Spatial and temporal variation in relative numbers of grapsid crabs (Decapoda: Grapsidae) in northern Australian mangrove forests

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ABSTRACT

Crabs belonging to the family Grapsidae are possibly one of the most important components of the fauna of mangrove forests globally, in part because of their influence in nutrient cycling by feeding on litterfall. This study investigated spatial and temporal patterns in relative numbers of 11 grapsid species in northern Australian mangrove forests. The results indicated that *Perisesarma* spp*., Neosarmatium meinerti* and an undescribed species of *Episesarma* were most abundant, followed by *Clistocoeloma merguiensis, Ilyograpsus paludicola, Sesarmoides borneensis, Metopograpsus frontalis* and *Sarmatium* spp. Mangrove assemblage was the most important spatial factor affecting the distribution and abundance of these species. *Perisesarma* sp. was most abundant in mid- and low-intertidal assemblages, whereas *N. meinerti* and *Episesarma* sp. were largely limited to high intertidal assemblages. In many cases, crab species occurrence and abundance were specific to certain assemblages, areas, aspects, and times during the two-year study period, which probably reflects the specificity of species to particular environmental conditions.

KEYWORDS: crab abundance and distribution, environmental conditions, habitat, mangroves, Grapsidae, *Perisesarma, Episesarma, Neosarmatium*.

INTRODUCTION

Grapsid crabs are one of the most abundant and important faunal components of intertidal mangrove forests globally (Golley *et al.* 1962; Jones 1984; Smith III *et al.* 1991; Lee 1998), particularly in the Indo-west Pacific. Recent studies of their activities in mangrove forests indicate that by attacking mangrove seeds and seedlings they may affect forest structure (Smith III 1987; McGuinness 1997) by feeding on litterfall (Fig. 1), and by burrowing they influence nutrient cycling and alter the sediment geochemistry (Robertson 1986; Smith III *et al.* 1991; Kristensen 2008; Nerot *et al.* 2009). There is also evidence of competition between grapsid crabs and other invertebrate species in the forest (Fratini *et al.* 2001).

Although there have been some studies of grapsid diversity (Davie 1982; Abele 1992), studies of distribution and abundance in mangrove forests, at both local and geographic scales, are limited. Investigations of temporal patterns are even rarer. Spatial patterns in abundance have only been studied in Australia, Africa and Hong Kong (Micheli *et al.* 1991; Smith III *et al.* 1991; Frusher *et al.* 1994; Lee & Kwok 2002; Metcalfe 2007). In Australia, these studies have found that species of crabs that occur in mangrove forests change across the continent, and so do their numbers (Smith III *et al.* 1991). On a local scale, the abundance and distribution of different species appear to change across intertidal zones, and also, along tidal creeks (Frusher *et al.* 1994).

The variation in species diversity, distribution, and abundance may result from differences in habitat within and among mangrove forests and the evolution of species to fit a particular niche. For instance, it is known that grapsid crabs have a wide range of feeding habits, varying from detritivory, to herbivory (feeding on leaves and propagules), and to carnivory (Nishihira 1984; Lee 1998). This difference in feeding behaviour among species makes it possible for crabs to live in a diversity of habitats.

There is no published information on spatial and temporal patterns in the population structure of grapsid crabs in mangrove forests. Characteristics of the population structure, such as size and gender distribution, and the presence of gravid females may also be affected by environmental conditions occurring in different locations (Lee & Kwok 2002), and would certainly influence crab energy requirements. Changes in energy requirements may result in alterations in food preferred by crabs and the quantity of food consumed, thus influencing the role that crabs play within the ecosystem.

Studies on activity and social behaviour are more numerous (e.g., Seiple 1981; Willason 1981; Seiple & Salmon 1982; Micheli *et al.* 1991; Smith III *et al.* 1991; Frusher *et al.* 1994; Kneib *et al.* 1999). Grapsid crabs may alter their behaviour according to the environmental
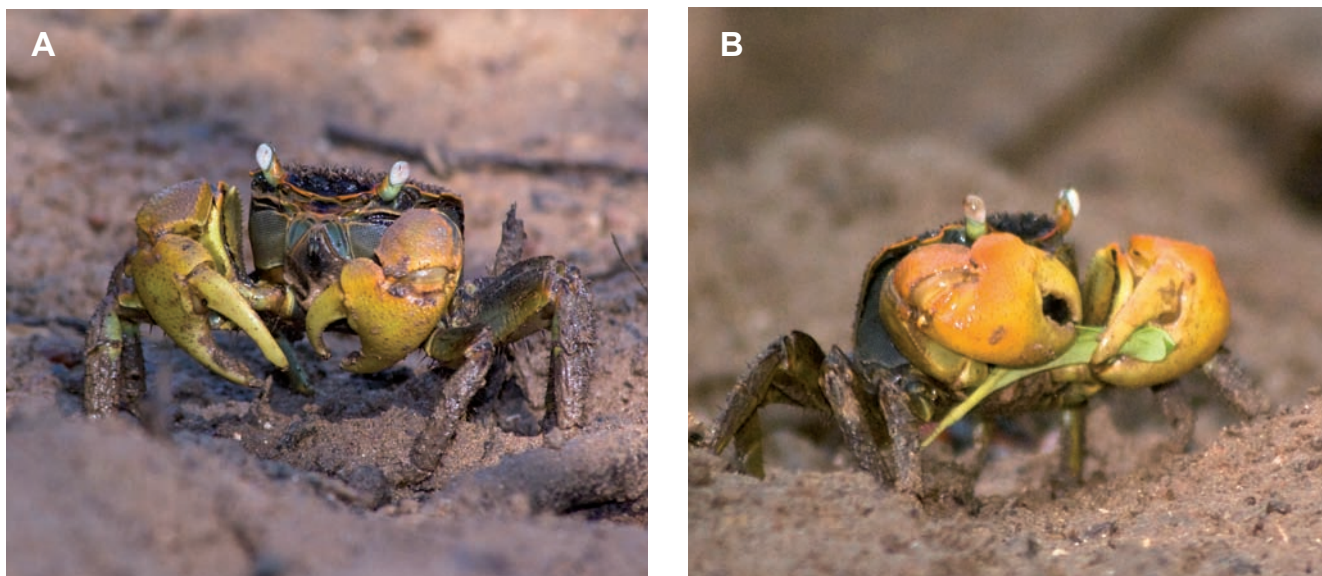
Fig. **1**. *Neosarmatium meinerti* is one of the most abundant grapsid crabs high in the intertidal zone in mangrove forests in Darwin Harbour. **A**, An adult foraging at low tide. **B**, An adult feeding on a fallen mangrove leaf. Photographs: Keith McGuinness.

