

Michaela A. Guest · Rod M. Connolly
Shing Y. Lee · Neil R. Loneragan · Mark J. Breitfuss

Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement

Received: 30 May 2005 / Accepted: 27 December 2005 / Published online: 7 February 2006
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Abstract In theory, carbon is highly mobile in aquatic systems. Recent evidence from carbon stable isotopes of crabs (*Parasesarma erythroactyla* and *Australoplax tridentata*), however, shows that in subtropical Australian waters, measurable carbon movement between adjacent mangrove and saltmarsh habitats is limited to no more than a few metres. We tested whether the pattern in crab $\delta^{13}\text{C}$ values across mangrove and saltmarsh habitats was explained by crab movement, or the movement of particulate organic matter. We estimated crab movement in a mark–recapture program using an array of pitfall traps on 13 transects (a total of 65 traps) covering an area of 600 m² across the interface of these two habitats. Over a 19-day period, the majority of crabs

(91% for *P. erythroactyla*, 93% for *A. tridentata*) moved <2 m from the place of initial capture. Crab movement cannot, therefore, explain the patterns in $\delta^{13}\text{C}$ values of crabs. $\delta^{13}\text{C}$ values of detritus collected at 2-m intervals across the same habitat interface fitted a sigmoidal curve of a similar form to that fitting the $\delta^{13}\text{C}$ values of crabs. $\delta^{13}\text{C}$ values of detritus were 2–4‰ more depleted in saltmarsh ($-18.5 \pm 0.6\text{‰}$), and 4–7‰ more depleted in mangroves ($-25.9 \pm 0.1\text{‰}$) than $\delta^{13}\text{C}$ values of crabs recorded previously in each habitat. Assimilation by crabs of very small detrital fragments or microphytobenthos, more enriched in ^{13}C , may explain the disparity in $\delta^{13}\text{C}$ values. Nevertheless, the pattern in $\delta^{13}\text{C}$ values of detritus suggests that crabs obtain their carbon from up to several metres away, but without themselves foraging more than a metre or so from their burrow. Such detailed measurements of carbon movement in estuaries provide a spatially explicit understanding of the functioning of food webs in saltmarsh and mangrove habitats.

Communicated by Tony Underwood

M. A. Guest · R. M. Connolly · S. Y. Lee
Centre for Aquatic Processes and Pollution, and School of Environmental and Applied Sciences, Gold Coast Campus, Griffith University, PMB 50, Gold Coast Mail Centre, 9726 Nathan, QLD, Australia

N. R. Loneragan · M. A. Guest · R. M. Connolly · S. Y. Lee
Cooperative Research Centre for Coastal Zone, Estuary and Waterway Management, Indooroopilly, QLD, Australia

N. R. Loneragan
CSIRO Marine Research, PO Box 120, 4163 Cleveland, QLD, Australia

M. J. Breitfuss
Kellogg, Brown and Root Proprietary Limited Company, PO Box 2177, 4066 Toowong, QLD, Australia

Present address: M. A. Guest (✉)
Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, GPO Box 252-49, 7001, Hobart, TAS, Australia
E-mail: michaela.guest@utas.edu.au
Tel.: +61-3-62277207
Fax: +61-3-62278035

N. R. Loneragan
Centre for Fish and Fisheries Research, School of Biological Sciences and Biotechnology, Murdoch University, 6150 Murdoch, WA, Australia

Keywords Crab movement · Carbon movement · Crustacean · Estuaries · Stable isotopes

Introduction

In aquatic systems, water facilitates the movement of carbon as dissolved or particulate matter, or in the bodies of animals, across spatial boundaries so that aquatic animals, even sedentary ones, may obtain food from sources remote from the habitats in which they reside (Polis et al. 1997). In marine systems, examination of the apparent large-scale transport of carbon from inshore to offshore waters (e.g. Odum et al. 1979; Lee 1995) has been central to our understanding of the ultimate source of nutrition for marine and estuarine animals. In some estuaries, the 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 trophic linkages.

Grapsid and ocypodid crabs are common residents in mangrove (e.g. MacIntosh 1984; Kwok and Lee 1995) and saltmarsh habitats (e.g. Pennings et al. 1998). In several tropical mangrove systems, they are the dominant benthic macrofauna in terms of both abundance (Jones 1984) and biomass (Golley et al. 1962). The activities of crabs have also been shown to substantially alter the abiotic and biotic properties of intertidal habitats (Smith et al. 1991). For example, sesarmid crabs (Grapsidae) contribute substantially to leaf litter degradation [up to 80% of annual litterfall (Robertson and Daniel 1989)] and subsequent nutrient cycling and energy flow (Lee 1995, 1997; Skov and Hartnoll 2002).

