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Quantifying the density of mangrove crabs: Ocypodidae and Grapsidae

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Abstract Numerous studies have highlighted the importance of crabs within mangrove ecosystems, but tested methods of enumeration are virtually non-existent. The aim of the present study was to assess the accuracy of quick, non-invasive methods for estimating the population density of three species of mangrove crabs in East Africa: *Uca annulipes*, *Sesarma guttatum* and *Neosarmatium meinerti*. Methods employed depended on the behaviour and habitat of each species. Counts of *U. annulipes* and *N. meinerti* individuals that were active on the surface (visual counts) and burrow counts (of *U. annulipes*) were compared to actual densities. Actual densities were determined by excavation of *U. annulipes*, and by multiplying counts of *N. meinerti* burrows by the mean number of crabs per burrow. Visual counts of marked individuals of *S. guttatum* were compared to known densities of marked crabs. For *N. meinerti* two visual counting methods were tested: (1) instant counts – crabs were counted every 5 min during 0.5 h and the highest count taken; and (2) continuous counts – all burrows were tagged, and those from which a crab emerged during 0.5 h were totalled. For *U. annulipes* on Inhaca Island (Mozambique) visual counts underestimated excavated numbers by 27%, whereas burrow counts overestimated numbers by 46%. These

values were similar for both sexes, and on both spring and neap tides. Burrow counts and visual counts estimated absolute numbers of *U. annulipes* with equal consistency. At Mida Creek (Kenya) visual counts underestimated *U. annulipes* numbers by 37%, again with no differences between spring and neap tides. In Zanzibar 81% of *N. meinerti* burrows contained a crab. The instant visual count underestimated *N. meinerti* numbers by 41%, the continuous count, by 12%. Visual counts of *S. guttatum* in Zanzibar (Tanzania) underestimated crab numbers by 49%.

Introduction

Crabs of the Grapsidae and Ocypodidae are key components of Indo-Pacific mangroves (Lee 1998). Ocypodids such as fiddler crabs (*Uca*) are a characteristic feature of the forest floor and may occur at very high densities (e.g. Hartnoll et al. 2002). They can alter both sediment topography (Warren and Underwood 1986) and the composition of sediment microflora (Olafsson and Ndaró 1997). Sesarmids (Grapsidae: Sesarminae) are likewise of great importance to Indo-Pacific mangrove ecosystems (review: Lee 1998). Their burrowing and feeding activities may significantly affect mangrove primary productivity (Smith et al. 1991), tree colonisation (Dahdouh-Guebas et al. 1997), nutrient cycling and energy flow (Lee 1997; Skov 2001; Skov and Hartnoll 2002). Unfortunately, the trophic importance of such crabs cannot be clearly resolved because satisfactory methods for the estimation of mangrove crab density have been lacking (Lee 1998).

Direct quantification of mangrove crabs is rarely possible. Netting cannot be done because of roots and trees. Many species dig burrows into which they retreat if disturbed. Burrow excavation is practically impossible in areas of high root density, certainly on the scale of most quantitative studies. Digging is also not an option if repeated observations are required. Manual catching

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is difficult, because a proportion of crabs invariably escapes under root systems or into burrows. Four indirect techniques have been employed as alternatives to direct methods: pitfall trapping (e.g. Frusher et al. 1994), mark–release–recapture (e.g. Hockett and Kritzler 1972), counting burrow openings (e.g. Mouton and Felder 1996), and counting crabs that are active on the surface (visual quantification) (e.g. Golley et al. 1962). The adequacy or suitability of these census techniques remains largely unclear. Few have been critically assessed (but see for mark–release, Hockett and Kritzler 1972; for visual counting, Nobbs and McGuinness 1999), and only four studies have compared their estimates of crab density to absolute density (Krebs and Valiela 1978; Spivak et al. 1991; Macia et al. 2001; Skov and Hartnoll 2001). To our knowledge, techniques for counting mangrove grapsids have never been compared.

We have tested pitfall trapping and found it selective (by crab size, sex and species) and that it takes several days to complete. Mark–release–recapture can only be applied to free-roaming or migrating species and is as selective as trapping because it relies on the capture of crabs. We have found visual counting (by binoculars) and burrow counting the most suitable techniques. Both methods are quick and non-invasive. Visual counting can be descriptive (no. of species, males/females) and used for quantification of non-burrowing species. Burrow counts and measurements of burrow apertures may lead to precise estimates of crab density, biomass and population structure (Krebs and Valiela 1978; Warren 1990; Skov and Hartnoll 2001). However, visual counts will be lowered if crabs are not active on the surface during observation, and burrow counts will increase if crabs create more than one entrance per burrow, or decrease if burrows are plugged. For visual counts the relationship between counts and absolute densities must therefore be known. For burrow counts the ratio between crab numbers and burrow numbers must be known.

