

# Movement of carbon among estuarine habitats: the influence of saltmarsh patch size

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**ABSTRACT:** We used carbon stable isotopes to examine the influence of the size of saltmarsh patches on the trophic contribution of saltmarsh grass and mangroves to 2 species of resident crabs (*Parasarsarma erythroductyla* and *Australoplax tridentata*). Crabs were collected at different distances across the saltmarsh–mangrove interface at each of 10 saltmarshes of different sizes (0.01 to 8.10 ha) adjacent to mangrove forests (each >4 ha). The  $\delta^{13}\text{C}$  values of crabs at all 10 marshes fitted a sigmoidal curve, with rapidly changing  $\delta^{13}\text{C}$  values across the saltmarsh–mangrove interface (the transition zone). The size of saltmarsh patches had a significant effect on  $\delta^{13}\text{C}$  values of *P. erythroductyla* collected in the saltmarsh, with a similar trend shown by *A. tridentata*. On large saltmarshes (>0.4 ha),  $\delta^{13}\text{C}$  values of crabs (*P. erythroductyla*,  $-15.9\text{‰}$ ; *A. tridentata*,  $-15.4$ ) collected >5 m onto the saltmarsh matched that of the saltmarsh grass *Sporobolus virginicus* ( $-15.5$ ). Carbon movement and assimilation by crabs was limited to <5 m. On small saltmarshes (<0.3 ha),  $\delta^{13}\text{C}$  values of saltmarsh crabs ( $-18.1$  and  $-16.8$ , respectively) were depleted, indicating assimilation of carbon from *S. virginicus*, but also from a more depleted allochthonous source, e.g. mangroves ( $-28.1$ ), microphytobenthos ( $-23.7$ ), or phytoplankton (ca.  $-20$ ). Saltmarsh patch size did not affect the extent of carbon movement or assimilation by crabs in mangroves. Given that habitat patch size can influence pathways of carbon supply to invertebrates, the role of estuarine habitats in food webs cannot be assumed to be independent of the size and configuration of habitats.

**KEY WORDS:** Landscape ecology · Trophic ecology · Stable isotopes · *Avicennia marina* · Crustacea

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## INTRODUCTION

The influence of landscape structure on the abundance and distribution of organisms is a basic tenet of landscape ecology (Forman & Godron 1986). Landscape structure, or what has more recently been termed landscape mosaics (e.g. Arguiar & Sala 1999), refers to the distribution, orientation, age, size, shape and number of habitat patches, where 'patches' are commonly defined as an area that is visually distinct from its surroundings (Forman & Godron 1986). Much of the effort examining the biological consequences of landscape structure has focused on terrestrial land-

scapes (e.g. Robinson et al. 1992), but ecoscapes in the sea (Kneib 2000) are the subject of increasing attention (e.g. Hemminga et al. 1998, Frost et al. 1999).

In both terrestrial and marine settings, counts of animal and plant diversity and abundance are common means by which the response of organisms to characteristics of landscape structure is assessed (Cadenasso et al. 2004). For example, a review of 20 terrestrial studies of habitat fragmentation found that most focused on the effects of habitat size on species richness or on abundances of individual species (Debinski & Holt 2000). Other aspects of terrestrial landscape structure commonly explored using measures of diver-

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sity and abundance of organisms are comparisons between 'edge' and 'core' habitat (Fox et al. 1997), as well as the age of habitat patches (Brooks et al. 1999). In marine settings, patch size has also been the most commonly explored aspect (Bell et al. 2001), often with reference to the influence of edge and core habitat. In contrast to the structure of populations and assemblages of animals, the relationship between ecological processes and landscape structure has received much less attention, particularly in marine systems (however, for predator-prey interactions across habitat boundaries, see e.g. Donovan et al. 1997, Cantrell et al. 2001).

Food webs are an aspect of ecological processes central to our understanding of how natural systems are organised (Polis et al. 1997). One focus of food web processes in marine and estuarine settings has been the movement of carbon from intertidal habitats to off-shore environments (e.g. Kneib 2000, Bouillon et al. 2004), thus creating the first link between large-scale landscape structure and trophic contribution. Few marine or estuarine studies, however, have examined the relationships between food web processes and detailed characteristics of landscape structure such as patch size (but see Gremillet et al. 2004). Understanding the trophic function of small patches of habitat provides empirical evidence with which to evaluate the relative conservation value of habitats for inclusion into Marine Protected Areas at a scale more consistent with the scale of management in estuarine systems (Stevens & Connolly 2004).

We used stable isotopes of carbon and naturally fragmented saltmarsh habitat adjacent to mangrove forests to examine the influence of habitat size on the movement of carbon and its assimilation by resident invertebrates. These saltmarsh and mangrove habitats are suited to isotope analysis because the  $\delta^{13}\text{C}$  values of the dominant autotrophs are clearly separated (Guest et al. 2004a). As water is the principal vector for the transport of carbon across habitat boundaries in aquatic systems (Polis et al. 1997), animals within these habitats, even sedentary ones, may derive their carbon from sources outside the habitat they occupy. Sedentary animals are therefore useful test organisms, because their home range is limited and carbon sources can be more clearly differentiated into those produced locally and those produced further away. Results from the same estuary as that used in the current study (Guest & Connolly 2004, Guest et al. 2004a) showed that the movement of carbon and its assimilation by resident invertebrates in adjacent saltmarsh and mangrove habitats is limited to <10 m where the sizes of saltmarshes were all about 2 ha. The current survey measured the influence of habitat size on the small-scale movement of carbon and its assimilation by 2 resident, detritivorous crab species.