conditions in the mangrove forests that they inhabit. These alterations, for instance, may be in the time spent feeding or burrowing. This is relevant to studies of abundance, as changes in crab activity can influence estimates of relative abundance. Several studies report high crab activity during spring tides (Seiple 1981; Micheli *et al.* 1991, Smith III *et al.* 1991; Frusher *et al.* 1994), so trapping has been done during this period of the tidal cycle. These studies were however, done on the east and south-east coast of Australia, and it is not known if the pattern exists in more tropical regions.

Underwood (2000) wrote: "There is no possible doubt that observations of patterns or lack of patterns are the fundamental starting-blocks for ecological study. Until patterns have been described, there is no basis for invoking explanatory models about processes". The aims of this present study were to test for, and describe, spatial and temporal patterns in the abundance of the most common grapsid crabs in Darwin Harbour, and briefly to investigate their relationship to environmental conditions. This is an important first step in investigating the ecology of these animals. The specific objectives of this study were: (1) to test for spring–neap patterns in relative abundance; (2) to determine the best phase for the subsequent long-term, large-scale studies; and (3) to test for spatial (within plots, among assemblages, between aspects, and between areas) and temporal patterns in the relative abundance, and population structure, of the dominant grapsid crabs.

MATERIALS AND METHODS

Darwin Harbour is located in tropical northern Australia, between latitudes 12º20' and 12º45' S and longitudes 130º45' and 131º05' E (Fig. 2). It supports mangrove forests occupying about 20 000 ha and containing 36 of the world's 70 true species of mangrove (Polidoro *et al.* 2010). The mangrove communities of the Harbour have

been identified as a significant resource, comprising about 5% of the total area of mangroves in the Northern Territory and approximately 0.1% of remaining world mangrove areas (Brocklehurst & Edmeades 1996).

Brocklehurst & Edmeades (1996) identified 10 mangrove associations, or assemblages, in the Harbour forests and the three most common were studied: (a) tidal creek (dominated by *Rhizophora stylosa* Griffith and *Avicennia marina* (Forsskål) Vierh.; (b) tidal flat (dominated by *Ceriops australis* Ballment, Smith & Stoddart; that was mentioned in Brocklehurst & Edmeades (1996) by the older name of *Ceriops tagal* Robinson); and (c) hinterland (dominated by *Ceriops australis*). A fourth assemblage (d) mixed-species woodland (dominated by *Ceriops australis* with *Lumnitzera racemosa* Willd. and *Excoecaria ovalis Endlicher* co-dominant or locally dominant) was also
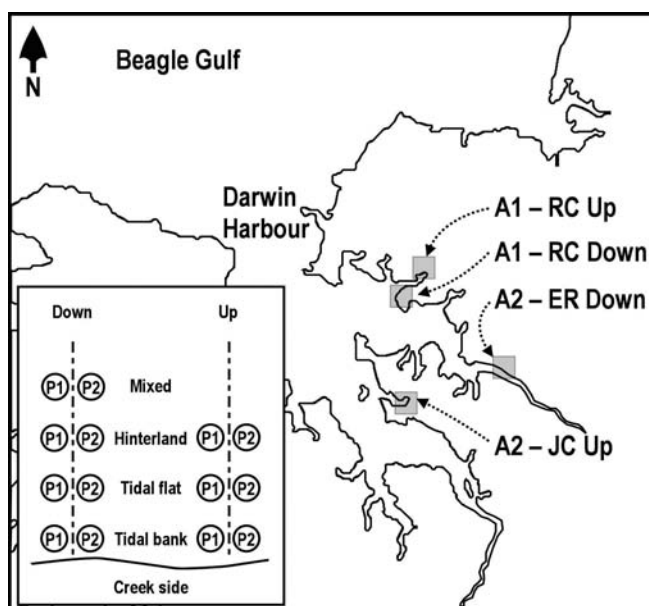
Fig. **2**. Location of study sites along Reichardt Creek (Area 1), Elizabeth River and Jones Creek (Area 2) within Darwin Harbour.

included as it was an important component in the areas studied.