Two crab species, *Parasesarma erythroactyla* (Grapsidae) and *Australoplax tridentata* (Ocypodidae), are ubiquitous throughout saltmarsh and mangrove habitat patches in southeast Queensland, Australia (Snelling 1959). The distribution of these crabs, and their known ecological importance, make them ideal organisms to test theories about carbon movement in estuaries. We have previously capitalised on these characteristics of *P. erythroactyla* and *A. tridentata* to examine the movement of carbon and its subsequent assimilation by crabs across the saltmarsh–mangrove interface at the scale of metres (Guest et al. 2004; Guest and Connolly 2004). Carbon movement across the saltmarsh–mangrove interface, as indicated by the $\delta^{13}\text{C}$ values of crabs, was shown to be limited to about 5–8 m, a much smaller scale than had previously been considered [see below for reproduction of crab isotope values from Guest and Connolly (2004)]. This small-scale movement of carbon occurred either side of the habitat interface, but crabs residing more than about 8 m into each habitat assimilated predominantly autochthonous carbon.

The conclusion by Guest and Connolly (2004) that crab isotope values indicate limited carbon movement rests on the assumption that the crabs themselves move and forage over distances much less than the 5–8 m of carbon movement described above. Previous studies that examined the movement of grapsid or ocypodid crabs suggest that patterns of movement vary among species. For example, the non-burrowing crab, *Hemigrapsus sanguineus* (Grapsidae), was found to move on average about 7 m over a 24-h period (Brousseau et al. 2002), and *Pachygrapsus marmoratus* (Grapsidae) was found to range over an area of up to 10 m² (Cannicci et al. 1999). The distances moved by these crabs would be sufficient to explain the pattern in $\delta^{13}\text{C}$ of crabs recorded by Guest and Connolly (2004). By contrast, other species that have high burrow fidelity are less mobile. For example, the majority of individuals of the grapsid, *Sesarma*

guttatum, remained within 1 m of where they were captured, 10 days after initial capture (Skov et al. 2002). For *Scopimera globosa* (Ocypodidae), few individuals moved between microhabitats along an intertidal gradient (Koga 1995).

We tested two models that can explain the pattern in $\delta^{13}\text{C}$ values of crabs across the saltmarsh–mangrove interface shown by Guest and Connolly (2004): (1) crabs move and forage at a scale of 5–8 m perpendicular to the saltmarsh–mangrove interface (model 1, movement of crabs), or (2) carbon moves as particulate matter at a scale of 5–8 m perpendicular to the saltmarsh–mangrove interface (model 2, movement of particulate organic matter). The models are not mutually exclusive; both mechanisms might operate simultaneously.

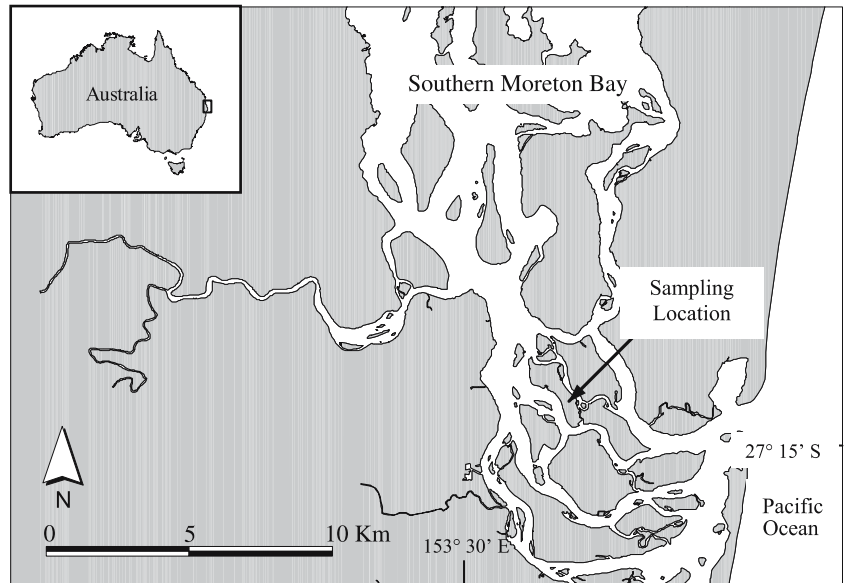
Materials and methods

Crabs and organic matter were sampled in February 2004 (late austral summer) in southern Moreton Bay, Queensland, Australia (Fig. 1); the same location and time of year previously used to examine movement and assimilation of carbon across the saltmarsh–mangrove interface (Guest et al. 2004; Guest and Connolly 2004). *Sporobolus virginicus* was the dominant vegetation in the saltmarsh habitat, and *Avicennia marina* the most common mangrove species. The saltmarsh habitat was defined visually by the presence of discrete boundaries marked by an abrupt change in vegetation type and was 2.4 ha in area. The adjacent mangrove forest was about 22 ha in area. The saltmarsh had low relief (<0.5 m) and was inundated on one high tide during each 24-h sampling period. The saltmarsh/mangrove interface is inundated daily for approximately 2 out of every 4 weeks in southern Moreton Bay over summer, and the maximum tidal amplitude is about 2 m.

