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Fine-scale movement and assimilation of carbon in saltmarsh and mangrove habitat by resident animals

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Abstract

Despite theories of large-scale movement and assimilation of carbon in estuaries, recent evidence suggests that in some estuaries much more limited exchange occurs. We measured the fine-scale movement and assimilation of carbon by resident macroinvertebrates between adjacent saltmarsh and mangrove habitats in an Australian estuary using $\delta^{13}C$ analysis of animals at different distances into adjacent patches of habitat. $\delta^{13}C$ values of crabs (*Parasesarma erythrodactyla* –15.7 ± 0.1‰, *Australoplax tridentata* –14.7 ± 0.1‰) and slugs (*Onchidina australis* –16.2 ± 0.3‰) in saltmarsh closely matched that of the salt couch grass *Sporobolus virginicus* (–15.5 ± 0.1‰). In mangroves, $\delta^{13}C$ values of crabs (*P. erythrodactyla* –22.0 ± 0.2‰, *A. tridentata* –19.2 ± 0.3‰) and slugs (–19.7 ± 0.3‰) were enriched relative to those of mangroves (–27.9 ± 0.2‰) but were more similar to those of microphytobenthos (–23.7 ± 0.3‰). The $\delta^{13}C$ values of animals across the saltmarsh-mangrove interface fitted a sigmoidal curve, with a transition zone of rapidly changing values at the saltmarsh-mangrove boundary. The width of this transition indicated that the movement and assimilation of carbon is limited to between 5 and 7 m. The $\delta^{13}C$ values of crabs and slugs, especially those in saltmarsh habitat, clearly indicate that the movement and assimilation of carbon between adjacent saltmarsh and mangrove habitat is restricted to just a few metres, although some contribution from unmeasured sources elsewhere in the estuary is possible. Such evidence demonstrating the extent of carbon movement and assimilation by animals in estuarine habitats is useful in determining the spatial arrangement of habitats needed in marine protected areas to capture food web processes.

Introduction

The source of energy or carbon to consumers and its movement among habitats has been a key focus in ecology. In marine systems, high offshore secondary production adjacent to inshore waters, rich in primary productivity, led to a hypothesis of large-scale transportation of carbon from inshore to offshore habitats (e.g., Odum 1968; Kneib 2000). For some estuaries however, such large scale movement of carbon has proved to be negligible (e.g., Loneragan et al. 1997; Chong et al. 2000), and more recent evidence suggests that the movement of carbon in estuarine habitats can occur at a finer scale than has previously been considered. For example, in a study examining the carbon isotopes of ocypodid crabs at sites separated by hundreds of metres, Hsieh et al. (2002) found that the crabs derive their carbon from the sites in which they reside rather than from further afield. A study of the movement and assimilation of carbon by shore crabs in an Australian estuary, however, showed that crabs appear to obtain their nutrition from

sources within the surrounding tens of metres (Guest et al. in press), a much finer scale than even the site-specific work of Hsieh et al. (2002).

Stable isotope analysis of carbon is one of the most effective methods of tracing energy transfer from autotrophs to consumers, and has been used successfully at scales of hundreds of metres (Hsieh et al. 2002) as well as larger scales (Deegan and Garritt 1997). This method is able to distinguish among carbon sources where autotrophs have different ratios of $^{13}C/^{12}C$, and consumers take on the ratio of their food source (Peterson and Fry 1987). Stable isotope analysis has advantages over other techniques used to study food web processes as the $\delta^{13}C$ values of consumers experience only minor enrichment across trophic levels (typically $< 1‰$, McCutchan et al. 2003). This means that despite multiple trophic shifts (for example, via a microbial loop or through the consumption of small invertebrates) stable isotope analysis of carbon can trace the original source of carbon (autotrophs) and therefore does not rely on the direct consumption of plant material by the study organism.

In this study we use the stable isotopes of carbon to examine the movement and assimilation of carbon by sedentary crabs and slugs across the boundary of adjacent saltmarsh and mangrove habitat. These habitats are ideally suited to stable isotope analysis as the $^{13}C/^{12}C$ ratios of the dominant autotrophs in each habitat are clearly separated. Sedentary animals are also ideal test organisms because their home range is limited, and thus carbon sources can be more clearly differentiated into those produced locally and those produced further away. The crabs are thought to consume detritus, which consists of plant material, microbes and small invertebrates. The slugs are either grazers and/or detritivores. As water is the primary vector for the transport of nutrients, detritus and animals both within habitats and across habitat boundaries in aquatic systems (Polis et al. 1997), animals within these habitats, even sedentary ones, may derive their carbon from sources remote to the habitat they occupy.