Movement of carbon among estuarine habitats occurs at least partly as particulate matter, and we based our hypotheses on the concept that larger patches would generate more particulate matter and that some of this would be available for dispersal to adjacent habitats. We predict, therefore, that, for large saltmarsh patches, saltmarsh carbon will move further into adjacent mangrove habitat and be assimilated by the mangrove crabs (Fig. 1). This means that in mangroves adjacent to large saltmarsh patches, the  $\delta^{13}\text{C}$  values of mangrove crabs will reflect the assimilation of some saltmarsh carbon. Crabs in mangroves adjacent to small patches of saltmarsh, where the total pool of particulate saltmarsh material is predicted to be small, should show little assimilation of saltmarsh carbon. In this scenario, mangrove crab  $\delta^{13}\text{C}$  values will be similar to the dominant autotroph in the mangroves (i.e. mangroves or microphytobenthos). In large saltmarsh patches, the  $\delta^{13}\text{C}$  values of crabs resident in saltmarsh are predicted to be similar to that of the dominant autotroph in the saltmarsh (i.e. saltmarsh grass). For small saltmarsh patches, mangrove carbon will move into the adjacent saltmarsh and be assimilated by the crabs. We predict that in these small saltmarsh patches, the  $\delta^{13}\text{C}$  values of the saltmarsh crabs will be more similar to the dominant autotrophs of the adjacent mangroves than to the saltmarsh in which they reside.

## MATERIALS AND METHODS

Saltmarsh and mangrove habitats were sampled in April 2003 in southern Moreton Bay, Queensland, Australia (Fig. 2). Ten sites of adjacent saltmarsh and mangrove habitat were chosen where saltmarsh habitat was dominated by the saltmarsh grass *Sporobolus virginicus* and the mangroves by *Avicennia marina*. These species were chosen over other estuarine species in southern Moreton Bay because of the clear separation of their carbon isotope values (Guest et al. 2004a), their proximity to each other and their abundance throughout the study region. Patches of saltmarsh were defined visually by an abrupt change in vegetation type on 3 sides, with the fourth bounded at the upper intertidal edge by estuarine water. Saltmarsh patches were between 0.01 and 8.10 ha in area (see Fig. 3), and adjacent mangrove forests were at least 4 ha. We selected saltmarsh patches approximately rectangular in shape, with the longer edge of the rectangle abutting the mangroves, to standardise the potential influence of patch orientation and perimeter to area ratio across patches. The saltmarshes had low relief (<0.5 m change in elevation) and were inundated on at least 1 high tide per day for 2 wk out of the 4 wk sampling period, with a tidal range of about 1.3 m.

