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A comparison of alternative methods for estimating population density of the fiddler crab *Uca annulipes* at Saco Mangrove, Inhaca Island (Mozambique)

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Abstract

Visual counts of surface-active crabs both by binocular and burrow counting methods have been used in many studies to estimate population density. However, their reliability has not yet been assessed comparatively. Three methods for estimating the abundance of fiddler crabs *Uca annulipes* in a mangrove forest (Inhaca Island, Mozambique) were compared from three different sub-areas: two sub-areas inundated only during spring tides and one sub-area inundated in both spring and neap tides. Burrow, binocular and direct (excavation) counting methods were performed by plotting ten 0.25 m^2 quadrats in each sub-area over the four moon phases. Overall densities (per 0.25 m^2) differed according to method, sub-area and lunar phase. Burrow count overestimated crab density by up to 20%, while binocular count underestimated density by up to 41%. Correlation coefficient estimated for both counting methods showed that burrow count gives better density estimates than binocular count (0.91 and 0.56, respectively). Sex ratios were also investigated within the three sub-areas and at the moon phases. Males are dominant throughout the studied period except during new moon and first quarter, indicating that when the number of gravid females is low, sex ratio bias for binocular count is minimal.

Introduction

Distribution patterns and taxonomic status of fiddler crabs belonging to the genus *Uca* have been studied in great detail (Crane, 1975). The fiddler crab *Uca annulipes* has a widespread distribution in the southern hemisphere and typically is a dominant species in mangrove crab communities (MacIntosh, 1988). The activity patterns of *Uca* species are largely dependent on tidal periodicity, which is in turn moderated by moon phase.

Several methods have been used to estimate the population densities of crabs inhabiting mangroves (Cammen et al., 1984; Colby & Fonseca, 1984; Nobbs & Mcguinness, 1999). Due to their habit of emerging from burrows during ebb tide, population size can be estimated using a variety of methodologies. Absolute estimates can be produced through direct excavation of crabs from their burrows, while direct visual counts can be made of surface-active animals, or of their burrows.

Both visual counts of surface-active crabs and burrow counts have been used in many studies to estimate population density (e.g. Crane, 1975; Macintosh, 1988; Von Hagen, 1993; Nobbs & Mcguinness, 1999). The popularity of these methodologies is partly a consequence of the difficulties associated with excavating crab burrows in mangrove habitats. Furthermore, they are considered appropriate for generating accurate indices of relative abundance, whilst resulting in minimum impact on sensitive mangrove habitats.

A problem with visual counts of surface-active animals is that they tend to underestimate population size because some individuals (for example moulting crabs or ovigerous females) remain inside their burrows, and juveniles are easily overlooked (Crane, 1975; MacIntosh, 1988). Conversely, burrow counts tend to overestimate population density because a proportion of burrows are unoccupied or have more than one opening (Macintosh, 1988). No previous studies have attempted to quantify the relationship between estimates generated by these different methods in relation to absolute counts.

In this study, we compare three methods of estimating the population density of the fiddler crab *Uca annulipes* through burrow, binocular and absolute counts at an East African subtropical mangrove, the Saco da Inhaca, Inhaca island, southern Mozambique. In addition, a comparison of the impact of tidal and lunar phases on the different counting methods and population sex ratios was made.

Materials and methods

Study area

The Saco da Inhaca (26° 07′ S, 32° 56′ E) is an enclosed bay fringed by extensive mangrove forest (Fig. 1) for which detailed descriptions of the general ecology, fauna and flora have been carried out (Kalk, 1995; Guerreiro et al., 1996; De Boer & Longamane, 1996; Abdurremane, 1998; Halare, 1999; Quincardete, 1999; De Boer, 2000).

The study was conducted in three different sub-areas characterised by differing tidal inundation periods. Two of the areas were in the mangrove forest, under the upper *Avicennia marina* (area A) and the mid *Avicennia marina* belts (area B). The third was a low sandbank in the inner part of the intertidal zone (area C). The two mangrove sub-areas were not inundated during neap tides, while the sandbank was inundated during all tides.

