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Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae: *Uca*) in mangrove habitats

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Abstract Counting the number of individuals emerging from burrows is the most practical method for estimating the apparent abundance of Australian *Uca* species living in mangrove habitats. Experiments were conducted to investigate the effect on counts of quadrat design, distance of observer, quadrat size, recovery time and observational technique. Significant differences in the apparent abundance of one species were found when the subjects were within 2 m of the observer, and when a conspicuous quadrat was used. The largest quadrat tested provided the least variability in counts but an intermediate size (0.56 m^2) was more practical. Most *Uca* active within a 30-min period emerged during the first 10 min regardless of site, species, sex or season. There was a linear correlation between scanning and continuous observation indicating that the former method could be useful when sampling time was limited. Temporal changes in the apparent abundance of *Uca* suggest that long-term sampling and more detailed studies will be worthwhile.

Key words: Darwin Harbour, sampling methods, *Uca flammula*, *Uca elegans*, *Uca mjobergi*, *Uca signata*.

INTRODUCTION

Fiddler crabs (*Uca* spp.) are among the most abundant animals in tropical mangrove forests (Jones 1984; Davie 1994). The species found in Darwin Harbour are small crabs (up to 3.5 cm carapace width) which usually live singly in burrows at a density of up to 15 per m^2 (M. Nobbs pers. obs. 1996). They emerge at low tide to feed on the substratum close to the burrow entrance and frequently visit the burrow presumably as a refuge from environmental stress (Montague 1980). While there are numerous studies of species in North America (e.g. Teal 1958; Kerwin 1971; Wolf *et al.* 1975; Ringold 1979; Bertness & Miller 1984; Cammen *et al.* 1984; Mouton & Felder 1996), and in southeast Asia (e.g. Frith & Brunenmeister 1980; Chakraborty & Choudhury 1992), species in Australia have been largely ignored (but see Hagen & Jones 1989; Hagen 1993). This may be due, in part, to the difficulties involved in estimating the abundance of burrowing mangrove species (Warren 1990).

Several methods have been used to estimate the true abundance of crabs inhabiting soft sediments, but few of these are suitable for use in tropical mangroves. Some workers have excavated burrows (Frith & Brunenmeister 1980; Cammen *et al.* 1984; Colby & Fonseca 1984; Chakraborty & Choudhury 1992) but this would cause unacceptable disturbance to the habitat, even if it were practical. Mark–recapture (Hockett & Kritzler 1972) and removal sampling (Wolf *et al.* 1975) methods have given good estimates in those situations where the behaviour of the subjects is appropriate. The former method requires random mixing of the marked individuals into the population which occurs in droving species, and the latter requires quick and efficient capture of subjects without disturbing the habitat. Darwin Harbour species do not form droves and are not easily captured.

Faced with these difficulties, most workers have attempted to estimate only the number of crabs active on the surface. This apparent abundance is likely to underestimate true abundance, as some crabs may not emerge because of abiotic (Crane 1975; Powers & Cole 1976; Nakasone 1982) or biotic (Crane 1958; Christy 1978; Krebs & Valiela 1978; Goshima & Murai 1988) factors. Two methods that have been used to estimate the number of crabs active on the surface are pitfall traps (Salmon & Hyatt 1983) and video recordings (Colby & Fonseca 1984). Australian *Uca*, however, rarely fall into traps (M. Nobbs unpubl. data) and video recording is impractical for large-scale sampling programs. Some workers have counted burrows (e.g. Icely & Jones 1977; McGuinness 1997a) to estimate abundance but these estimates can be unreliable (Spivak *et al.* 1991).

