Spatiotemporal distribution and abundance of mangrove ecosystem engineers: burrowing crabs around canopy gaps

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Abstract.   The burrowing and feeding activities of fiddler and sesarmid crabs have considerable impacts on ecosystem functioning, accordingly they are considered ecosystem engineers. Identifying the factors influencing spatial and temporal variability in crab distribution and abundance would allow us to make predictions of their engineering impacts over a variety of habitats, which is essential for understanding the functionality of mangrove ecosystems. Here we determined the spatial and temporal distributions and abundances of fiddler crabs and sesarmids around canopy gaps in the mangroves of Darwin Harbour, Australia. We sampled three microhabitats at each canopy gap (site): gap center, gap edge and forest edge. We counted crabs and measured selected environmental variables at thirty sites stratified by height within two creek systems during a single season and at six sites within one creek system over two years. Fiddler crabs were generally more abundant in gap centers with *Uca flammula* preferring lower sites than *Uca elegans* or *Uca signata*, while sesarmids favored low to mid-height vegetated sites. Canonical Correspondence analyses showed spatial abundances to be partitioned and the main driving factors were canopy density and site height, as well as substrate features (sediment mounds, soil moisture, soil penetrability, soil surface temperature). Temporal abundances were either highly variable (*U. signata*) or showed significant seasonal variation only at exposed (*U. flammula*) or higher (*U. elegans*) sites. The main factors driving temporal partitioning were humidity, wind speed, sunshine, and soil and air temperatures. Our results indicate that the distribution and abundance of crabs in mangroves varies over time and space, and with sampling scale. Substrate and environmental variables had been largely overlooked by previous studies describing the distribution and abundance of mangrove crabs. We, accordingly, suggest that studies designed to understand mangrove functionality include fine-grained spatial and temporal assessments of ecosystem engineers.

Key words: abiotic factors; biotic factors; course-grained sampling; Darwin Harbour; ecosystem engineers; fine-grained sampling; microhabitats; Sesarmidae; tropical ecosystem; *Uca elegans*; *Uca flammula*; *Uca signata*.

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INTRODUCTION

Ecosystem engineers are organisms that mod- ulate resource flows and in doing so modify, maintain and create habitats for other organisms (Jones et al. 1994, 1997, Odling-Smee et al. 2013).

Consequently, ecosystem engineers have direct and indirect positive and negative influences on the ecological interactions and fitness of organisms that share their environment (Jones et al. 1994, 1997, Erwin 2008, Odling-Smee et al. 2013). Engineering impacts are often greatest when abiotic factors such as soils are modified because they integrate many resources (living space, nutrients, prey, etc.) within one locale (Jones et al. 1994, 1997). Organisms with small individual impacts can also have huge ecological effects, providing they occur at sufficiently high densities over large areas (Jones et al. 1994). Since their influence on an ecosystem is disproportional to their biomass, ecosystem engineers may be considered keystone position organisms (Mills et al. 1993, Paine 1995, Bond 2001, Crain and Bertness 2006).

Within mangrove forests, deposit-feeding fiddler crabs (Uca, Ocypodidae) and sesarmids (Grapsidae, Sesarminae) affect availability of resources for other living things in mangroves through burrow construction and maintenance, sesarmid processing of plant litter and fiddler crab forcing of the microbial distribution and activity in sediment (Smith et al. 1991, Lee 1998, 2008, Kathiresan and Bingham 2001, Reinsel 2004, Thongtham and Kristensen 2005, Kristensen and Alongi 2006, Kristensen 2008). While sesarmids have long been known to play a significant role in promoting nutrient recycling and shaping mangrove structure (McGuinness 1994, Lee 1998, 2008, Dahdouh-Guebas et al. 2002, Thongtham and Kristensen 2005, Kristensen and Alongi 2006), it is only recently that the importance of fiddler crabs has been widely recognized (Cannicci et al. 2008, Kristensen et al. 2008, Penha-Lopes et al. 2009). Fiddler crabs and sesarmids are considered engineers of mangrove ecosystems because they have a considerable impact on ecosystem functionality (Smith et al. 1991, Cannicci et al. 2008, Kristensen 2008, Penha-Lopes et al. 2009). Since the engineering effects are different for sesarmid and fiddler crabs, presumably due to foraging differences, comparative work on the distribution and abundances of sesarmids and fiddler crabs is required (Kristensen 2008).

The impact of an ecological engineer depends upon the spatial and temporal scale of its actions (Jones et al. 1994, 1997). Therefore, quantifying fiddler crab and sesarmid abundance allows scaling of their engineering impact, which is important for understanding the structure and function of mangrove ecosystems and for providing essential information such as their trustworthy global carbon budgets (Jones et al. 1997, Kristensen et al. 2008). Identifying the environmental conditions influencing the spatial and temporal distribution and abundance of these crabs would allow us to make predictions of engineering impacts over a wide variety of habitats, which is essential given the inherent environmental variability of mangrove systems (Kristensen et al. 2008). Mechanisms influencing the spatial and temporal distribution of sesarmids have been described in mangroves from Australia (Frusher et al. 1994, McGuinness 1997, Salgado Kent and McGuinness 2006), the Americas (Sieple 1979, Inés et al. 2005), and Africa (Emmerson 1994). However, despite their ecological impact (Lee 1998, Nobbs and McGuinness 1999, Kristensen and Alongi 2006, Kristensen 2008), the factors driving the spatial and temporal abundance of fiddler crabs within mangroves are not known (but see Nobbs and McGuinness 1999, Nobbs 2003, Inés et al. 2005).