Study sites. Three creeks within Darwin Harbour were selected for the study: Reichardt Creek, Elizabeth River and Jones Creek (Fig. 2). Reichardt Creek is on the northern side of the Harbour, referred to here as Area 1. Elizabeth River and Jones Creek are to the south, a location referred to here as Area 2. Within each of these areas, an upstream location and a downstream location, referred to here as 'aspects', were selected along the creeks. In Area 1, these locations were both on Reichardt Creek. In Area 2 these were upstream on Elizabeth River and downstream on Jones Creek.

Downstream aspects included four assemblages: tidal creek, tidal flat, hinterland and mixed-species woodland. Upstream aspects, due to the natural distribution of assemblages, included only the tidal creek, tidal flat, and hinterland. The word 'site' used in this paper refers to a combination of an assemblage, aspect, and area. Sampling was conducted within two replicate circular plots, 20 m in diameter, at each site.

Crab sampling. Pitfall traps were used to estimate relative abundance of grapsid crabs for three reasons: (a) they were most effective among an array of methods tested for sampling multiple species in the same location over time (Salgado Kent & McGuinness 2006); (b) they sampled all species with little disturbance to the habitat (c) they allowed information on population characteristics to be collected. Salgado Kent & McGuinnes (2006) found that observational and photographic methods were useful only for sampling consistently surface-active species (i.e., species that were surface-active infrequently were not accurately represented), while excavation was too destructive for accurate repeated measures of abundance in the same location over time. While the use of pitfall traps has been suggested potentially to result in size-biased sampling (towards larger crabs; Salgado Kent & McGuinness 2006), the usefulness of measuring this parameter is not diminished since insight into spatial patterns can be obtained from comparisons of relative size (Salgado Kent & McGuinness 2006).

Two replicate traps were placed at random locations – chosen by identifying a reference tree in the centre of each plot then moving a random direction and distance (as in Smith III *et al.* 1991) – within each plot at each sampling time. As some species were observed travelling one or two metres from their burrows while foraging, traps were placed at least 3 m apart.

Traps were set during low tides and checked daily for two days (Salgado Kent & McGuinness 2006). Grapsids caught were identified, sexed, and had their carapace width measured to the nearest 0.01 mm, at the widest point including the spines (Davie 1992). Any ovigerous female was noted. Before release, the crabs were marked on their carapace with a blue permanent marker pen (known to last at least three days) to avoid duplicate counts. Some crabs drowned in traps when they drained slowly during heavy rain or extreme spring high tides, so this mortality were noted as well. The effects of mortality on estimates from trap captures are discussed below.

Crabs were identified to the lowest taxonomic level which could be easily distinguished in the field. As a consequence, *Perisesarma darwinensis* Campbell and *Perisesarma semperi* Bürger were grouped together as *Perisesarma* sp. *Sarmatium unindentatus* Davie, *Sarmatium hegerli* Davie and *Sarmatium germaini* Milne Edwards were recorded as *Sarmatium* sp. The species of *Episesarma* was easily identified but, as it has been neither described nor named at present, is referred to simply as *Episesarma* sp. *Neosarmatium meinerti* de Man (Fig. 1), *Clistocoeloma merguiensis* de Man, *Ilyograpsus paludicola* Rathbun, *Sesarmoides borneensis* Tweedie and *Metopograpsus frontalis* White could all be readily distinguished morphologically. All these genera are common to the Indo-west Pacific and/or Africa and only two species appear to be endemic; *Perisesarma darwinensis* and *Episesarma* sp. Because grouping species according to their congeners was required for some species (to reduce errors from misidentification in the field), meaningful information for these species is drawn from the species grouping level, rather than the species level.

Spatial and temporal patterns in relative abundance. Crabs were sampled on spring tides on 12 occasions from January 1999 to December 2000. During each year, crabs were sampled once in the early wet season (January), once in the late wet season (March), once in the wet to dry transition (May), once in the early dry season (July), once in the late dry season (September), and once in the dry to wet transition (November).

To explore spatial and temporal patterns in abundance, PERMANOVA analyses (which have no assumptions of normality such as does ANOVA) were conducted. Analyses were limited to species with very large numbers (*Perisesarma* sp.). Included in the analysis were the following factors: sample time (six levels, fixed), year (two levels, fixed), area (two levels, random), aspect (two levels, fixed), and assemblage (three levels, fixed). The mixed-species woodland assemblage was not included since there were virtually no *Perisesarma* sp. in this assemblage, and inclusion would have only potentially introduced zero inflation into the analysis. Data were log transformed for analysis since this resulted in more equal variances (a recommendation for PERMANOVA).

ANOVAS were done on carapace width, proportion of females, and proportion of ovigerous females, for species with sufficient captures (since assumptions for ANOVA were met). The number of factors, included in the latter analyses was dependent upon the number of crabs captured, but included one or more of the following: sample time (six levels, fixed), assemblage (two levels, fixed) and area (two levels, random). Assemblage for *Perisesarma* only included the tidal flat and tidal creek.