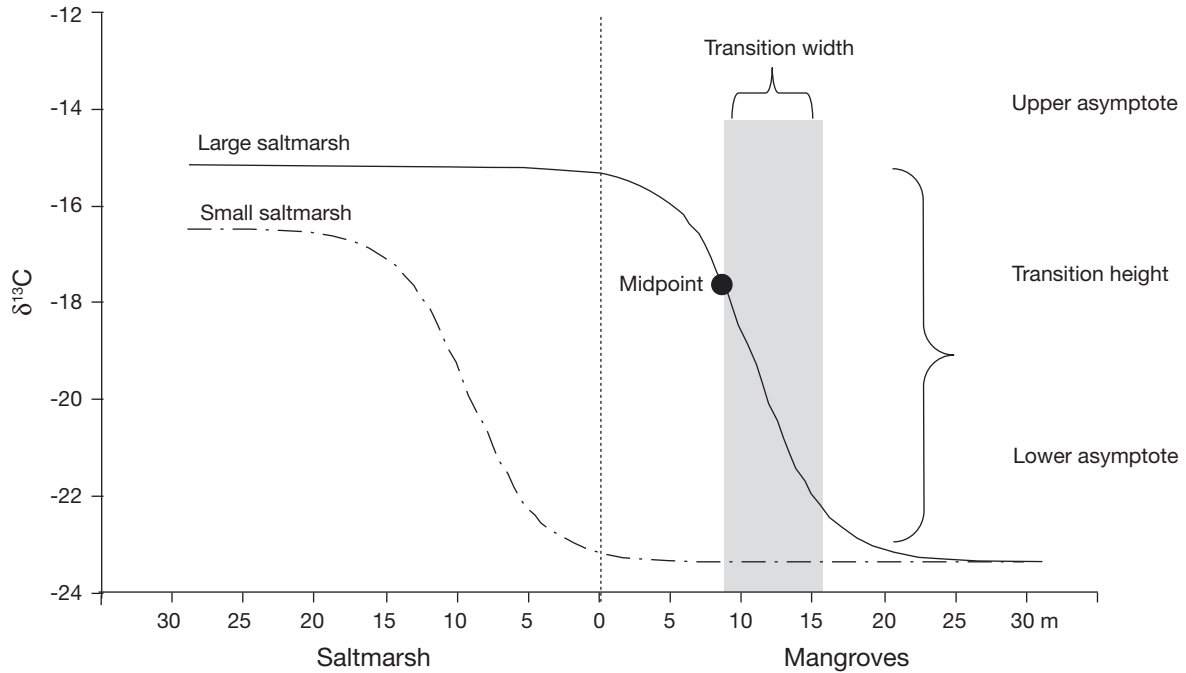


Fig. 1. Predicted non-linear patterns of invertebrate isotope values at different distances from the saltmarsh–mangrove interface in large and small marshes. The parameters expected to best describe these patterns are labelled (upper asymptote, the  $\delta^{13}\text{C}$  value of crabs in saltmarsh; lower asymptote, the  $\delta^{13}\text{C}$  value of crabs in mangroves; transition height, the difference in  $\delta^{13}\text{C}$  values between the upper and lower asymptote; midpoint, the centre of the transition zone along the x-axis; transition width, the distance carbon moves into the adjacent habitat from the midpoint)

Two crab species, *Australoplax tridentata* (Ocypodidae) and *Parasesarma erythroductyla* (Grapsidae), were chosen for analysis, because they are found in both saltmarsh and mangroves and because they rarely move >1 m from their burrows (Guest 2004). Their carbon isotope values therefore provide a good

test of the movement and assimilation of carbon among adjacent habitats.

At each of the 10 locations, samples of both crab species were collected at the saltmarsh–mangrove interface (or zero point), and at 2, 4, 8, 16 and 30 m positions from the zero point into both saltmarsh and mangroves. However, some saltmarsh patches were too small to permit collections 30 m into the saltmarsh, and, in the smallest patch, crabs could only be collected up to 8 m into the saltmarsh. Crabs of a similar size (mean  $13.7 \pm 0.1$  mm carapace width for *Parasesarma erythroductyla* and  $10.6 \pm 0.1$  mm for *Australoplax tridentata*) were collected at each position to minimise the possibility of intraspecific variability in isotope ratios of carbon due to ontogenetic shifts in diet (France 1998). The flesh from 2 to 3 crabs was pooled to provide enough tissue for analysis for each sample in each patch.

Three samples of *Sporobolus virginicus* and *Avicennia marina* were collected 30 m from the saltmarsh–mangrove interface at each site (i.e. 3 samples per site). Carbon isotope values of both *S. virginicus* (Guest et al. 2004b) and *A. marina* (Connolly et al. 2003) from different positions within a patch have previously been shown to be within 1‰. Carbon isotope values of microphytobenthos (MPB) collected at 30, 10 and 2 m positions in saltmarsh and mangrove habitats

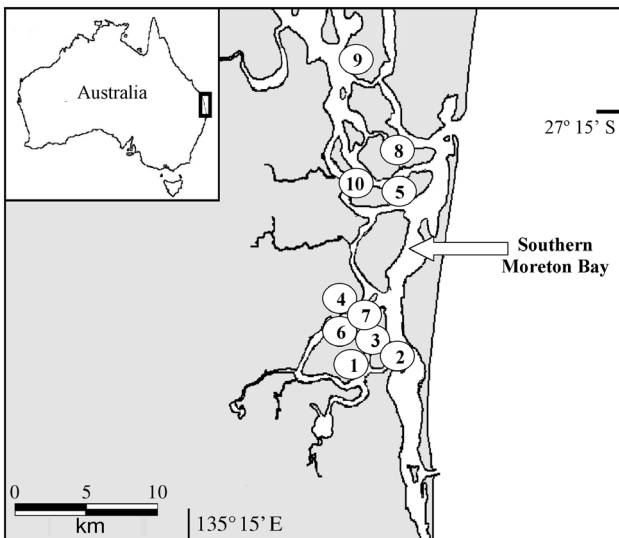


Fig. 2. Study area in southern Moreton Bay, with adjacent saltmarsh and mangrove sites numbered in order of size