Biotic factors, such as the abundance and distribution of vegetation are thought to substantially affect the distribution of mangrove fauna (McGuinness 1994, Kristensen and Alongi 2006, Cannicci et al. 2008, Nagelkerken et al. 2008). For instance, sesarmids are abundant in vegetated areas and rarely seen in canopy gaps (Osborne and Smith 1990, Salgado Kent and McGuinness 2006). Fiddler crabs on the other hand may prefer vegetated or non-vegetated areas depending on the species (Hagen and Jones 1989, Skov et al. 2002, Nobbs 2003). Previous estimates of fiddler crab spatial distributions in mangroves nevertheless were based on course-grained transect sampling across forest zones (Costa and Negreiros-Fransozo 2002, Dahdouh-Guebas et al. 2002, Skov et al. 2002), so the environmental factors influencing distribution at fine-grained scales could not be identified (Lee 2008). Because tropical mangroves provide a wide range of faunal microhabitats (Kathiresan and Bingham 2001, Nagelkerken et al. 2008) that has confounded many previous efforts to quantify mangrove crab populations (Lee 1998), and fiddler crabs can be spatially isolated within

microhabitats (Salmon and Hyatt 1983, Kathiresan and Bingham 2001), fine-grained stratified sampling based on the presence or absence of vegetation and specified environmental variables would be a better method for identifying the biotic and abiotic processes that influence the spatial distribution and abundance of fiddler crabs (see Macintosh et al. 2002, Ysebaert and Herman 2002).

There have been few studies that directly quantify fiddler crab abundance over time (but see Nobbs 1999, Litulo 2005a, b). Hence, the temporal influences on the distribution of different fiddler crabs in mangroves are poorly defined. Indirect observations have shown tropical fiddler crabs to be relatively abundant year round (Litulo 2005a, Bennetti et al. 2007), with abundance peaking during spring tides and ebbing during neap tides (Palmer 1995, Stillman and Barnwell 2004).

Here we performed two surveys using stratified sampling across creeks, sites and microhabitats coupled with multivariate modelling to quantify the factors influencing the spatial and temporal distribution of burrowing crabs in and around canopy gaps in a tropical Australian mangrove. The first survey investigated the spatial relationship between fiddler crab and sesarmids and a range of factors pertaining to vegetation. The second survey investigated the fine grained influences on the temporal distribution of mangrove crabs across two coarse grained variables: season and tidal elevation (Mouton and Felder 1996).

METHODS

Canopy gaps stratified by height

We performed the following procedures in the mangroves of Darwin Harbour, Australia, where the tides are semi-diurnal with a spring tidal range of up to 8 m. As the distribution of fiddler crabs can vary between creek systems (Hagen and Jones 1989), we sampled two systems—Ludmilla Creek and inner Harbour (see McGuinness [1997] for details). We identified 15 canopy gaps within the mid-upper intertidal zone (above high water neap) of each creek system ($N = 30$ in total) on topographic maps and numbered and classified them as follows according to their height above sea level.

1) Low gaps (~6.2 m above sea level) numbered 1–5, were small and their exact locations more arbitrary than at the other sites. They had muddy soil close to tidal creeks, usually with numerous sediment mounds, and occurred in areas corresponding to a tidal creek habitat (see Semeniuk [1985] for more details).
2) Mid-height gaps (~6.6 m above sea level) numbered 1–5, were relatively large and distinctive (Ludmilla Creek: 621 ± 376 m^2: Inner Harbour: 156 ± 93 m^2) with muddy, flat soil occurring in areas corresponding to a tidal flat habitat (Semeniuk 1985).
3) High gaps (~6.9 m above sea level) numbered 1–5, were extremely large and distinctive (Ludmilla Creek: $3,654 \pm 2,420$ m^2: Inner Harbour: $13,804 \pm 26,894$ m^2) with loamy soil and a flat surface.

Study sites subdivided into microhabitats

The area within each gap and the area of the forest that surrounded each gap (up to 1 m from the edge of the gap) we called a 'site'. The area covered by each of the 30 sites was subdivided into the following three microhabitats (see Fig. 1): (1) gap center is the area at the center of the canopy gap at least 2 m from the forest; (2) gap edge is the area of the canopy gap that is within 1 m of the forest; and (3) forest edge is the area of the forest that is within 1 m of the canopy gap.

We accordingly sampled a total of 90 microhabitats (45 at Ludmilla Creek and 45 at inner Darwin Harbour). All of the sites had sparse leaf litter cover on the surface.

