Making up for lost time: Biophysical constraints on the temporal abundance of two fiddler crabs in wet–dry tropical mangroves

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Abstract   Biophysical models are used to predict the spatial distributions of organisms. Nevertheless, understanding factors influencing the temporal distributions of animals may often be additionally required. It is expected that intertidal macrofauna of the wet–dry tropics face a multitude of temporal challenges because there is not only seasonal drying but also variation in surface moisture over the circatidal cycle. Activities of fiddler crabs (*Uca* spp.) depend on adequate surface moisture being available for feeding and respiration. A recent study monitored crab abundance during spring tides and found that one *Uca* species in the mangroves of Darwin Harbour, Australia, *U. flammula*, is most abundant in the wet season, while another, *U. elegans*, is most abundant in the dry season. We hypothesized here that these seemingly contradictory abundance patterns are driven by temporal variation in the availability of soil moisture within each species habitat. We thus monitored crab abundance and measured soil moisture content across four types of habitat (low gap centres, low gap edges, mid-height gap centres and high gap centres) seasonally and across the circatidal cycle. We found that crab abundance and soil moisture both varied over time among habitat types. We used a log-linear model to show that habitat type influenced soil moisture and this in turn influenced crab abundance. Sampling across the circatidal cycle showed that *U. flammula* was more abundant in the wet season, as reported previously, while the abundance of *U. elegans* did not vary between seasons. Our model suggested that *U. elegans* 'makes up for lost time' in the dry season by undertaking all activities during spring tide low water as only at this time is the substratum moist enough for feeding and respiration. We highlight the importance of measuring multiple variables across habitats over small and large scales when assessing temporal abundance patterns of intertidal tropical organisms.

Key words: biophysical parameters, intertidal organisms, log-linear model, Ocypodidae, *Uca elegans*, *Uca flammula*.

INTRODUCTION

Biophysical models may be combined with geographical information systems (GIS) to provide a powerful means of assessing the spatial niche dynamics of organisms based on their physiological requirements (Gates, 1980; Campbell and Norman, 1998; Guisan and Thuiller, 2005; Sillero, 2011). Many ectothermic animals have physical requirements for optimal development, growth, foraging and reproduction that have been implicated in influencing their spatial distributions (Tracy, 1982; Kearney and Porter, 2004; Buckley *et al.*, 2013; Higgins *et al.*, 2014). Unfortunately, the dynamic responses of most animals to changes in their environments over time are not well known or are difficult to determine so biophysical models are sparingly used for explaining animal temporal distributions

(Guisan and Zimmerman, 2000). Nevertheless, there is a growing need to estimate the temporal impacts of environmental changes on animals to facilitate management. Researchers are thus increasingly using spatial information to model animal temporal niche dynamics (Campbell and Norman, 1998; Pearman *et al.*, 2008; Kearney and Porter, 2009). Non-linear models such as log-linear models and logistic regression can be utilized to determine ecological associations between different organisms and specified environmental parameters. Moreover, the relative influences of competing predictor variables on nominated response variables can be assessed (Christensen, 1997). Accordingly, such models present a viable means of using spatial data to make inferences about temporal ecological processes.

Organisms may experience seasonal fluctuations in abiotic parameters such as air and surface temperature, solar radiation, wind speed, rainfall and humidity (Wolda, 1978; Brown and Shine, 2006). Accordingly, many animals adjust their seasonal activities and/or

behaviours to cope with such fluctuations (Brown and Shine, 2006; Kearney and Porter, 2009; Buckley *et al.*, 2013; Buckley and Nufio, 2014). Macrofauna inhabiting intertidal areas have unique biophysical challenges as they experience daily fluctuations in water cover, temperature, salinity and splash forces in addition to seasonal climatic fluctuations (Helmuth and Hoffman, 2001; Helmuth, 2002; Denny and Dowd, 2012).