Variation in numbers during spring and neap tides. A preliminary test for spring-neap changes in activity was conducted by sampling at these two stages in the tidal cycle (Spring: 4–7 June 2000; Neap: 10–13 June 2000). Due to time constraints, only one spring-neap cycle could be sampled and only on the upstream aspect of Reichardt Creek (so there was no replication of tide). Here two plots in each of the three assemblages present (the hinterland, the tidal flat and the tidal creek) were sampled. Data for *Perisesarma* sp., the only abundant species, were analysed with a three-factor ANOVA (all assumptions were met). Factors included tide (two levels, fixed), assemblage (three levels, fixed) and plot (two levels, random and nested in assemblage).

Spatial and temporal variation in *N. meinerti* burrow counts. While pitfall traps certainly capture *N. meinerti*, Salgado Kent & McGuinness (2006) found that they may not provide reliable estimates of abundance. Hence, the abundance of this species was also estimated by burrow counts, a method that is practical because their large, hooded burrows are easily identifiable (Micheli *et al.* 1991) and because burrows do not last more than about three weeks (hence overestimates from abandoned burrows are not likely to be large; Micheli *et al.* 1991; Emmerson & McGwynne 1992). Emmerson (2001) however, found in some cases multiple crabs inhabiting one burrow, which could lead to underestimates. No attempts were made here to differentiating active burrows, abandoned burrows, or co-inhabited burrows because this would have required destruction of the burrows. Burrows were counted, on the day that pitfall traps were first buried, in two randomly placed 1 × 1 m quadrats in each plot. Burrow counts were, however, not started until part-way through the main sampling program (September 1999), so did not span two full years.

RESULTS

Variation in numbers during spring and neap tides. Forty-one crabs were captured during this study: 24 *Perisesarma* sp., 5 *N. meinerti*, 5 *Episesarma* sp., 5 *S. borneensis*, and 2 *Ilyograpsus paludicola*. More individuals of all species caught during the spring tide (17 *Perisesarma* during the spring tide and 7 during the neap; all 5 *N. meinerti* and 5 *Episesarma* during the spring tide; 4 *S. borneensis* during the spring tide and 1 during the neap, and both *I. paludicola* during the spring tide). Only *Perisesarma* were sufficiently abundant for analysis. For this species, there was a significant interaction between tide and assemblage ($F_{2,6} = 22.17$, $P < 0.05$), due to the number of crabs decreasing during the neap tide in the tidal flat (spring = 3.00 ± SE per trap; neap = 0.25 ± SE) but remaining stable in the other two assemblages (tidal creek spring = 0.00; neap = 0.25; hinterland spring = 1.25; neap = 1.25).

Spatial and temporal variation in relative grapsid numbers. *Perisesarma* was the most abundant (554 individuals) of the 11 species of grapsids captured during the two-year study. Numbers of crabs for the other seven species sampled were: 67 *N. meinerti* (and 201 burrows), 39 *Episesarma*, 27 *C. merguiensis*, 25 *I. paludicola*, 18 *S. borneensis*, 14 *M. frontalis* and 8 *Sarmatium*. Proportions of crabs surviving in traps were: *C. merguiensis*, 100% (based on 12 traps with crabs); *I. paludicola*, 89% (22 traps); *S. borneensis*, 80% (15 traps); *Episesarma*, 75% (28 traps); *N. meinerti*, 63% (53 traps); *Perisesarma*, 62% (263 traps); *M. frontalis*, 50% (12 traps); and *Sarmatium*, 29% (7 traps).

There were complex spatial and temporal patterns in the abundance of *Perisesarma*. Overall, *Perisesarma* was almost entirely absent in the mixed-species assemblage (n=2), so this assemblage was excluded from the analysis. In the analysis, many interactions among factors were significant, with the main effects of year and assemblage, and interactions among area, assemblage and aspect being associated with particularly large mean squares (Table 1). Interactions between year and assemblage were significant, although to a lesser extent. Regardless of area or aspect, *Perisesarma* were always uncommon in the hinterland (Fig. 3). The crabs were more abundant in the other two assemblages – tidal creek and tidal flat – but the relationship between these differed among areas and aspects. In area 1, the crabs were more abundant in the tidal creek downstream and the tidal flat upstream, whereas in area 2 they were more abundant in the tidal flat downstream with little difference upstream. Overall abundance decreased from 1999 to 2000 in the tidal creek and tidal flat, but not in the hinterland (Table 1, Fig. 4).

Because of the fewer numbers associated with *Neosarmatium meinerti*, no statistical analyses were conducted because of the clear pattern in distribution. *Neosarmatium meinerti* crabs were more abundant in the higher shore assemblages – hinterland (mean = 0.22 per trap ± 0.05 SE) and mixed-species woodland (0.23 ± 0.05) – than in the lower shore assemblages where they were virtually absent – tidal creek (0.01 ± 0.01) and tidal flat (0.02 ± 0.01). Greater numbers of *N. meinerti* were caught during the second year of the study but other consistent temporal trends were not evident (Fig. 5).

Table 1. PERMANOVA of spatial and temporal patterns in relative numbers of *Perisesarma* crabs in Darwin Harbour in 1999 and 2000. Analyses were done using both areas, both aspects (upstream and downstream) and three assemblages (hinterland, tidal flat, and tidal creek). Only interactions which were significant in at least one analysis, or had one of the five largest mean squares, are listed.

