</i> (Large-scaled grinner) *	9	12.83	(0.47)	14	14.12	(0.40)
<i>Sillago ciliata</i> (Sand whiting) *	12	11.45	(0.20)	15	10.98	(0.18)

For sand whiting, carbon isotope ratios varied much more strongly with distance up the estuary (range > 5 ‰) than over the same distance between plume and non-plume areas (range < 0.5 ‰, Figure 3). Individuals from the middle reaches were strongly depleted in ^{13}C (< -20 ‰), gradually becoming more intermediate until in the lower estuary, ratios were markedly enriched (> -15 ‰; Figure 3).

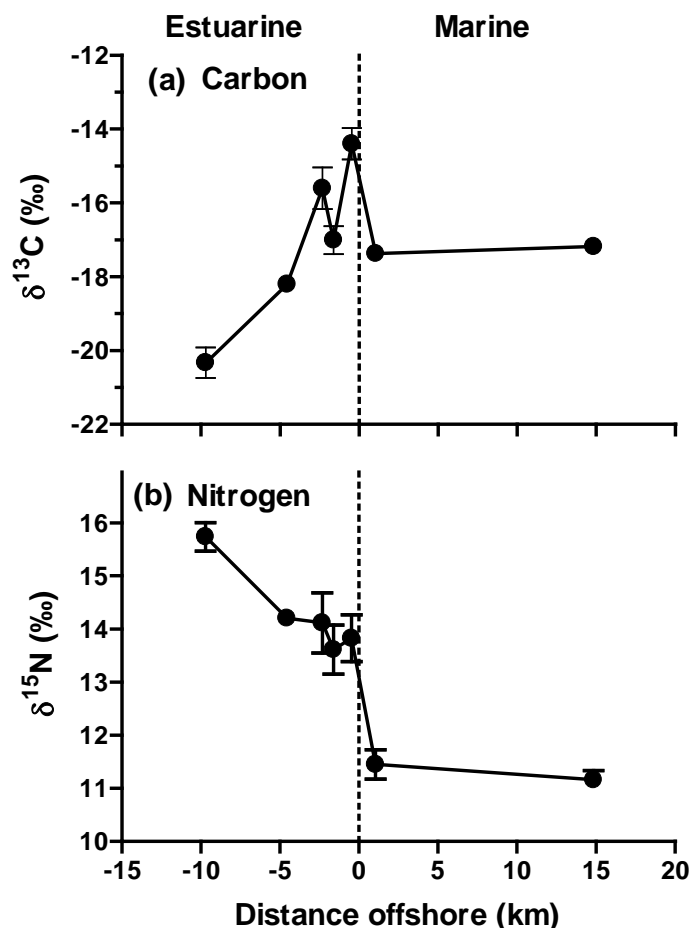


Figure 3 Spatial gradients in mean (SE) carbon and nitrogen isotope ratios in sand whiting (*Sillago ciliata*) from the Maroochy estuary to shelf areas 15 km offshore. Shaded side is up estuary.

Nitrogen

Spatial differences in nitrogen isotope ratios in animals from plumes and non-plume areas generally indicated some extent of river influence in a pattern similar to differences in carbon isotopes. More enriched nitrogen isotope ratios, which are indicative of uptake of terrestrial matter, were detected in two-thirds of marine consumers caught under plumes. Differences between plume and reference non-plume sites ranged up to 1.3 ‰, and most were between 0.5 and 1.0 ‰ (Table 1). Significant spatial differences consistent with a model of land-ocean coupling were evident in five species, whereas fewer species showed an opposite and generally small (< 0.5 ‰) and non significant change; a single species (*Saurida undosquamis*) was significantly more enriched by 1.3 ‰ outside plumes.

Nitrogen isotope ratios of sand whiting in the estuary were, as for carbon, much more variable (range 4 ‰) than between plume and non-plume areas (range < 0.5 ‰, Figure 3). The mean ratio was highly enriched (> 15 ‰) in the middle reaches and remained elevated at all other estuarine sites. The transition from the lower estuary to the sea coincided with the largest change in nitrogen ratios of these fish (Figure 3).

Discussion

Our stable isotope survey demonstrates that riverine organic matter is incorporated into nearshore, marine food webs. Delivery of this material occurs via small rivers that discharge directly onto high-energy, exposed coastlines. Despite the presence of an overall signal of land-ocean coupling in the food webs under river plumes, the absolute strength of trophic subsidies by riverine organic matter was not large. The marine fisheries species sampled in this study obtain their nutrition overwhelmingly from marine sources, complemented by a smaller contribution of externally delivered material of estuarine and terrestrial provenance. Such marine dominance reflects the small size and ephemeral nature of the plumes against a background of massive sediment and organic matter inputs from rivers to coastal seas on a global scale (Schlünz and Schneider 1999; Devlin et al. 2001; Wooldridge et al. 2006).

Shifts in carbon isotope ratios of animals in plume areas relative to non-plume areas were the same as in studies of plumes of larger rivers, denoting the presence of a terrestrial/estuarine signal in the tissues of marine consumers. However, the magnitude of isotopic depletion in marine consumers from areas influenced by river discharge (maximum of 1.5 ‰, but generally < 0.5 ‰ in the current study) is smaller than that detected for larger rivers (Lee 2000; Darnaude 2005; Banaru and Harmelin-Vivien 2006). Even in larger plumes, however, isotopic differences between plume and non-plume areas vary among species, in a similar fashion to the current study. In such larger systems, it is typically detritivorous invertebrates that show the strongest signal for a terrestrial component in their diet, and this propagates to fish preying on those invertebrates (Darnaude et al. 2004b). Overall, though, the smaller rivers studied by us contributed less to the diet of marine consumers, despite our deliberate sampling at the end of the wet season, when any river influence should have been maximised (Banaru and Harmelin-Vivien 2006).

