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## Movement of carbon among estuarine habitats and its assimilation by invertebrates

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**Abstract** We measured the extent of movement of carbon and its assimilation by invertebrates among estuarine habitats by analysing carbon stable isotopes of invertebrates collected along transects crossing the boundary of two habitats. The habitats were dominated by autotrophs with distinct isotope values: (1) mudflats containing benthic microalgae (mean  $-22.6$ , SE  $0.6\%$ ) and (2) seagrass and its associated epiphytic algae (similar values, pooled mean  $-9.8$ ,  $0.5\%$ ). Three species of invertebrates were analysed: a palaemonid shrimp, *Macrobrachium intermedium*, and two polychaete worms, *Nephtys australiensis* and *Australonereis ehlersi*. All species had a similar narrow range of isotope values ( $-9$  to  $-14\%$ ), and showed no statistically significant relationship between position along transect and isotope values. Animals were relying on carbon from seagrass meadows whether they were in seagrass or on mudflats hundreds of metres away. Particulate organic matter collected from superficial sediments along the transects had similar values to animals (mean  $-11.1$ , SE  $1.3\%$ ) and also showed no significant relationship with posi-

tion. The isotope values of these relatively immobile invertebrates and the particulate detritus suggest that carbon moves from subtidal seagrass meadows to mudflats as particulate matter and is assimilated by invertebrates. This assimilation might be direct in the case of the detritivorous worm, *A. ehlersi*, but must be via invertebrate prey in the case of the carnivorous worm, *N. australiensis* and the scavenging shrimp, *M. intermedium*. The extent of movement of carbon among habitats, especially towards shallower habitats, is surprising since in theory, carbon is more likely to move offshore in situations such as the current study where habitats are in relatively open, unprotected waters.

**Keywords** Crustacea · Estuary · Polychaeta · Stable isotopes · Trophic subsidy

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### Introduction

The question of where an animal gets its food is a central organising theme in ecology, and energy movement within and among habitat patches is a crucial component of landscape ecology (Polis et al. 1997). The movement of energy sources across spatial boundaries is influenced by the permeability of habitat boundaries and the structural complexity of the landscape (Holt 2002). The potential exchange of material across habitat boundaries has pushed ecologists to consider patch edges as functional units rather than structural aspects of the landscape (Pickett and Cadenasso 1995). In aquatic systems, energy (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).

In marine systems, high offshore secondary production adjacent to inshore waters, rich in primary productivity, led to a theory of large-scale movement of carbon from inshore to offshore habitats (Odum et al. 1979). This theory provided the framework for numerous subsequent empirical studies of estuarine systems

(Kneib 2000), based around the concept that animals can be spatially segregated from the ultimate autotrophic source on which they rely. The most common technique for examining energy flows became carbon stable isotope analysis (Peterson and Fry 1987). In some estuaries, large-scale movement of carbon proved to be negligible (e.g. Loneragan et al. 1997; Dittel et al. 2000), and the focus shifted to carbon movement between areas within estuaries. Results of studies that examined the within-estuary movement of carbon indicated that animals were ultimately deriving their nutrition from local sources (e.g. Marguillier et al. 1997; Deegan and Garritt 1997; Bouillon et al. 2004). The distances between sampling locations in such studies were typically measured in kilometres, but the work nevertheless pointed towards smaller-scale spatial resolution of food webs. For example, Hsieh et al. (2002) used carbon isotopes to show that the ultimate autotrophic source of nutrition for invertebrates on mudflats adjacent to mangroves varied between two sites separated by hundreds of metres, suggesting that even finer scales of analysis of food webs might be useful.

A recent study in a subtropical estuary in Australia analysed carbon isotopes of relatively immobile invertebrates collected across the boundary of saltmarsh and mangrove habitat patches to measure the extent of carbon movement and assimilation by invertebrates (Guest et al. 2004). All species showed the same pattern of large differences in carbon isotope values between individuals collected in the two adjacent habitats, showing that animals derived their carbon predominantly from sources in their immediate surrounds (within 15 m). Subsequent sampling at an even finer scale showed that carbon isotope values of invertebrates changed rapidly across the saltmarsh–mangrove boundary, with  $\delta^{13}\text{C}$  values shifting up to 8‰ in a narrow transition zone. Carbon movement and assimilation by these invertebrates was limited to 5–7 m either side of the habitat boundary (Guest and Connolly 2004).