Estimating crab abundance

We ascertained an index of crab abundance by counting the number of individual fiddler crabs and sesarmids that emerged from their burrows within three 0.56-m^2 haphazardly placed quadrats over 10 min (Nobbs and McGuinness 1999). We counted crabs during the four hours of daytime low water during spring tides (i.e., between approximately 1200 and 1600 h) to minimize the between and within day variation (Nobbs and McGuinness 1999). We identified all fiddler crabs to sex and species, with three species principally identified: *Uca flammula* (Crane), *U. elegans* (George and Jones), and *U. signata* (Hess). Sesarmids were not identified to species or sex.
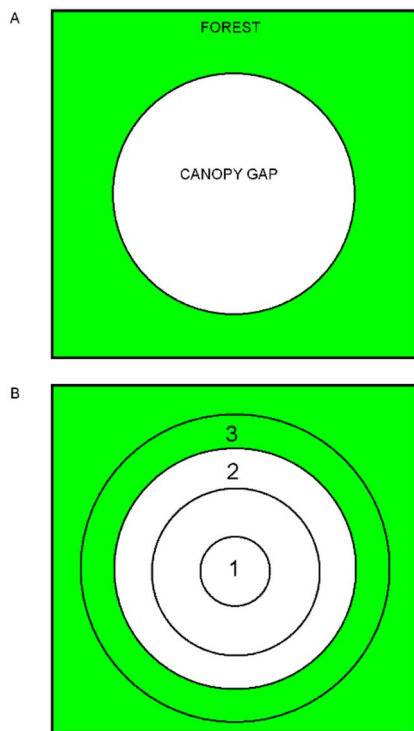
Fig. 1. Diagrammatic representation of a forest canopy gap (A), which we divided into three microhabitats (B). (B) The gap centers (1) were located in a gap at least 2 m from the forest, the gap edges (2) were within the gaps <1 m from the forest, and the forest edges (3) were areas of forest <1 m from the gap.

Spatial survey

We sampled crabs in each microhabitat at all 30 sites at Ludmilla Creek and inner Darwin Harbour over nine days during the 1998 dry season (24–29 June and 12, 14 and 15 July) after each site had been wetted by the spring high tide (heights: 6.72–7.15 m).

Environmental variables.—We measured the following environmental variables at each of the 90 microhabitats during the 1998 dry season.

1) Average soil penetrability: A metal bolt (length = 21.5 cm, weight = 344.58 g) was held flush inside the top of a length of PVC pipe (length = 114.8 cm, diameter = 3.0 cm), and then released. The PVC pipe was taken away and the distance that the bolt penetrated into the soil was determined by measuring the length of bolt above the soil

and subtracting this from 215 mm. Three measurements were taken at low water during spring and neap tides.

2) Root mat depth: During spring tides, a wooden pole (length = 93.2 cm, diameter = 3.0 cm) was pushed into the soil as far as the root mat would allow, and the depth recorded. It was not pushed further than 5.2 cm so that there was 8 cm of the pole remaining above the soil, which was enough to enable it to be pulled free. Three measurements were taken at haphazardly chosen positions within each microhabitat within one day.

3) Soil moisture and soil organic content: Six soil surface samples were collected from each microhabitat. Three samples were collected during spring tides and three were collected during neap tides. These samples were taken to the laboratory at Charles Darwin University, Darwin, where the soil was weighed and dried to a constant weight for two weeks at 105°C. The percentage of mass lost by drying each sample was assumed the percentage due to moisture. The dry soil that had been collected during spring tides was placed in a muffle furnace at 5000°C for 36 hours. The ash-free dry weight was determined and the mass lost was calculated and assumed to represent the organic content.

4) Percentage shade: Percentage shade was estimated by a hand-held engraved spherical densiometer with a convex reflecting mirror (CPS, Model A, Bartlettsville OK, USA) held approximately 10 cm off the ground at three haphazardly chosen positions in each microhabitat.

5) Peg roots, soil mounds and soil temperature: After sampling crab abundance, the numbers of peg roots and soil mounds within each of the quadrats were counted and recorded. In addition, two readings from each quadrat were taken of soil temperature using a temperature sensitive probe (Fluke, Type K, Everett, WA, USA). One reading was taken with the probe lying on the surface of the soil and the other with the probe inserted 15 cm into the soil.

Temporal survey

For the temporal survey we determined crab abundances as described above and sampled environmental variables at the three microhabitats at six sites (low sites 1 and 2; mid-height sites 1 and 2; and high sites 1 and 2), giving a total of 18 microhabitats. We sampled over two days, during spring tide cycles at four times of year: the dry, dry-wet transition, wet, and wet-dry transition seasons over two years (1997 and 1998), sampling 1728 quadrats overall.

Environmental variables.—The following measurements were taken at each of the 18 microhabitats at Ludmilla Creek at the abovementioned four times of year over two years (1997 and 1998) prior to counting crab abundances.

Air temperature and relative humidity were measured using a Type K temperature and humidity probe held approximately 10 cm off the ground. Soil temperature was measured by inserting the probe approximately 15 cm into the soil. Daily figures for hours of sunshine, rainfall and maximum wind speed were recorded approximately 1 km away at Darwin airport by the Bureau of Meteorology. The Northern Territory Department of Transport and Works supplied us with tidal height data.

Analyses

Spatial survey.—For all data collected an average from each of the 90 microhabitats was determined and used in the ensuing analyses. Crab counts were divided by 0.56 in order to quantify abundance as the number of crabs per m^2. One factor ANOVAs were done to compare fiddler crab and sesarmid abundances, and environmental variables across heights (low sites vs. mid-height sites vs. high sites) and across microhabitats at each height (gap center vs. gap edge vs. forest edge).

A Canonical Correspondence Analysis (CCA) ordination (Ter Braak 1986) was used to identify the environmental factors influencing the abundance of the three fiddler crab species and sesarmids. Environmental data were examined for asymmetry and multicollinearity. Since CCA performs well regardless of these issues (Palmer 1993), we left the data unmodified. Out of the 12 environmental variables collected at each site, four were removed on a priori grounds (sensu Ter Braak 1986). The variables removed included

soil hardness during neap tides, which was the only environmental variable that was highly correlated to other environmental variables (Tolerance = 0.084, VIF = 11.84) and root depth, which was the only environmental variable with a bimodal distribution, presumably because of the way the data was measured. Distributions of our species data were right-skewed due to a disproportional number of zeroes so we added 0.01 to the crab counts prior to analysis. Although some workers have used logarithmic or square-root transformations to down-weigh disproportional abundances (Ter Braak 1986, Ter Braak and Verdonschot 1995), CCA performs well with skewed species distributions (Palmer 1993) so we made no transformations.