Crab movement

The two crab species, *A. tridentata* (Ocypodidae) and *P. erythroactyla* (Grapsidae), were sampled repeatedly using pitfall traps made of PVC pipe (15 cm diameter, 10 cm deep) buried flush with the sediment surface. The bottom of the trap was a PVC disc that could be removed and inserted upside down to prevent crabs entering the traps when not being sampled. Perforations in the PVC disc, however, allowed normal tidal water-level fluctuations in both open and closed traps. The pitfall traps are a variation on those previously used in mangroves (Smith et al. 1991) and saltmarsh [see Chapman et al. (1998), who give a detailed description of the traps]. Sixty-five traps were placed in 13 transects parallel to the saltmarsh–mangrove interface, where each transect was separated by 2 m (traps were spread over a distance of 24 m across the saltmarsh–mangrove interface, 12 m into each habitat) and each trap within a transect was separated by 5 m. The traps were kept shut

Fig. 1 Sampling location in southern Moreton Bay, Queensland



for the 3 days following their installation to condition crabs to the presence of traps.

Upon first capture, crabs were individually marked by gluing a numbered plastic disc (2 mm diameter, Swienty, Queen Bee marker kit, Germany) to the carapace, and then released alongside the pitfall trap (now closed) in which they were captured. The species, sex, carapace width (CW) and location of capture were recorded for all new and re-captured crabs. Crabs < 6 mm CW were too small to mark and were released without marking. Pitfall traps were opened at dusk and checked just after dawn the following day after an overnight flooding tide had receded, on 9 days between 8 and 26 February 2004. Sampling was done in blocks of 2 (8 and 9 February), 4 (13–16 February) and 3 days (23–26 February) compatible with flooding tides where each block is referred to as a sampling event. The diel stage of sampling was chosen to optimise the capture of *P. erythroductyla* that is considered to be active during the night, whilst ensuring individuals of *A. tridentata*, that become active during daylight hours, were also likely to be captured. It was also important to sample the crabs after the marsh had been inundated as these crabs do not often emerge from their burrows when the sediment surface is dry. After traps were checked on each day within a sampling event, they remained closed for at least 7 h before being re-opened. Traps were kept closed between sampling events. Traps were therefore opened at dusk on the first day of each sampling event, and checked the following morning at which time they were closed until dusk (within a sampling event), or remain closed until dusk of the next sampling event. Trap closure at the end of each sampling event, and breaks between sampling within an event, were intended to limit the degree to which trapping and handling might affect crab movement.

Crab movement was estimated for each recaptured crab by measuring the distance, perpendicular to the

saltmarsh–mangrove interface, moved between the point of last capture and the recapture position. Only perpendicular movements were of interest since the hypothesis being tested was about movement perpendicular to the habitat interface. Thus, the 13 transects represent the possibility of recording one of 13 distance categories (i.e. 0–24 m) for recaptured crabs. Only those categories that registered more than one crab capture were analysed. Non-parametric Kruskal–Wallis tests were used for each species to determine whether the number of crabs within each distance category was significantly different. Crab captures on each of the nine sampling days were considered replicates within each of the five distance categories. Where there were significant differences among distance categories, post-hoc Mann–Whitney tests were used to determine which medians were driving those differences. The *P*-values for these multiple comparisons were adjusted using a Bonferroni correction ($P < 0.003$ at experiment-wise error rate $\alpha = 0.05$). As an indication of whether crab behaviour was altered by the presence of the pitfall traps, and whether crabs were avoiding or favouring capture, the number of days between captures (i.e. days at liberty) was calculated for each crab species. If the majority of crabs had only 1–2 days at liberty between captures, this would be interpreted as a positive bias of trapping on crab behaviour. Days at liberty were calculated using all recaptures across the 19-day sampling period and therefore includes days in which no crabs were sampled.

