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INFLUENCE OF BIOTOPE CHARACTERISTICS ON THE DISTRIBUTION OF *UCA ANNULIPES* (H. MILNE EDWARDS, 1837) AND *U. VOCANS* (LINNAEUS, 1758)(CRUSTACEA: BRACHYURA: OCYPODIDAE) ON PULAU HANTU BESAR, SINGAPORE

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***ABSTRACT*. –** Density and distribution patterns of two species of fiddler crabs, *Uca annulipes* (H. Milne Edwards, 1837) and *U. vocans* (Linnaeus, 1758) were studied on Pulau [=Island] Hantu Besar, Singapore. Twenty-five and 26 $1m^2$ quadrats were sampled at the upper and lower shore levels of the lagoonal beach. Sediment samples from each quadrat were analysed for %sand, %mud and %organic content. A two-way analysis of variance (ANOVA) of crab density against species and shore level position showed the interaction term, 'Species × Shore level' to be significant (p<0.05), with *Uca annulipes* being more abundant on the upper shore and *U. vocans* preferring the lower shore. A General Linear Model for Multivariate Analysis of Variance (MANOVA) was used to further analyze the biotope-related variables (sand, mud and organic content) against crab species and shore level position. This time 'Species × Shore level' interaction was not significant (p>0.05). After this interaction term was removed from the model, only the main factor, 'Species', was significant (p<0.05). Subsequent ANOVAs showed *U. annulipes* was significantly (p<0.05) associated with sediments containing higher sand content regardless of shore level, and *U. vocans* was significantly (p<0.05) associated with sediments that had higher mud content. These results provide quantitative data to support and explain qualitative observations that *U. annulipes* are generally found in sandier habitats than *U. vocans*.

KEY WORDS. – Distribution, density, *Uca annulipes*, *Uca vocans*, biotope characteristics.

INTRODUCTION

Crane (1975), in her major revision of the fiddler crab genus *Uca*, compiled information on the distribution and habitats of the 59 species then recognised. Most *Uca* species were reported as being restricted in distribution, being closely associated with specific biotopes. 'Biotope' as used by Crane, and in the present study, was defined by Hesse et al. (1951) as "an area showing uniformity in the principal habitat conditions".

Two sympatric populations of fiddler crabs, *Uca annulipes* (H. Milne Edwards, 1837) and *U. vocans* (Linnaeus, 1758) inhabit the lagoonal shore on Pulau [=Island] Hantu Besar, off Singapore. *Uca annulipes* [referred to by Crane (1975) as *Uca* (*Celuca*) *lactea*] was reported to characteristically co-occur with *Uca vocans* throughout most of its range. In addition, "although burrows often mingle, *lactea* occupies higher levels on the shore" (Crane, 1975). Frith & Frith (1977, 1978) similarly reported that *U. lactea annulipes* occurs in muddy sand, *U. vocans vocans* inhabits firm mud, while both species co-exist in sandy mud substrates. The objectives of the present study were to test: 1) whether these two sympatric species differ significantly in population density according to position on the shore; and 2) if they are distributed differently, whether shore level position (e.g. different inundation/exposure requirements), or sediment characteristics is the major determinant.

MATERIALS AND METHODS

The study was conducted at the lagoonal beach of Pulau Hantu Besar, Singapore (Fig. 1). Field work and laboratory analyses were carried out from November to December 1997. Both species of *Uca* (i.e., *U. annulipes* and *U. vocans*) were found in abundance, but patchy in distribution on the lagoonal shore. Five 40 m transects, set 20m apart, were established in the intertidal zone on the lagoonal shore. Sampling stations at 5 m intervals were established along each transect. Stations were classified as either upper or lower shore based on their locations on the shore, i.e., stations within 0 to 20m of the transect were recorded as 'upper' shore and those that are established from 21m to 40m (i.e., towards the middle of the lagoon) were classified as 'lower' shore (Fig. 1).

At each station, the species of *Uca* and the number of burrows found in a $1m^2$ quadrat were recorded; after which, a core of 12cm depth of the sediment was removed for sediment particle size analysis. The top 5mm of sediment in an area, 15cm×15cm, within the quadrat was collected for organic content analysis. All samples were placed in airtight bags and brought back to the laboratory. Samples were stored at –20°C until analyses. A total area of 51 m^2 on the lagoonal shore was surveyed with 25 quadrats in the upper shore and 26 at the lower shore level.

Sediment particle size analysis was carried out using the wet-sieving method as outlined in Buchanan (1984). Organic content was determined using the percentage by weight of organic material lost using the ignition method as in Reinsel & Rittschof (1995).