Sampling

Sampling was performed between January and March 1999 at the three sub-areas, and once at each of the four lunar phases (first quarter, full moon, last quarter and new moon). Each phase was sampled twice over a 2–3 day period, from the first day of each type of tide, starting 1–2 h after high tide. Twenty stations were allocated in each of the sub-areas, of which 10 were chosen randomly for sampling (quadrats of 0.25 m^2). Each randomised quadrat was observed for 5 min from a distance of 4 m, and the number of emerging crabs was counted using binoculars with 8×40 magnification. After each 5 min observation, the number of burrows within the plots was counted. Afterwards, the same plot was excavated with a corer to a depth of 25 cm. All crabs were collected, identified and sexed (females checked for eggs). Other species excavated while digging were recorded and discarded.

Burrow and binocular counts were converted to percentage of absolute count. Hourly sampling was also made in order to assess the variation of sex ratio, starting 1 h after high tide until low tide, during one spring tide at two sites, the upper *Avicennia marina* (A) and the mid *Avicennia marina* (B) areas. Regressions of absolute *versus* binocular counts and absolute *versus* burrow counts were computed for the three sub-areas. All quadrats without excavated crabs or burrows were excluded from this analysis. Pearson's correlation coefficients were calculated in order to assess the degree of relationship between the direct values (excavated) and the binocular and the burrow counts.

Sex ratio was calculated for male *versus* total crabs (M:T) for the three sub-areas and separately for each moon phase. One-way ANOVA was performed to test the hypothesis that there was no difference between the counting methods, the three areas and lunar phases. Post Hoc comparisons were made using the Tukey HSD test for unequal N.

Results

Average density estimates of crabs, based on binocular, burrow and absolute counts, varied between sub-areas (Fig. 2). The binocular method density estimates are lower than those based on direct counts, while burrow counts are higher than the direct counts.

It is clear that area C on the sand bank presented the lowest densities of crabs by all counting methods. Upper (A) and mid *Avicennia marina* (B) sub-areas contained the highest numbers of crabs, and presented no clear differences. Density estimates differed between sub-areas (Anova, $p<0.00001$, indicating significant differences between sub-areas A and B in relation to C), moon phases (Anova, $p<0.001$, indicating significant differences between full moon and last quarter in relation to new moon, and also between first quarter and full moon), and sampling method (Anova, $p<0.0001$, indicating significant differences between all 3 methods). Global results of the 3 performed Anovas are presented in Table 1.

On the whole, a total of 5952 individuals were counted by the direct excavation method. Binocular counts gave a total of 3533 individuals (59% of direct count), while burrow counts indicated 7487 individuals (126% of direct count). The results show