Source	df	Mean Squares
Year (Yr)	1	0.87**
Time (Ti)	5	0.09
Area (Ar)	1	0.01
Aspect (Asp)	1	0.01
Assemblage (Abg)	2	1.94***
Yr×Abg	2	0.33*
Ar×Asp×Abg	2	0.93***

With respect to the six less common species, four species – *Clistocoeloma merguiensis*, *I. paludicola*, *M. frontalis* and *Sarmatium* – showed broadly similar patterns to *Perisesarma*, being most abundant in the tidal creek and tidal flat (Figs 6, 7). *Clistocoeloma merguiensis* and *I. paludicola* were caught in similar numbers in both

aspects but *M. frontalis* was more common upstream and *S. borneensis* was rarely captured downstream (Fig. 7). *Episesarma*, like *N. meinerti*, was most abundant in the higher shore assemblages, hinterland and mixed-species woodland (Fig. 6), and was rarely captured in the tidal creek or tidal flat. *Episesarma* was, however, also rarely
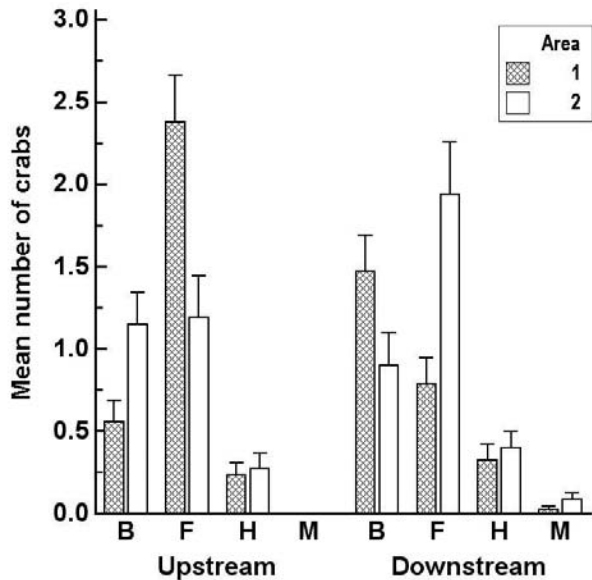

Fig. 3. Mean number of *Perisesarma* (per trap) in the two areas, two aspects and four assemblages in Darwin Harbour (mean + SE). Assemblages include tidal creek (B), tidal flat (F), hinterland (H), and mixed-species woodland (M).

Fig 5. Mean number of *Neosarmatium meinerti* (per trap) over the two years of the study for the assemblages in which the species was common. Circles are area 1; squares are area 2. For clarity, error bars are not plotted but the vertical line shows the average standard error.
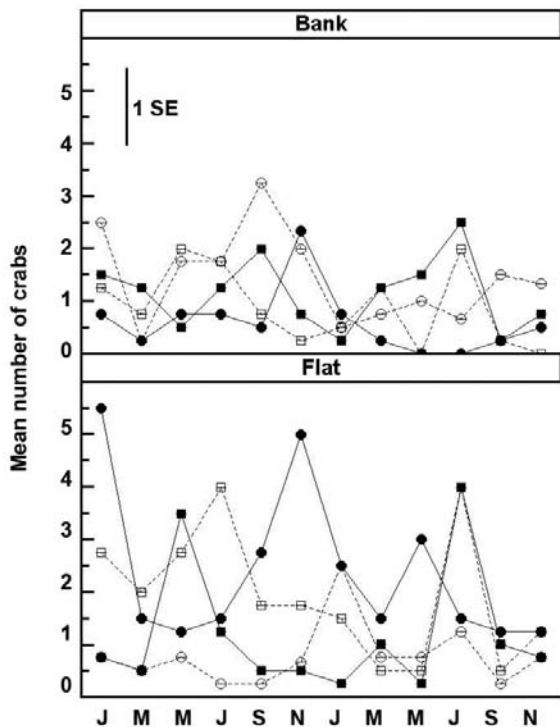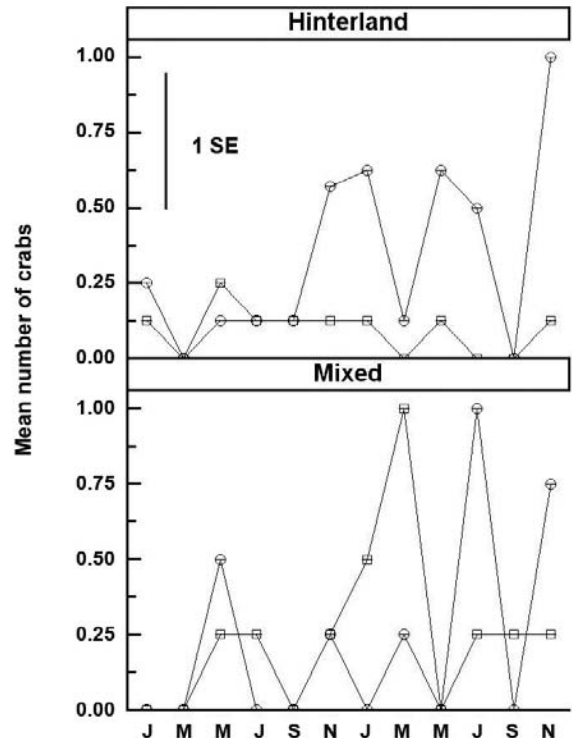