This paper investigates whether the density of three of the most common East African mangrove crabs – *Uca annulipes* (H. Milne Edwards), *Sesarma (Perisesarma) guttatum* A. Milne-Edwards, and *Neosarmatium meinerti* (De Man) – can be reliably estimated by visual counts or burrow quantification. Crabs and burrows were counted within quadrats, and absolute densities were derived differently for the three species depending on their behaviour, habitat and the required quadrat sizes. *U. annulipes* was excavated because it creates shallow burrows (<0.4 m) in soft sediment, and its high density means that only small areas need to be excavated. Excavation was not practicable for *N. meinerti* given its low density and deep (0.8–1.8 m) burrows. Instead burrows were cast with cement to determine the number of crabs per burrow, and absolute density determined from burrow counts and mean occupancy. *S. guttatum* is a highly active, free-roaming species that only burrows when other shelter (root systems, crevices) is unavailable; it is therefore not amenable to excavation or burrow casting.

Specimens were marked, and known numbers released within quadrats. Visual counts of marked crabs were then compared to these known densities.

U. annulipes was studied at two East African locations (Mozambique and Kenya), and the results compared to a previous study from Zanzibar (Tanzania) (Skov and Hartnoll 2001) to determine whether the difference between observed counts (crabs or burrows) and absolute densities varied geographically. *S. guttatum* and *N. meinerti* were each studied in two Zanzibar (Tanzania) mangroves to assess local variation. *S. guttatum* occurs from high to low mangroves, and a top shore *Avicennia marina* stand and a low shore *Rhizophora mucronata* stand were compared. *N. meinerti* is normally restricted to the top shore, so two high shore *A. marina* stands were compared.

Fiddler crabs are deposit feeders and require water for sediment sorting (Miller 1961), so surface activity may be reduced and burrow plugging increased during neap periods when the sediment is dry (Zucker 1978). Macia et al. (2001) and Skov and Hartnoll (2001) found that the relationship between observed counts (visual, burrows) and absolute densities varied between spring and neap periods. Here we compare spring and neap observations of *U. annulipes*. For *S. guttatum* the variation in activity over the spring–neap tidal cycle is less marked, so this species was observed throughout the spring–neap tidal cycle and a mean taken. Observations of *N. meinerti* concentrated on days following spring tides, when surface activity is at a maximum and visual counts are most appropriately done (Skov, unpublished data).

Nobbs and McGuinness (1999) found that instant visual counts of *Uca* accounted for a lower proportion of actual numbers compared to continuous counts (adding up individuals recorded during observation). We tested the difference between instant and continuous visual counts on populations of *N. meinerti*.

Materials and methods

Study areas

Four mangroves were involved in the study (Table 1). Saco da Inhaca (Saco) is a creek mangrove on Inhaca Island, Mozambique (descriptions: MacNae 1968; Paula et al. 1998). Sampling occurred within the western limits of the mangrove, in a habitat similar to that used for *Uca annulipes* observations by Skov and Hartnoll (2001): mid/upper mangrove, sandy substrate, dominated by *U. annulipes* and *Avicennia marina*. The zone was bordered down-shore by the central mud flats of the Saco mangrove. Mida Creek (Mida) is a creek mangrove in Kenya. Sampling occurred within the “Mida” stand (descriptions: Micheli et al. 1991; Fratini et al. 2000), in a habitat similar to that at Saco. The zone was situated above a larger *Rhizophora mucronata* zone. Maruhubi mangrove (MH) is a fringing mangrove situated on Unguja Island, Zanzibar (description: Machiwa 1998). Sampling took place within a high shore stand dominated by *A. marina* and muddy to medium sandy substrates. MH bordered the terrestrial fringe. Kisakasaka mangrove is a creek mangrove on Unguja. Two areas were sampled: a high shore stand dominated by *A. marina* and fine and silty

Table 1. Descriptions of study areas. “Area” refers to the entire mangrove, whereas “shore level” is the height above chart datum of study zones