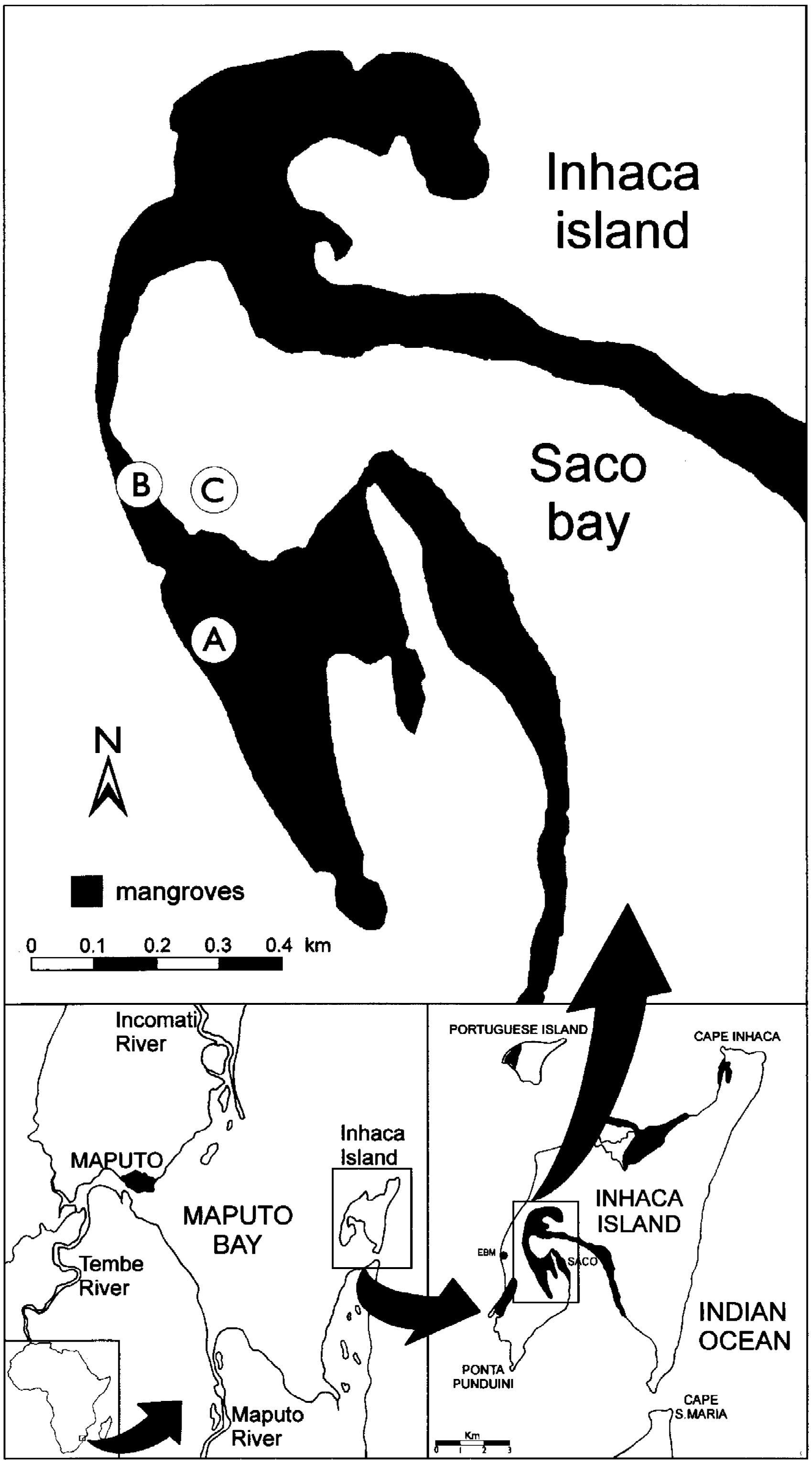

Figure 1. Map of Saco bay at Inhaca island, showing position of sampling areas.

Table 1. Results of 1-way ANOVA performed for the estimation method, area and moon phase

	df Effect	MS Effect	df Error	MS Error	*F*	*p*-level
Method	2	7736.061	2056	49.178	157.308	0.00001
Area	2	7661.165	2056	49.251	155.555	0.00001
Moon phase	3	376.215	2055	56.182	6.696	0.00017

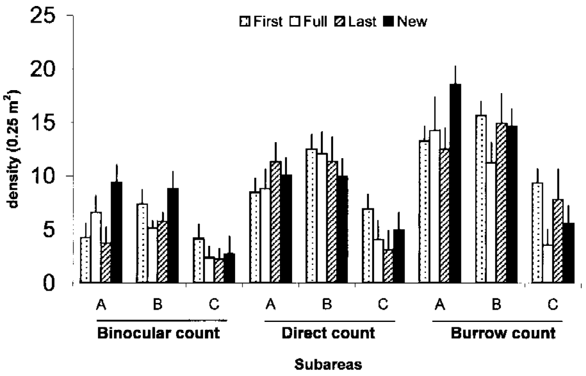

Figure 2. Density of *Uca annulipes* estimated by binocular, burrow and absolute counts, in the 3 sampling areas (Upper – A, Mid – B, Lower – C) during the 4 lunar phases. Vertical lines indicate +1 standard error.

that burrow counts overestimate density by around 25%, while binocular counts underestimate density by around 40%.

The relationships of binocular counts and burrow counts to excavated counts are shown in Figure 3. The correlation coefficients for these relationships were calculated. The correlation values are highly significant and strongly positive (for binocular *versus* direct counts r=0.40, $p<0.001$, and for burrow *versus* direct counts r=0.61, $p<0.001$).

Figure 4 presents the variations in sex ratio over the 4 lunar phases. At all areas sampled, there was a permanent male bias during the 4 lunar phases. Highest proportion of males is reached during full moon at areas B and C, and lowest was found during new moon at areas A and B.

Hourly variation in sex ratio during the ebb tide period is shown in Figure 5. Sex ratio is male-biased during all the ebbing tide period. This result is more pronounced at area B. In both areas, however, there is a slight increase of surface active male crabs throughout the ebb tide period.