Temporal survey.—We chose sites where the mean abundances of each *Uca* species were greater than three crabs per m^2, which corresponded to: low sites for *U. flammula*, mid-height gap centers and high gap centers for *U. elegans*, and mid-height gap edges, high gap edges and high forest edges for *U. signata*. At these sites, two-factor ANOVAs were used to compare temporal abundances across seasons (dry, dry-wet transition, wet and wet-dry transition) and years (1997 and 1998). The average count from the three quadrats at each site was calculated and used in these analyses.

A CCA ordination was used to examine the relationships between the temporal distribution of different crabs and factors in their environment. All data were left unmodified. All seven environmental variables were included in the analysis. Environmental data and crab counts from sites 1 and 2 within each height for each season within each year were pooled then averaged giving a total of 72 (24 × 3) rows in the data set.

Cochran's tests were used to check that all variances were equal and distributions normal prior to performing ANOVAs. Data that failed Cochran's test ($P < 0.05$) were $X^{0.25}$ transformed. Tukey's HSD post hoc tests were conducted when significance was detected by ANOVA. Significance levels were Bonferroni corrected to account for multiple testing where appropriate (Quinn and Keough 2002). All ANOVAs and tests of assumptions were performed using STATISTICA version 12.0 (StatSoft, Tulsa, OK, USA). CCA ordinations were performed using

Table 1. Crab abundances (no./m^2; mean ± SE) within different microhabitats at each height ($N = 10$) and within all microhabitats at different heights ($N = 30$), recorded during the spatial survey.

Location	Uca flammula	Uca elegans	Uca signata	Sesarmids
Low sites				
Gap center	7.4 ± 1.1	0.0	3.2 ± 1.8	4.7 ± 0.8
Gap edge	4.5 ± 1.0	0.0	0.5 ± 0.2	5.0 ± 0.8
Forest edge	2.3 ± 0.5	0.0	0.4 ± 0.4	4.4 ± 0.8
Mid sites				
Gap center	0.1 ± 0.1	7.2 ± 1.6	**7.2** ± 2.3	0.5 ± 0.2
Gap edge	1.3 ± 0.7	0.4 ± 0.3	**3.9** ± 1.3	**5.9** ± 1.0
Forest edge	0.4 ± 0.2	0.0	0.1 ± 0.1	**6.6** ± 1.0
High sites				
Gap center	0.0	10.0 ± 1.3	0.7 ± 0.4	0.1 ± 0.1
Gap edge	0.3 ± 0.2	**2.1** ± 1.2	11.1 ± 2.0	1.2 ± 0.8
Forest edge	1.7 ± 0.9	**0.1** ± 0.1	5.8 ± 2.0	2.9 ± 1.1
All microhabitats				
Low sites	4.7 ± 0.7	0.0	1.4 ± 0.6	**4.7** ± 0.5
Mid sites	**0.6** ± 0.2	2.5 ± 0.8	3.8 ± 1.0	**4.3** ± 0.7
High sites	**0.7** ± 0.3	4.1 ± 1.2	5.9 ± 1.2	1.6 ± 0.3

Notes: Mean abundances of each kind of crab within different microhabitats at each height and within all microhabitats at different heights were compared by one factor ANOVAs. Tukey's (HSD) tests to compare the means were done where significance was detected by ANOVA. Similar means found by Tukey's (HSD) tests ($P \geq 0.05$) appear in boldface.

Microsoft XLSTAT 2014.3.

RESULTS

Spatial survey

We found significant differences between mean abundances of fiddler crabs and sesarmids on the basis of height and microhabitat (Table 1). *Uca flammula* were most abundant in the gap centers at low sites ($F = 7.3$, $P < 0.01$) and were rarely observed at higher sites. *Uca elegans* were never observed at low sites, being most abundant in the gap centers compared to the other microhabitats at higher sites (Mid-height sites: $F = 30.3$, $P < 0.001$; High sites: $F = 14.6$, $P < 0.001$). *Uca signata* were present at all sites but mean abundances became greater as height increased ($F = 4.2$, $P < 0.05$). At mid-height sites, they were most abundant in gap centers and gap edges ($F = 5.9$, $P < 0.01$), but at high sites they were most abundant in gap edges ($F = 7.4$, $P < 0.01$). Sesarmids were less abundant at high sites ($F = 16.2$, $P < 0.001$), being found predominantly in gap edges and forest edges at mid-height sites ($F = 14.6$, $P < 0.001$), and in all microhabitats at low sites.

Compared to the higher sites, the low sites had cooler, wetter, softer sediment with more mounds and a higher organic content, a shallower root mat and greater peg root density (Table 2). Environmental variability among microhabitats differed with height, with low sites having one differing variable and mid-height and high sites having six and nine differing variables respectively (Table 2).