The apparent variability in results among studies of movement of carbon from inshore to offshore waters led to a refinement of theories about outwelling of energy. The most important factor in determining the extent of carbon movement is likely to be the degree of openness of an estuary or embayment to the open sea (Odum et al. 1979; Nixon 1980). Where an estuary is separated from coastal waters by barrier islands, for example, there is likely to be less trophic subsidy of coastal waters. In such situations, movement of carbon is expected to occur among habitats within estuaries (Odum et al. 1979). The work of Guest et al. (2004) in subtropical Australia was in an estuarine system largely separated from coastal waters by barrier islands. This makes the very restricted movement and assimilation of carbon by invertebrates among estuarine habitats shown by Guest et al. (2004) more surprising. There may be some difference simply due to the height of habitats in the intertidal zone (Taylor and Allanson 1995), but the influence of other environmental factors such as tidal

regimes on carbon movement has not yet been determined.

Guest et al. (2004) proposed a model in which estuarine invertebrates rely on autotrophic sources in their immediate surrounds. We tested the generality of this model by measuring carbon isotopes of invertebrates across a different habitat boundary in the temperate waters of southern Australia. We utilised adjacent estuarine habitats with distinct carbon values for the dominant autotrophs, in this case, shallow subtidal seagrass (and its epiphytic algae) and intertidal mudflats supporting benthic microalgae. Extensive mangrove forests, with another distinct carbon isotope value for the dominant autotroph, lay on the shoreward side of the mudflats. As test organisms, we used three invertebrate species with restricted mobility and different feeding modes (scavenging omnivore, carnivore, detritivore).

## Methods

The upper section of Gulf St Vincent in South Australia is a large, sheltered embayment (Fig. 1), receiving minor freshwater inputs but supporting well-developed estuarine habitats. Extensive tracts of *Posidonia sinuosa* seagrass (with some *P. australis* and *Heterozostera tasmanica*) occur subtidally, giving way intertidally to mudflats lacking macrophytes but containing benthic microalgae. Further up the intertidal gradient the mudflats are backed by forests of the mangrove *Avicennia marina*, which in turn give way to saltmarsh consisting of low, turf-forming glasswort (*Sarcocornia quinqueflora*) and bushes (predominantly *Halosarcia halocnemoides*). The amplitude of spring tides is about 2 m and all intertidal habitats are inundated daily, except saltmarsh which is fully inundated only on spring tides.

Four transects were selected by first delineating four general sections of coastline separated by several

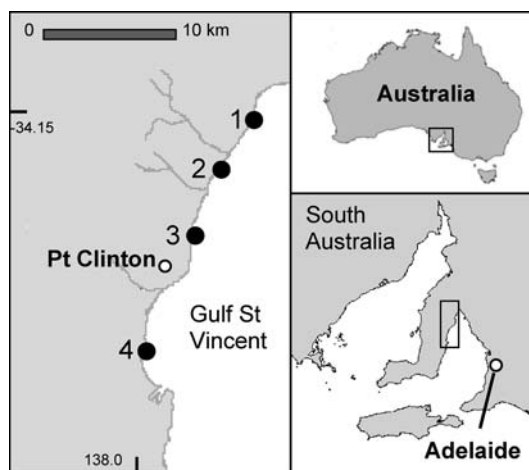


Fig. 1 Map showing the locations of the four transects in upper Gulf St Vincent, South Australia

kilometres. A GPS coordinate in each section was then randomly selected to use as a starting point for transects running perpendicular to the coastline. The transects ran both ways from the boundary of the seagrass and mudflats (designated as distance 0), about 400 m seaward into the seagrass habitat, and 200 m up the shore to the upper edge of the mudflat habitat (to within 15 m of the lower edge of the mangrove forest, for each transect) so that the transects were about 600-m long in total.