Fig. 4. Mean number of *Perisesarma* (per trap) over the two years of the study for the assemblages in which the species was common. Open symbols are for the upstream aspect; hatched for the downstream. Circles are area 1; squares are area 2. For clarity, error bars are not plotted but the line shows the average standard error.
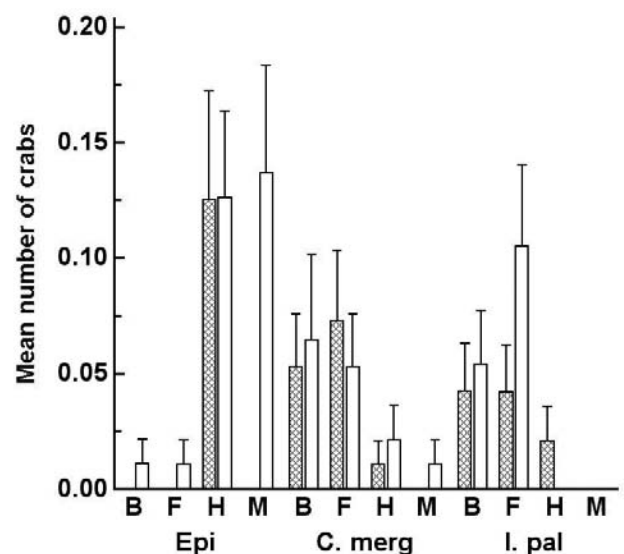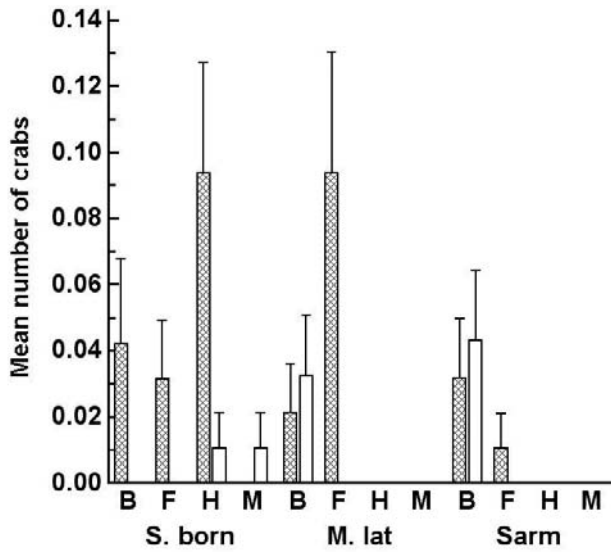

Fig. 6. Mean numbers of three species of crabs (per trap) in two aspects and four assemblages in Darwin Harbour (mean + SE). Assemblages include tidal creek (B), tidal flat (F), hinterland (H), and mixed-species woodland (M). Aspects were downstream (open bars) and upstream (hatched bars). Species were: Epi = *Episesarma*; C. merg = *C. merguiensis*; I. pal = *I. paludicola*.

Fig. 7. Mean numbers of three species of crabs (per trap) in two aspects and four assemblages in Darwin Harbour (mean + SE). Assemblages include tidal creek (B), tidal flat (F), hinterland (H), and mixed-species woodland (M). Aspects were downstream (open bars) and upstream (hatched bars). Species were: S. born = *S. borneensis*; M. lat = *M. frontalis*; Sarm = *Sarmatium*.

caught in the hinterland of Area 2 (Salgado Kent 2004). In terms of temporal patterns, *I. paludicola* variability was greater during both March and May, and for *N. meinerti* only in May (Salgado Kent 2004). For *Perisesarma* there was greater variability during March, May, and July than at other times, but this was only true for 1999 (Salgado Kent 2004). *Metopograpsus frontalis* had high variability between plots during March and December of 2000, and only during December in 1999 (Salgado Kent 2004).

Numbers of N. meinerti burrows. About 3.7 times as many burrows were counted as crabs were caught (201 burrows versus 54 crabs, for the period September 1999 onwards, when both variables were recorded). Mean, per plot, burrow counts and *N. meinerti* numbers were significantly, but weakly, correlated (r = 0.41, n = 224, P < 0.001; the comparison was done on a 'per plot' basis because crab traps and burrow quadrats were in different, randomly selected, locations in each plot). As for trap captures, the number of burrows was greater in the hinterland than in other assemblages, and particularly in the downstream of Area 1 (mean = 1.33 per quadrat ± 0.22 SE), the hinterland in the upstream aspect of Area 2 (1.17), than in other combinations of these factors (other means ≤ 0.71).

Population structure: size, sex ratio, and proportion of ovigerous females. The largest crabs, on average, were *N. meinerti*, followed, in order from the largest to the smallest, by *S. borneensis*, *Perisesarma*, *Sarmatium*, *Episesarma*, *C. merguiensis* and *I. paludicola* (Table 2). Overall, there were many more male crabs captured than females and ovigerous females were only observed for *Perisesarma* and *C. merguiensis*.

Differences in size of *Perisesarma* were observed between areas ($F_{1, 166}$ = 3.86, P<0.5), with area 1 having larger

Table 2. Means and standard errors for carapace width, proportion female and proportion of ovigerous females of crabs caught. For each species and variable, n is the number of traps (not crabs) for which data were available (*i.e.* which contained crabs).