Landscape structure and animal use of habitat edges or 'interfaces' has been extensively studied in terrestrial landscape ecology (e.g., Burkey 1993; Robinson et al. 1995; Bolger et al. 2000). Edge habitats have been considered both areas of high biodiversity and productivity due to the interchange of biotas from adjacent habitats (e.g., Davies-Colley et al. 2000), and areas of increased predation risk and disturbance (Flaspohler et al. 2001). As such, ecological processes linked to edge habitats (e.g., movement of carbon in the form of animals, plants, detritus or nutrients) may differ from their interior counterparts (Fagan et al. 1999), and may act to functionally couple adjacent habitats. Thus, the inclusion of habitat edges as buffer zones in terrestrial protected area design is often recommended. By contrast, there has been limited research on aquatic interfaces, and aquatic ecology has yet to fully recognise the potential differences in these edge environments. Conventional food web theory developed for terrestrial systems does not fully explain marine food web processes (e.g., Link 2002), and the link between the habitat interface and food web processes in marine systems is less well understood. In this study we examine the movement and assimilation of carbon across the saltmarsh-mangrove interface. Understanding the scale of estuarine food web processes and the transfer of energy between adjacent habitats may be useful in evaluating the use of buffer zones in the design of aquatic protected areas (France 1998).

Specifically, this study was designed to examine the metre-scale movement and assimilation of carbon for resident crab and slug species in adjacent saltmarsh and mangrove habitats in an Australian estuary. Results from the same estuary showed that the movement and assimilation of carbon for resident animals in adjacent saltmarsh and mangrove habitats is less than 30 m (Guest et al. 2004b). The current survey was designed to measure more precisely the extent of carbon movement and assimilation by sedentary invertebrates by sampling at more frequent spatial intervals across the habitat interface.

Materials and methods

Saltmarsh and mangrove habitats were sampled in March 2003 in southern Moreton Bay, Queensland, Australia (Figure 1). Three sites of adjacent saltmarsh and mangrove habitat were selected. Saltmarsh habitat was a pure stand of the salt couch grass, *Sporobolus virginicus*, and the dominant species in the mangroves was *Avicennia marina*. Saltmarsh sites were defined visually by the presence of discrete habitat boundaries marked by an abrupt change in vegetation type. Saltmarsh areas were between 1 and 2 ha, and adjacent mangrove forests were at least 10 ha. The sites had a tidal range of approximately 1.3 m. The saltmarshes had low relief (< 0.5 m) and

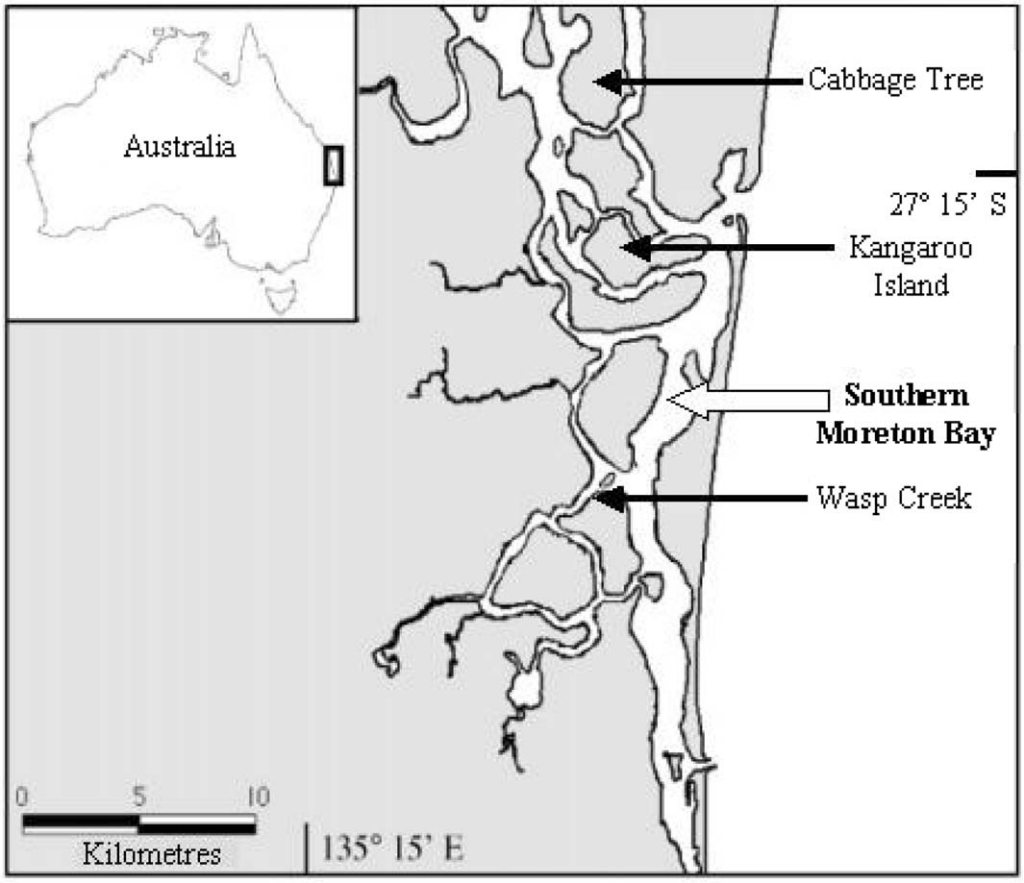

Figure 1. Map of study area in southern Moreton Bay with labeled sampled sites of saltmarsh adjacent to mangroves.

were inundated on at least one high tide per day for two weeks out of the four-week sampling period.