Samples of seagrass leaves (*P. sinuosa* at all points, and *H. tasmanica* where it occurred) were collected at two points along each transect. In the laboratory, epiphytic algae consisting of diatoms and very short (<10 mm) filaments of brown algae were scraped from seagrass leaves. Green leaves of mangroves (*A. marina*) and the two dominant saltmarsh plants (*H. halocnemoides*, *S. quinqueflora*) were also collected at each transect. The assemblage of unicellular algae on mudflats consisted almost exclusively of pennate diatoms. This benthic microalgae (BMA) was extracted from superficial mud collected at two positions on each transect. The mud was washed through 53- $\mu\text{m}$  mesh to remove infauna. Material passing through the mesh was then washed through 5- $\mu\text{m}$  mesh. Material retained on this mesh was centrifuged in colloidal silica (density=1.21) until a band of diatoms formed at the top of the tube. This band was removed and again washed through 5- $\mu\text{m}$  mesh to remove silica and any remaining microbes. Inspection of samples showed that they consisted predominantly of diatoms with occasional contamination by very fine detrital fragments.

We attempted to collect phytoplankton in the intertidal zone by towing a 37- $\mu\text{m}$  mesh plankton net in the water column at each transect at high tide. Samples had few algal cells, however, and instead consisted of sediment and fragments of plant material. This material were therefore analysed as evidence of the  $\delta^{13}\text{C}$  values of seston, after digestion in HCl to remove carbonates.

To determine which animals would have a distribution wide enough to make good test species, we first sampled all epibenthic and infaunal invertebrates to determine occurrence across both habitats at all transects. Three species were selected because of their wide distribution, different feeding modes and relative lack of mobility. We then attempted to collect each of these species by sieving sediment at about 50-m intervals along each transect. None of these species occurred in the adjoining mangrove or saltmarsh habitats. *Macrob- rathium intermedium* (striped shrimp) is a caridean decapod (family Palaemonidae). It is a scavenging omnivore capable of swimming short distances but having a strongly benthic habit (Walsh 1994). Where available, three specimens (total length up to 40 mm) were collected at each sampling point to give a pooled sample. Carapaces and guts were removed, leaving muscle tissue for processing. *Nephtys australiensis* and *Australonereis ehlersi* are errant, infaunal polychaete worms widely distributed in Australian estuaries (Scanes

et al. 1993). *N. australiensis* is carnivorous and *A. ehlersi* is detritivorous (Glasby et al. 2000). Both species are considered to have restricted movement given their infaunal habit (Scanes et al. 1993), although both species are at times caught in plankton tows. For each of the two species, several specimens (about 10, individual lengths up to 12 mm) were collected at each sampling point (where available), to give a pooled sample. Worms were left for 4 h to clear their guts before being processed.

All samples were dried, ground, placed into tin capsules and analysed on an Isoprime mass spectrometer. The ratios of  $^{13}\text{C}/^{12}\text{C}$  for all samples were calculated as the relative per mil (‰) difference between the sample and the recognised international standard (Pee Dee Belemnite limestone carbonate) and expressed as  $\delta^{13}\text{C}$  values. Precision of the mass spectrometer, calculated using values from duplicate samples, was 0.2‰.

Samples of detritus (large fragments of particulate organic matter) from the top 5 mm of sediment were collected at nine points (spread over the different transects). These samples were washed through a 2-mm and 125- $\mu\text{m}$  sieve. We used only the material retained on the 125- $\mu\text{m}$  mesh. Larger animals and shells of dead molluscs were removed by the 2 mm screening, and benthic microalgae were lost through the 125- $\mu\text{m}$  mesh. We removed any animals remaining in samples by hand during inspection under magnification. The detritus samples were dried, acid digested to remove carbonates, and analysed on the mass spectrometer as for other samples.

#### Statistical analysis

The main objective was to test for a relationship between the  $\delta^{13}\text{C}$  values of animals and their position along transects. Initially, animal values were tested using the analysis of covariance (ANCOVA), where treatments were the different transects and the covariate was distance along the transect. ANCOVA tested first for differences among slopes of the relationship between animal isotope values and distance along transects at individual transects. If slopes are homogeneous, it is valid to then test for differences among mean isotope values of animals at individual transects, after accounting for any relationship with distance. If no differences in slope or among mean isotope values of animals at individual transects were found, we pooled data from individual transects and used linear regression to test for any relationship between  $\delta^{13}\text{C}$  values of animals and their positions along transects. Linear regression was used because non-linear ANCOVA can only test homogeneity of shape of multiple curves if shape is defined a priori, and in this case, we had no a priori understanding of the shape to expect (and only limited samples numbers on each transect to estimate shape). Raw data met the ANCOVA assumption of homogeneity of variances and no transformation was used. Sample sizes (number of sampling points) for each

species differed among transects but ranged between 3 and 6 (mean 4.4); degrees of freedom were adjusted to account for unequal sample sizes.