Visual counts of the numbers of crabs active on the surface have been used in several studies (Golley *et al.* 1962; Nakasone 1982; Zucker 1983; Hagen 1993) but

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a variety of protocols have been used. For instance, observation times vary, although workers have typically used periods of 20 min or less (e.g. Warren 1990; Hagen 1993). Most workers have made continuous records of all crabs during the observation period but some took only quick scans (e.g. Zucker 1983). Little attention has been given to how such differences might affect results and to the extent to which they confound comparisons among species or habitats. Frix *et al.* (1991), for example, found that re-emergence times varied significantly between *U. pugilator* (Bosc) and *U. pugnax* (Smith). Peterson & Black (1994) recently emphasized the importance of investigating these method–species and method–habitat interactions.

This study aimed to determine the influence of some aspects of visual sampling protocols on counts of several species of *Uca* in different habitats. It had five specific objectives.

(1) Test if the physical structure of the quadrat affected counts of active crabs of different species and at different sites. Some *Uca* respond to certain shapes (Herrnkind 1968; Langdon 1985; Cameron & Forward 1993) and casual observations suggested that some might avoid conspicuous quadrats.

(2) Test whether the distance of the quadrat from the observer affected counts of different species and at different sites. Casual observations suggested that some species might be slow to emerge if the observer was close.

(3) Test whether the size of the quadrat affected either the mean or standard error of counts of different species and at different sites. Smaller quadrats are easier to count but might give less reliable results.

(4) Test whether observation period differentially affected counts of different species, between the sexes and at different sites. Wilson (1989) found that the mean re-emergence time of four species of mangrove crabs of Florida Bay was 10 min in summer but longer (22 min) in winter (when temperatures fall to 20–21°C during the day).

(5) Test whether continuous observations and quick scans gave similar results for different species and at different sites. Results might vary according to observational technique because *Uca* make frequent visits to their burrows and move short distances from their burrows to feed, taking them out of or into the quadrat. Quick scans might save time but not be as precise as the continuous observation method.

METHODS

Study sites

Three main sites were studied in the mangrove forest at Ludmilla Creek, Darwin Harbour (see McGuinness 1994, 1997a,b for general descriptions): a tidal creek bank site, a muddy clearing and a sandy clearing. All sites were above the high water neap level and had only small amounts of leaf litter on the soil surface. The tidal creek bank site was 7.5 m × 12.5 m and 6.36 m above sea-level. Its surface was uneven, due to the presence of numerous mounds of soil, and it was adjacent to a dense zone of tall *Ceriops tagal* var. *australis* C. White. *Uca flammula* (Crane) and *U. signata* (Hess) dominated at this site. The muddy clearing was a saltpan 23.0 m × 40.0 m and 6.68 m above sea level. *Uca elegans* (George and Jones) was the dominant species in the centre of the clearing. This species, and *U. flammula* and *U. signata*, occurred towards the edges of the clearing where, in places, mangroves were colonizing and the substratum was uneven. The sandy clearing was 30.0 m × 35.0 m, 6.14 m above sea level and close to the creek mouth. The substratum was flat and inhabited by *U. elegans* and *U. mjobergi* (Rathbun). Without the aid of binoculars an experienced observer could identify crabs up to 4 m away to species by their size, shape and colour.

Four additional sites were used for the distance experiment. There was a second tidal creek bank site (9.0 m × 22.5 m, 6.30 m above sea-level), two additional muddy clearings (15.5 m × 56.5 m, 6.68 m above sea-level, and 10.5 m × 17.0 m, 6.60 m above sea-level), and a large loamy clearing (72.5 m × 79.0 m, 6.92 m above sea-level).

Quadrat design

Six 0.25 m^2 plots, marked with thin wooden stakes, were haphazardly placed in each of the three main sites. Each plot was first sampled with a quadrat made of thick black plastic tubing (14 mm diameter), then with a second of thin wire (3 mm diameter), and finally with a third of fishing line (strung around the stakes). The three designs were used at each plot so that the behaviour of the same individuals could be compared and to minimize variation in results due to the uneven distribution of crabs. Plots were observed for 10 min after the quadrat was placed and the number of crabs emerging from burrows within the quadrat was recorded. At least 30 min were allowed to elapse between repeated observations of the same plot to give the crabs time to recover. Observations were made on 17–19 May 1996.