	Mangrove location				
	Mida Creek	Maruhubi	Kisakasaka 1	Kisakasaka 2	Saco da Inhaca
Site designation	Mida	MH	K1	K2	Saco
Country	Kenya	Zanzibar	Zanzibar	Zanzibar	Mozambique
Latitude	03°21'S	06°09'S	06°14'S	06°15'S	26°01'S
Longitude	39°59'E	39°12'E	39°17'E	39°17'E	32°58'E
Area (hectares)	~150	<100	~200	~200	~150
Tidal range (m)	3.6	4.0	4.0	4.0	3.5
Shore level (m)	2.9–3.4	3.6–4.0	3.5–4.0	2.5–2.9	2.8–3.2
Dominant tree	<i>Avicennia marina</i>	<i>A. marina</i>	<i>A. marina</i>	<i>Rhizophora mucronata</i>	<i>A. marina</i>
Studied species	<i>Uca annulipes</i>	<i>N. meinerti</i> , <i>S. guttatum</i>	<i>Neosarmatium meinerti</i>	<i>Sesarma guttatum</i>	<i>U. annulipes</i>

substrates (K1), and a low shore stand dominated by *R. mucronata* and fine and muddy substrate (K2). K1 bordered the terrestrial fringe, and K2, the main creek at Kisakasaka.

Methods for counting crabs

Transects and quadrats

Crabs were counted using quadrats located in transects. One transect was placed centrally in each study area (for *Neosarmatium meinerti* there were two transects at stations MH and K1. They were placed centrally, 300 m apart). Transects were 40 m wide (cross-shore) and 80 m (MH, K1, K2) or 100 m long (Saco, Mida). Transects were divided into plots (0.5×0.5 m for *U. annulipes*; 2×2 m for *Sesarma guttatum* and *N. meinerti*), ignoring clearings, drainage channels and areas without the study species. Plots were then randomly selected, and quadrats erected using pegs and string 3 days prior to observation.

Visual counting and burrow counting

Visual counts were conducted according to Skov and Hartnoll (2001). Observations took place in the morning (0700–1030 hours) and were made through binoculars (8×40 magnification) from a distance of 3.5 m. Crabs within quadrats were counted after observers had remained motionless for 15 min (*U. annulipes* and *S. guttatum*) or 30 min (*N. meinerti*), which is sufficient time for resumption of full activity (Cannicci and Skov, unpublished data). Burrows were counted after the visual counts.

Counting *U. annulipes* [adult carapace width (CW): 7–18 mm]

Sampling took place at Saco (July and August 1999) and Mida (February and March 1998). At Saco 12 quadrats were observed on five spring-tide days and 12 quadrats on four neap-tide days. At Mida, 11 spring (one quadrat failed) and 12 neap quadrats were observed on five neap- and five spring-tide days. Following observation, all quadrats were excavated to the water table. Sediments were sieved (2 mm mesh), crabs extracted and counted, and those > 3 mm CW sexed.

Counting *S. guttatum* (adult CW: 10–28 mm)

S. guttatum was observed at stations MH and K2 during May 1999. There were 12 quadrats per station. Ten *S. guttatum* were caught inside each quadrat, sexed, measured (CW), marked and released into the quadrat (density in two K2 quadrats was low, and only seven and nine crabs were marked). Crabs were marked by super-gluing PVC squares (<6 mm) to the carapace. Laboratory trials showed that tags remained intact until moulting and had no

apparent detrimental effect. Two shapes (circles and triangles) and five colours made all ten crabs per quadrat identifiable. Tagging animals < 8 mm CW was not possible, so the study is not valid for these. Each quadrat was observed six times over the following 10 days (day 1, 2, 4, 6, 8 and 10). Observations lasted 30 min, during which time the number of marked crabs and each crab's position relative to the quadrat were recorded. Each crab was counted only once. After 30 min the surrounding 5 m area was scanned, and positions of marked crabs relative to the quadrat were recorded.

Counting *N. meinerti* (adult CW: 24–47 mm)

N. meinerti observations were conducted in two transects at stations MH (transects MH1 and MH2) and at K1 (KIS1 and KIS2) from January to March 2000. The mean crab-to-burrow ratio was determined using six quadrats per transect. Burrows of *N. meinerti* inside each quadrat were numbered, and three were randomly selected. Cement of paint-like viscosity was poured into burrows 3–4 days after spring tides. Burrow casts were excavated 3 days later. Casts were broken into fragments (<10 mm diameter), and numbers of crabs caught in the cement were recorded.