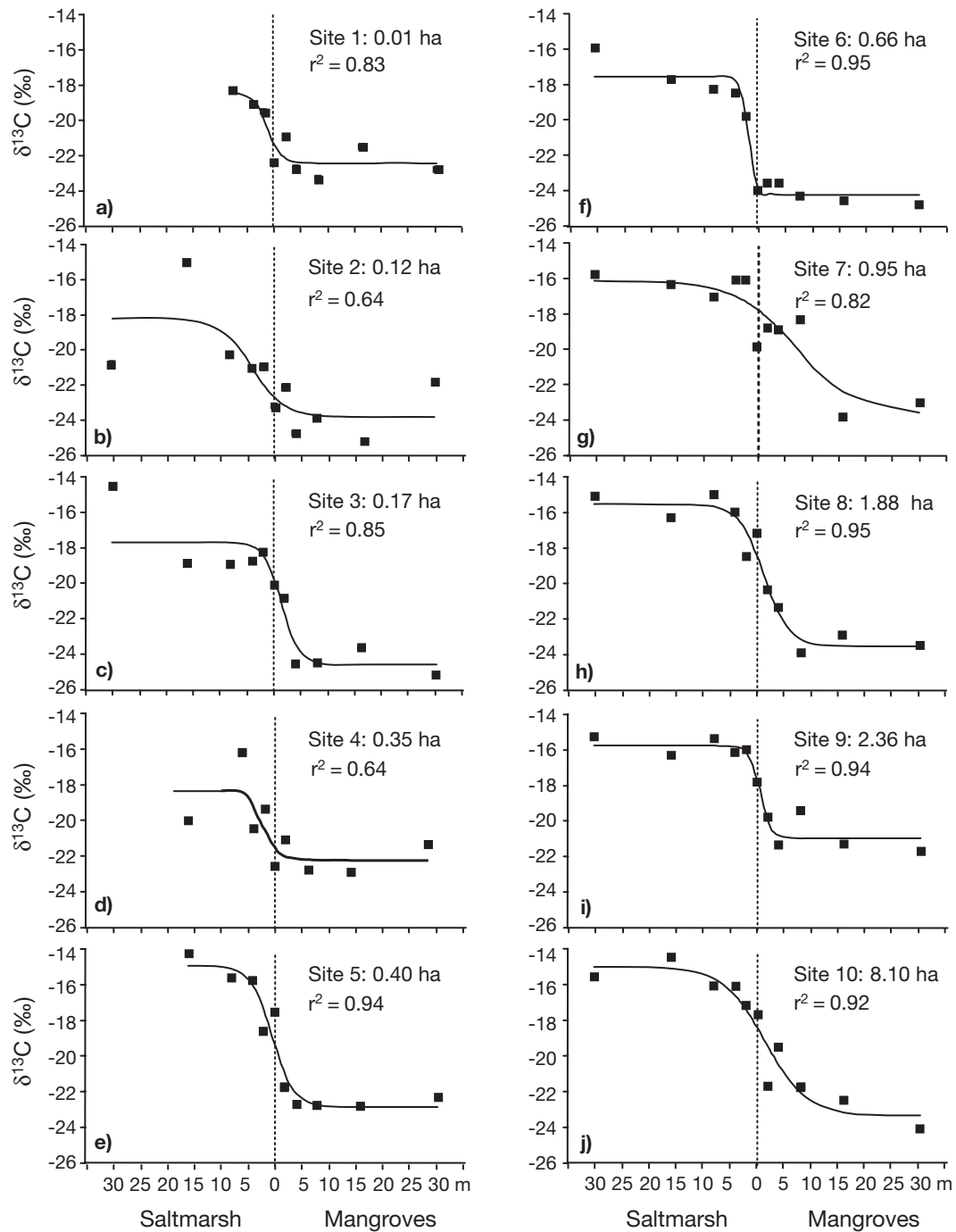


Fig. 3. *Parasesarma erythroductyla*. Non-linear regression line of best fit for  $\delta^{13}\text{C}$  values and sampling positions for each site. Sites are numbered 1 to 10 in increasing order of saltmarsh patch size

at 3 of the 10 sites had previously been reported (Guest & Connolly 2004), and these values were used again here. MPB samples consisted predominantly of diatoms isolated by centrifuging superficial sediment in silica gel (Guest et al. 2004a).

All samples were dried and ground (for crabs, the exoskeleton, shell and gut were removed), and their isotopic values were analysed on an Isoprime mass spectrometer. The ratios of  $^{13}\text{C}/^{12}\text{C}$  were calculated as the relative difference (‰) between the sample and the

recognised standard (Pee Dee belemnite limestone carbonate). Precision of the mass spectrometer, calculated using values from duplicate samples, was 0.2‰.

At each location, the relationship between  $\delta^{13}\text{C}$  values of each crab species and sampling positions across saltmarsh and mangrove habitats was clearly curvilinear. We therefore used non-linear regression in SPSS (Release 11.5.0, 2002, standard version for Windows) to determine the best fitting sigmoidal curve, of the form:

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

where  $a$  is the transition height, i.e. the difference in  $\delta^{13}\text{C}$  between upper (saltmarsh) and lower (mangrove) asymptotes;  $b$  is the transition midpoint, i.e. the centre of the transition zone along the  $x$ -axis; and  $d$  is the value of  $y$  when  $x$  approaches its smallest value, i.e. the lower asymptote (Fig. 1). The transition width equals  $2.197c$  (obtained from Tablecurve 2D, Version 5, 2000, AISN Software) and is the distance that carbon moves along the  $x$ -axis from the transition midpoint, and is symmetrical around the midpoint (Fig. 1).  $c$  is a non-zero constant, and reflects the steepness of the transition width. The initial values for parameters were estimated from visual plots of the data to reduce the number of iterations when calculating the best-fitting sigmoidal curve.

The influence of the size ( $\log_{10}$ ) of the saltmarsh patch on the trend in  $\delta^{13}\text{C}$  values of each crab species among sampling positions was analysed using simple linear regression. Parameter estimates (derived from

the non-linear model above) that describe the trend in the  $\delta^{13}\text{C}$  values of crabs were selected *a priori* for analysis, according to the predicted influence of patch size on the  $\delta^{13}\text{C}$  values of crabs at sampling positions across the saltmarsh–mangrove interface (Table 1).