Two crab species, *Australoplax tridentata* (Ocypodidae) and *Parasesarma erythrodactyla* (Grapsidae), and an estuarine slug, *Onchidina australis* (Pulmonata: Onchidiidae), were analysed. These species were chosen because they are found in both saltmarsh and mangrove habitats, and whilst there is little documentation of the movement of *A. tridentata* and *P. erythrodactyla*, they appear to be faithful to their burrows (pers. obs.) and are therefore assumed to have restricted home ranges. Personal observation suggests the movement of *O. australis* is predominantly vertical within the sediment profile, using crab holes during high tide periods, and feeding on the mud surface at low tide.

At each of the three sites, animal samples were collected at the saltmarsh-mangrove interface (or zero point), and at 2 m positions from the zero point to 20 m into both saltmarsh and mangrove habitats (Figure 2). Additional samples were also taken 30 m into of the saltmarsh habitat, and 30 and 50 m into the mangrove habitat. It was not possible to take samples 50 m into the saltmarsh habitat because that distance was too close to the opposite edge of the saltmarsh, and measurements intending to indicate an interior habitat would be confounded by proximity to the opposite saltmarsh edge. For all animal species, the animal size between sampling positions was similar. For crabs, samples from each sampling position were composites of 2-3 individuals to obtain enough tissue for analysis, while for *O. australis* only one individual was needed for each sampling position. Three samples of *Sporobolus virginicus* were collected 30 m from the saltmarsh/mangrove interface at each site (i.e., 3 samples per site), as previous collections at 30 m and 0 m sampling positions indicate that the $\delta^{13}C$ values of *S. virginicus* were within 1‰ (Guest et al. 2004a). Three samples of *Avicennia marina* were collected 30 m and 2 m from the

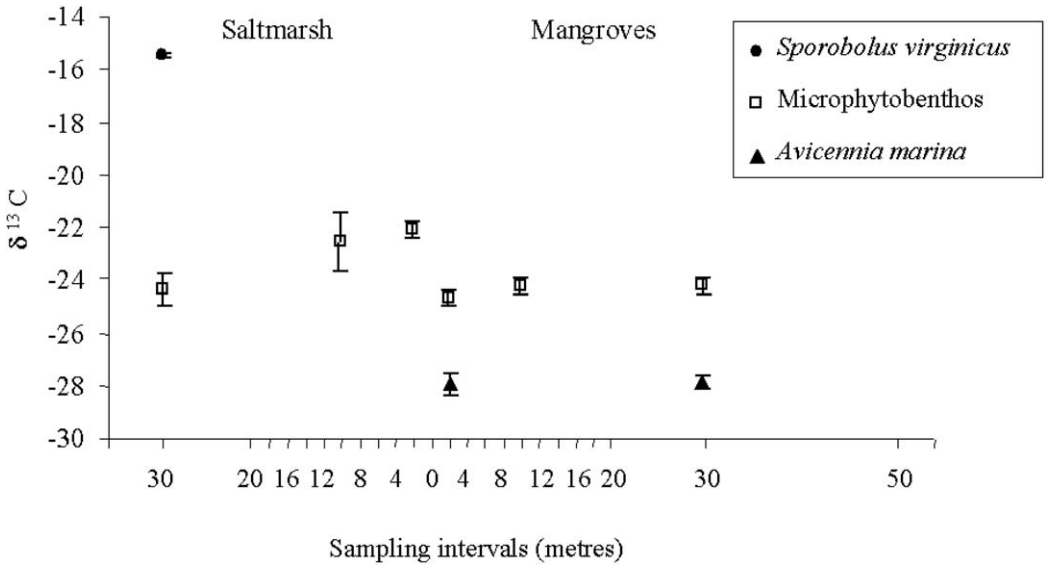

Figure 2. $\delta^{13}C$ values for autotrophs at sampling positions within saltmarsh and mangrove habitat. Values are averaged across the three sites ± 1 SE (SE too small to see in some cases).

saltmarsh/mangrove interface. Apart from the dominant autotrophs, numerous but inconspicuous algal and cyanobacteria cells are found in the superficial sediment of both habitats. One sample of this microphytobenthos (MPB) was collected at 30 m, 10 m and 2 m positions in both saltmarsh and mangrove habitat at each site (i.e., 6 samples per site). Samples were collected adjacent to where collections of animals were made, by scraping the top 1 cm of sediment from the surface of the mud.