The data were analysed using a two factor repeated measures ANOVA. The factors were Species at site (5 levels: *U. elegans* at the muddy clearing and the sandy clearing, *U. mjobergi* at the sandy clearing, *U. flammula* at the creek bank, and *U. signata* at the creek bank) and Quadrat design (repeated measure). Cochran's test was not significant ($P > 0.05$) after data were square root transformed.

Distance of observer

Each species was sampled at two sites: *U. flammula* at the two creek bank sites, *U. elegans* at the centres of the muddy and loamy clearings, and *U. signata* at the edges of the two additional muddy clearings. At each of the six sites, three 0.56 m^2 wire quadrats were haphazardly placed at 2 m, 4 m and 6.5 m from the observer, giving a total of nine quadrats per site. After 10 min, all nine quadrats were scanned and the number of *Uca* in each recorded. Observations were made on 7 June 1997.

The numbers of crabs of each species were analysed by separate two factor ANOVAs with the factors Site (2 levels) and Distance (3 levels). Data were untransformed and Cochran's test was not significant ($P > 0.05$). Tukey's tests were used to compare means at the three distances for each combination of site and species.

Size of quadrat

At each of the three main sites, four different sizes of wire quadrat, 0.12 m^2, 0.25 m^2, 0.56 m^2 and 1.00 m^2, were compared. At each site, the four quadrats were simultaneously observed for 15 min. The species, sex and time of appearance of each crab that emerged from a burrow within the quadrat were recorded. This procedure was repeated six times at each site. Observations were made on 17–19 July 1996.

The results for each of the four sizes of quadrat were converted to numbers per m^2 and analysed by a two factor repeated measures ANOVA. The factors were Species at site (4 levels: *U. elegans* at the muddy clearing and the sandy clearing, *U. flammula* at the creek bank and *U. mjobergi* at the sandy clearing) and Quadrat size (repeated). Cochran's test was not significant ($P > 0.05$).

Recovery times

At each of the three main sites, six haphazardly placed 0.25 m^2 wire quadrats were observed for 30 min. The species, sex and time of appearance of each crab that emerged from a burrow within the quadrat were recorded. Observations were made on 22–23 May and 2 June 1996.

The number of crabs observed during the first 10 min was expressed as a percentage of the total number of crabs that emerged during the 30 min observation period. These data were analysed by a two factor ANOVA with the factors Species at site (4 levels: *U. elegans* at the muddy clearing and sandy clearing, *U. flammula* at the creek bank, and *U. mjobergi* at the sandy clearing) and Sex. Cochran's test was not significant ($P > 0.05$) after data were transformed by arcsin $\sqrt{(x/100)}$.

During the 30 min observation period no crabs emerged after the first 15 min. The number of crabs that emerged from burrows after 10 min was expressed as a percentage of all crabs that had emerged after 15 min. Data from this and the previous experiment were analysed by a two factor ANOVA with the factors Habitat (3 levels: creek bank, sandy clearing and muddy clearing) and Month (2 levels: May/June and July). Cochran's test was not significant ($P > 0.05$) after data were transformed by arcsin $\sqrt{(x/100)}$.

Data from these two experiments were also used to compare the apparent abundance of *Uca* between May/June and July. Counts of crabs after 10 min were analysed by a three factor ANOVA with the factors Species at site (4 levels: *U. flammula* at the creek bank, *U. elegans* at the muddy clearing, *U. elegans* at the sandy clearing, and *U. mjobergi* at the sandy clearing), Time and Sex. Cochran's test was not significant ($P > 0.05$).