## RESULTS

The  $\delta^{13}\text{C}$  values of autotrophs could be separated into 3 bands: *Sporobolus virginicus* ( $-15.4 \pm 0.1\text{‰}$ ), MPB ( $-23.7 \pm 0.3\text{‰}$ , Guest & Connolly 2004) and *Avicennia marina* ( $-28.1 \pm 0.1\text{‰}$ ). The  $\delta^{13}\text{C}$  values of MPB did not vary greatly between habitats ( $-23.0 \pm 0.5\text{‰}$  in saltmarsh,  $-24.4 \pm 0.5\text{‰}$  in mangroves).

For both crab species, and at all sites, the sigmoidal regression model provided a close fit of the relationship between  $\delta^{13}\text{C}$  values and the position of a crab in each habitat ( $p < 0.001$  for all; Figs. 3 & 4). The relationship between  $\delta^{13}\text{C}$  values and crab position was negative, with more enriched  $\delta^{13}\text{C}$  values in the saltmarsh habitat and increasingly depleted  $\delta^{13}\text{C}$  values with greater proximity to mangroves. The explanatory power of the sigmoidal regressions (measured as  $r^2$ ) in estimating  $\delta^{13}\text{C}$  from positions of invertebrates was high ( $r^2 > 0.80$ ) for all sites except at Sites 2 and 4 for both species (0.64 for both sites for *Parasesarma erythroductyla*; 0.67 and 0.50 for *Australoplax tridentata* at Sites 2 and 4, respectively; Figs. 3 & 4).

Most parameter estimates were not correlated with the size of the saltmarsh patch (Table 1), but their averages across the 10 sites indicated the extent of carbon movement and assimilation across the saltmarsh–mangrove interface. The average transition midpoint over all 10 patches was 0.2 m ( $\pm 0.9$ ) into the mangroves for *Parasesarma erythroductyla* and 2.0 m ( $\pm 0.9$ ) into the mangroves for *Australoplax tridentata* (estimated from the 0 m position that demarcates the saltmarsh–mangrove interface). The extent of carbon movement and assimilation into each habitat measured from the transition midpoint, and referred to as the transition width, was 5.0 m ( $\pm 1.0$ ) for *P. erythroductyla* and 3.8 m ( $\pm 0.7$ ) for *A. tridentata*.

The transition height was similar for both species ( $6.4 \pm 0.5\text{‰}$  for *Parasesarma erythroductyla*,  $5.6 \pm 0.7\text{‰}$  for *Australoplax tridentata*). The upper and lower asymptotes (see Figs. 3 & 4) represent invertebrate  $\delta^{13}\text{C}$  values at sampling positions within saltmarsh and mangrove habitats, excluding the

Table 1. *Parasesarma erythroductyla*, *Australoplax tridentata*. Regression analysis ( $r^2$ ) and significance ( $p$ ) of relationships between saltmarsh patch size and parameter estimates derived from the non-linear regression model (upper and lower asymptotes,  $\delta^{13}\text{C}$  values for crabs in saltmarsh and mangroves, respectively; midpoint, centre of the transition zone along the  $x$ -axis; transition width, distance carbon moves into the adjacent habitat from the midpoint; distance saltmarsh carbon moves into mangroves, measure of the intrusion of saltmarsh carbon [in m] into adjacent mangrove habitat based on crab  $\delta^{13}\text{C}$  values; distance mangrove carbon moves into saltmarsh, same measure but of intrusion of mangrove carbon into saltmarsh; asterisk denotes significance,  $n = 10$  in all cases)

Parameter	<i>Parasesarma erythroductyla</i>		<i>Australoplax tridentata</i>	
	$r^2$	$p$	$r^2$	$p$
Upper asymptote	0.58	0.011*	0.26	0.131
Lower asymptote	0.00	0.849	0.03	0.606
Midpoint	0.19	0.207	0.00	0.947
Transition width	0.10	0.374	0.03	0.627
Distance saltmarsh C moves into mangroves	0.01	0.739	0.02	0.661
Distance mangrove C moves into saltmarsh	0.17	0.241	0.01	0.790