Our CCA ordination showed that the sites and species are linearly related to the sites/variables data (permutation test: 500 permutations, pseudo-$F = 0.731$, $P < 0.0001$) and total inertia in the data was 1.775 (49.4% constrained). Six principal axes were derived and 93.58% of the inertia was carried by the first two axes. We inferred the first axis to represent canopy density and the second axis to represent a height gradient (Table 3). The CCA ordination diagram (Fig. 2) shows that male and female *U. flammula* abundances were associated with shaded, lower sites. Male and female *U. elegans* abundances, however, were in the opposite quadrant from the canopy density vector thus their abundances were associated with an open canopy. Sesarmids and male and female *U. signata* abundances were more closely associated with soil characteristics (e.g., moisture, sediment mounds and surface temperature) than height or canopy density. Sesarmids were associated with cooler, wetter, more penetrable soils with more mounds, while *U. signata* was associated with warmer, drier, less penetrable soil with fewer mounds.

Temporal survey

Analysis of our temporal data on mean fiddler crab abundances revealed three patterns (Fig. 3). Firstly, significant temporal variations in *U.*

Table 2. Environmental variables ($N = 30$; mean $\pm$ SE) at different heights, recorded during the spatial survey.

Environmental variable	Low sites	Mid sites	High sites	F
Canopy density (%)	58.2*** ± 3.3	**31.5*** ± 5.0**	**29.9*** ± 4.8**	12.5***
Soil moisture {S} (%)	**44.5 ± 1.5**	**41.8*** ± 2.1**	29.9 ± 1.2	23.8***
Soil moisture {N} (%)	**42.6 ± 1.8**	**37.3*** ± 2.8**	22.7** ± 1.7	17.0***
Depth of root mat (cm)	21.3 ± 2.9	**53.8*** ± 5.0**	**57.2*** ± 4.8**	20.3***
Soil penetrability {S}(cm)	**5.2 ± 0.2**	**5.0*** ± 0.3**	4.1 ± 0.1	9.4***
Soil penetrability {N}(cm)	**4.6 ± 0.2**	**4.2***† ± 0.2**	2.7 ± 0.2	15.4***
Soil organic content (%)	**16.1 ± 0.9**	**18.3* ± 1.2**	12.8 ± 0.7	7.3***
Soil surface temperature (°C)	26.5 ± 0.7	**28.1** ± 0.9**	**30.7** ± 0.7**	7.8***
Soil 15 cm temperature (°C)	24.1 ± 0.1	23.4 ± 0.3	23.3* ± 0.3	3.6*
Sediment mounds per m²	**3.8 ± 0.6**	**6.4*** ± 0.9**	1.4 ± 0.7	19.2***
Peg roots per m²	87.2 ± 13.8	**8.0 ± 7.7**	**19.1*** ± 6.9**	31.7***

Note: F values are shown for one-factor ANOVAs with Height the factor at three levels (low, mid and high sites). Significance is indicated as: $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. Similar means found by Tukey's (HSD) tests appear in boldface. Data from each height was further analyzed by one-factor ANOVA with Microhabitat the factor at three levels (gap center, gap edge and forest edge). Some variables were measured during periods of Spring {S} and Neap {N} tides.

† Cochran's test was significant ($0.01 < P < 0.05$), therefore significance in the ANOVA was set at $P = 0.01$.

flammula and *U. elegans* abundance occurred in areas where conditions were hypothetically more stressful. At low sites *U. flammula* abundance varied temporally in the gap centers (Season × Year: $F = 7.9$, $P < 0.001$) and gap edges (Season: $F = 6.2$, $P < 0.001$) but not in the forest edges (Fig. 3A). In gap centers *U. elegans* abundance varied temporally at high sites (Season × Year: $F = 12.2$, $P < 0.001$) but not at mid-height sites (Fig. 3B).

Secondly, differences in seasonal abundances varied between *U. flammula* and *U. elegans* (Fig. 3A, B). We found *U. flammula* were in greater abundance in the wet and dry-wet transition

seasons than the dry and wet-dry transition seasons in low gap centers and low gap edges ($F = 12.7$, 6.2, respectively, $P < 0.001$). The reverse was the case for *U. elegans* in high gap centers who were in greater abundance in the dry and wet-dry transition seasons than the wet and dry-wet transition seasons ($F = 39.4$, $P < 0.001$).

Thirdly, the abundance of *U. signata* showed temporal patterns that were unlike the other two species (Fig. 3C). Year was the most influential factor influencing the temporal abundance of *U. signata* ($F > 9.5$, $P < 0.01$ in all microhabitats tested). In addition seasonal variation depended upon microhabitat and height (Fig. 3). In high gap edges *U. signata*, like *U. elegans*, were more abundant in the dry and wet-dry transition seasons ($F = 4.6$, $P < 0.01$). In high forest edges and mid-height gap centers *U. signata*, like *U. flammula*, were less abundant in the dry season ($F = 3.5$, 11.0 and $P < 0.01$, 0.001, respectively).

Our CCA ordination showed that the sites and species were linearly related to the sites/variables data (permutation test: 1000 permutations, pseudo-$F = 0.389$, $P < 0.0001$) and total inertia in the data was 1.290 (57.7% constrained). Two principal axes were derived and 100% of the inertia was carried by the two axes. We inferred the first axis to represent sunshine and soil temperature, and the second axis to represent a moisture gradient that is negatively associated with tide height, air temperatures, rainfall and humidity (Table 3). Our CCA ordination diagram (Fig. 4) showed *U. flammula* abundances were associated with high humidity and low wind speeds. *Uca elegans* abundances were associated with high

Table 3. Regression coefficients of the first two axes derived by canonical correspondence analysis on species abundance data and the environmental variables collected during the spatial and temporal surveys.