Comparison of continuous observation and instantaneous scan sampling

The previous experiments testing quadrat design, size of quadrat and recovery times used continuous observation as a method of sampling and the distance of observer experiment used instantaneous scans. In order to compare these observational techniques three 0.56 m^2 plots were haphazardly placed at the centre of each site and at the edge of the muddy clearing. For 10 min, all crabs that emerged from burrows within the quadrat were counted (continuous observation). Crabs which went up and down a burrow several times were not recounted and those which entered the quadrat from outside were not counted at all. At the end of this period, the number present, regardless of method of entry, was recorded (instantaneous scan sampling).

Data were analysed by a two factor repeated measures ANOVA with the factors Species at habitat (6 levels: *U. elegans* at the centre of the muddy clearing, *U. elegans* at the edge of the muddy clearing, *U. signata* at the edge of the muddy clearing, *U. elegans* at the sandy clearing, *U. signata* at the creek bank, and *U. flammula* at the creek bank) and Sampling method (repeated measure). Cochran's test was not significant ($P > 0.05$).

The ratio of the number of crabs seen by scanning to those seen by continuous observation was compared among habitats by a one factor ANOVA (4 levels: sandy clearing, creek bank, centre of muddy clearing, and edge of muddy clearing). Cochran's test was not significant ($P > 0.05$) after data were transformed by arcsin $\sqrt{(x/100)}$.

RESULTS

Quadrat design

Fewer *U. elegans* were counted at the muddy clearing in the black plastic quadrat than in the other designs ($P < 0.01$). Quadrat design had no effect on

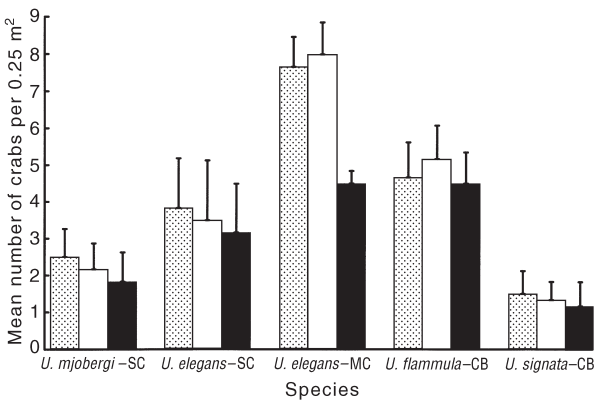

Fig. 1. The effect of quadrat design on the apparent abundance of *Uca*. Each bar represents the mean of the counts from six 0.25 m^2 quadrats; the error bars give + 1 SE. ▨, wire quadrats; □, fishing line quadrats; ■, black plastic tubing quadrats. SC, Sandy clearing; MC, muddy clearing; CB, creek bank.

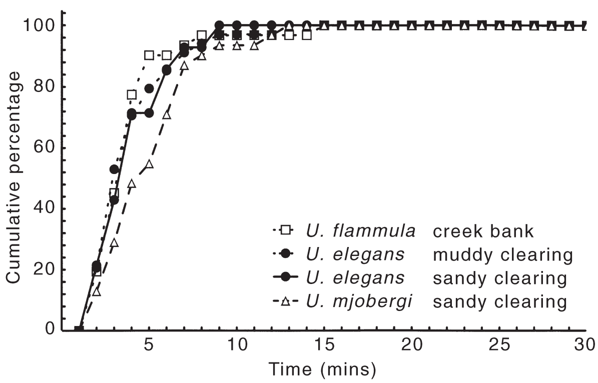

Fig. 2. The cumulative percentage of crabs emerging from burrows following a disturbance. Each point represents the sum of counts of six 0.25 m^2 quadrats and gives the percentage of the total number of crabs which would emerge in those six quadrats during a 30-min period. Percentages were calculated for each one min interval during the 30 min observation period.