Fiddler crabs (genus *Uca*) are deposit feeding crabs that live in intertidal areas. Accordingly, they limit their activity to the low tide when the intertidal substratum is exposed. Some temperate species are active by day and night in the summer but remain underground during the winter (Crane, 1975; Salmon, 1987; Wolfrath, 1993; Kashyap, 2001). Most tropical species on the other hand are active all year round and rarely nocturnal (Crane, 1975; Salmon, 1987; Kashyap, 2001; Mokhtari *et al.*, 2008).

The wet–dry tropical region of northern Australia is characterized by a dry season (June–August) when rainfall is exceptionally scarce, and a monsoon (wet) season (December–March) when heavy rain falls daily (Taylor and Tulloch, 1985). The wet–dry (April–May) and dry–wet (September–November) intervening periods experience intermediate amounts of rainfall. Daytime temperatures are similar (~30–35 °C) between the wet and dry seasons. Thus, as a consequence of the extreme seasonal variations in rainfall, fiddler crabs in the intertidal habitats of the wet–dry tropics of Australia experience many seasonal and daily physiological and ecological challenges (Hagen and Jones, 1989; Nobbs, 2003; Nobbs and Blamires, 2015).

Water is an essential requirement for feeding and respiration in fiddler crabs (Smith and Miller, 1973; Thurman, 1998, 2004, 2005). Indeed, water availability has been shown to limit the daily and seasonal distributions of many crabs (Thurman, 1998; Stillman and Barnwell, 2004). Accordingly, we expect fiddler crabs in Australian wet–dry tropical mangroves to restrict their activities to times when the substrate is the wettest, that is either during the wet season or during low water following a spring high tide. Nevertheless, a recent assessment of the influence of abiotic and biotic factors on the seasonal abundances of different fiddler crabs in the upper intertidal zone of a wet–dry tropical Australian mangrove found some incongruent patterns (Nobbs and Blamires, 2015). One species, *Uca flammula*, was most abundant during the wet season while another, *U. elegans*, was most abundant during the dry season. These findings nonetheless were based on observations of crab abundance only during spring tides.

These two crab species do not co-occur so they do not affect each other's temporal abundance. *Uca flammula* associates with shady low-elevation canopy gaps, while *U. elegans* associates with large, flat, high-elevation gaps (Nobbs and Blamires, 2015). Occupying less shaded

habitats may render *U. elegans* more prone to drying than *U. flammula*. This may be extenuated during neap tides and/or low water in the dry season. We have certainly noticed that the soil surface of *U. elegans* habitats often appears dry and cracked at these times, which is never the case for the surface of *U. flammula* habitats. As a consequence, periodic variation in substratum water availability might induce physiological stress and force *U. elegans* to limit their dry season activities to times of low water during the spring tides; whereas *U. flammula* might be able to maintain activity during both the spring and neap tides all year round. Hence, we monitored the seasonal abundance of *U. flammula* and *U. elegans* during both the spring and neap tides within the mangroves at Darwin Harbour, Northern Territory, Australia, in the wet and dry season over two years. We then measured soil moisture in each species habitat to test the prediction that water availability in the substratum constrains the temporal activities of both species and that excessive drying during neap tides limits the activities of *U. elegans* to times of low water during spring tides in the dry season.

MATERIALS AND METHODS

Sites and crab abundance determination

Within the mid-upper intertidal zone of Ludmilla Creek, Darwin Harbour, Northern Territory, *U. flammula* and *U. elegans* were spatially partitioned within and among canopy gaps (Nobbs and Blamires, 2015). In order to sample both species within this zone where they were abundant, we selected a total of eight sites, two each of the following habitat types:

1. Low gap centres: The centre (at least 2 m away from the forest; Nobbs and Blamires, 2015) of two small (145.3 $\pm$ 51.6 m^2), low-elevation canopy gaps (6.33 $\pm$ 0.03 m above mean sea level). *Uca flammula* were abundant, but *U. elegans* absent.
2. Low gap edges: The edge (within 1 m of the forest; Nobbs and Blamires, 2015) of the same two small, low-elevation canopy gaps. *Uca flammula* were abundant, but *U. elegans* were absent.
3. Mid-height gap centres: The centre of two large (655.9 $\pm$ 269.1 m^2) mid-elevation gaps (6.67 $\pm$ 0.01 m above mean sea level). *Uca elegans* were abundant, but *U. flammula* were absent.
4. High gap centres. The centre of two very large (6,175.0 $\pm$ 465.6 m^2) high-elevation gaps (7.10 $\pm$ 0.18 m above mean sea level). *Uca elegans* were abundant, but *U. flammula* were absent.

We sampled each site during the wet and dry seasons in two consecutive years: 1997 and 1998. Within a season, each site was sampled on two consecutive days during the spring tide and two consecutive days during the neap tide.

Our sampling consisted of counting the number of individual *U. flammula* or *U. elegans* that emerged from their burrows over 10 min within three 0.56 m^2 quadrats haphazardly placed within each site during diurnal low water. No acclimation period to account for observer presence was necessary in these habitats because over 90% of the *Uca* spp. active within a 30-min period emerge during the first 10 min regardless of site, species, sex or season (Nobbs and McGuinness, 1999). The mean number of crabs per square metre (calculated as the mean number of crabs per quadrat divided by 0.56) was used as an index of crab abundance at each site (Nobbs and McGuinness, 1999; Nobbs, 2003; Nobbs and Blamires, 2015). Crab abundance data from 1997 and 1998 were summed prior to analyses.

Soil moisture measurements

Six soil samples were collected from the soil surface at each of our sites, three at each site were collected during one spring-tide period and one neap-tide period in the wet season of 1998. Soil samples were not collected at other times. The soil samples were taken to the laboratory at Charles Darwin University where they were weighed and dried at 105 °C in an oven until a constant weight was attained, in accordance with Australian standard test method (AS1289 B1.1; Department of Sustainable Natural Resources, 1977). The percentage weight lost by each sample as a consequence of drying was calculated as the percentage moisture for each sample.

Analyses

First, we ascertained whether crab abundances and soil moisture varied among habitat types over time. We compared the abundances of *U. flammula* and *U. elegans* using two three-factor analyses of variance (ANOVA) with the factors habitat type (two levels: low gap centre and low gap edge for *U. flammula* and mid gap centre and high gap centre for *U. elegans*), season (two levels: wet and dry) and tide (two levels: spring and neap). Tukey's (honest significant difference) tests were conducted where the interactions of the factors on crab abundance were significant. We then compared soil moisture across sites by a two factor ANOVA with the factors habitat type (four levels: low gap centre, low gap edge, mid gap centre and high gap centre) and tide (two levels: spring and neap tides). Cochran's tests were used to confirm that all variances were equal, and distributions appeared normal when assessed visually. Data that failed Cochran's test ($P < 0.05$) were square-root transformed as appropriate. Variances of untransformed data for the abundance of *U. elegans* were significantly heterogeneous according to a Cochran's test ($0.01 < P < 0.05$); therefore, the significance level for ANOVA was adjusted to $P = 0.01$.

Second, we used non-linear models to distinguish the relative influences of two predictor variables on crab spatial abundance to make inferences about their temporal abundances. We used three way (x, y, and z) log-linear models for each species of fiddler crab (*U. flammula* and *U. elegans*) to determine the relative influences of habitat type (the x variable, recorded as either low gap centre, low gap edge, mid gap centre or high gap centre) and soil moisture (the y variable) on crab abundance (the z variable, 1998 data only). The model tested four hypotheses: (i) that soil moisture influenced crab abundance and habitat type influenced soil moisture ($xy + yz$); (ii) that habitat type influenced soil moisture and crab abundance independently ($xy + xz$); (iii) there were three-way interactions between habitat type, soil moisture and crab abundance ($xy + xz + yz$); or (iv) the null hypothesis that habitat type, soil moisture and crab abundance varied independently. We used G^2 goodness-of-fit tests to identify significant interactions in the model and an Akaike information criterion score to identify the model best-fitting the data. All statistical analyses were performed using STATISTICA version 12.0 (StatSoft, Tulsa OK, USA).