## Results

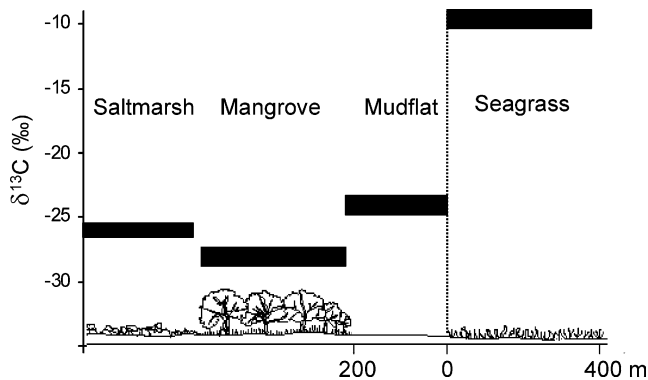
$\delta^{13}\text{C}$  values of the dominant autotrophs in the two adjacent habitats were distinct and showed little variability among positions within habitats and among transects. For seagrass, values from all transects and all positions, for both *P. sinuosa* and *H. tasmanica*, lay in a narrow range from  $-8.0\text{‰}$  to  $-11.7\text{‰}$  (mean  $-9.4\text{‰}$ , SE  $0.4\text{‰}$ ,  $n=12$ ). Algae epiphytic on seagrass fell in a similar range ( $-9.2$  to  $-13.8\text{‰}$ , mean  $-10.6\text{‰}$ , SE  $1.1\text{‰}$ ,  $n=8$ ). Isotope values of seagrass and its epiphytes were therefore indistinguishable for our purposes and were combined (Fig. 2).  $\delta^{13}\text{C}$  values of BMA were depleted relative to seagrass, lying in the range  $-19.2$  to  $-24.4\text{‰}$  (mean  $-22.6\text{‰}$ , SE  $0.6\text{‰}$ ,  $n=8$ ).  $\delta^{13}\text{C}$  values for autotrophs in neighbouring habitats were more depleted again, with the mean mangrove value at  $-28.0\text{‰}$  (SE  $0.6\text{‰}$ ,  $n=8$ ) and the mean for both saltmarsh species, combined, at  $-26.6\text{‰}$  (SE  $0.3\text{‰}$ ,  $n=8$ ).

All animal  $\delta^{13}\text{C}$  values across all species and all transects were towards the enriched end of the range for the autotrophs, lying between  $-9.4\text{‰}$  and  $-14.5\text{‰}$ , which is similar to the values for seagrass and its epiphytes. None of the species showed any significant relationship between  $\delta^{13}\text{C}$  values and position along transects. The pattern for *N. australiensis* is typical of the other species and is shown with data combined from all transects and in detail at individual transects (Fig. 3). An ANCOVA on  $\delta^{13}\text{C}$  values of *N. australiensis* did not show any departure from homogeneity of slopes of individual transects (Fig. 3;  $F_{3,11}=1.35$ ,  $P=0.307$ ), nor any significant difference among means of individual transects ( $F_{3,14}=0.70$ ,  $P=0.569$ ). Data from all tran-