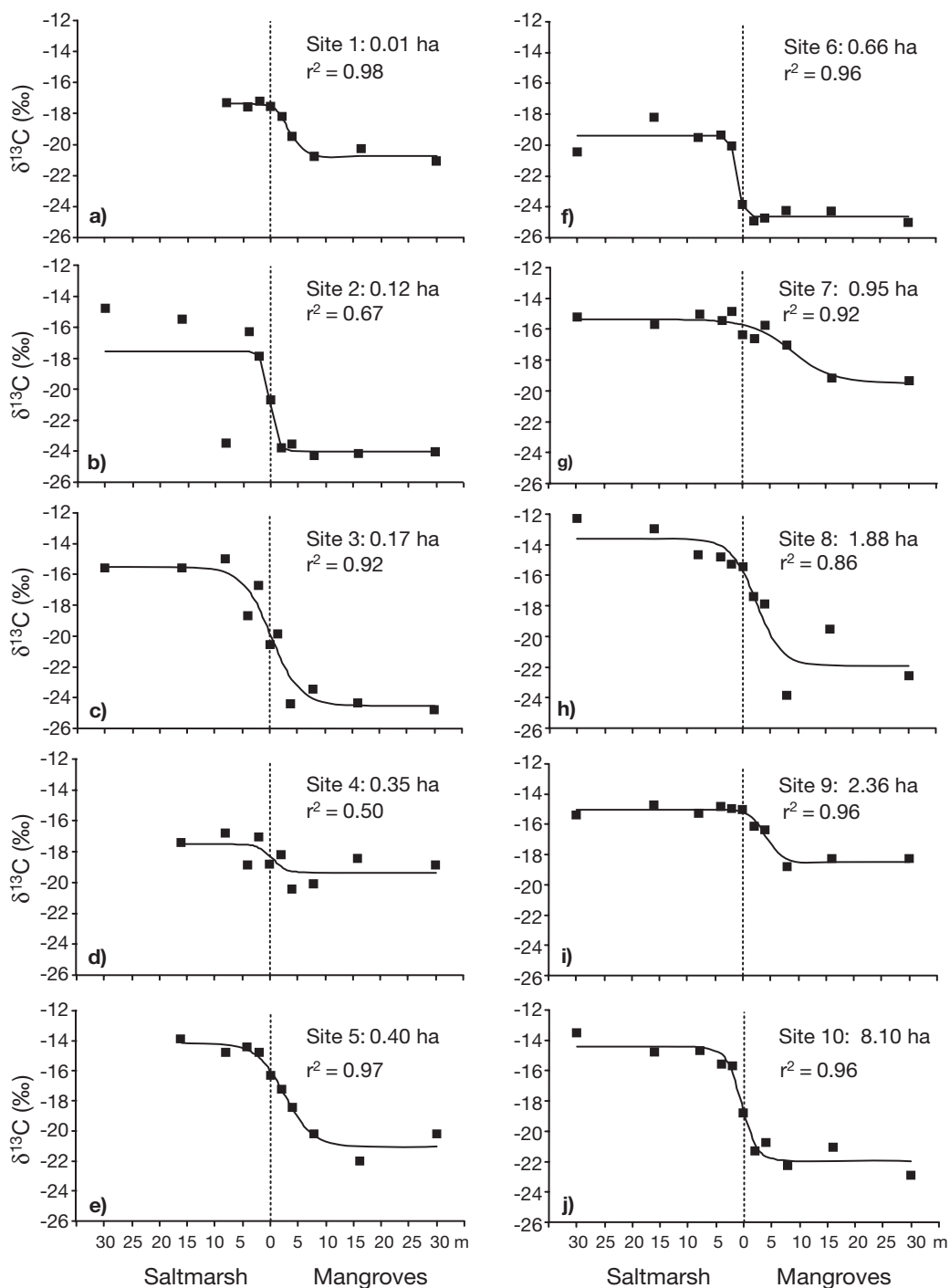


Fig. 4. *Australoplax tridentata*. Non-linear regression line of best fit for  $\delta^{13}\text{C}$  values and sampling positions for each site. Sites are numbered 1 to 10 in increasing order of saltmarsh patch size

saltmarsh–mangrove interface. In the saltmarsh, the invertebrate  $\delta^{13}\text{C}$  values closely matched the  $\delta^{13}\text{C}$  values of the saltmarsh grass. In the mangroves, invertebrate values were more enriched than the mangrove values, and were closer to, but still slightly more enriched than, the  $\delta^{13}\text{C}$  values of MPB.

From the regression analyses of parameter estimates and saltmarsh size, only the relationship between the upper asymptote (i.e. the  $\delta^{13}\text{C}$  values of crabs in saltmarsh habitat) and saltmarsh size was significant, and only for *Parasesarma erythroactyla* (Table 1, Fig. 5a). The  $\delta^{13}\text{C}$  values of *P. erythroactyla* in small saltmarsh

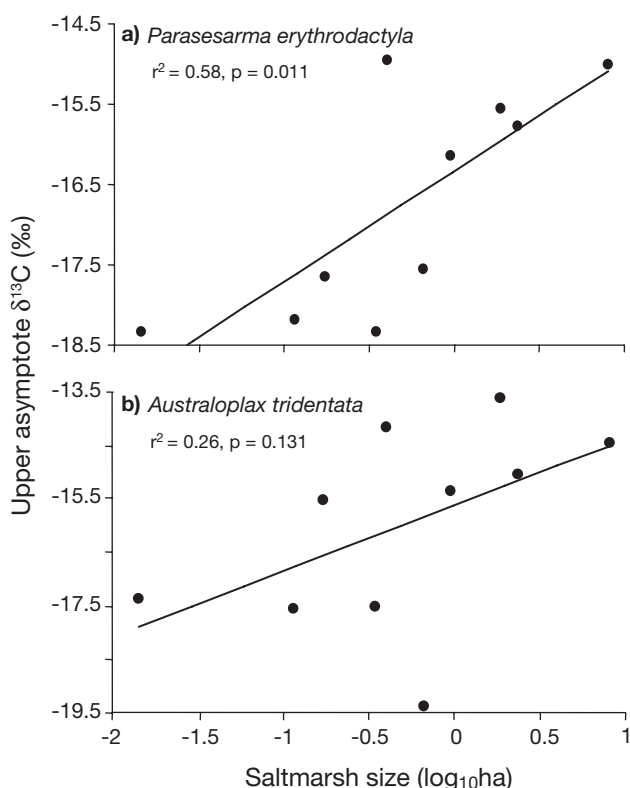


Fig. 5. (a) *Parasesarma erythroductyla*, (b) *Australoplax tridentata*. Upper asymptote values ( $\delta^{13}\text{C}$ ) for different-sized saltmarshes ( $\log_{10}$ ) ( $n = 10$  crabs)