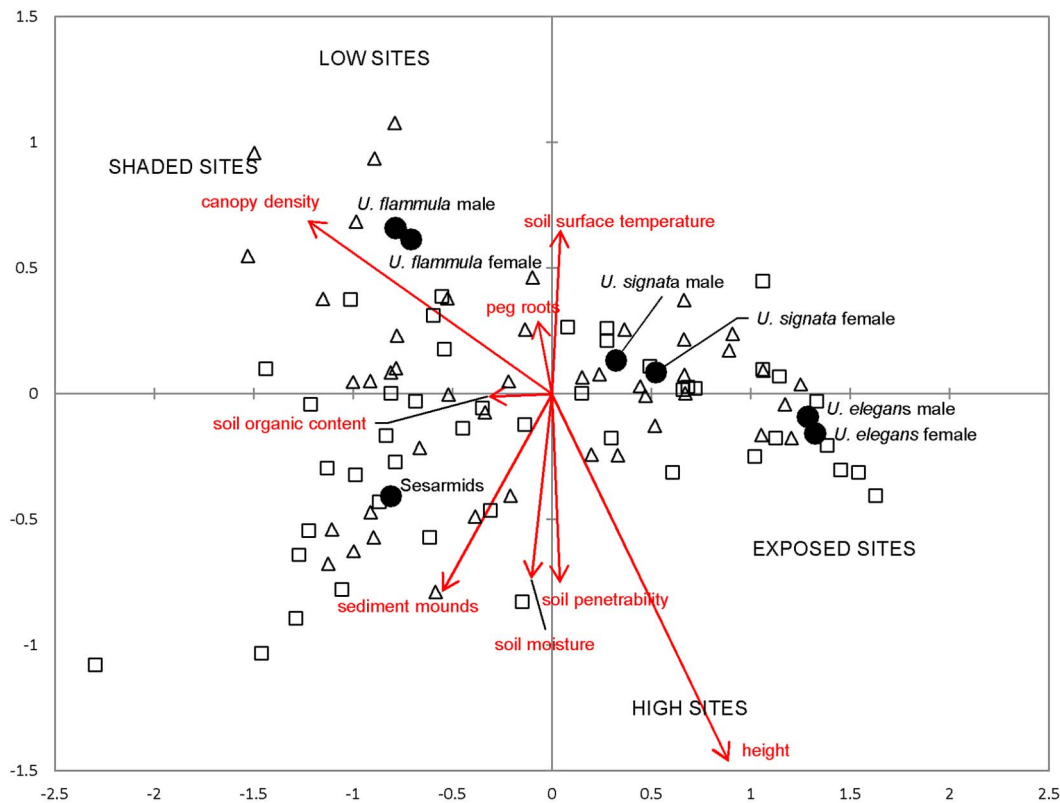| Environmental variable	F1	F2
Spatial survey		
Height of site	0.444	−0.732
Canopy density	−0.617	0.346
Sediment mounds	−0.276	−0.395
Soil organic content	−0.161	−0.005
Temperature soil surface	0.021	0.328
Soil moisture spring tides	−0.052	−0.369
Soil penetrability spring tides	0.020	−0.378
Peg roots	−0.036	0.148
Temporal survey		
Previous high tide height	0.075	−1.167
Temperature in soil	1.398	1.451
Air temperature	−0.282	−1.244
Air humidity	−0.469	−1.005
Wind speed	0.662	0.580
Rainfall	0.978	−1.244
Hours of sunshine	1.443	−0.322

Fig. 2. CCA ordination diagram with crab species (solid circles) and environmental variables (red arrows) recorded during the spatial survey. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.69 and 0.13, respectively; the eigenvalue of axis 3 (not displayed) is 0.04. Open squares identify Ludmilla Creek sites and open triangles identify Inner Harbour sites.

soil temperatures and more hours of sunshine, and *U. signata* abundances were associated with high air temperatures.

DISCUSSION

The abundances of intertidal organisms within tropical mangroves are often partitioned spatially (Hagen and Jones 1989, Frusher et al. 1994, Polgar and Crosar 2009). Indeed, the three most abundant and identifiable species of fiddler crab (*Uca flammula*, *U. elegans*, and *U. signata*) in the mid-upper intertidal zone of Darwin Harbour were spatially partitioned within and among our study sites. *Uca flammula* were abundant in small, shady and low elevation canopy gaps, while *U. elegans* were abundant in large, flat, high canopy gaps. *Uca signata* appeared to take advantage of mangrove shade to extend their vertical distribution, as described for *U. tetragonon* on an East

African shore (Icely and Jones 1978). While fiddler crabs were abundant in gaps that may be more conducive to their method of communicating by visual waving displays (Nobbs 2003, Zeil and Hemmi 2006, How et al. 2007), sesarmids that do not appear to communicate in this way were abundant in vegetated sites with numerous sediment mounds at low to mid-height tidal elevations. Thus sociality and other behaviors of crabs may be integral to their spatial distribution in and around canopy gaps.