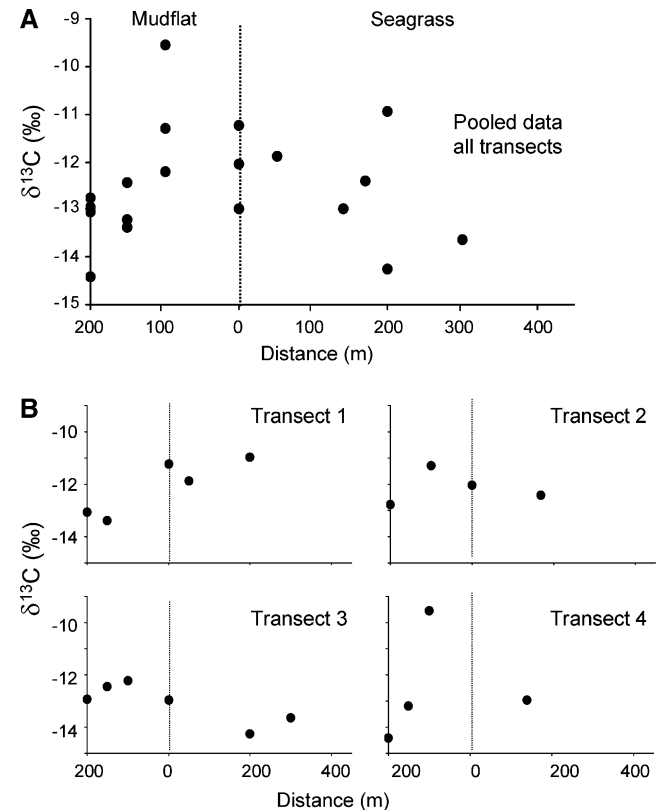
sects were therefore pooled. A linear regression on these pooled data found no significant relationship between  $\delta^{13}\text{C}$  values of animals and their positions (Fig. 3;  $df_{1,17}$ ,  $R^2=0.01$ ,  $P=0.993$ ).  $\delta^{13}\text{C}$  values of *N. australiensis* were very similar across the whole distance over which they were collected. Examination of residuals of the (non-significant) line of best fit showed that several values from worms collected in the upper 50 m of the mudflats (adjoining mangroves) had slightly depleted  $\delta^{13}\text{C}$  values, but these values nevertheless remained within the range of values for worms collected in seagrass.

The other two species (*A. ehlersi* and *M. intermedium*) also showed no pattern in  $\delta^{13}\text{C}$  values with position along transects (Figs. 4, 5). They showed the same similarity of values among transects and the absence of a relationship between  $\delta^{13}\text{C}$  values and positions on pooled data demonstrated for *N. australiensis* (pooled data only shown on Figs 4, 5; ANCOVA and regression  $P$  values non-significant ( $P>0.05$ ) for both species).

$\delta^{13}\text{C}$  values of detritus in superficial sediments were towards the enriched end of the range of autotroph values, and lay between  $-6.8\text{‰}$  and  $-14.0\text{‰}$  (mean  $-11.1$ , SE  $0.3\text{‰}$ ). No pattern was evident in detritus  $\delta^{13}\text{C}$  values with position along transect and the values matched those of the animals (Fig. 6).  $\delta^{13}\text{C}$  values of seston were also very enriched, ranging between  $-11.2$  and  $-14.5$  (mean  $-12.3\text{‰}$ , SE  $0.1\text{‰}$ ,  $n=9$ ).

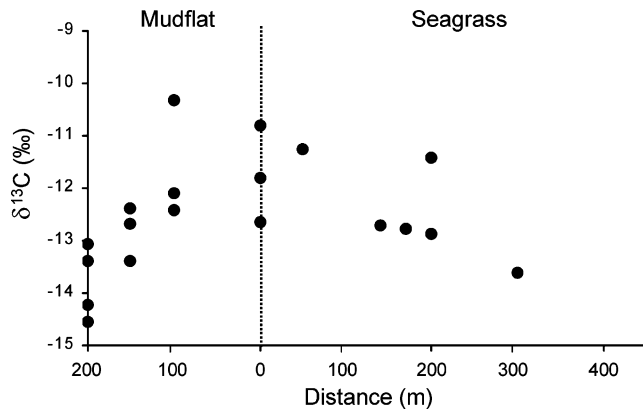


**Fig. 2** Diagram of shallow subtidal and intertidal habitats with  $\delta^{13}\text{C}$  values of dominant autotrophs in each habitat (shown as bands centred on the mean and 1 SE either side). Values in seagrass habitat are for seagrass and epiphytic algae combined, on mudflat habitat are for benthic microalgae, in mangrove habitat are for the single species occurring there, and in saltmarsh are for the two dominant species combined



**Fig. 3**  $\delta^{13}\text{C}$  values for *Nephtys australiensis* showing **a** data combined from all transects, and **b** data from individual transects. Values at each point are a single analytical result for a combined sample of several individuals