Movement of particulate organic matter

Patterns of movement of organic matter are likely to vary though time. Rather than trying to collect detritus in the water column at many different times, we collected detritus on the sediment surface at one

time. This detritus can be considered to be an amalgamation of organic matter settling over days or weeks prior to collection (Holmer and Bachmann Olsen 2002). It should be representative of detritus available to *P. erythro-dactyla* and *A. tridentata*. Detritus was collected adjacent to the pitfall traps about 1 week after the completion of the crab movement study. This ensured detritus samples were representative of the detritus within the array of traps, and were temporally relevant but would have no effect on crab movement. Detritus samples were collected by scraping the top 1 cm of sediment from the surface of the mud at three randomly selected points along 16-, 12-, 8-, 6-, 4-, and 2-m transects into both saltmarsh and mangroves, with three additional samples taken from the 0-m transect that demarcates the saltmarsh–mangrove interface. The sediment was first washed through 1-mm mesh to remove larger animals, and then through 125- μ m mesh allowing microalgae, other small particles, and microfauna to be washed away. Any animals remaining on the 125- μ m mesh were removed under microscopic examination and the retained material was used as the detritus sample. Detritus samples were dried, ground and acid digested, and then placed into tin capsules and their isotopic values 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. Analytical precision was determined as being within $\pm 0.2\%$, based on duplicates of samples. The relationship between $\delta^{13}\text{C}$ values of detritus and sampling positions across saltmarsh and mangrove habitats was clearly curvilinear and was analysed using the non-linear regression equation described by Guest and Connolly (2004). The form of this relationship is shown in Fig. 5a.

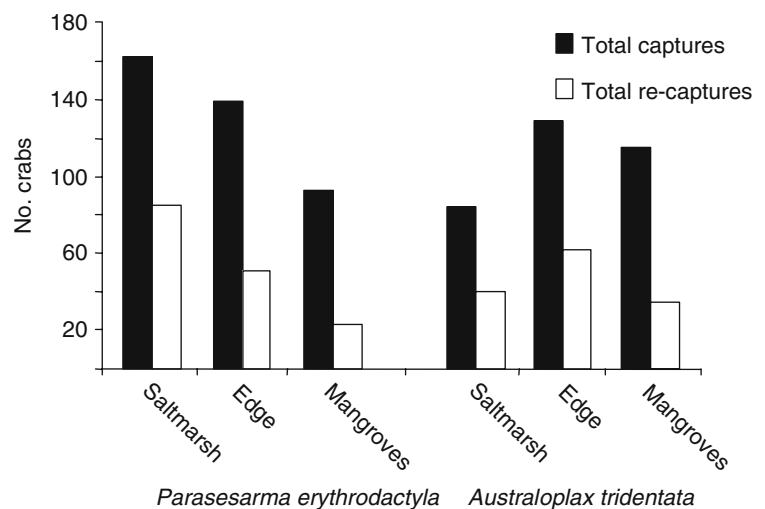
Fig. 2 The total numbers of crabs captured and recaptured for *Parasesarma erythro-dactyla* and *Australoplax tridentata* for each habitat. *Saltmarsh* Traps along transects at 6–12 m into the marsh, *Edge* traps from 4 m into the marsh to 4 m into mangroves, *Mangroves* traps 6–12 m into the mangroves

Results

Crab movement

A total of 394 *P. erythro-dactyla* and 328 *A. tridentata* were captured over the 9 sampling days within the 19-day interval. Of these initial captures, the total number of re-captured crabs was 159 for *P. erythro-dactyla* (40.3%) and 137 for *A. tridentata* (41.7%). The average CW of re-captured crabs was 15 mm (± 0.3 , SE) for *P. erythro-dactyla* and 10 mm (± 0.3) for *A. tridentata*. These sizes are similar to those of crabs used in previous carbon-movement studies (Guest et al. 2004; Guest and Connolly 2004). More male than female crabs were captured for both *P. erythro-dactyla* and *A. tridentata*, with males representing 67% and 71% of the recaptures respectively, but the pattern of movement was the same for both sexes. Crabs re-captured a second time represented 25.7% of re-captures for *P. erythro-dactyla* and 20.4% for *A. tridentata*. The highest capture rates were in saltmarsh for *P. erythro-dactyla*, and in edge habitat for *A. tridentata* (Fig. 2). Mangrove habitat had the lowest capture rates for *P. erythro-dactyla* and saltmarsh habitat for *A. tridentata* (Fig. 2). The time interval between captures was ≥ 3 days for 59% of individuals of *P. erythro-dactyla* and 62% for *A. tridentata* (Fig. 3).