The dissociation between sesarmids and fiddler crabs suggests that there may be competitive, antagonistic and/or predator-prey interactions between them. The low nitrogen availability in mangrove litter forces sesarmids to supplement their diet by preying on small animals including other brachyurans (Kristensen et al. 2008). We have indeed often seen sesarmids harass, kill and eat fiddler crabs at our study site,
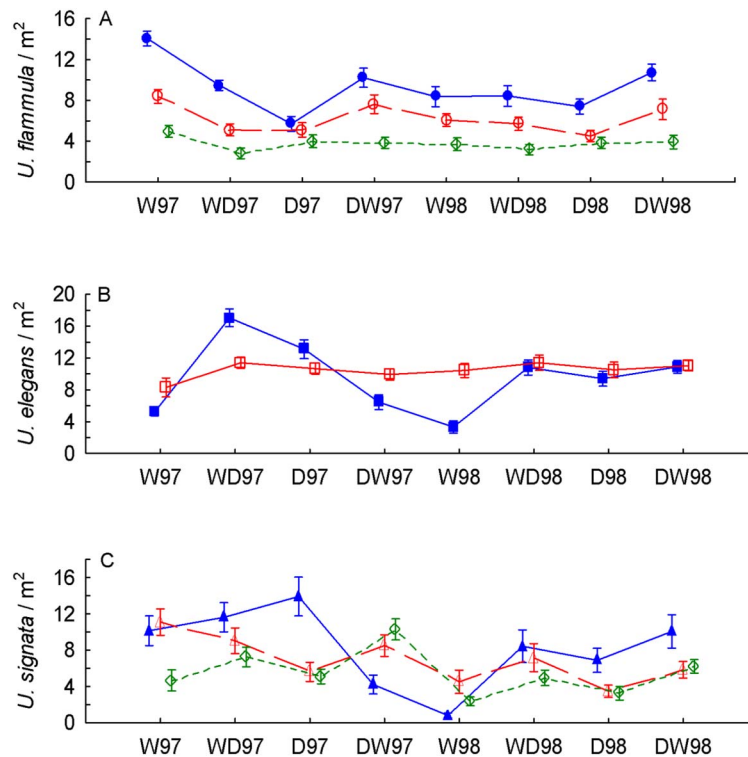
Fig. 3. Crab abundances per m^2 ($N = 24$; mean $\pm$ SE) across the wet (W), wet-dry transition (WD), dry (D) and dry-wet transition (DW) seasons over two years (1997 and 1998). (A) *U. flammula* abundances at low gap centers (solid blue circles), low gap edges (open red circles) and low forest edges (open green diamonds). (B) Counts of *U. elegans* at high gap centers (solid blue squares) and mid gap centers (open red squares). (C) Counts of *U. signata* at high gap edges (solid blue triangles), high forest edges (open red triangles) and mid gap edges (open green diamonds).

and in North Australian mangroves sesarmid predation excludes a small snail, *Cerithidea anticipata* Iredale, from forests (McGuinness 1994). We have also observed homolopsine snakes consuming crabs within forests in our study area (Nobbs and Blamires 2004). Sesarmids have good stereoscopic vision (Zeil et al. 1986) and we suggest that these three fiddler crabs may have differential susceptibility to predation or harassment by sesarmids due to differences in their conspicuousness. It seems likely that individuals of *U. flammula* are less conspicuous than the other two species due to their darker colouration reducing their contrast against the substrate, and the lower frequency of male waving (Nobbs 1999).

Previous work has shown vegetation to principally influence the spatial distributions and abundances of crabs within mangroves (Bertness

and Miller 1984, Kristensen and Alongi 2006, Cannicci et al. 2008, Nagelkerken et al. 2008). Our analyses, nevertheless, identified the importance of substrate features (sediment mounds, soil moisture, soil penetrability, soil surface temperature) as well as canopy density and site height over the spatial abundance of fiddler crabs and sesarmids in Darwin Harbour mangroves. The ameliorating effect of shade on temperature and moisture levels may be especially significant in the upper intertidal zone of tropical mangroves, where environmental conditions are severe during neap tides (McGuinness 1994). The significance of substrate features is unsurprising given the importance of the burrow to *Uca* survival. The density and depth of root mat and vegetative structural elements, and consolidation of substrate may determine where crabs can burrow, burrow longevity, potential for providing struc-
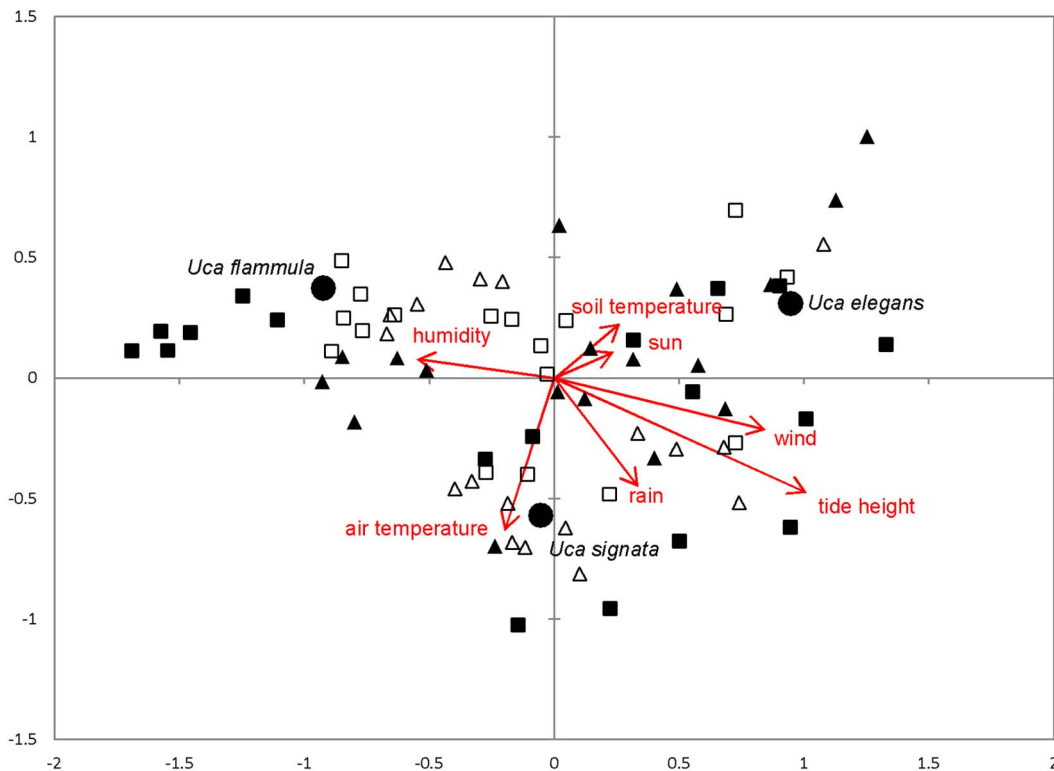
Fig. 4. CCA ordination diagram with *Uca* species (solid circles) and environmental variables (red arrows) recorded during the temporal survey. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.55 and 0.19, respectively. Solid squares identify wet season data, solid triangles identify dry/wet transition data, open squares identify dry season data and open triangles identify wet/dry transition data.