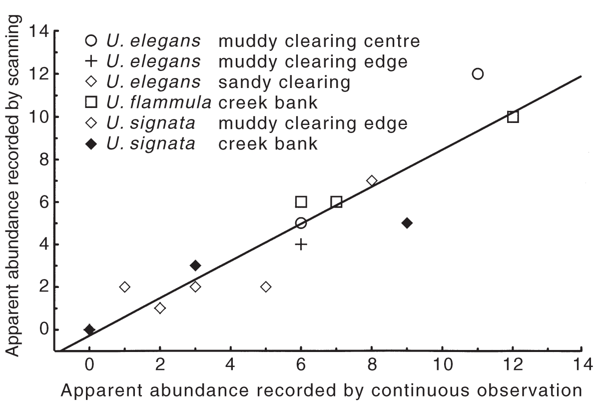

Fig. 3. The relationship between the number of crabs recorded by scanning and continuous observation. Each point represents the count from one 0.56 m^2 quadrat.

the apparent abundance of *U. elegans* at the sandy clearing, or on the other species (Fig. 1).

Distance of observer

Fewer *U. elegans* were counted 2 m from the observer than at greater distances in the loamy clearing ($P < 0.01$). Distance had no effect on counts of *U. elegans* at the muddy clearing, or on the other species (Table 1).

Size of quadrat

When adjusted for area, quadrat size had no effect on apparent abundance. The standard error decreased with increasing quadrat size for all sites (Table 2).

Recovery times

Over 90% of the crabs emerged in the first 10 min of the observation period (Fig. 2). There were no significant differences among species at site, or sexes, in the percentage of crabs which emerged during the first

Table 1. The effect of distance of observer on apparent abundance of *Uca* (n = three 0.56 m quadrats at each distance)

	Uca flammula			*Uca elegans*			*Uca signata*		
	2 m	4 m	6.5 m	2 m	4 m	6.5 m	2 m	4 m	6.5 m
Site A									
Mean	2.33	2.33	2.67	1.33	9.00	8.00	11.67	13.00	9.67
SE	0.33	0.88	0.88	0.67	1.00	1.00	0.67	2.52	1.76
Site B									
Mean	2.33	2.00	2.00	4.33	5.67	5.00	14.33	11.00	12.67
SE	0.33	0.58	0.58	0.33	1.67	1.15	0.88	1.15	0.33

Tukey's tests compare the means and three distances for each combination of site and species. Underline used to denote equal means.

Table 2. The effect of quadrat size on apparent abundance of *Uca* as numbers per m^2 (n = six quadrats of each size)

	Uca flammula	*Uca elegans* (MC)	*Uca elegans* (SC)	*Uca mjobergi*
Mean				
0.12 m^2	8.00	9.33	9.52	8.16
0.25 m^2	9.33	10.67	8.00	8.67
0.56 m^2	9.67	15.00	6.22	6.81
1.00 m^2	9.67	13.83	6.33	6.00
SE				
0.12 m^2	2.07	2.46	2.51	3.65
0.25 m^2	2.46	1.69	2.07	3.49
0.56 m^2	1.58	1.13	1.36	1.61
1.00 m^2	0.67	0.79	0.88	1.44

Table 3. The effect of observational technique on the apparent abundance of *Uca* (n = six 0.56 m^2 quadrats)

	Uca elegans			*Uca flammula*	*Uca signata*	
	Muddy clearing		Sandy clearing	Creek bank	Muddy clearing	Creek bank
	Clearing	Edge	Clearing	Clearing	Edge	Clearing
Observational technique						
Continuous	8.0	2.6	4.3	8.3	4.3	4.0
Scan	7.6	1.6	3.3	7.3	3.3	2.6
Percentage (scan/continuous)*100						
Mean	92.7	38.8	108.5	89.6	68.0	51.8
SE	8.2	20.0	47.5	5.2	10.8	28.9

Table 4. Analysis of variance comparing the counts of *Uca* emerging within the first 10 min in six 0.25 m^2 quadrats between May/June and July

Source	d.f.	SS
A: Species at Site	3	11.36*
B: Time	1	25.01***
C: Sex	1	11.34**
A*B	3	5.11
A*C	3	1.45
B*C	1	5.51*
A*B*C	3	1.78

Data from the quadrat size and recovery time experiments. All data were untransformed. Significance is indicated thus: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

10 min ($P > 0.05$). There were also no significant differences between habitats, or over time (between May/June and July), in the percentage of crabs emerging during the first 10 min ($P > 0.05$).