The overall patterns in distances moved by crabs were consistent among habitats for both species (Fig. 4). The patterns of movement were also similar for males and females of both species (data not shown since graphs are almost identical). For both species, all crabs were recaptured in one of five or six, of the possible 13, distance categories. The median number of crabs recorded in each of the five or six distance categories differed for both *P. erythro-dactyla* and *A. tridentata* (Kruskal–Wallis: $P < 0.001$ for both species). Movement between captures was overwhelmingly at the 0- to 2-m category



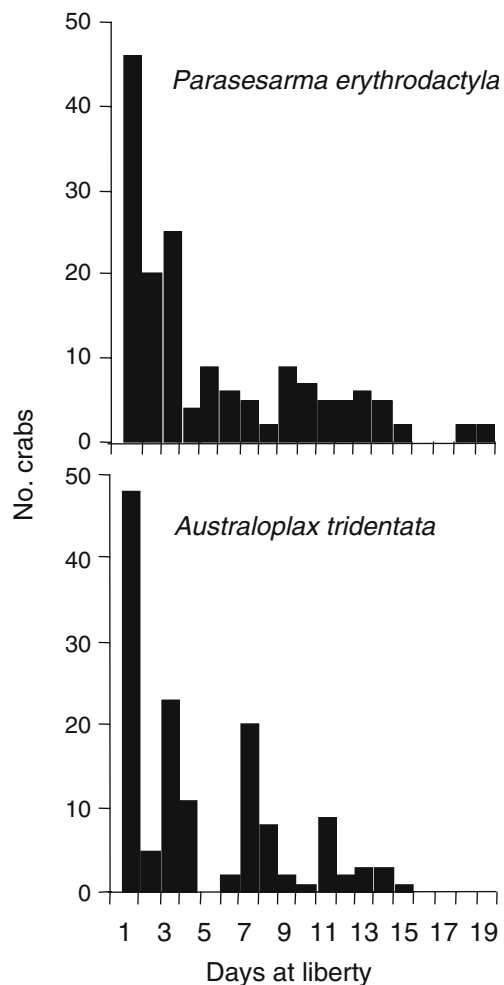


Fig. 3 The number of days between capture (*Days at liberty*) for each recaptured crab of *P. erythroductyla* and *A. tridentata* from all 19 days within the sampling period (9 days of which were actually sampled)

for both species (91% of recaptures for *P. erythroductyla*, 93% for *A. tridentata*; Fig. 4). This was supported by post hoc Mann–Whitney tests that showed that median numbers of crabs were greatest in the 0- to 2-m category, and found no differences amongst medians of the other categories. For *P. erythroductyla*, 11 individuals were recaptured 2 m from the place of last capture, two individuals moved 4 m, one individual 6 m, and another individual was captured 16 m from the place of last capture (Fig. 4). For *A. tridentata*, three individuals were captured in each of the 2- and 4-m-distance categories from the place of last capture, and one individual was captured at each of the 6-, 8- and 16-m-distance categories from the place of last capture (Fig. 4).

Detrital isotope values

The trend in $\delta^{13}\text{C}$ values of detritus across the saltmarsh–mangrove interface was negative, with more enriched $\delta^{13}\text{C}$ values in the saltmarsh habitat, and

increasingly depleted $\delta^{13}\text{C}$ with greater proximity to mangroves (Fig. 5). This pattern is similar to that of the $\delta^{13}\text{C}$ values of both crab species found by Guest and Connolly (2004), reprinted here in Fig. 5. However, the $\delta^{13}\text{C}$ values of detritus were more depleted than those of crabs in both saltmarsh and mangroves. The explanatory power of the sigmoidal regression (measured as r^2) in estimating the $\delta^{13}\text{C}$ values of detritus from position was 0.98. The transition midpoint for the $\delta^{13}\text{C}$ of detritus was 2.8 m into the saltmarsh habitat from the 0-m position that demarcates the saltmarsh–mangrove interface. This differs a little from previously recorded midpoints for both crab species (Guest and Connolly 2004) of 1–4 m into the mangroves. The extent of detrital movement into each habitat as measured from the transition midpoint, and referred to as the transition width, was 5.7 m and is similar to the transition width for crabs [5.30 m for *P. erythroductyla* and 4.90 m for *A. tridentata* (Guest and Connolly 2004)]. The top and bottom asymptotes represent detrital $\delta^{13}\text{C}$ values at sampling positions within saltmarsh and mangrove habitat, excluding the saltmarsh–mangrove transition zone. The difference in detrital $\delta^{13}\text{C}$ values between the top and bottom asymptotes (i.e. the transition height) was 8.4‰, larger than that recorded for crabs (4–7‰, Fig. 5).