Two visual techniques were used. For the instant count, crabs were enumerated every 5 min during 30 min, and the highest count taken. For the continuous count, all burrows were tagged 3 days before observation, which did not influence crab activity; those from which a crab emerged during 30 min were totalled. Instant counts were recorded in 12 quadrats per transect, and continuous, in 6 of these.

Statistical analysis

Visual counts of crabs and burrow counts (only *U. annulipes* at Saco) were compared to estimated absolute densities of crabs. For *U. annulipes*, absolute densities were excavated numbers. For *N. meinerti*, absolute densities were taken as the burrow count multiplied by the mean crab-to-burrow ratio. For *S. guttatum*, visual counts of marked crabs (VIS_m) were compared to actual numbers of marked crabs within release quadrats (N_m). N_m was calculated as the number of initially marked crabs minus emigrants (crabs not seen again after day 2) and crabs recorded outside the quadrat. Remains or moults of four (3.3%) MH- and two (1.7%) K2-marked *S. guttatum* were discovered during the trials. These crabs were excluded from analysis.

Paired *t*-tests were used to compare the observed numbers of crabs with the assumed actual numbers (H_0 : mean observed-actual number = 0). Paired *t*-tests were chosen over ANOVA because the actual number of crabs was considered an independent variable without variance; ANOVA was unsuitable since it would have treated actual numbers on an equal basis with estimated numbers.

For *U. annulipes*, the difference between estimated numbers [visual counts (VIS) or burrows] and absolute numbers (excavated,

EX) was expressed as a percentage of absolute numbers [e.g. (EX–VIS)/EX]. The percent differences from EX were then compared between males and females, and between spring and neap tides, by two-sample *t*-tests. The data were arcsine transformed for analysis.

The mean number of *N. meinerti* per burrow and the mean ratio between visual counts and actual counts were compared between mangroves (MH and KIS) and transects (MH1, MH2, KIS1, KIS2) using nested ANOVA. Transects (fixed) were nested within mangroves (fixed). The analysis was conducted using means per quadrat. Data sets did not need transformation. Burrow casts of one KIS2 quadrat failed. The quadrat was discarded, reducing numbers of quadrats in KIS2 from six to five. Since nested ANOVA cannot be conducted on unequal sample sizes, one quadrat was randomly extracted from the remaining three transects. Quadrats were not extracted from other analyses. One *N. meinerti* cement-casting burrow was found to have two exits on excavation. It was treated as two burrow casts in the analysis.

Statistical analyses were performed according to Zar (1984) and Sokal and Rohlf (1995). Mean values are reported with 95% confidence intervals (95% CI). Degrees of freedom (*df*) are listed as subscripts to *F*- (ANOVA) or *t*- (*t*-tests) values (e.g. $F_{(2)}; df=2$).

Results

Uca annulipes

Saco da Inhaca (Mozambique)

The mean densities for excavated (EX), visual (VIS) and burrow (BUR) counts are listed in Table 2. EX did not vary significantly between spring- and neap-tide periods ($t_{(23)}=0.4$, $P=0.7$). Absolute numbers (EX) were underestimated by visual counting and overestimated by burrow counting on both spring and neap tides (Table 2: paired *t*-tests). The percent difference from EX did not vary significantly between tides for either technique (VIS: $t_{(23)}=1.0$, $P=0.3$; BUR: $t_{(23)}=0.2$, $P=0.9$). The percent difference from EX did not vary significantly between VIS and BUR (spring: $t_{(23)}=1.3$, $P=0.2$; neap: $t_{(23)}=1.9$, $P=0.08$). VIS and BUR resembled EX with similar accuracy, the mean differences from EX having similar coefficients of variance (Table 2), indicating the techniques to be equally effective at estimating the true numbers.

The sex ratio of excavated *U. annulipes* at Saco was 0.53 ± 0.03 males/total. Paired *t*-tests (Table 2) showed

that male numbers were significantly underestimated on both spring and neap tides, as were female numbers. There was no significant variation between male and female percent differences from excavated counts (spring: $t_{(23)}=-0.75$, $P=0.5$; neap: $t_{(23)}=1.3$, $P=0.2$), indicating that males and females were quantified equally well by visual counts.

Since neither tide nor sex affected differences from EX, spring and neap counts were pooled, and overall mean percentage differences were calculated [based on Table 2: (mean EX–count)/mean EX]. This indicates that VIS at Saco should be corrected for a mean 27% underestimate, whereas BUR should be corrected for a mean 46% overestimate.