Comparison of continuous observation and instantaneous scan sampling

Fewer crabs were seen with the instantaneous scan method ($P < 0.05$), but the percentage of crabs not counted using this method did not differ significantly between the species ($P > 0.05$; Table 3). There was a good linear relationship between the numbers of crabs recorded with the two methods ($r = 0.94$, Fig. 3).

Changes over time

Fewer *U. elegans* were seen in the sandy clearing than in the muddy clearing (Table 4). Fewer crabs were also counted in July compared to May/June ($P < 0.001$) at all sites. The number of male crabs was greater during May/June but the number of female crabs did not differ.

DISCUSSION

A visual count of the individuals active on the surface was the only practical and reliable method of estimating the apparent abundance of crabs in these mangrove forests in large-scale studies. The present experiments reveal that although some aspects of the sampling protocol—such as quadrat size, recovery time or counting method—did not interact with either species or habitat, other aspects should be carefully considered when designing studies employing this method.

Counts of *U. elegans* were reduced at some sites when the observer used a conspicuous quadrat or was close to it. These effects were observed at those habitats with rather flat terrain, no vegetation and a prominent horizon. Land and Layne (1995) suggested that *U. pugilator* inhabiting flat beaches used the horizon to distinguish friend or foe: predators appear above the crab's horizon and conspecifics below it. The conspicuous quadrat and close observer were apparently regarded as threatening and avoided at sites where the horizon was prominent.

The absence of these effects at the other species–site combinations has two significant implications. First, it indicates that all three designs of quadrat, and the observer at all distances, were regarded as equally threatening. Although it is quite likely that these other species were unaffected by all of the quadrats, because the fishing line was inconspicuous, it is possible that they reacted to the observer even at the furthest distance tested here. It would be interesting to test this point but the results might be of little practical significance because identifying individuals at the longer distances becomes much harder. Second, it emphasizes the importance of evaluating methods in different situations. As Peterson and Black (1994) discuss, workers cannot assume that artefacts or biases will be similar in different habitats.

The results allow us to decide on the most appropriate method to use. First, an observation period of 10 min appears to be a good compromise, being long enough to provide reasonable accuracy while allowing several replicates to be made. Second, although larger quadrats give less variable results, the 0.56 m^2 quadrat is more practical because it is easier to track individuals: those that go up and down their burrows and those that enter the quadrat from outside can be recognized. Third, the instantaneous scan method may be useful in some studies, because many replicates can be collected quickly (observation time for scans: 15 min for six replicates), but it recorded, on average, only 75% of the individuals seen by continuous observations. Continuous observation may be costly in terms of time (observation time: 1 h for six replicates) but is more accurate in terms of numbers of crabs and for recording specific habitat differences because crabs that burrow elsewhere but wander into the quadrat are not counted.

With this protocol, we were able to document spatial and temporal patterns in the apparent abundance of *Uca* in the mangrove forests at Ludmilla Creek. Species exhibited clear differences in abundance among sites and habitats (species at site was significant, $P < 0.01$, for quadrat design experiment), and there were changes in abundance between May/June (transitional period between Wet and Dry Seasons) and July (Dry Season) ($P < 0.001$). These results are only preliminary but indicate that more detailed and longer-term studies will increase our understanding of behavioural ecology of these abundant animals. Patterns in the abundance and activity of *Uca* may be related to environmental factors as already discussed. Close monitoring of these factors would enable hypotheses about such patterns to be developed and tested in further studies. Such studies could also test whether the regional differences documented for some aspects of the ecology of mangrove communities (Smith *et al.* 1989; Robertson 1991; McGuinness 1997a) also influence *Uca*.

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