Statistical analyses **–** A two-way Analysis of Variance (ANOVA) using MINITAB software (MINITAB Inc., Release 14, 2003) was used to analyse how density of crabs of the two species varied across the two shore levels. A General Linear Model (GLM) procedure on MINITAB (MINITAB Inc., Release 14, 2003) for Multivariate Analysis of Variance (MANOVA) was used to analyze the biotope-related variables (sand, mud and organic content) against species and shore level position. Sediment variables, i.e., percentage of sand, mud (i.e., clay + silt) and organic content were arc-sine transformed before statistical analyses. Non-significant higher order interaction terms were systematically discarded until only significant terms remained in the model for subsequent interpretation. Tukey's multiple comparison tests were carried out when main effects ANOVA tests were significant.

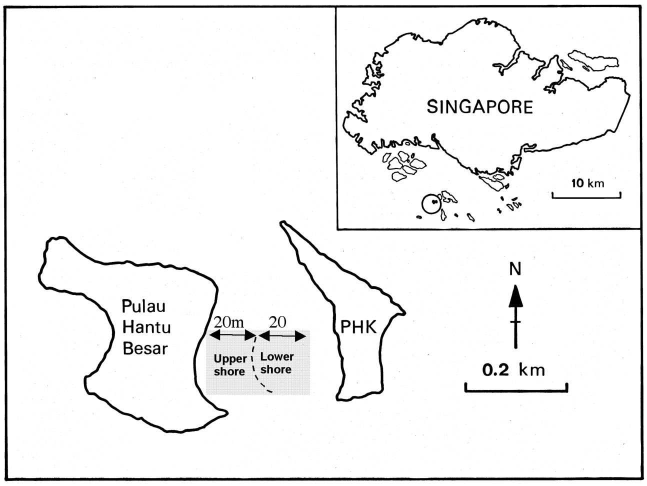

Fig. 1. Study site at the lagoon of Pulau Hantu Besar showing location of sampling area: upper and lower shores of the lagoon where 51 quadrats were taken (not drawn to scale). Inset: Map of Singapore and offshore islands with Pulau Hantu islands encircled. (PHK: Pulau Hantu Kechil). ▭ Region of shore that was surveyed.

RESULTS

The lagoonal shore is a sandy-mud biotope with more than 90% sand at both shore levels (Table 1). Ignition tests showed a uniformly low level of organic content (about 2%) (Table 1). The interaction term, 'Species × Shore level' of the two-way ANOVA was significant ($p<0.05$); thus, no further analysis of the main effects was carried out. The interaction can be clearly seen in Fig. 2: mean density of *U. annulipes* was higher at the upper shore ($\bar{x} \pm$ S.E. = 5.71 ± 1.15) than at the lower shore level ($\bar{x} \pm$ S.E. = 2.44 ± 0.47) but the reverse was observed for *U. vocans* where mean density was higher at the lower shore ($\bar{x} \pm$ S.E. = 10.35 ± 3.04) than at the upper shore level ($\bar{x} \pm$ S.E. = 1.73 ± 0.48).

Results of the full-model MANOVA showed that the interaction term for 'Tide level × Species' was not significant ($p>0.05$) (Table 2a). Of the two main factors, only 'Species', was significant ($p<0.05$) in the subsequent reduced-model MANOVA (Table 2b). Regardless of shore level, *U. annulipes* was found to be significantly associated with sediments that contained higher sand content (ANOVA, $p<0.05$) while *U. vocans* were significantly associated with sediments with higher mud content (ANOVA, $p<0.05$) (Table 2c). There was no significant association (ANOVA, $p>0.05$) between the two species of crabs with organic content (Table 2c).

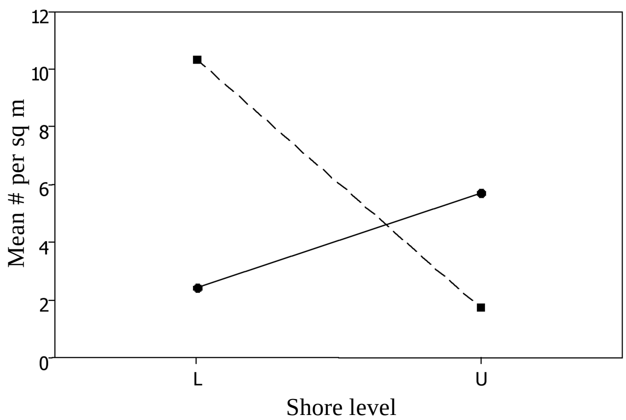

Fig. 2. Interaction plot of fitted means of density of *Uca annulipes* and *U. vocans* across the upper and lower shores of the lagoonal beach at Pulau Hantu Besar, Singapore. L: Lower shore level; U: Upper shore level. ●——● *Uca annulipes*; ■------■ *U. vocans*

Table 1. Mean percentage of sand, mud and organic content ± S.D. across two shore levels of the lagoonal shore on Pulau Hantu Besar, Singapore. (n = number of $1m^2$ quadrats sampled at each shore level).