The proportion of ovigerous females along the lunar phases is presented in Figure 6. The lowest val-

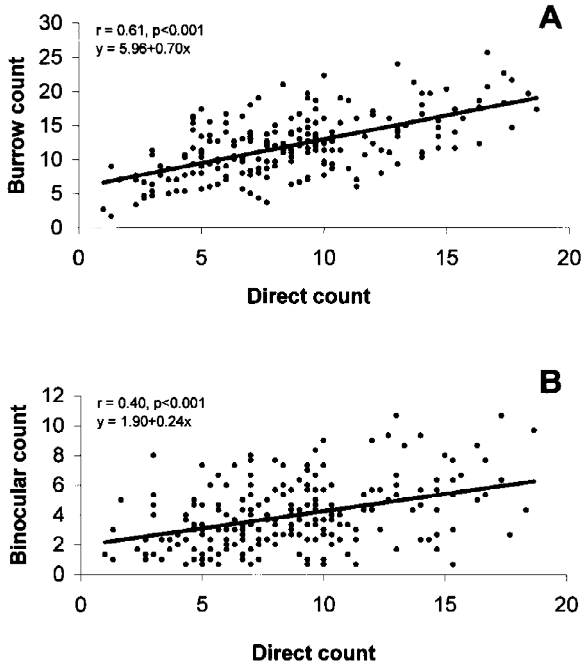

Figure 3. Regression in relation to direct excavation count for *Uca annulipes* of (A) burrow and (B) binocular counts.

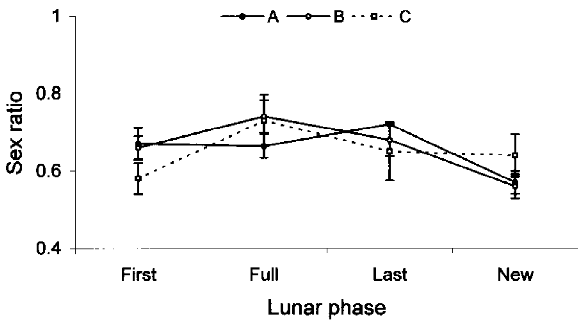

Figure 4. Fluctuation of sex ratio (males:total) for *Uca annulipes* along the lunar phases at the 3 sampling areas. Vertical lines indicate ±1 standard error.

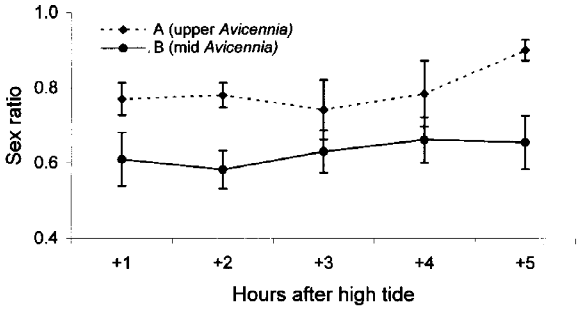

Figure 5. Fluctuation of sex ratio (males:total) for *Uca annulipes* during the ebb tide period for sampling areas A and B. Vertical lines indicate ±1 standard error.

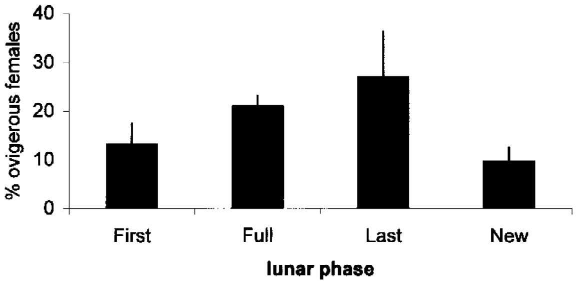

Figure 6. Fluctuation of proportion of ovigerous females of *Uca annulipes* along the lunar phases, the 3 sampling areas combined. Vertical lines indicate +1 standard error.

ues were obtained during new moon and first quarter counts, generally around 10%. Maximum values were observed during last moon quarter, reaching on average around 25%.

Discussion

The average densities differed greatly between the three sub-areas and between methods. The mid *Avicennia* zone seems to offer better suitability conditions compared to the other sub-areas, therefore the average number of crabs was higher compared to the other sub-areas. Some of the relevant conditions could be the amount of water and probably the organic content in the soil.

Density estimates obtained from the three different methodological approaches indicated that in relation to direct counts, burrow counts tend to overestimate crab population while binocular counts underestimate density of the crabs. MacIntosh (1988) and Firth & Firth (1979) reached a similar conclusion in their studies of fiddler crabs on mangrove shores in Malaysia and Thailand. These authors have suggested that the higher number of burrows in relation to the real number of the crabs can be attributed to the crabs' need to improve the opportunity for escape from predators and aggression from neighbouring conspecifics, and also because burrows are sometimes abandoned or lost.