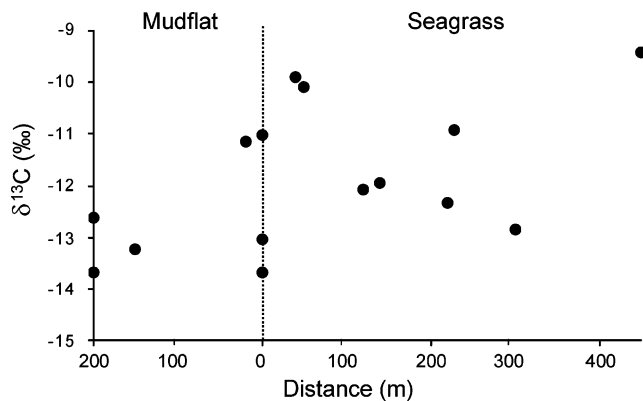




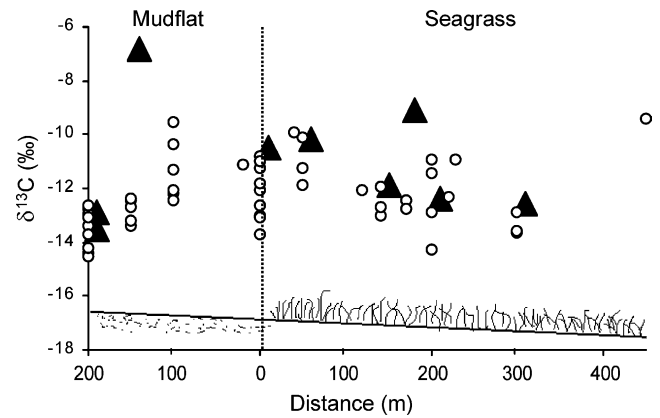
**Fig. 4**  $\delta^{13}\text{C}$  values for *Australonereis ehlersi* showing data combined from all transects. Values at each point are a single analytical result for a combined sample of several individuals

## Discussion

The lack of relationship between  $\delta^{13}\text{C}$  values and positions along transects for all three species is a clear indication that these invertebrates do not always rely on autotrophic sources in their immediate vicinity. The data are therefore inconsistent with the model developed from subtropical Australian waters by Guest et al. (2004). The rapid shift in  $\delta^{13}\text{C}$  values across a habitat boundary shown by Guest et al. (2004) did not occur in the present study. Rather, invertebrates in seagrass meadows and on mudflats relied on the same source, in this case, organic material from seagrass meadows (either seagrass itself or epiphytic algae). Animals in seagrass meadows might be obtaining nutrition ultimately from sources within their immediate surrounds, but this cannot be confirmed using the present data. Animals on mudflats were certainly not relying to any meaningful extent on the source (BMA) in their immediate surrounds. Furthermore, organic material from the mangroves and saltmarsh higher in the intertidal played no role in the nutrition of most of the animals on mudflats,



**Fig. 5**  $\delta^{13}\text{C}$  values for *Macrobrachium intermedium* showing data combined from all transects. Values at each point are a single analytical result for a combined sample of several individuals



**Fig. 6**  $\delta^{13}\text{C}$  values for detritus samples (closed triangles) and all animal species together (open circles), pooled for all transects

although some contribution to animals immediately alongside mangroves cannot be excluded.

The  $\delta^{13}\text{C}$  values for seston and detritus point to the mechanism underlying the patterns observed for animals. Energy can be transferred among different areas of estuaries either as particulate organic matter, as dissolved matter (Twilley 1988), or via animal movements in a set of predator-prey interactions known as trophic relay (Kneib 2000). The enriched  $\delta^{13}\text{C}$  values of seston at all transects show that particulate organic matter in the water column consisted predominantly of material from seagrass meadows, even over mudflats. Detrital particulate matter on mudflats had the same enriched  $\delta^{13}\text{C}$  values, demonstrating that particulate matter in the water column is deposited on the sediment. The simplest explanation for the enriched  $\delta^{13}\text{C}$  values of animals on mudflats is that they rely ultimately on seagrass and/or epiphytic algal material borne as particulate matter on water currents and incorporated into mudflat sediments. For the detritivore (*A. ehlersi*), uptake would be through direct consumption of detrital material along with bacteria and other microbes feeding on the detritus. For the other species, uptake would be via detritivorous intermediaries, either partly in the case of the omnivore (*M. intermedium*) or fully for the carnivore (*N. australiensis*). Although this is the simplest explanation for the patterns in animal  $\delta^{13}\text{C}$  values, our results cannot exclude the possibility that energy moved as dissolved material or in the bodies of small animals. Only further studies of dissolved material and the movements of small animals could fully resolve whether movement of particulate matter is the main pathway for energy from seagrass meadows to adjacent mudflats.