Mida Creek (Kenya)

Table 3 shows the mean densities of VIS and EX at Mida. There were no significant differences between spring and neap tide EX ($t_{(22)}=-0.98$, $P=0.4$). Paired *t*-tests showed that VIS significantly underestimated EX on both spring and neap tides (Table 3). The percentage difference from EX did not vary significantly between tides ($t_{(22)}=0.6$, $P=0.6$), and when tides were pooled VIS underestimated EX by a mean of 37% [based on Table 3: (mean EX–VIS)/mean EX].

The mean sex ratio at Mida was 0.56 ± 0.07 males/total. Male VIS did not differ significantly from EX during spring tides, but was significantly lower during neaps (Table 3). The opposite was true for females, with VIS significantly lower than EX during spring tides, but not during neaps (Table 3). Overall males were underestimated by 38% on neaps, while females were underestimated by 62% on spring tides.

Sesarma guttatum

Crabs displayed great fidelity to the area where they had been caught and re-released (Fig. 1). Ten days after release 66% (MH) and 75% (K2) of the released crabs were within 1 m of quadrats; of these 54% (MH) and

Table 2. *Uca annulipes*. Saco (Mozambique): mean densities ($\pm 95\%$ CI, in parentheses) according to excavated (EX), visual (VIS) or burrow (BUR) counts. Coefficient of variance relates to EX-count values. For paired *t*-tests, H_0 : mean EX-count=0. Significance: * $P < 0.05$, *** $P < 0.001$

Tide	Total count			Male count		Female count	
	EX	VIS	BUR	EX	VIS	EX	VIS
Spring tide (12 quadrats)							
Mean density (0.25 m^{-2})	101.5 (13.6)	77.0 (11.0)	158.8 (24.1)	57.2 (8.9)	41.2 (6.0)	44.3 (6.5)	35.8 (6.9)
Mean EX-count	–	24.5 (9.4)	–57.3 (19.5)	–	16.0 (5.4)	–	8.5 (6.5)
Coefficient of variance	–	78.2%	–69.4%	–	–	–	–
Paired <i>t</i> -test (<i>t</i> -value)	–	4.4***	–5.0***	–	5.0***	–	2.2*
Neap tide (12 quadrats)							
Mean density (0.25 m^{-2})	96.8 (16.5)	68.0 (10.6)	131.3 (24.6)	51.2 (11.7)	37.7 (8.2)	45.7 (6.4)	30.3 (5.2)
Mean EX-count	–	28.8 (9.5)	–34.4 (10.6)	–	13.5 (7.0)	–	15.3 (4.3)
Coefficient of variance	–	63.1%	–58.8%	–	–	–	–
Paired <i>t</i> -test (<i>t</i> -value)	–	5.5***	–5.9***	–	3.5***	–	6.5***

Table 3. *Uca annulipes*. Mida Creek (Kenya): mean densities ($\pm 95\%$ CI, in parentheses) according to excavated (EX) and visual counts (VIS). For paired *t*-tests, H_0 : mean EX-VIS=0. Significance: ^{NS}not significant, ** $P < 0.01$, *** $P < 0.001$

Tide	Total count		Male count		Female count	
	EX	VIS	EX	VIS	EX	VIS
Spring tide (12 quadrats)						
Mean density (0.25 m ⁻²)	18.4 (4.0)	10.6 (2.5)	8.0 (2.0)	6.6 (1.6)	10.4 (3.2)	4.0 (1.2)
Mean EX-VIS	–	7.1 (3.9)	–	1.4 (2.6)	–	6.4 (2.8)
Paired <i>t</i> -test (<i>t</i> -value)	–	3.8**	–	1.0 ^{NS}	–	4.5***
Neap tide (12 quadrats)						
Mean density (0.25 m ⁻²)	17.5 (3.1)	11.4 (1.8)	11.2 (1.8)	7.0 (1.3)	6.3 (2.1)	4.4 (1.2)
Mean EX-VIS	–	6.1 (2.6)	–	4.2 (1.3)	–	1.9 (2.2)
Paired <i>t</i> -test (<i>t</i> -value)	–	4.6***	–	6.1***	–	1.7 ^{NS}