patches were more negative (Site 1,  $-18.3 \pm 1.1\text{‰}$ ; Fig. 5a) than those collected from larger patches (Site 10,  $-15.0 \pm 1.2\text{‰}$ ; Fig. 5a). Whilst the upper asymptote of  $\delta^{13}\text{C}$  values of *Australoplax tridentata* were not significant (Site 1,  $-17.4 \pm 0.3\text{‰}$ ; Site 10,  $-14.4 \pm 0.6\text{‰}$ ; Fig. 5b), it followed the same trend with saltmarsh size as that of *P. erythroductyla*.

## DISCUSSION

### Influence of saltmarsh size on food web processes

The relative trophic contribution of small patches (<0.3 ha) of saltmarsh was less than that of larger patches (0.4 to 8.1 ha) for the resident crab *Parasesarma erythroductyla*. This was shown by the significantly more negative  $\delta^{13}\text{C}$  values of *P. erythroductyla* collected >5 m into the saltmarsh (and representing the upper asymptote in the model) in small patches (<0.3 ha) than in large patches. The patterns of  $\delta^{13}\text{C}$  values of *Australoplax tridentata* were not significant, although they followed a similar trend. No other para-

eters from the non-linear regression model of crab position across habitats and carbon isotope value varied significantly with saltmarsh size for both crab species.

Few other studies have examined the influence of habitat size on food web processes, but studies of terrestrial vertebrates (e.g. Stamps et al. 1987) suggest that the influence of habitat size is greater where the permeability (i.e. the ease of movement across habitats) of the habitat boundary is high (Marquet et al. 1993). In the present study, permeability refers to the ease with which carbon moves across the saltmarsh–mangrove interface and is assimilated by crabs. In large saltmarsh patches, the similarity of saltmarsh crab  $\delta^{13}\text{C}$  values to those of *Sporobolus virginicus* and the narrow transition width of  $\delta^{13}\text{C}$  values across the saltmarsh–mangrove interface indicate that permeability is low and limited to 5 m or less on either side of the saltmarsh–mangrove interface. Whilst the transition width in small saltmarsh patches was similar to that of large patches, the depleted  $\delta^{13}\text{C}$  values of crabs in the saltmarsh indicate that small saltmarsh patches are more susceptible or ‘permeable’ to the intrusion of allochthonous carbon sources, such as carbon from mangroves or phytoplankton.

### Scales of carbon movement and assimilation

The movement of carbon and its assimilation by resident crab species in large saltmarsh patches adjacent to mangroves was restricted to a scale of several metres (<5 m). This result is consistent with the trend of other recent smaller-scale studies on the movement of carbon and its subsequent assimilation by invertebrates (Jennings et al. 1997). For example, in a study of the  $\delta^{13}\text{C}$  values of ocypodid crabs at sites separated by hundreds of metres, carbon sources varied enormously (Hsieh et al. 2002).

In a study of saltmarshes approximately 2 ha in area (Guest & Connolly 2004), the  $\delta^{13}\text{C}$  values of crabs collected more than about 7 m from the saltmarsh–mangrove interface were close to those of *Sporobolus virginicus*. The  $\delta^{13}\text{C}$  values of crabs collected >7 m into the mangroves were intermediate between mangroves and MPB. The similarity in the  $\delta^{13}\text{C}$  values of crabs with the dominant autotroph in the habitat in which they reside, and the separation of isotope ratios between the 2 habitats, indicate the extent of carbon movement and assimilation occurring within a transition zone about 7 m either side of the saltmarsh–mangrove boundary. These results, and those of large saltmarshes from the current study, provide strong evidence that the movement of carbon is occurring at a scale much smaller than has typically been examined

in previous studies. For small saltmarshes, however, our results demonstrate depletion in the  $\delta^{13}\text{C}$  values of crabs right across the saltmarsh, indicating a larger contribution from allochthonous sources of carbon to crabs.

The transition midpoints of the sigmoidal curves also help to describe the movement and assimilation of carbon, and were close to the saltmarsh–mangrove interface for both crab species. This indicates that even for large saltmarshes, 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 than from mangroves into the saltmarsh (i.e. the midpoint described by the model for *Parasesarma erythro-dactyla* was  $0.2 \pm 0.9$  m and for *Australoplax tridentata*  $2.1 \pm 0.9$  m into the mangroves). The transition widths of large saltmarshes, however, suggest limited carbon movement (<5 m either side of the transition midpoint for both species) and are at the smaller end of the scale that was measured.