RESULTS

Crabs of both species were more abundant during spring tides, and the abundance of *U. flammula* was greater during the wet season than the dry season, while the abundance of *U. elegans* did not vary significantly between seasons (Table 1; Fig. 1). Crab abundance nevertheless varied between habitat types. During the wet season and spring tides, there were more *U. flammula* in the low gap centres compared with the low gap edges, but *U. flammula* counts did not vary significantly between habitat types during the dry season and neap tides. Abundance of *U. elegans* was greater at the mid-height gap centres compared with the high gap centres during the wet season, but did not vary significantly between habitat types during the dry season.

Percentage soil moisture varied significantly, with habitat type ($F_{3, 40} = 83.5$, $P < 0.0001$), tide ($F_{1, 40} = 299.9$, $P < 0.0001$) and their interaction ($F_{3, 40} = 20.8$, $P < 0.0001$). We found that soil was wettest at the low gap edges during the spring tide and driest at the high gap centres and mid gap centres during the neap tide (Fig. 2).

We performed a subsequent log-linear analysis and identified our data to best fit hypothesis (1) for both *U. flammula* and *U. elegans*; that is, that soil moisture influenced abundance of both crabs and that habitat type influenced soil moisture (Table 2). The previously mentioned results accordingly suggest that water availability constrains temporal abundance in both crabs.

DISCUSSION

Our study is one of a handful to show biophysical parameters affecting the temporal activities of intertidal organisms at multiple scales (but refer to Helmuth and Hoffman, 2001; Helmuth, 2002; Denny and Dowd, 2012). We monitored, over two years, the temporal

Table 1. Results of analyses of variance comparing mean abundance (crabs per m^2 $\pm$ 1 SE) of *U. flammula* and *U. elegans* during the spring and neap tides in the wet and dry seasons of 1997 and 1998

Factor	df	Counts of *U. flammula* sqrt			Counts of *U. elegans*		
		MS	F	P	MS	F	P
A: Habitat type	1	1.0	4.5	0.035*	64.2	6.5	0.012
B: Season	1	22.8	102.4	0.000***	7.1	0.7	0.398
C: Tide	1	28.0	125.8	0.000***	1699.2	171.0	0.000***
A × B	1	1.3	5.9	0.016**	100.1	10.1	0.002**
A × C	1	2.7	12.2	0.001**	19.8	2.0	0.160
B × C	1	1.9	8.6	0.004**	419.4	42.2	0.000***
A × B × C	1	0.2	0.9	0.355	38.9	3.9	0.050
Error	120	0.2			10.0		

Cochran's test was not significant ($P > 0.05$) for square-root transformed *U. flammula* data. Variances of untransformed data on *U. elegans* abundance were significantly heterogeneous by Cochran's test ($0.01 < P < 0.05$); therefore, the significance level for ANOVA was increased to $P = 0.01$. *$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.
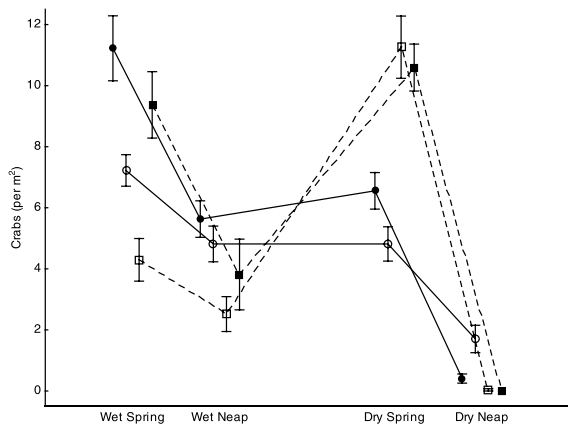