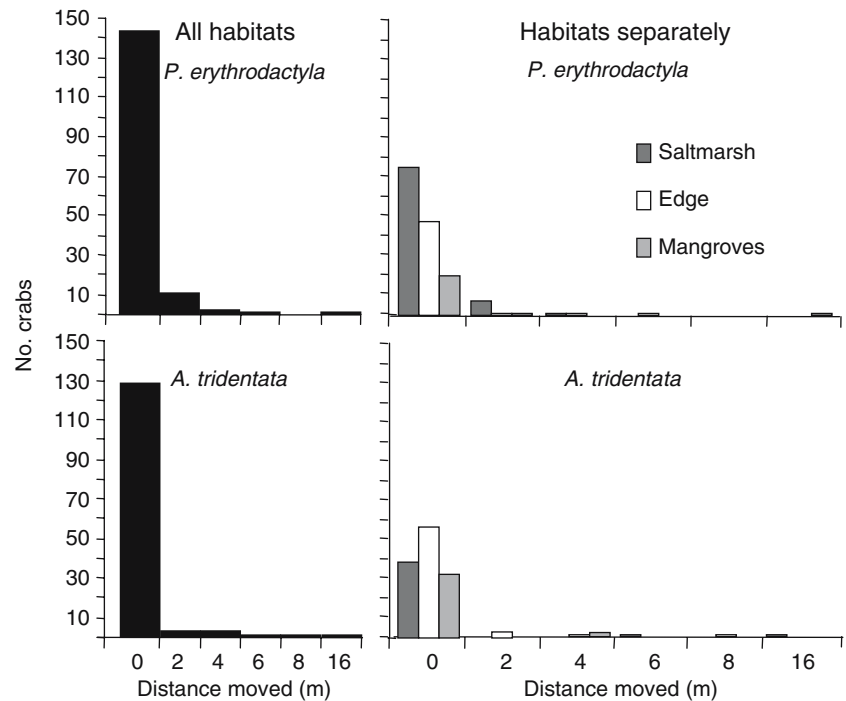
Discussion

Our data are consistent with only one of the two models potentially explaining the previously described patterns in $\delta^{13}\text{C}$ values of crabs across the saltmarsh–mangrove interface. Crabs rarely move up or down the shore perpendicular to the habitat interface, and certainly did not forage regularly at distances of 5–8 m from their burrows. Patterns of crab movement (model 1) cannot, therefore, be used to explain the patterns in crab isotope values. The $\delta^{13}\text{C}$ values of detritus (model 2), on the other hand, showed the same general pattern of change across the habitat interface as crab isotope values. Although isotope values of detritus did not match exactly those of crabs, it seems likely that at least some particulate organic matter from the two producers is assimilated by crabs. Importantly, they apparently obtain this carbon from up to several metres away, but without foraging more than a metre or so from their burrow.

Crab movement

The limited movement of crabs is consistent with the findings of several other studies that have examined the mobility of burrowing (particularly sesarimid) crabs. For example, the majority of *Sesarma guttatum* (Grapsidae) individuals were found within 1 m of the point of capture, up to 10 days after their initial capture (Skov et al. 2002). Fratini et al. (2000) examined the competitive interactions of *Neosarmatium smithi* (Grapsidae) and a

Fig. 4 Distance moved (m) by recaptured crabs from all habitats combined, and separated into saltmarsh, edge and mangrove habitats for *P. erythroductyla* and *A. tridentata*. For habitats, see Fig. 3



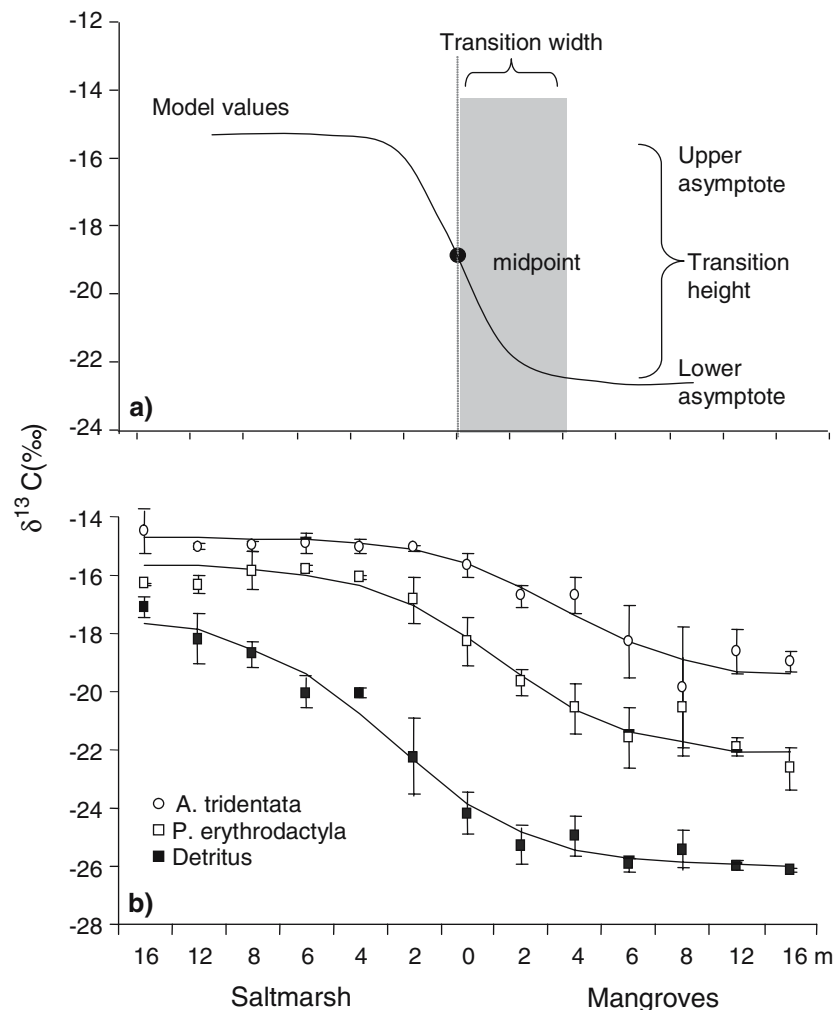
mangrove snail, *Terebralia palustris* in Kenya. They found that *N. smithi* did not move further than 80 cm from its burrow in order to retrieve a mangrove leaf, with the average foraging area estimated to be about 2 m² (Fratini et al. 2000). Burrowing crabs have also been shown to defend their burrow territory vigorously from a potential intruder. Hemmi and Zeil (2003) report the territorial behaviour of the burrowing crab *Uca vomeris*, and the crab's heightened response to an intruder when crabs are located at greater distances from their burrow at the time of disturbance. Thus, it appears that the territorial behaviour common in burrowing crabs may limit the distance crabs move away from their burrow. Both species of crabs examined here are burrowing crabs, and personal observation indicates that they defend their burrow territory in response to a disturbance (e.g. conspecifics or other predators) and this may explain the limited movement recorded in this study.