tural support, and burrow depth and thereby access to the water table (Bertness and Miller 1984).

Season has been ascribed as influential over the temporal distribution and abundance of fiddler crabs living in saltmarsh (Mouton and Felder 1996) and mangrove habitats (Skov et al. 2002, Litulo 2005*a*). We found significant seasonal patterns of abundance in fiddler crabs at higher or more exposed areas of their habitat range, presumably where they were under greater ecophysiological stress. We identified wind, humidity, temperature and sunshine as more proximally influential over crab temporal distribution and abundance during spring tides, than season or year. These factors are significant because they affect the atmospheric saturation deficit, therefore influencing the ability of crabs to regulate their body temperature by transpiration (Wilkens and Fingerman 1965), as well as the amount of surface water available for crabs to

access in order to deposit-feed and respire. We would predict crabs to be more abundant during the wet season, which was the case at the lowest sites. We hypothesize that the increased abundance of *Uca* in the highest gaps during the dry season was a function of the greater drying of the substratum during neap tides at this time thereby restricting feeding activities to spring tide periods when the substratum is wet.

Conclusions and implications

We described the results of our survey of the abiotic and biotic influences on the spatial and temporal distribution and abundance of three species of fiddler crabs and unidentified sesarmids in the mangroves of Darwin Harbour. We sampled crabs at spatial scales ranging from creek systems to microhabitats and at temporal scales ranging from days, tidal cycles, seasons and years to expand on other studies describing tropical mangrove crab distributions (cf. Emmer-

son 1994, Costa and Negreiros-Fransozo 2002, Skov et al. 2002, Inés et al. 2005). Our study is the first to determine the influences on crab abundances at multiple spatial scales, i.e., from ecosystem to microhabitat. We identified microhabitat factors such as soil temperature and canopy cover as influential over crab spatial abundance and seasonal variations in environmental factors such as wind speed and temperature as influential over fiddler crab temporal abundance. We suggest that sampling at too course a scale results in many environmental variables that describe the distribution and abundance of fiddler crabs in mangroves becoming overlooked, resulting in a misrepresentation of the functional factors within mangrove ecosystems.

As fiddler crabs and sesarmids are ecosystem engineers, identifying the factors influencing spatial and temporal variability in their distribution and abundance is imperative in understanding their impact on mangrove functionality. The spatial partitioning of habitats between sesarmids and *Uca* species is a significant consideration given their different engineering impacts (Kristensen 2008, Penha-Lopes et al. 2009). We found additional spatial and temporal partitioning of habitats among fiddler crab species, and since the influence of fiddler crabs on substrate surface nutrient availability has cascading effects through mangrove food chains (Silliman and Bertness 2002, Kristensen and Alongi 2006), we expect that other organisms (e.g., algae, plants, fish) might also be spatially partitioned as a consequence. As a large crab, *Uca flammula* is likely to have comparatively large, deep burrows (Bertness and Miller 1984, Hagen and Jones 1989), and this coupled with their association with low, vegetated sites means that *U. flammula* may play a more significant role than other fiddler crabs in nutrient turnover within mangroves; perhaps an equivalent role to that played by sesarmids in mangroves (Smith et al. 1991, Kristensen 2008).

Mangroves are ecologically and economically important ecosystems that are under threat of destruction around the world (Polidoro et al. 2010, Sandilyan and Kathiresan 2012). Accordingly, their effective management relies on the identification of the underlying processes influencing the distribution and abundance of eco-

system engineers and keystone organisms (Tanner and Hughes 1994, Bond 2001, Ernest and Brown 2001, Manning et al. 2006). We suggest that future studies designed to understand functionality of mangrove ecosystems include assessment of the influences on the spatiotemporal distribution and abundance of fiddler crabs and sesarmids at multiple scales. We further suggest that studies include temporal sampling of the size of individuals to facilitate estimates of the population dynamics of these ecosystem engineers.

Acknowledgments

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