Slugs were left for approximately 8 h before freezing to allow extrusion of gut contents. All other samples were frozen immediately after collection. Samples were thawed and rinsed in distilled water prior to processing. The exoskeleton, shell and gut were removed from the crabs, and for both crabs and slugs, the soft flesh was selected for analysis. All samples were dried and ground, placed into tin capsules and their isotopic values analysed on an Isoprime mass spectrometer. MPB samples were 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 (9 mL) to a centrifuge tube containing 21 mL of colloidal silica (LUDOX^{TM} AM30, density = 1.21) and centrifuged at 10 000 rpm for 10 minutes. A band of diatoms, some organic matter and silica particles formed at the top of the centrifuge tube. This band was removed and again washed through a 5 μm mesh to remove the silica and any remaining microbes. Inspection of samples showed that they consisted predominantly of microalgae (mainly diatoms) with occasional contamination by very fine detrital fragments. The ratios of $^{13}C/^{12}C$ 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 $\delta^{13}C$ values. Analytical precision was determined as being within +/- 0.5 ‰.

Differences in isotope signatures of plants at different positions within each habitat (sites were pooled) were tested using a one-way analysis of variance for each taxon. Data were checked for homogeneity of variances using Cochran's test and no transformations were necessary. Where the position factor was significant, differences among positions were tested using the Student-Newman-Keuls (SNK) test. The relationship between $\delta^{13}C$ values of animals and sampling positions across saltmarsh and mangrove habitats was clearly curvilinear. We therefore used non-linear regression in SPSS (2002) to determine the best fitting sigmoidal curve, of the form:

$$y = \frac{a}{1 + \exp\left[-\frac{x-b}{c}\right]} + d$$

where a = the transition height, i.e., the difference in

$\delta^{13}C$ between upper (saltmarsh) and lower (mangrove) asymptotes; b = the transition midpoint, i.e., the centre of the transition zone along the x-axis; and d = the value of y when x approaches its smallest value, i.e., the lower asymptote. The transition width = $2.197c$ (obtained from Tablecurve 2D (2000) software), and is the distance that carbon moves along the x-axis from the transition midpoint, and this movement is symmetrical around the midpoint. The rate of change in $\delta^{13}C$ with distance across the transition zone is the slope, and we calculated slope as transition height/transition width. Initial estimation of parameters was by graphical inspection. This was done for each site separately and for data averaged across all three sites.

Results

Autotrophs

The $\delta^{13}C$ values of autotrophs could be separated into three bands (Figure 2), *Sporobolus virginicus* (–15.5 $\pm$ 0.1‰), MPB (–23.7 $\pm$ 0.3‰) and *Avicennia marina* (–27.9 $\pm$ 0.2‰). The $\delta^{13}C$ values of MPB were marginally significantly different between sampling positions across saltmarsh and mangrove habitats (one-way ANOVA: $P = 0.040$), and although a post-hoc SNK test could not distinguish which means were different, means values in saltmarsh tended to be more enriched than those in mangroves (Figure 2). The $\delta^{13}C$ values of *Avicennia marina* (Figure 2) did not vary between 2 m and 30 m sampling positions.

Consumers

For all animal species, and at all sites, the non-linear regression model provided a close fit of the relationship between $\delta^{13}C$ values and the position of an animal (Figures 3, 4 and 5). The trend was negative, with more enriched $\delta^{13}C$ values in saltmarsh habitat, and increasingly depleted $\delta^{13}C$ with greater proximity to mangroves. For each species, the patterns at individual sites were similar (shown for *P. erythrodactyla* in Figure 3b as an example), so analyses were done on data averaged across the three sites (Figures 3a, 4 and 5). The explanatory power of the sigmoidal regressions (measured as r^2) in estimating $\delta^{13}C$ from position of an animal was strongest for *P. erythrodactyla*, intermediate for *A. tridentata* and weakest for *O. australis* (Figures 3, 4 and 5).

For all species, the transition midpoint was within 1–4 m of the 0 m position that demarcates the saltmarsh-mangrove interface (Table 1), and was always in the mangroves. The extent of carbon movement and assimilation into each habitat as measured from the transition midpoint, and referred to as the transition width, was approximately 5 m for *P. erythrodactyla* and *A. tridentata* and $<$ 7.5 m for *O. australis*. The rate of change in $\delta^{13}C$ values across the transition zone was greatest for *P. erythrodactyla*, intermediate for A. *tridentata*, and lowest for *O. australis* (Table 1).

The difference in consumer $\delta^{13}C$ values between the top and bottom asymptotes (i.e., the transition height) was large, ranging from 4 to 7‰ for different species (Table 1). The top and bottom asymptotes (see Figures 3, 4 and 5) represent animal $\delta^{13}C$ values at sampling positions within saltmarsh and mangrove habitat, excluding the saltmarsh-mangrove transition zone. In the saltmarsh, the animal $\delta^{13}C$ values closely matched the $\delta^{13}C$ values of the salt couch grass. In the mangroves, animal values were more enriched than the mangrove values, and were closer to, but still a little more enriched than, MPB values.