The similarity in patterns of  $\delta^{13}\text{C}$  values for the three species suggests that the results can probably be generalised to other invertebrates at this location. Further examination of filter feeding species would be useful, however, given that in other estuaries they have been shown to rely on fine suspended matter rather than macrophyte detritus (Schlacher and Wooldridge 1996).

An alternative explanation for the patterns in  $\delta^{13}\text{C}$  values of animals in the present study is that individuals

of the three species move freely between seagrass meadows and mudflats. This would mean that individuals collected on mudflats could have been in seagrass just prior to our sampling, and obtained their nutrition whilst in the seagrass. Under this scenario, animals might have obtained their energy from sources immediately surrounding them whilst in the seagrass. Although the infaunal polychaetes are at times found in the plankton, the enriched isotope values of polychaetes on mudflats could only have arisen if there was consistent, unidirectional movement over hundreds of metres. Where polychaetes have been used previously to examine food webs on mudflats, they have been considered resident except during seasonal mass movements (Meziane and Retiere 2001); there was no sign of such mass movements during the current study. Shrimp are more mobile and individuals probably go back and forth between seagrass and mudflat near the boundary of the habitats. It remains unlikely, however, that the enriched  $\delta^{13}\text{C}$  values of shrimps, so consistent across the entire mudflat, would be due to all of these shrimp having come from seagrass prior to our sampling.

Stable isotope analysis of animals tests only the movement *and* assimilation of carbon. It is possible that carbon may move among habitats in ways different to that presented, but not be assimilated by the consumers sampled (Duarte and Cebrián 1996). Since we aimed to determine the trophic importance of discrete habitats, only the movement and assimilation of carbon has been examined, and carbon movement that does not contribute to trophic dynamics has not been considered.

The difference in results of the present study from those of Guest et al. (2004) in subtropical Australian waters demonstrates the variability in patterns of carbon movement and assimilation. In theory, carbon movement among habitats within estuaries is more likely in estuaries having restricted exchange with open coastal waters than those open to the sea (Odum et al. 1979). Our own data, however, point to the opposite being true. Guest et al. (2004) found very restricted movement of carbon between saltmarsh and mangrove habitats in a subtropical estuary separated from coastal waters by barrier islands, while in the present study in an embayment open to coastal waters we found more extensive movement of carbon. We presume other environmental variables (e.g. patterns of tidal currents) are important in determining the extent of carbon movement and its assimilation by invertebrates. Further spatially explicit measurements of carbon movement among habitats in other estuaries will help to discern general patterns in the characteristics of estuaries that correlate with the extent of movement among habitats.

Our data also provide a demonstration of invertebrates in an intertidal habitat assimilating carbon from an adjacent subtidal habitat. This has been demonstrated previously for invertebrates of sandy beaches (Robertson and Lenanton 1984) but not estuaries. Early studies using stable isotopes to examine movement and assimilation of estuarine carbon emphasised, quite

rightly, the possible outwelling of organic material from intertidal habitats (Lee 1995). In estuaries where outwelling is not important, it seems animals may rely on carbon from habitats anywhere in the estuary, and a focus on these within-estuary pathways will be important for an understanding of the role of different habitats in supporting secondary production.

The utilisation of organic material from seagrass meadows by animals occurring in the meadows is consistent with previous studies examining the contribution of seagrass and epiphytes to animals living in seagrass meadows that report seagrass and/or epiphytes to be the ultimate source of nutrition (e.g. Marguillier et al. 1997, Moncreiff and Sullivan 2001). The role of organic material from seagrass meadows in the nutrition of animals living elsewhere has not been well documented. It is known that seagrass meadows produce far more organic matter than can be utilised by consumers living in the meadows (Duarte and Cebrián 1996), and excess production is potentially available for use in detrital food webs in adjacent habitats (Slim et al. 1996; de Boer 2000; Wooller et al. 2003). Assimilation of seagrass carbon by larval fish has been demonstrated in waters offshore of Tasmania, Australia (Thresher et al. 1992). Our data provide evidence of movement of carbon from subtidal seagrass meadows to an intertidal habitat, and its subsequent assimilation by invertebrates. There is also evidence that these invertebrates are consumed by fish. A previous broad-scale survey in South Australia that included the current study area found that polychaete worms were consumed by yellowfin whiting (*Sillago schomburgkii*), an important fisheries species occurring mainly over mudflats and in mangrove creeks (Connolly et al. 2005). Stable isotope values of yellowfin whiting tissue were consistent with a major contribution of seagrass (Connolly et al. 2005).