Species	Carapace width (cm)			Proportion female			Proportion ovigerous		
	n	Mean	SE	n	Mean	SE	n	Mean	SE
C. merguiensis	23	1.07	0.06	22	0.36	0.10	10	0.10	0.10
Episesarma	26	1.12	0.06	25	0.13	0.07	4	0.00	0.00
I. paludicola	20	0.49	0.07	5	0.00	0.18	5	0.00	0.00
N. meinerti	52	2.24	0.09	51	0.28	0.06	17	0.00	0.00
S. borneensis	15	1.30	0.10	14	0.39	0.13	5	0.00	0.00
Sarmatium	7	1.18	0.12	6	0.17	0.17	1	0.00	–
Perisesarma	263	1.24	0.02	252	0.33	0.02	123	0.25	0.04

crabs than area 2 (means = 1.33 and 1.26, respectively). The proportion of *Perisesarma* females did not vary among sample times, assemblages, years or areas (all P > 0.05), however the proportion of ovigerous females increased during the wet season months ($F_{5, 85}$ = 2.66, P < 0.05; means were Jan: 0.43; Mar: 0.39; May 0.13; Jul: 0.09; Sep: 0.43, Nov: 0.39). Also there were more ovigerous females in the tidal creek than in the tidal flat assemblage ($F_{1, 85}$ = 4.41, P<0.05; means = 0.38 and 0.16).

There was no significant variation in *N. meinerti* carapace width among sample times or between years, but the proportion of females did vary between years with more females caught in 1999 than in 2000 ($F_{1, 39}$ = 6.51, P< 0.05; means = 0.47 and 0.18).

DISCUSSION

Effects of crab mortality on estimates from trap captures. Mortality of crabs during sampling can be a concern in studies that involve temporal sampling since crab densities would be reduced artificially by traps each time the crabs are sampled. Even though the percentage of crabs surviving in pitfall traps was 62% for the most abundant species sampled (*Perisesarma*), the mean mortality was not more than one crab in each circular 20 m diameter plot. This mortality rate was insignificant since the mean true abundance of *Perisesarma* crabs across assemblages in Darwin Harbour was 1.35 crabs per m² (Salgado Kent & McGuinness 2006). For *Sarmatium*, the species of grapsid with the highest mortality and lower abundance, there was an average mortality of 71% of crabs caught in pitfall traps. Densities estimated in Salgado Kent and McGuinness (2006) during that period were one *Sarmatium* per 3 m². Captures of *Sarmatium* in traps were rare enough so that less than one in about every 100 crabs in a plot would be removed from the population by mortality. This number is also insignificant and indicates that trap related mortality did not interfere with results.

Variation in grapsid numbers during spring and neap tides. Crabs were more active during spring tides than during neap tides. Although results from this experiment were

restricted by the limited spatial and temporal replication included in the experiment, the results suggest that crabs in Darwin Harbour have similar patterns of activity to those found elsewhere (Micheli *et al.* 1991; Frusher *et al.* 1994; Nobbs 1999). Micheli *et al.* (1991) found much of the greatest activity of *N. meinerti* during spring tides was due to increased time digging (presumably digging is easier when soil is moist) and suggested that this may be required when a high water level causes burrows to collapse.

The absence of a spring-neap pattern in the activity of grapsids in the tidal creek assemblage may reflect the regular pattern of tidal inundation, which results in consistently high soil saturation in this habitat. This is consistent with the observations of Micheli *et al.* (1991) of a reduced spring-neap difference in activity of the land crab, *Cardisoma carnifex* Herbst, during a period of high soil and air moisture (caused by a full moon spring tide and nocturnal rain showers). Similar observations have been made in other studies on land crabs (Goshima *et al.* 1978).

Comparison of *N. meinerti* number and *N. meinerti* burrow counts. The relative abundance of *N. meinerti* estimated by burrow counts in the majority of cases was almost four times the estimate of numbers of *N. meinerti* captured in pitfall traps. The relationship between pitfall trap captures and burrow counts was significant but the R^2 was small. Of the two methods, burrow counts most likely provided a better estimate as *N. meinerti* appear to spend little time on the surface.

Population structure. The apparent difference in size of *Perisesarma* between areas is difficult to explain as there were no obvious patterns in soil condition or litter fall rates (unpublished data) to account for it. Lee & Kwok (2002) suggested that difference in size of crabs between mangroves forests in Hong Kong was due to variations in the dominant mangrove species. In this study, however, the areas had similar mangrove composition, so other environmental differences (as also suggested by Lee & Kwok 2002) may play a role.

For most species of crabs in this study, more males were caught than females. This is consistent with a study by Lee & Kwok (2002) on *Perisesarma bidens* de Haan and *Parasesarma affinis*, but contrasts with findings on *Aratus pisonii* Milne Edwards populations in New World mangroves (Conde & Diaz 1989). The dominance of males could simply reflect a trap bias. Traps tend to capture larger crabs more often than smaller crabs, and males are slightly larger than females in most species in this study. Furthermore, larger males (with larger chelae) may be less susceptible to predation and therefore be more active on the surface than females.