The recapture rates we recorded are relatively high (e.g. Brousseau et al. 2002; Skov et al. 2002) presumably because the crabs do not move very far, and are thus likely to repeatedly encounter the same pitfall trap. An alternative explanation is that the crabs are favourably disposed towards capture, and actively enter the traps (i.e. are "trap-happy"). This is considered unlikely as the majority of individuals of both crab species (59–62%) were recaptured 3 days or more after initial capture. Furthermore, as the days at liberty measure was calculated using the time between capture for all recaptured crabs, and included all days within the sampling period, including those days not actively sampled, the recaptures separated by only a small number of days are inflated.

For example, the period between initial and subsequent capture for crabs sampled during the last sampling event (3 days), cannot be >3 days. Only those crabs recaptured in the first and second sampling event had the chance of a 3-day or more separation between initial and subsequent capture.

It is possible that un-recovered crabs escaped capture by moving large distances beyond the sample area, causing the movement of crabs to be underestimated. Clearly a small number of individuals of *P. erythroductyla* and *A. tridentata* were capable of moving longer distances, as shown by the three crabs that were recorded 16 m from the place of last capture. For the majority of crabs, however, movement beyond the sampling area is considered unlikely, since although crabs were frequently sighted on the sediment surface when the traps were being checked, no marked crabs were sighted during regular inspection of the sediment surface outside the sampling area. As the sampling area was large (24 m deep and 25 m wide) relative to crab movement recorded in previous studies, the possibility of any but a few marked crabs moving and remaining undetected over large distances was also minimised. Even the largest movements recorded for similar-sized crabs in mangroves or saltmarsh, for *Hemigrapsus sanguineus*, are 7–16 m/day (Brousseau et al. 2002). Given that we targeted sub-adult crabs, un-recovered crabs were more likely to have escaped recapture by taking refuge during moulting, making them unavailable for capture, and resulting in the subsequent loss of the mark. Observations during sampling confirm this as we saw several moulted carapaces with our mark intact on the sediment surface in the sampling area.

Fig. 5 a Model data describing non-linear regression equation used to analyse $\delta^{13}\text{C}$ values and sampling positions for detritus, and for *P. erythrodractyla* and *A. tridentata*. **b** $\delta^{13}\text{C}$ values of detritus, averaged from two replicates at each position, ± 1 SE (SE too small to see in some cases). Values for *P. erythrodractyla* and *A. tridentata* are shown for comparison [values from Guest and Connolly (2004) for reference, being data averaged across three sites, including the one in the current study]. *Upper asymptote* $\delta^{13}\text{C}$ values of detritus/crabs in saltmarsh, *Lower asymptote $\delta^{13}\text{C}$ values of detritus/crabs in mangroves, *Transition height* difference in $\delta^{13}\text{C}$ values between the upper and lower asymptotes, *midpoint* centre of the transition zone along the *x*-axis, *Transition width* distance that carbon moves into the adjacent habitat from the midpoint, For habitats, see Fig. 3*