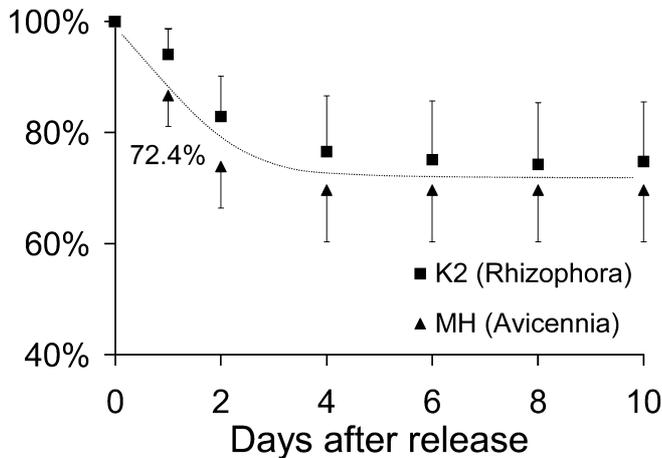


Fig. 1. *Sesarma guttatum*. Fidelity of marked specimens to release quadrats. N/M_0 (%) = fidelity, where N is the number of marked crabs observed inside or < 1 m from quadrat and M_0 is the number of marked crabs released (minus mortalities). Data points are means of 12 quadrats ($\pm 95\%$ CI). Details on stations K2 and MH, see Table 1

47% (K2) were inside quadrats. Fig. 1 indicates that $> 70\%$ of crabs restricted their activity to an area of < 4 m across [quadrat (2 m) + 1 m on each side].

The ratio between visual counts of marked crabs (VIS_m) and the actual number of marked crabs (N_m) ranged between 0.21 and 0.78, with means of 0.53 ± 0.08 (MH) and 0.48 ± 0.09 (K2), and a pooled mean of 0.51 ± 0.06 . A two-sample *t*-test (on means of 6 days per quadrat) showed that the ratio did not vary significantly between mangrove stands ($t_{(23)} = 0.9$, $P = 0.4$). A paired

t-test on the pooled data showed that overall VIS significantly underestimated *S. guttatum* numbers ($t_{(24)} = 13.3$, $P < 0.001$) by 49%.

Neosarmatium meinerti

Burrow occupancy

Crabs (CW: 21–43 mm) were found in 56 of the 70 burrow casts (Table 4) – all were *N. meinerti*. In addition four juvenile *N. meinerti* (< 10 mm CW) were found in narrow side branches of adult burrows. Nested ANOVA showed that the crab-to-burrow ratio did not vary between mangroves ($F_{(1)} = 0.02$, $P = 0.9$) or transects ($F_{(2)} = 0.9$, $P = 0.4$). A paired *t*-test showed that burrow numbers exceeded crab numbers ($t_{(43)} = 2.9$, $P = 0.008$), and the overall mean crab-to-burrow ratio was 0.81 (Table 4).

Visual quantification

Table 5 shows burrow numbers, visual counts and estimated actual numbers of *N. meinerti* ($Crabs_B = burrows \times 0.81$). Nested ANOVA showed that the ratio between instant visual counts and $Crabs_B$ (Table 5) was significantly lower at Kisakasaka than at Maruhubi ($F_{(1)} = 17.0$, $P < 0.001$), but did not vary significantly between transects ($F_{(2)} = 0.2$, $P = 0.8$). Ratios between continuous counts and $Crabs_B$ also varied between mangroves ($F_{(1)} = 9.1$, $P = 0.007$), being lower at Kisakasaka than Maruhubi, again with no difference

Table 4. *Neosarmatium meinerti*. Zanzibar: results of burrow casting in transects at Maruhubi (MH1, MH2) and Kisakasaka (KIS1, KIS2) (95% CI, in parentheses). Sex ratio is males/total

Transect	Quadrats	Casts	Crabs	Sex ratio	Crab/Burrow ratio
Maruhubi	12	37	30	0.36	0.818 (0.159)
MH1	6	19 ^a	17	0.18	0.917 (0.214)
MH2	6	18	13	0.54	0.720 (0.346)
Kisakasaka	11	33	26	0.50	0.832 (0.147)
KIS1	5	15	12	0.42	0.900 (0.196)
KIS2	6	18	14	0.57	0.775 (0.288)
Overall	23	70	56	0.38	0.811 (0.105)

^a One burrow with two exits

Table 5. *Neosarmatium meinerti*. Zanzibar: mean ($\pm 95\%$ CI, in parentheses) burrow counts, visual counts (*Instant* or *Continuous*) and estimated actual counts ($Crabs_B = \text{burrows} \times 0.81$ crabs per burrow) per 4 m^2 . Ratios between visual counts and $Crabs_B$ are also shown