For the purposes of testing the model by Guest et al. (2004) in the present study, we were able to consider seagrass and epiphytic algae as a single source produced in seagrass meadows, and their relative importance was not critical to our conclusions. However, in estuarine systems generally the relative contributions of macrophytes and epiphytic algae to the nutrition of animals has been a long-standing topic of investigation (Moncreiff and Sullivan 2001). The similarity of carbon isotope values of seagrass and epiphytes in the current study prevents us from distinguishing between these two sources, and further work will be needed to resolve their contributions. Recent developments in stable isotope analysis using sulphur (Moncreiff and Sullivan 2001; Connolly et al. 2004) and experimental manipulation of autotroph isotope values (Winning et al. 1999; Mutchler et al. 2004) are likely to be useful.

The lack of assimilation of carbon from BMA by the animals occurring on mudflats in the present study is unusual, given the trend in recent years to uncover a greater role for BMA in estuarine food webs than had previously been considered. It has been shown, for example, that BMA on mudflats is assimilated by mei-

ofauna (Middelburg et al. 2000) and to some extent by fish (Melville and Connolly 2003). Macroinvertebrates in mangrove forests (Bouillon et al. 2002b) and saltmarsh (Wainright et al. 2000) have also been shown to assimilate BMA from intertidal sediments. The contribution of BMA to food webs may depend on algal productivity. In another temperate Australian estuary, for example, the contribution of BMA to the nutrition of a callianassid shrimp was shown to be low, and BMA biomass was also very low (Boon et al. 1997). Unfortunately, estimates of productivity on mudflats in temperate Australian waters are unavailable, but such data might help us to understand why BMA have a greater role in some locations than others.

Despite the large area of mangroves adjacent to mudflats, the lack of contribution of mangrove carbon to the nutrition of invertebrates on mudflats was expected. While early studies used the high productivity of mangrove forests to argue that they must be important contributors to food webs (Odum and Heald 1972; Rodelli et al. 1984), evidence is accumulating that they contribute little (Lee 1995; Newell et al. 1995; Loneragan et al. 1997; Bouillon et al. 2002a). Much of the carbon from mangroves is consumed by invertebrates occurring there (Boto and Bunt 1981; Bouillon et al. 2002b), and may be predominantly recycled within the mangrove forest. Some studies have detected a gradient in  $\delta^{13}\text{C}$  values of invertebrates in habitats adjacent to mangroves, with more depleted values near mangroves (Marguillier et al. 1997; Bouillon et al. 2002b). In the current study, invertebrates on the mudflats within about 30 m of mangroves had slightly depleted  $\delta^{13}\text{C}$  values, although this pattern was not significant. Even this weak signal, however, may not be a result of assimilation of mangrove carbon. The general depletion in  $\delta^{13}\text{C}$  values of autotrophic sources, including algae, in mangrove forests can confound gradient analysis of animal  $\delta^{13}\text{C}$  values adjacent to the forests (France 1998; Bouillon et al. 2004).

The lack of contribution of saltmarsh plants in the nutrition of animals in our study also comes as no surprise. The importance of saltmarsh carbon to consumers occurring in adjacent habitats is well established for marshes along the east coast of North America (Peterson and Howarth 1987; Currin et al. 1995; Weinstein et al. 2000), where marshes are lower in the intertidal zone, frequently inundated, and support extensive stands of tall cordgrass (*Spartina*). As yet, however, there is little evidence of saltmarsh production providing a trophic subsidy to other parts of estuaries in Australia, where marshes are inundated only infrequently.

In summary, our findings highlight the variability in energy pathways in different places, and we encourage detailed spatial analysis of food webs using carbon isotopes in other locations. We recommend that tidal amplitude and position of habitats within the intertidal/subtidal gradient be taken into account when selecting further test locations. In the current study area, we found widespread movement of carbon from subtidal

seagrass meadows to intertidal habitats. This “inwelling” results in utilisation of organic matter from seagrass meadows by invertebrates and probably fish in intertidal habitats.

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