Discussion

Scales of carbon movement and assimilation

This study found that carbon movement and assimilation by resident animals between adjacent saltmarsh and mangrove habitat was most likely restricted to a scale of several metres. These results are in contrast to the wider expectation of large-scale carbon movement and assimilation in estuarine habitats (e.g., Kneib 2000), but are consistent with recent studies on the movement and assimilation of carbon between adjacent habitats at smaller scales. For example, in a study of the carbon isotopes of ocypodid crabs at sites separated by hundreds of metres (Hsieh et al. 2002), crabs collected from a river site derived their carbon from terrestrial grass nearest to the river site. MPB was considered to be the main source of carbon for crabs collected from a creek site 600 m from the river site, but a mixed diet of algae, particulate organic matter or the detritus of a terrestrial grass was also plausible. Sampling done at a smaller scale than that by Hsieh et al. (2002), however, found that the movement and assimilation of carbon by crabs and snails was occurring at $<$ 30 m (Guest et al. 2004b).

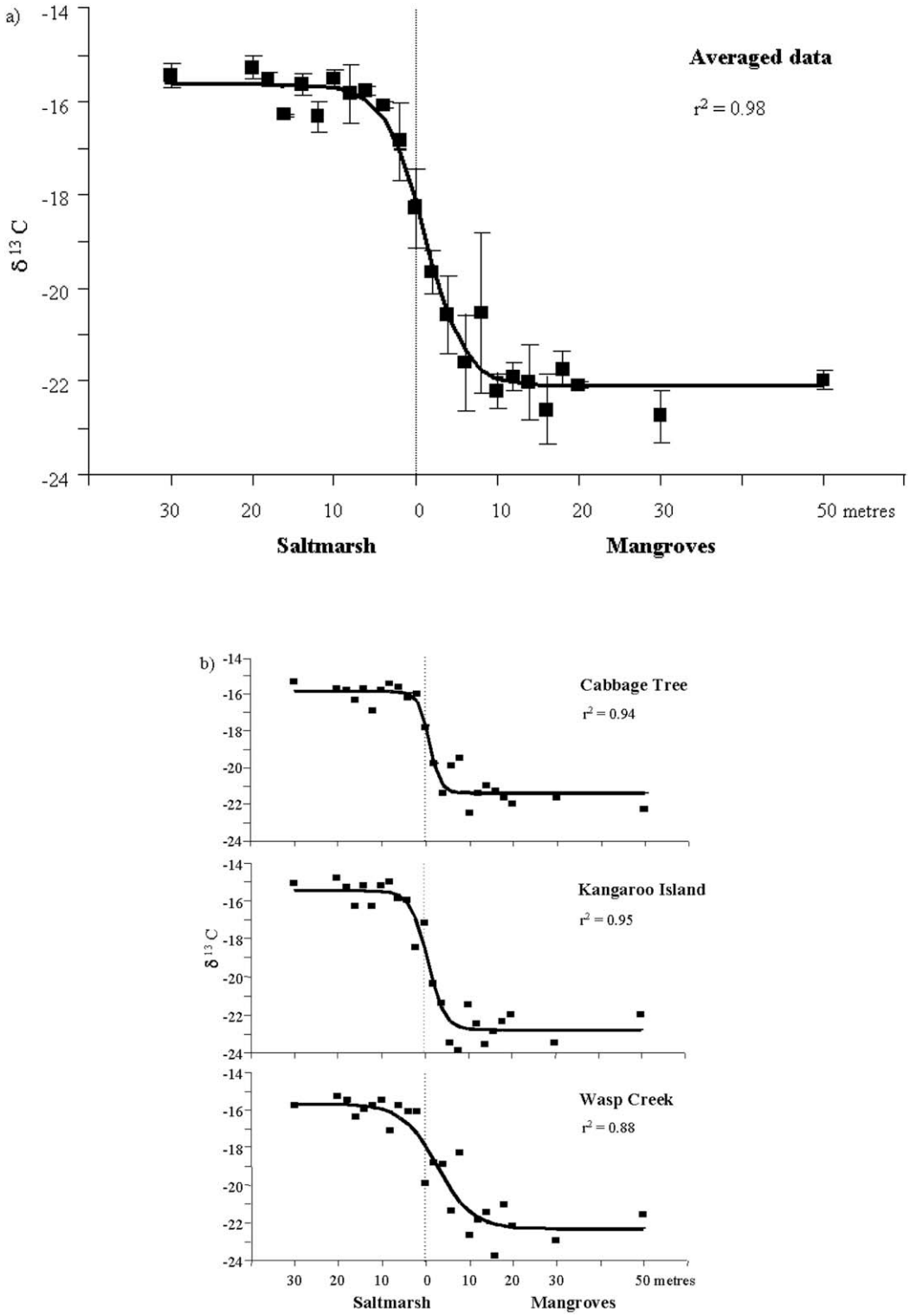

Figure 3. Parasesarma erythrodactyla: non-linear regression line of best fit for $\delta^{13}C$ values and sampling positions for (a) data averaged across the three sites, and (b) for each site.