Transect	Burrows		Instant		Continuous	
	Count	$Crabs_B$	Count	Count/ $Crabs_B$	Count	Count/ $Crabs_B$
Maruhubi	23.2 (4.8)	18.8 (3.9)	13.0 (2.6)	0.74 (0.12)	21.1 (7.2)	1.07 (0.17)
MH1	29.5 (6.8)	23.9 (2.8)	16.8 (3.1)	0.76 (0.15)	29.7 (5.5)	1.20 (0.36)
MH2	16.9 (4.8)	13.7 (2.0)	9.2 (3.0)	0.73 (0.24)	12.5 (9.0)	0.93 (0.23)
Kisakasaka	29.2 (2.7)	23.7 (2.2)	9.9 (1.7)	0.43 (0.08)	15.6 (5.0)	0.69 (0.17)
KIS1	31.3 (4.1)	25.3 (1.7)	10.3 (2.7)	0.40 (0.11)	19.5 (9.0)	0.72 (0.36)
KIS2	27.1 (3.1)	22.0 (1.3)	9.5 (2.1)	0.46 (0.14)	11.7 (2.8)	0.67 (0.31)
Overall	26.2 (2.8)	21.2 (2.3)	11.4 (1.6)	0.59 (0.09)	18.3 (4.4)	0.88 (0.15)

between transects ($F_{(2)} = 1.3$, $P = 0.3$). Visual counts approximated actual *N. meinerti* numbers closer at Maruhubi than at Kisakasaka, irrespective of visual technique.

Paired *t*-tests showed that instant visual counts significantly underestimated crab numbers by 25.7% at Maruhubi ($t_{(24)} = 4.42$, $P < 0.001$), by 56.8% at Kisakasaka ($t_{(24)} = 11.45$, $P < 0.001$), and overall by 41.3% ($t_{(48)} = 9.25$, $n = 48$, $P < 0.001$). Continuous counts of crabs per quadrat did not vary significantly from actual crab numbers at Maruhubi ($t_{(12)} = -0.5$, $P = 0.63$), but significantly underestimated crab numbers at Kisakasaka by 30.6% ($t_{(12)} = 3.56$, $P = 0.005$) and overall by 11.8% ($t_{(24)} = 2.17$, $P = 0.04$). Continuous counts were always closer to actual counts than instant counts; the former is clearly more accurate.

Discussion

Visual counts of *Uca annulipes* from Saco da Inhaca (Mozambique) underestimated absolute abundance by 27%, compared to 37% at Mida Creek (Kenya). On Inhaca Island Macia et al. (2001) found visual counts underestimated absolute abundance by 40%, with some variation between tidal phases. Skov and Hartnoll (2001) found visual counts underestimated absolute abundance in Zanzibar (Tanzania) by 45% (spring tide) and 51% (neap tide). For this species the difference between visual counts and absolute abundance can clearly vary between locations, but a substantial underestimate invariably occurs.

Visual counts of male and female *U. annulipes* were equally precise at Saco, but at Mida there were differences between the sexes; males were underestimated during neap tides, but females were underestimated during spring tides. The results differ from Zanzibar, where females were best quantified on spring tides, but for males there were no differences between tidal phases (Skov and Hartnoll 2001). There are four main differences between male and female behaviour; all may influence visual census, but only the fourth may influence burrow quantification. (1) Counts of surface-active crabs may underestimate females. Females often retreat into burrows sooner than males, and *U. annulipes* and

Neosarmatium meinerti females in Kenya and Zanzibar take longer to re-surface (Cannicci and Skov, unpublished results). Disturbance may therefore cause underestimation of females. (2) Male fiddler crabs may migrate long distances from burrows to feed (Hockett and Kritzler 1972; Murai et al. 1983), the distance and duration of migration depending on species and location, whereas females tend to stay close to burrows (Salmon 1984). This effect will be limited if animals are quantified immediately after burrow emergence – at dawn or after tidal retreat. (3) Males of some species of fiddler crabs feed for longer than females (Salmon 1968, 1984; Valiela et al. 1974; Weissburg 1992), so visual census favours males. This problem can be minimised by counting shortly after crabs emerge to feed. (4) Several authors have described how ovigerous female crabs stay buried or hidden. This is particularly notable for fiddler crabs (Zucker 1978; Salmon and Hyatt 1983; Nakasone and Murai 1998), but is also characteristic of sesarmids such as *Sesarma ortmanni* (Crosnier) and *S. guttatum* (Skov, personal observations). Choice of technique can reduce, but not eliminate, sexual bias.