The increased number of ovigerous *Perisesarma* females captured during the wet season is potentially of some significance and could be associated with the strong wet and dry seasons in northern Australia (Rabalais & Cameron 1982). The tidal creek also had a noticeably greater proportion of ovigerous female *Perisesarma* crabs than the

tidal flat assemblage, possibly because it has conditions which are more suitable for the production of eggs and dispersal of larvae (see Thurman II 1985) for use of tides by *Uca* for dispersal). In particular, the nearby tidal creek may be used for dispersal, as has been found for crabs in other estuarine systems (Christy & Morgan 1997), where larvae are conspicuous to predators and dispersal is important to avoid predation.

Spatial and temporal variation in relative grapsid numbers. During the two year study on relative abundance of grapsids in the assemblages studied in Darwin Harbour, *Perisesarma* was the most abundant crab species, followed in order of abundance by *N. meinerti*, *Episesarma* sp., *C. merguiensis, I. paludicola, S. borneensis, M. frontalis* and *Sarmatium* spp. Underestimates of *Episesarma* may have been possible because these crabs, like *N. meinerti*, may have limited activity (Sivasothi 2000) since they live in relatively dry assemblages in Darwin Harbour.

In general, mangrove forest assemblage was the most important factor influencing the distribution and relative abundance of grapsid crab species within the Harbour. This observation is consistent with other studies conducted elsewhere (Micheli *et al.*1991; Frusher *et al.* 1994). Of the grapsids that were most abundant in this study, *Perisesarma* dominated the lower intertidal assemblages, while *N. meinerti* dominated high intertidal mangroves. These patterns are also similar to those from other sites elsewhere (Micheli *et al.* 1991; Emmerson & McGwynne 1992).

The observed distribution of grapsid crabs among assemblages is probably related to soil conditions such as soil moisture and salinity. Frusher *et al.* (1994), examined the relationship of grapsid numbers to environmental conditions (pore-water salinity, Eh, pH, and percent silt, clay and organic matter) in the Murray River mangrove forests. The two most numerous crabs in that study, *Sesarma messa* Campbell and *Sesarma brevipes* de Man, were most common in forests with sandy sediments. *Sesarma messa* was also in greater numbers in forests with sediment containing a high organic matter content while the abundance of *S. brevipes* appeared to increase with increasing sediment acidity. Frusher *et al.* (1994) indicated, however, that these environmental variables did not appear to explain the limited distributional patterns observed in *Perisesarma semperi* or *Sesarma brevicristatum* Campbell. *Perisesarma semperi* was present in much lower numbers than were *S. messa*, *S. brevipes*, and *S. brevicristatum*, and only occurred in the low intertidal habitats of the river mouth.

Both *Perisesarma semperi* and *P. darwinensis* appear to be fairly widespread in Darwin Harbour, at least one species of this genus occurring in all assemblages, areas, and aspects. It seems possible, therefore, that the three more abundant species in the study by Frusher *et al.* (1994) (i.e., *S. messa*, *S. brevipes, and S. brevicristatum*) may outcompete *P. semperi* for the more desirable habitats in that region. It is also possible, however, that *P. darwinensis* (only occurring in northern Australia) has, in part, filled the ecological niche

occupied by other sesarmids that occur on the Murray River. Smith (1998) suggested that, although *P. semperi* and *P. darwinensis* appear to overlap in distribution in Darwin Harbour, the former may prefer lower intertidal zones, and the latter higher zones. Competition between these species may explain some of the patterns in distribution that are not explained by environmental conditions.

Of the species that were less abundant in the assemblages sampled during this study, *Sesarmoides borneensis* showed consistent patterns of greater numbers upstream than downstream. Frusher *et al.* (1994) observed a similar difference in abundance upstream and downstream of the Murray River, but for different species of crabs. In that study, *Sesarma brevipes* dominated the upstream sites, whereas *Perisesarma semperi* was restricted to the river mouth. The distribution of *S. brevipes* in the Frusher *et al.* (1994) study appeared to be related to soil acidity.

Metopograpsus frontalis had the most specific distribution, in that it occurred almost entirely in the tidal flat and tidal assemblage of the upstream of area 2. This species was also commonly observed in the shoreline forest, an assemblage not included in this study that is lower in elevation than the tidal creek. The shoreline forest is dominated by the mangroves *Rhizophora stylosa* and *Sonneratia alba* Smith, and is commonly inundated by tides. The tidal flat and tidal creek assemblages upstream of area 2 appeared to be inundated by tides more often than the same assemblages at other sites, so factors such as tidal flow or elevation gradient may be important for *M. frontalis,* and merit further study.

Finally, *Episesarma* sp. was the only species to show a distinct increase in numbers during the wet season months. Metcalfe (2007) observed a similar increase in grapsid abundance during the wet season in the hinterland margin in Darwin Harbour. It is difficult to know whether this is a result of an actual change in population size, or whether surface activity of crabs simply increased due to wetter conditions from wet season rains (Frusher *et al.*1994; Nobbs 1999; Lee & Kwok 2002).

Overall, there were strong general patterns in distribution among assemblages for the majority of the species of crabs in this study, however the large number of interactions among factors indicates that crab species occurrence and abundance were often specific to certain plots, assemblages, areas, aspects, and times during the study. These interactions indicated that while clear patterns existed, crab distribution and abundance were often patchy and fluid through space and time. In conclusion, this study has confirmed the importance of habitat heterogeneity on demarcating broad distributional ranges of grapsids observed in studies elsewhere. The work has also highlighted the likely role of environmental variability and change on the fluid nature of abundance, distribution, and population structure of grapsid crabs in mangrove forests.

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