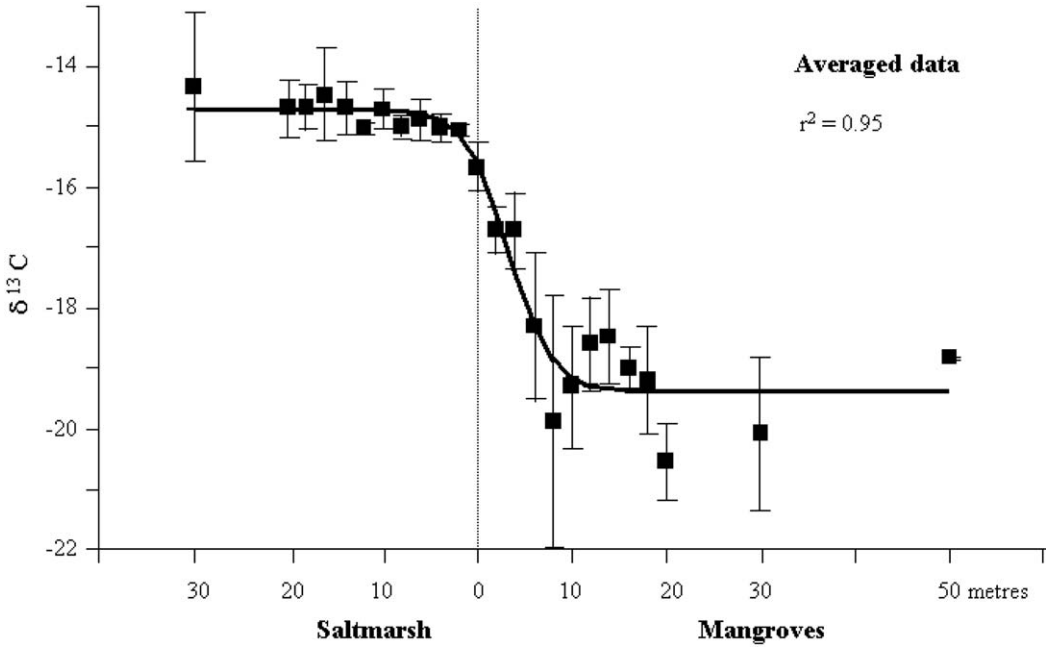

Figure 4. Australoplax tridentata: non-linear regression line of best fit for $\delta^{13}C$ values and sampling positions for data averaged across the three sites.

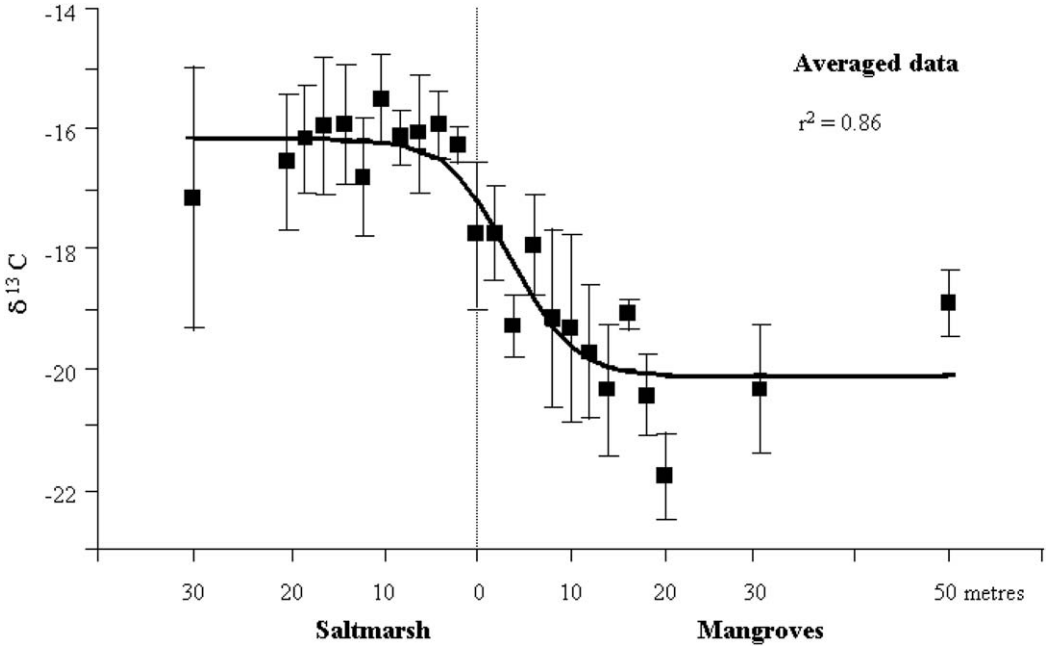

Figure 5. Onchidina australis: non-linear regression line of best fit for $\delta^{13}C$ values and sampling positions for data averaged across the three sites.

The current study gives greater precision to our understanding of carbon movement and assimilation by resident animals in adjacent estuarine habitats, and is consistent with our predictions of restricted carbon movement and assimilation.

Table 1. Parameter estimates in the non-linear regression model for each animal species, on data averaged across sites. Transition height is the upper minus lower asymptote, transition midpoint is the centre of the transition zone along the x-axis (negative numbers represent mangrove habitat), and transition width is the distance carbon moves into the adjacent habitat from the midpoint. The slope is the transition height/transition width (with negative numbers indicating the direction of the curve). Numbers in brackets are ± 1 SE for parameters estimated directly from the model.