Our conceptual understanding of trophic dynamics in small plumes is that phytoplankton are stimulated by inorganic nitrogen (Gaston et al. 2006), whereas direct assimilation of riverine carbon by animals in the water column is smaller. Work on larger plumes has shown, however, that riverine organic matter is incorporated into the benthos (Alliot et al. 2003; Banaru et al. 2007), and that benthic invertebrates and fish in plumes areas assimilate terrestrial carbon (Riera and Richard 1997; Lee 2000). We therefore expected that any trophic influence of smaller plumes would be greatest in benthic food webs. Indeed, we have previously shown that these small rivers deliver appreciable quantities of terrestrial organic carbon to the sea floor under plumes (Gaston et al. 2006).

The weaker isotopic signal of riverine influence measured by us might result from the variable nature of plume events generated by smaller rivers. Plumes off the Mooloolah and Maroochy estuaries are not only small in physical dimensions, but are also short-lived events, typically lasting only for a few days following heavy rainfall (Gaston et al. 2006). Thus, inputs of terrestrial matter to nearshore marine waters are erratic and ephemeral in nature, presumably limiting the contribution of this carbon to recipient food webs. Isotope ratios in

marine consumers are therefore a composite of feeding on marine sources for long periods, supplemented by pulsed intakes of terrestrial material.

Another possible reason that only a weak terrestrial signal was found in the plume area is that animals move in and out of the area of plume influence. Animals caught in the plume area during the study might have lived and fed elsewhere during the preceding weeks and months, imparting a marine signature on tissue isotope ratios. Animals may derive a trophic subsidy from pulsed plume events, but this is masked by marine signals when feeding outside plume areas. It is also possible that freshwater discharge from the estuaries could initiate movement of animals to more marine areas and thus a subsequent shift to different carbon sources.

The two species showing significantly more depleted carbon isotope ratios in plume than in non-plume areas (three spot crab, *Portunus sanguinolentus*, and large-toothed flounder, *Pseudorhombus arsius*) both feed on other fish and benthic invertebrates (Blaber 1980; Sukumaran and Neelakantan 1997). The three spot crab is a more active predator than the flounder, which is an ambush predator, but both species are strictly benthic, and we assume would be thoroughly enmeshed in the benthic food web. These species are harvested as part of the trawl fishery on the east coast of Australia (Williams 2002); assimilation of terrestrial carbon by these species indicates a direct link between riverine organic matter and fisheries productivity.

For nitrogen isotopes, there was the same small but distinct estuarine signal in consumers collected from the plume areas. This shows that while many other studies have used the enriched nitrogen isotope ratios from anthropogenic sources to delineate the extent of eutrophication in the sea (Nixon and Buckley 2002; Gaston et al. 2004; Costanzo et al. 2005), anthropogenic nitrogen with its enriched nitrogen isotope signal is also a useful tracer of riverine influence in marine food webs (Peterson 1999; West et al. 2006).

The patterns in isotope ratios of sand whiting throughout the Maroochy estuary provide a context for the differences in ratios at marine sites. Isotopic variation in fish is much larger across estuarine gradients than over the same spatial scale in the sea off the estuary. The relatively large changes in the estuary had different causes for carbon and nitrogen. For carbon, the sharp changes in isotope ratios reflect the changing prominence of different sources of organic matter available to animals. Major shifts in putative carbon sources for fish have been well described in estuaries (Schlacher and Wooldridge 1996), where animals often rely on local sources of carbon (Deegan and Garritt 1997). In the Maroochy system, the relatively depleted carbon isotope ratios of sand whiting in the middle estuary probably reflect uptake of terrestrial and mangrove carbon (Eyre 1998; Schlacher et al. 2007; Bouillon et al. 2008). Nearer the estuary mouth, strikingly enriched ratios reflect a localised influence of seagrass production, which is known to be enriched in ^{13}C (Melville and Connolly 2005). Such small scale patterns in animal isotope ratios in estuaries are known from several recent studies, implying localised consumption of available resources and limited movement of consumers (e.g. Riera et al. 1999; Hsieh et al. 2002; Guest et al. 2004; 2006). This would explain how sand whiting from the lower estuary obtain enriched carbon ratios by preying on invertebrates in or around seagrass patches (Connolly et al. 2005), despite an overall depleted organic carbon pool moving from the estuary to the sea. Temporal variability in carbon pathways has been shown from the lower reaches of estuaries elsewhere, including in response to freshwater flows (Wissel and Fry 2005).

Similar to carbon, spatial differences in nitrogen isotope ratios of sand whiting inside the estuary reflect localised uptake of different nitrogen sources. In the Maroochy estuary, changes to the nitrogen pool occur mainly from the release of large quantities of sewage nitrogen to the middle reaches of the estuary (47 t per year, Schlacher et al. 2005). The very high ratios in the middle estuary, with reduced but still enriched ratios lower in the estuary, is the same, consistent pattern described for sand whiting collected in other years in the Maroochy estuary (Schlacher et al. 2007), corroborating the influence of wastewater on estuarine fish. This consistency in spatial patterns also indicates a reasonable degree of site fidelity within the estuary for this species.

In summary, small plumes from relatively small rivers deliver enough organic matter to provide small trophic subsidies to benthic food webs in coastal seas. The ephemeral nature and small extent of the plumes does, however, set limits to the extent of terrestrial influence both in terms of the number of species that assimilate this carbon and the contribution it makes to the energy requirements of consumers. Although terrestrial carbon might be utilised by pelagic species, benthic fisheries species probably show the highest degree of assimilation of terrestrial material, and demonstrate land-ocean coupling in marine fisheries productivity.

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