Detrital movement

The $\delta^{13}\text{C}$ values of detritus examined here indicate that carbon moves in the form of particulate material in the range of about 5–8 m across the saltmarsh–mangrove interface. This was best indicated by the transition width (i.e. the distance that carbon moves along the *x*-axis from the transition midpoint) that was 5.7 m into each habitat, and is consistent with that recorded previously for both crab species (Guest and Connolly 2004). However, the positive value of the transition midpoint for detritus indicates that there was a slightly greater movement of mangrove carbon into saltmarsh. Whilst the current study did not measure the availability of carbon to consumers, the greater area of adjacent mangrove (approximately 9 times that of saltmarsh) compared to saltmarsh may explain the slightly greater intrusion of mangrove carbon into the saltmarsh. The net movement of carbon towards shallower, more elevated habitats is opposite to the expected direction, but has previously been recorded in temperate Australian waters (Robertson and Lenanton 1984; Connolly et al. 2005a, b).

Equally, mangrove carbon may be carried further into the saltmarsh due to the “settling and scour lag” described by Woodroffe (2003). Material is typically deposited on the slack high tide when water velocity is reduced, but material is carried further landward with the slowing flood tide due to a time delay in the settlement of sediment (settlement lag), and in the reduction of water velocity below a critical threshold (Woodroffe 2003). The strength of the ebb tide is not sufficient for material to be resuspended and transported seaward (scour lag) thus resulting in a net landward flux. Additionally, the transportation capacity of tides can be influenced by tidal range (Chadwick and Largier 1999). For the sites examined here, however, no data are available on the potential disparity in the strength of ebb and flood tides. It remains for future studies to examine the role of tides in the transportation of carbon among adjacent habitats.

The $\delta^{13}\text{C}$ values of detritus closely match those of crabs (Guest and Connolly 2004), and indicate that detritus forms a major component of the diet of *P. erythrodractyla* and *A. tridentata*. However, the disparity between the $\delta^{13}\text{C}$ values of detritus compared

to crabs (in saltmarsh, 2‰ for *P. erythrodractyla*, and 4‰ for *A. tridentata*, and in mangroves 4 and 7‰ respectively) suggest that incorporation of an unmeasured food source more enriched in ^{13}C may also be possible. In a previous study, for example, $\delta^{13}\text{C}$ values of microphytobenthos in mangroves ($-23.7 \pm 0.3\text{‰}$) were intermediate between those of crabs (*P. erythrodractyla*, $-22.0 \pm 0.2\text{‰}$; *A. tridentata*, $-19.2 \pm 0.3\text{‰}$) and mangrove leaves [$-27.9 \pm 0.2\text{‰}$ (Guest and Connolly 2004)]. Bouillon et al. (2002) also found that only a limited number of mangrove invertebrates assimilated mangrove-derived carbon, and suggested that microalgae were an important source of carbon for benthic invertebrate mangrove communities. The small disparity in the position of the transition midpoint for detritus (in saltmarsh) and crabs (in mangroves) may also be explained by the incorporation of an alternative food source by crabs over the transition zone.

Crabs may utilise detrital fragments smaller than those collected. Whilst there is no information on the selection of particle size for these species, given the small size of the crabs examined (about 10 mm), they may actively select the smaller detrital fragments. These smaller fragments may be more important for *A. tridentata* as ocypodid crabs have previously been described as being capable of selectively filtering food items from their buccal cavity (Miller 1961). If smaller detrital particles have a different isotope signature to larger particles, this may explain the greater disparity in the $\delta^{13}\text{C}$ values of *A. tridentata* and detritus. It does not, however, alter our overall conclusion that carbon movement, not crab movement, explains the patterns in isotope values of crabs across the saltmarsh–mangrove habitat boundary.

Conclusion

We tested two models potentially able to explain previously described patterns in $\delta^{13}\text{C}$ values of crabs across the saltmarsh–mangrove interface. Model 1, that crabs move (and subsequently forage) distances of 5–8 m across the saltmarsh–mangrove interface, was not supported, since crab movement was typically very limited (< 2 m). $\delta^{13}\text{C}$ values of detritus, however, were consistent with movement of particulate organic matter across the habitat interface at the scale of several metres (model 2). Crabs apparently forage close to their burrow but assimilate, at least partly, organic matter transported from up to several metres away. The results from the current study therefore provide evidence that carbon movement among habitats in the upper intertidal occurs at a scale of no more than about 8 m. Our results show that carbon in the form of detrital material displays a pattern of variation within this distance and thus, the previously described patterns of carbon movement are not the result of crab movement.

Acknowledgements We thank D. Gorman for laboratory assistance, several volunteers for help in the field, and are grateful for funding from the CRC for Coastal Zone, Estuary and Waterway Management. All work complied with Australian government law.

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