Species	Transition height (‰)	Transition midpoint (m)	Transition width (m)	Slope (‰ m^{-1})
Parasesarma erythrodactyla	6.45 (± 0.23)	–1.14 (± 0.43)	5.30	–1.22
Australoplax tridentata	4.66 (± 0.28)	–3.29 (± 0.69)	4.90	–0.95
Onchidina australis	3.94 (± 0.46)	–3.64 (± 1.52)	7.24	–0.54

The transition midpoints of the sigmoidal curves describing the movement and assimilation of carbon were close to the saltmarsh-mangrove interface for all species, indicating that there was a small amount of energy transfer across the interface in both directions. However, there was a slightly greater movement and assimilation of saltmarsh carbon into the mangroves as indicated by the negative value of the transition midpoints. The transition width indicated that the movement and assimilation of carbon into the each habitat measured from the transition midpoint was restricted to a scale of ~5–7.5 m for all species, the smaller end of the scale we measured. Measurement of energy transfer at this extreme end of the scale potentially becomes confounded with movements by the animals themselves (see below).

The relationship between sampling position across adjacent saltmarsh and mangrove habitats and $\delta^{13}C$ values of resident animals formed a clear sigmoidal trend. Spatial gradients in $\delta^{13}C$ values of consumers (more depleted with greater proximity to mangroves, e.g., Marguillier et al. 1997; Bouillon et al. 2002) have been identified in previous studies of carbon movement and assimilation. However, the coarse scale of sampling used in previous studies has prevented the detailed characterisation of the shape of the spatial gradients shown here. In this study, the top and bottom asymptotes of the sigmoidal curve indicated that there was no relationship between $\delta^{13}C$ values of animals and sampling position except near the habitat interface. This lack of relationship between $\delta^{13}C$ values and position for animals away from the interface is consistent with very small-scale movement and assimilation of carbon. However, the possibility of carbon movement and assimilation at a somewhat larger scale further inside habitats cannot be discounted, since it would not be detectable because of the homogeneous $\delta^{13}C$ values of autotrophs within habitats. It is also possible that sources such as seagrass from further afield may contribute to animal nutrition, particularly to animals in mangrove habitat.

Across the habitat interface, consumers derived their carbon from a mixture of saltmarsh and mangroves. Although the scale of sampling in previous studies has precluded detailing the rate of energy transfer across the habitat interface, in this study, the change in $\delta^{13}C$ values across the transition zone indicates the rate of carbon movement and assimilation between these adjacent habitats. The dietary shift from saltmarsh to mangrove-MPB carbon is between 0.54 and 1.22‰ m^{-1}. This type of information may be useful in any consideration of buffer zones in the design of Marine Protected Areas.

Animal diets

For animals collected at positions more than about 5 m into the saltmarsh habitat, the average $\delta^{13}C$ values closely reflected that of the salt couch grass, indicating that this was their main source of dietary carbon. The similarity in $\delta^{13}C$ values of the salt couch grass and animals collected in the saltmarsh supports the model that carbon movement and assimilation occurred at a scale of just a few metres (5–7.5 m).

No previous studies have examined the role of *Sporobolus virginicus* in macroinvertebrate food webs, but vascular plants such as *Spartina alterniflora* have previously been described as an important part of the diet of marsh snails (Haines and Montague 1979). Dietary analysis of deposit-feeding gastropods shows that they are able to assimilate organic matter from reed detritus under laboratory conditions (Kurata et al. 2001). Other studies have shown the diet of saltmarsh macroinvertebrates (Currin et al. 1995; Dittel et al. 2000) and selected finfish (Weinstein and Litvin 2000) to be comprised of a mixture of *S. alterniflora* and microalgae. Observations of the feeding behaviour of grapsid (Iribarne et al. 1997) and

ocypodid (Hsieh et al. 2002) crabs have included the consumption of saltmarsh plants and terrestrial grass.

$\delta^{13}C$ values of animals collected at positions more than about 5 m into the mangroves were more enriched than the mangroves in the present study. The animals in mangrove habitat most likely obtain their carbon from MPB, although their $\delta^{13}C$ values are also consistent with a mixture of carbon sources such as mangroves and salt couch grass, with or without contribution from MPB. In this latter scenario, values of mangrove animals suggest larger-scale movement of carbon than the 5–7 m range indicated by saltmarsh animals. Fractionation of carbon during metabolism, however, can be up to 2‰ (McCutchan et al. 2003), and it is equally possible that that the slightly enriched values of mangrove animals result from the assimilation of predominantly MPB sources.