### Crab diets

The clear separation in the  $\delta^{13}\text{C}$  values of crabs located more than about 5 m into the saltmarsh and those located more than about 5 m into the mangroves (as indicated by the transition height) means that crabs residing in saltmarsh and mangroves derive their carbon from different sources. This is consistent with the results of previous studies on the diet of ocypodid and grapsid crabs that suggest a lack of dietary specialisation for some crab species (e.g. *Sesarma leptosoma*, Dahdouh-Guebas et al. 1999). For example, grapsid crabs have been reported to consume both saltmarsh plants (Iribarne et al. 1997) and mangrove leaf litter (Lee 1997). Ocypodid crabs have been described as feeding on bacteria (Dye & Lasiak 1986), microalgae (Rodelli et al. 1984) and terrestrial grass (Hsieh et al. 2002).

In the current study, for crabs collected in large saltmarshes, their  $\delta^{13}\text{C}$  values closely matched that of the saltmarsh grass *Sporobolus virginicus*, indicating that this was their main source of dietary carbon. The  $\delta^{13}\text{C}$  values of crabs from small saltmarshes, however, were more depleted in  $^{13}\text{C}$  than those from large saltmarshes. The more depleted  $\delta^{13}\text{C}$  values of crabs from smaller saltmarshes suggest that these crabs assimilate an alternate and more depleted carbon source, e.g. mangrove, MPB, or phytoplankton (ca.  $-20\%$ , Fry 1984, Davenport & Bax 2002).

The  $\delta^{13}\text{C}$  values of crabs collected at positions more than about 5 m into the mangroves were more enriched than the mangroves at all sites, regardless of

the size of the adjacent saltmarsh. Thus, mangroves, saltmarsh grass and MPB may all contribute to the diet of mangrove crabs. Any contribution of saltmarsh grass to the diet of mangrove crabs suggests a larger-scale movement of carbon than the 5.0 m range indicated by saltmarsh crabs from large patches. However, a simpler explanation is that mangrove crabs rely predominantly on MPB and that the slight enrichment of crab values to MPB values (about  $1\%$ ) results from trophic fractionation (Peterson & Fry 1987).

In small saltmarshes, the  $\delta^{13}\text{C}$  values of saltmarsh crabs were more depleted than that of the saltmarsh grass. The  $\delta^{13}\text{C}$  values of phytoplankton and the proximity of the sites surveyed to open water make phytoplankton a possible carbon source for saltmarsh crabs, and this may explain the disparity between the carbon isotope values of consumers and the dominant autotroph within each habitat. However, phytoplankton may only be an irregular source of carbon to saltmarsh crabs, as it can only be deposited on the marsh during flooding tides. At the sites surveyed, flooding tides typically occur on spring tides, but more frequently in periods of prolonged rainfall. Seagrass with its epiphytic algae is also present in southern Moreton Bay, seaward of mangroves, and has an enriched  $\delta^{13}\text{C}$  signature ( $-12\%$ ) similar to that of saltmarsh grass (Melville & Connolly 2003). Seagrass meadows produce more carbon than can be consumed *in situ* by animals (Duarte & Cebrian 1996, Moncreiff & Sullivan 2001), and seagrass deposited at the marsh sites may contribute small amounts of carbon to the diet of saltmarsh crabs. Terrestrial vegetation is an unlikely contributor of carbon to the  $\delta^{13}\text{C}$  values of crabs, as the sites surveyed were several kilometres from terrestrial vegetation.

The trend in the  $\delta^{13}\text{C}$  values of crabs across the saltmarsh–mangrove interface may also be explained by the movement and subsequent foraging by crabs across this transition zone (Guest et al. 2004a). However, Guest (2004) has shown that crabs rarely move more than about 1 m up or down the shore. Crab movement across the saltmarsh–mangrove interface is therefore not a plausible alternative to explain the trend in the  $\delta^{13}\text{C}$  values of crabs from saltmarsh patches of varying sizes. Small-scale movement of detrital carbon is the most likely explanation for the trend in the  $\delta^{13}\text{C}$  values of crabs (Connolly et al. 2005). It is possible that carbon moves among habitats more than is shown by the present results, but that it is not assimilated by crabs (stable isotope analysis of crabs tests only the movement *and* assimilation of carbon). Any movement of particulate carbon not utilised by invertebrates could be detected in future work by measuring carbon isotope values of detritus in superficial sediments.



## CONCLUSIONS

The results of this study, where significant, are consistent with our predicted influences of saltmarsh patch size. Very small saltmarshes contribute less carbon to food webs supporting resident crab species than do larger patches of saltmarsh. Unfortunately, such small saltmarsh patches are typically not incorporated into landscape-scale mapping. Patches of *Sporobolus* saltmarsh <2 ha in area comprise more than a third of saltmarshes in the study region (data provided by Dowling & Stephens 1999), suggesting that small patches of saltmarsh may be relatively common throughout southern Moreton Bay. Our work shows that habitat patch size can influence pathways of carbon supply to invertebrates. The role of estuarine habitats in local food webs cannot be assumed to be independent of the size and configuration of habitats.

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