Fig. 1. Mean ($\pm$ SE) crab abundance (crabs per square metre) recorded at the four types of habitats during spring and neap tides in the wet and dry seasons of 1997 and 1998. Black circles with solid line indicate *U. flammula* in low gap centres. White circles with solid line indicate *U. flammula* in low gap edges. Black squares with dotted line indicate *U. elegans* at mid gap centres. White squares with dotted line indicate *U. elegans* at high gap centres.

abundance of two species of fiddler crab, *U. flammula* and *U.elegans*, from non-overlapping habitat types, and measured soil moisture across four arbitrary habitat types in a tropical Australian mangrove. We found distinct differences in the seasonal and circatidal activity patterns of each species. The soil moisture content within habitat types utilized by each of the species differed between the spring and neap tidal cycle. Our subsequent modelling confirmed that habitat type influenced soil moisture, which influenced the temporal abundance of the two species. This result concurs with our prediction that water availability acts as a constraint on the temporal activities of both fiddler crab species. Henceforth, we concluded that habitat

factors drive the differences in temporal abundance between species. Our results also confirm that water is essential for crab feeding and respiration and, as such, limits crab activities (Smith and Miller, 1973; Thurman, 1998, 2004, 2005).

We reported previously that *U. flammula* were more abundant during the wet season and *U. elegans* were more abundant during the dry season within their respective habitats (Blamires & Nobbs 2015). Because these results suggested that *U. elegans* confines its activity to drier periods, they seem incongruent with our expectation that substratum moisture is essential for crab activities. Nevertheless, by measuring soil moisture content while monitoring crab abundances across multiple sites during spring and neap tides we demonstrated that soil moisture availability within habitats differs daily and seasonally. This in turn seems to drive temporal abundances in different species of fiddler crab. Hence,
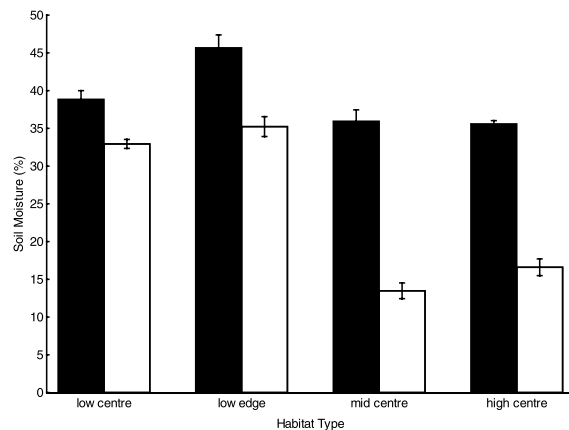

Fig. 2. Mean ($\pm$ SE) percentage soil moisture collected at the four types of habitats during one spring-tide period and one neap-tide period in the wet season of 1998. Black bars indicate spring tides. White bars indicate neap tides.

Table 2. Results of a three-way log-linear model determining the influence of habitat type (*x* variable) and soil moisture content (*y* variable) on crab abundance (*z* variable); measured as crabs per square metre

	Model	df	G^2-value	*P*-value	AIC_C
U. flammula	$xy + yz$	8	97.0	<0.0001	81.24*
	$xz + xy$	8	1.35	0.32	1.50
	$xz + xy + yz$	4	1.25	0.63	0.92
	Null	0	0		
U. elegans	$xy + yz$	8	40.31	<0.0001	46.32*
	$xz + xy$	8	1.41	0.46	1.67
	$xz + xy + yz$	4	2.22	0.19	1.14
	Null	0	0		