Studies that examine food web dynamics of resident mangrove animals typically apportion only minor contributions of mangrove carbon to macroinvertebrate diets (e.g., Bouillon et al. 2002; Hsieh et al. 2002). For several species of *Uca*, microalgae (Rodelli et al. 1984) and bacteria (Dye and Lasiak 1986) are considered important food sources. Feeding observations of grapsid crabs are diverse and include the carrying of mangrove leaf litter into their burrows (Lee 1998), but recent evidence from gut content analysis indicates a generalist mode of feeding and dietary assimilation for some species (e.g., *Sesarma leptosoma,* Dahdouh-Guebas et al. 1999). This generalist mode of feeding is consistent with the interpretation of a mixed diet described in the present study for crabs collected in mangroves, but further work in local estuaries is required to determine sources for the animals studied here.

Alternative sources

In addition to saltmarsh and mangroves, seagrass is also present in southern Moreton Bay, seaward of mangroves, and has an enriched $\delta^{13}C$ value similar to that of salt couch grass (–12‰, Melville and Connolly 2003). Seagrass carbon could potentially be deposited on marshes and be directly or indirectly used by crabs and slugs. However, as there was no seagrass in the vicinity of the sites surveyed, and no seagrass detritus observed, it is unlikely that seagrass contributed much, if at all, to the animal carbon source. Carbon isotope values for phytoplankton of ~ –20‰ (Fry 1984; Davenport and Bax 2002) make it an unlikely source of carbon for animals residing on the saltmarsh. Truly terrestrial vegetation can show similar isotopic values to that of mangroves (e.g., –27 to –30‰, Boon and Bunn 1994), but the sites used in this study were several kilometres from terrestrial sources, minimising the likelihood of terrestrial vegetation contributing to the isotopic values of the animals.

Previous studies frequently use the progressive enrichment of ^{13}C with increasing distance from mangroves as an indication of the progressive reduction in the assimilation of mangrove detritus (Rodelli et al. 1984; Lin et al. 1991; Hemminga et al. 1994). France (1998) however, argues that this interpretation of the dietary contribution of mangroves may be incorrect. He suggests that all organisms, regardless of trophic status, or whether they are ingesting mangroves directly, are ^{13}C depleted in mangroves due the high rates of decomposition, microbial activity and respiration. In our study, the more depleted $\delta^{13}C$ values of the crabs in mangrove habitat could have been obtained without any contribution from mangrove material. Recent work indicates that MPB has a greater role in invertebrate nutrition than mangrove material itself (Bouillon et al. 2002). Further work with alternative tracers is required to determine more precisely the autotrophs involved in crab and slug nutrition in mangrove habitats in Moreton Bay.

Factors influencing the potential movement and assimilation of mangrove carbon include geomorphology, inundation frequency, tidal range and sediment chemistry (Lee 1995; Ayukai et al. 1998). Measurements for these factors that would permit comparisons across different parts of Moreton Bay are unavailable, and it is therefore difficult to know how general the patterns shown here would be. At the sites in this study in southern Moreton Bay, tidal currents are strong, and we consider it unlikely that processes of energy transfer involving currents would be more limited here than elsewhere in the bay.

Whilst the aim of this study was to examine the metre-scale movement and assimilation of carbon across adjacent habitat boundaries, movement of the target animals could also explain the observed patterns in $\delta^{13}C$. If the movement of target animals is used to explain the patterns in $\delta^{13}C$ observed in the current study, the restricted range of carbon movement and assimilation remains the same, but the mechanism by which movement occurs is different. That is, under the animal movement scenario, carbon moves and is assimilated, not by the transport of particulate carbon, but via tropic relay as described by

Kneib (2000). Such movement is considered unlikely for both crabs and the estuarine slug. Little information on the movement of these animals is available, however the crabs are considered to be faithful to their burrows and are therefore assumed to forage in close proximity to their burrows. At the very small scale, there remains the possibility that the movement of crabs accounts for the transition of $\delta^{13}C$ values across the habitat interface. For slugs, personal observation indicates that their movement is predominantly vertical within the sediment profile.

It is possible that carbon may move among habitats at any of the scales presented but not be assimilated by the consumers sampled. Stable isotope analysis of consumers tests only the movement *and* assimilation of carbon. As this study set out to determine the trophic importance of discrete habitats over small spatial scales, only the movement and assimilation of carbon has been examined. Movement of carbon that does not contribute to trophic dynamics has therefore not been considered.

Conclusion

A previous study of the isotope ratios of invertebrates in the study area indicated that movement and assimilation of carbon by invertebrates occurred at a scale of $<$ 30 m. That provided the rationale for the detailed measurement of metre-scale movement in the present study. The most likely scenario is that the intertidal crabs and slugs used as test organisms here ultimately obtain their nutrition from very local sources; salt couch grass for animals in saltmarsh and probably microalgae for animals in mangrove habitat. Contributions from unmeasured autotrophic sources further afield cannot be totally excluded given the tidally driven current in these waters. The rapid change in isotopic ratios of animals across the saltmarsh-mangrove boundary nevertheless demonstrates a sharp change in the major local sources for these animals. The detailed spatial sampling gives greater precision to our understanding of carbon movement between discrete patches of estuarine habitat. Although further work is required to be able to generalise to more mobile animals, this type of information is useful to managers looking to incorporate habitat buffer zones into protected area design.

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