Shore level	n	Mean % sand content ± S.D.	Mean % mud content ± S.D.	Mean % organic content ± S.D.
Upper	25	94.38 ± 2.10	5.77 ± 1.91	2.27 ± 0.54
Lower	26	92.32 ± 3.06	7.73 ± 2.98	2.42 ± 0.62

Table 2. Results of (a) MANOVA (Full model) for the variables of sand, mud and organic content crossed with factors: crab species and shore level; (b) MANOVA (Reduced model) for the variables of sand, mud and organic content crossed with factors: crab species and shore level; (c) ANOVA (main factor: 'Species') and Tukey's test for density, sand content, mud content and organic content. (n.s.: not significant; sig.: significant; U. a.: *U. annulipes;* U. v.: *U. vocans*).

(a) MANOVA (full model)

Factor	Wilk's λ	p	
Species	0.719	0.005	
Tide level	0.995	0.981	
Species × Tide level	0.950	0.577	n.s.

(b) MANOVA (reduced model)

Factor	Wilk's λ	p	
Species	0.650	0.001	sig.
Tide level	0.997	0.988	n.s.

(c) ANOVA and Tukey's test for 'Species' factor

Variable	Factor	p		Tukey's test
Sand content	Species	0.000	sig.	U. a. > U. v.
Mud content	Species	0.000	sig.	U. v. > U. a.
Organic content	Species	0.133	n.s.	—

DISCUSSION

Information on the distribution of *Uca annulipes* and *U. vocans* populations in relation to abiotic factors are scant, except for a few studies, e.g., Chakraborty and Choudhury (1985, 1992); Icely and Jones (1978) and Lim and Diong (2003). In this study, we observed that *U. annulipes* was significantly more abundant on the upper shore on sandy substrates, while *U. vocans* was significantly more abundant on the normally muddier lower shore levels; *U. vocans* moved to the upper shore levels only where the substrate had higher mud content. These quantitative results support the qualitative observations of Crane (1975) and Frith & Firth (1977, 1978). Present results also substantiate that reported by Icely and Jones (1978) that *U. vocans* has a preference for the lower shore region and occupies regions where sediment particle sizes are finer than that of *U. lactea* (= *U. annulipes*).

Icely and Jones (1978) also observed that *U. vocans* was found in areas with higher organic content than *U. lactea* (= *U. annulipes*). This distributional association of the two species with organic content was not observed in the present study as organic content was similar at both shore levels in the lagoon, yet *U. vocans* was found in greater abundance at the lower levels.

The morphology of dominant species is usually specialised and adapted to some aspect of the substrate of the habitat in which they are found (Abele, 1974). Fiddler crabs are surface deposit feeders, and therefore the sediment type can be expected to be an important factor governing their abundance and distribution. In deposit-feeding crabs the mouthparts sort out food particles from the sediment for ingestion. The mouthparts of *Uca pugilator*, *U. minax* and *U. pugnax* are closely-linked to the habitats in which these crabs occur in abundance in the wild (Miller, 1961).

Crane (1975) concluded that the normal habitat of a given species, whether sandier or muddier, can be surmised by examining the setae on the endites of the second maxilliped: the more spoon-tips, the more nearly sandy the environment. Crane's (1975) observations were confirmed by Miller (1961) who reported that *Uca pugilator*, which inhabits sandy areas, had spoon-tipped setae on the second maxillipeds. In contrast, *U. pugnax* which is dominant in muddy habitats had woolly setae on its second maxillipeds. The modification of these maxilliped setae in *U. minax* was much less than that in *U. pugilator* and *U. pugnax*. Miller (1961) attributed this to the high availability of food in the marsh where *U. minax* lives. Quantitative comparisons of the second maxillipeds of *U. vocans* and *U. annulipes* collected from the same sampling site as this study showed that for any given size of crab, there were significantly more spoon-tipped setae in *U. annulipes* than in *U. vocans* (Lim, 2004). These results provide additional evidence that the mouthparts of the two species are closely-linked to the habitats in which they live, that is, more spoon-tipped setae in mouthparts of the sandy habitat-preferring *U. annulipes* and more woolly setae in the muddy habitat-dweller, *U. vocans*.

Besides substrate composition, other factors such as interspecific competition and burrowing activity can also determine the distribution of *Uca* species (Aspey, 1971, 1978; Jaramillo & Lunecke, 1988). When *U. pugnax* and *U. pugilator* co-exist, the reduced number of *U. pugilator* burrows was attributed to the agonistic display by *U. pugnax* (Aspey, 1971, 1978). Field and laboratory substrate-preference experiments conducted by Jaramillo and Lunecke (1988) showed that *U. pugilator* made burrows in both kinds of substrates whereas *U. pugnax* dug exclusively in muddy sediments. Further research is currently ongoing to test (i) substrate-preference in *U. vocans* and *U. annulipes* in various combinations of sand-mud proportions and (ii) if interspecific competition similarly influences the distribution of *U. vocans* and *U. annulipes* on Pulau Hantu.

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