The model tested four hypotheses: (1) that soil moisture influences crab abundance and habitat type influences soil moisture ($xy + yz$); (2) that habitat type influences soil moisture and crab abundance independently ($xy + xz$); (3) there were three-way interactions between habitat type, soil moisture and crab abundance ($xy + xz + yz$); or (4) the null hypotheses that habitat type, soil moisture and crab abundance varied independently.
*Indicates the model best fitting the data as determined by AIC_c.

our study highlights the need to measure environmental parameters at multiple temporal scales in multiple habitats to delineate their influences on the temporal activity of intertidal organisms (Helmuth, 2002, 2009). This may be even more imperative for organisms in the wet–dry tropics where rainfall and other abiotic conditions substantially co-vary between seasons (Taylor and Tulloch, 1985; Kathiresan & Bingham 2001; Brown and Shine, 2006).

Sampling across the circatidal cycle showed that *U. flammula* was more abundant in the wet season, as reported previously (Nobbs and Blamires, 2015). The abundance of *U. elegans* on the other hand did not vary between seasons. Unlike *U. flammula*, which occupies closed forests, *U. elegans* associates with high elevation canopy gaps. The substratum at the sites used by *U. elegans* is subject to periodic drying during the dry season, particularly during neap tides, when the surface often appears dry and cracked, so soil moisture is likely to be a restrictive influence over the timing of *U. elegans* activity. It is likely that *U. elegans* 'makes up for lost time' in the dry season by undertaking all of its activities during times of spring tide low water. Thus, our previous finding that *U. elegans* were more active in the dry season, unlike *U. flammula* (Nobbs and Blamires, 2015), appears to have been a consequence of only sampling during the spring tide.

We predicted that both species of fiddler crab required access to substantial moisture in order to feed, respire and thermoregulate (Wilkens and Fingerman, 1965; Smith and Miller, 1973; Thurman, 1998, 2004, 2005). *Uca elegans* and *U. flammula* select habitats that vastly differ in elevation and vegetation cover, thus have vastly

different substrate drying patterns. These may be coped with by the species behaviourally and physiologically adapting to changing conditions by different means. Members of the subgenus *Deltuca*, which includes *U. flammula*, generally have rapid transpiration rates so may be more susceptible to desiccation in the dry season than other fiddler crabs (Crane, 1975). Members of the subgenus *Australuca* on the other hand, which includes *U. elegans*, have low transpiration rates (Thurman, 1998); thus, they may not be prone to desiccation during the drier season, and hence are more free to move into novel habitats.

An additional observation we have made is that the carapace of large female *U. elegans* sometimes whiten (an effect called 'bleaching') when in full sun and large males may become more brightly coloured on sunny days. Both of these responses help to reflect solar radiation and lower body temperature (Wilkens and Fingerman, 1965). The dark carapaces of large adult *U. flammula* do not whiten in the sun, although juveniles are a light greyish blue (Hagen and Jones, 1989). We have also noticed that *U. elegans* uses mud from the substratum to wet its body when inhabiting open clearings during the dry season. Similar behaviours in other fiddler crabs have been described as a means of inducing evapotranspirative cooling (Smith and Miller, 1973; Thurman, 1998).

Biophysical and statistical modelling is an effective way of assessing the spatial distributions of organisms (Gates, 1980; Campbell and Norman, 1998; Guisan and Thuiller, 2005; Sillero, 2011). Nevertheless, they have been used relatively rarely for assessing temporal distributions. However, temporal changes to environments, such as those induced under climate change, threaten the survival of many marine and intertidal animals (Harley *et al.*, 2006; Sandilyan and Kathiresan, 2012), so the development of better temporal biophysical models is of paramount importance. Here, we used non-linear modelling of spatial data to ascertain the temporal abundances of fiddler crabs in an Australian wet–dry tropical mangrove. We found that the models presented a viable means for making inferences about temporal patterns in *Uca* spp. Similar assessments could be applied to the development of temporal biophysical models for other animals of interest, such as threatened tropical intertidal organisms.

ACKNOWLEDGEMENTS

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