Burrow counts of *U. annulipes* from Saco overestimated crab numbers by 46%, with no effect of tidal phase. Macia et al. (2001) found that burrow counts overestimated numbers on Inhaca by 25%. In Zanzibar, burrow counts exceeded true numbers by 35% during spring tides, but did not differ from true numbers during neaps (Skov and Hartnoll 2001). Overestimation by burrow counts is the norm.

Our results suggested that visual and burrow quantification were both applicable to the quantification of *U. annulipes*. It is important to know with what variation a census technique predicts absolute crab numbers; a less variable technique requires less replication to achieve reliable population estimates. Here, visual and burrow techniques matched absolute numbers with similar variation (coefficients of variance) between quadrats. However, coefficients of variance calculated from Table 2 in Skov and Hartnoll (2001) showed visual estimates to be less variable than burrow counts. Macia et al. (2001), on the other hand, found a higher correlation between burrow counts and excavated counts ($r^2 = 0.6$) than between visual and excavated counts ($r^2 = 0.4$), indicating that burrow counts were less

variable than visual counts. Hence, it is not clear which quantification technique is generally the least variable.

We have assumed that excavated counts of *U. annulipes* equalled absolute densities. However, some individuals may have escaped during digging, causing us to underestimate true density. Burrows that opened at the edge of quadrats but which terminated outside would not have been excavated. This should not have any effect, since, on average, an equal number of burrows would have opened outside quadrats, but terminated inside.

S. guttatum in Zanzibar remained close to preferred shelters, and similarly restricted movement has been documented in other non-burrowing mangrove crabs (Cannicci et al. 1995, 1996, 1999; Fratini et al. 2000). This limited mobility facilitates the census of marked specimens, and our visual counts recorded 51% of *S. guttatum*. Admittedly our trials had limited replication in time and space. However, some brief mark–release trials in Kenya and at Saco [Tippex-marked animals in three 36 m² (Mida) and two 100 m² (Inhaca) *R. mucronata* quadrats] indicated that visual surveys accounted for 37% (Mida) and 50% (Saco) of marked crabs (Cannicci, unpublished results). These values fall within the 21–78% range observed in Zanzibar.

Eighty-one percent of *N. meinerti* burrows contained a crab. Burrow casting revealed several narrow side branches to adult burrows, and within four of these small juveniles (7–10 mm CW) were found. Juvenile *N. meinerti* are always scarce, and until this study we had never encountered individuals < 10 mm CW. Emmerson (2001) also observed side branches to South African burrows, and proposed that juveniles might shelter in adult burrows during early life.

Instant and continuous visual counting estimated *N. meinerti* numbers better at one Zanzibar location than another. Reasons for differences between locations are unclear; they were worked simultaneously and had very similar fauna, flora and tidal regimes. Continuous counts always approximated true density closer than instant counts. Nobbs and McGuinness (1999) similarly noted that fewer *Uca* were seen by instantaneous visual counts than by continuous counting. Whilst these results indicate that continuous counting is best, this technique demands extra preparation. Burrows must be marked in areas of high density if crabs that emerge several times are not to be counted twice. At Inhaca *U. annulipes* reached densities of up to 564 crabs m⁻². Even in less dense populations burrow tagging is not possible without causing unacceptable disturbance to the habitat; for certain species instant scans may be the only option for visual census.

This study has shown how the match between visual or burrow counts and absolute density may vary between locations. This should be considered when quantifying mangrove crabs; accuracy may need evaluation at each new location. With regard to *U. annulipes*, the observed differences in accuracy between locations (Kenya, Zanzibar, Mozambique) could also be due to

temporal variation, a factor not examined here. *N. meinerti* was quantified simultaneously at the two Zanzibar locations; thus, the significant differences between them must be due to factors other than time.

Visual and burrow quantification techniques each have advantages and disadvantages, which must be considered when choosing between them. Visual observations permit estimates of sex ratios in species when males and females have different morphology. Different species can be identified by visual observations, but not from burrow observations unless burrows are sufficiently different to be easily recognised. Visual counts, on the other hand, may underestimate juvenile numbers, because these are difficult to see (Skov and Hartnoll 2001), and disturbance and temporal variation in crab surface activity usually affect visual quantification more than burrow quantification. Burrows do have one major advantage over visual techniques: they may enable estimation of population size distribution and biomass (Krebs and Valiela 1978; Mouton and Felder 1996; Emmerson 2001; Skov 2001).

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