Comparing binocular and burrow counting methods in relation to the direct count it is evident through the statistical tests and through the correlation coefficients obtained that the burrow count gives much better estimates of the real data than the binocular count. However, both methods have advantages and disadvantages that need to be discussed. Binocular count estimates fewer crabs per area, and the sexes can easily be confused especially for males lacking the larger chela and juveniles. The lunar phase, as well as the timing of the counting process in relation to ebbing tide, is also crucial. The incubation period for females, the distance from which the crabs are counted, as well as local disturbances can interfere seriously with crab behaviour, therefore resulting in a wrong interpretation of data. It is important to note that estimating population density using binocular counts should be confined to the non-breeding period in order to avoid missing gravid females. Females of *Uca annulipes* can be highly underestimated by the binocular method during incubation period. In this study, it was found that in periods with higher numbers of ovigerous females, fewer females were counted by the binocular method.

In spite of being a non-destructive method, the binocular method does not supply reliable results on the true density of crabs. Thus, it would not be recommended for rapid appraisal of crab density unless additional data (such as: emergence time, lunar phase, sex ratio variation in relation to tide, etc) on crabs in the area to be studied are carefully considered. Counting crabs after the ebbing tide shows variations in the sex ratios as the time increases. Lunar phase is also known to be a determinant for sex ratio variation in decapod crustaceans (see Crane, 1975; Macintosh, 1988; Emmerson, 1994).

Burrow count becomes an ambiguous method when the studied area is inhabited by several other burrowing crabs, even when burrow specific characteristics are well known. This is an important issue for crabs of the same genus. For example, in this study, *Uca inversa* coexists with *U. annulipes,* and it is quite difficult to determine which burrow belongs to which crab species before a survey is done, to check the dominant burrow sizes of both species. In this case, the exact percentage of occurrence of each species needs to be known in advance. Another problem is that, usually, the number of crabs dwelling within the same burrow is not known and the sex ratio can never be assessed.

Salmon (1987) found in his behavioural study that males of *U.thayeri* could be found in relation to the number of burrows in the following proportions: 3/2, 1/1, 1/3, 1/4, 1/9 and 1/11 (number of crabs/number of burrows). This example illustrates that, in spite of the relatively good correlation between the direct and the burrow counts, there will remain an important source of error. Before trying to study population density for *Uca annulipes* a similar study would be required in order to assess the consistency of the relation between the number of crabs occupying a certain amount of burrows. This will always constitute a limitation when a rapid assessment of density is required. If the burrow characteristics are well distinguished, and the species inhabiting the studied area are known, then this method can easily be applied and give fair results on density estimate. However, it is still important to bear in mind that the values obtained will usually be higher than the real ones.

Another aspect that may interfere with the number of counted crabs, as well as in their relationship with the burrow number, is the droving behaviour of *Uca annulipes.* It is known that these crabs drove from their burrowing areas to feed in other areas, presumably with higher organic content (P.Blackwell, pers. com.). During this study, many crabs where seen in patches away from their burrows in areas without any burrows. On the other hand, for some quadrats no crabs were encountered inside the area as well as within the burrows during excavation. This suggests movement towards other surrounding areas for feeding.

Males dominated throughout the study period and in all sub-areas. Sex ratio variation is less pronounced during new moon and during the first quarter, indicating that when the number of gravid females is low, sex ratio bias is minimal. More females are active during the first and new moon, therefore sex ratios are closer to parity during these periods for the three sub-areas. Female *Uca annulipes* are known to change their pattern of emergence during the incubation period (P.Blackwell, pers. com.), therefore affecting sex ratio. During all lunar phases, except new moon, females are proportionally more abundant at the surface in the lower bank (sub-area C) than in the other areas studied. This fact may be related to the fact that sub-area C is inundated by all tides and thus ovigerous females do not suffer the usual desiccation problems encountered in higher areas.

These results show that both binocular and burrow counting methods can be used to estimate the apparent abundance of *Uca annulipes* in mangrove areas. Both methods are 'mangrove friendly' since they do not destroy the environment. However, for both cases, a number of factors have to be taken into account in order to get the best validated approach to population density.

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