Cannibalistic interactions of juvenile mud crabs *Scylla serrata*: the effect of shelter and crab size

DO Mirera¹²* and P-O Moksnes³

¹ Kenya Marine and Fisheries Research Institute (KMFRI), PO Box 81651, Mombasa, Kenya
² Linnaeus University, School of Natural Sciences, Box 391 82, Kalmar, Sweden
³ University of Gothenburg, Department of Biology and Environmental Sciences, Box 461, 40530 Göteborg, Sweden

* Corresponding author, e-mail: dimirera@yahoo.com, dimirera@kmfri.co.ke

In the culture of mud crab *Scylla serrata*, cannibalism is often the greatest cause of mortality. A laboratory study was conducted to compare the influence of size class differences and shelter on cannibalism and limb loss in juvenile mud crabs (20–70 mm internal carapace width; ICW). Four size classes of juvenile crab (A: 21–30 mm, B: 31–40 mm, C: 41–50 mm and D: 51–70 mm ICW) were tested in all possible combinations using four different substrata with varying degree of shelter (seaweed, plastic strings, bamboo tubes and open sand substratum) in 48 h trials. Results suggest that cannibalistic interactions are heavily influenced both by size differences of crabs and the availability of shelter. Cannibalism on the smallest size class (20–30 mm ICW) increased about 10 times in the presence of the largest crab (51–70 mm) compared with treatment with only same-size crabs (control treatment). Shelter provided little refuge for the smallest crabs, whereas cannibalism in larger size classes decreased by >50% in all the shelters compared with the sand substratum. The findings suggest that both size-grading and provision of shelter could minimise cannibalism in the culture of mud crabs.

**Keywords:** cannibalism

**Introduction**

The culture of mud crabs *Scylla serrata* is commercially developed in South-East Asia (Keenan 1999, Agbayani 2001) and has been a focus over the past decade in the Western Indian Ocean (WIO) region (Mwaluma 2002, Rönnbäck et al. 2002, Mirera 2009, 2011). Aquaculture expansion in South-East Asia has been documented to have caused a decline in wild seed supply that has impacted both culture and capture fisheries (Keenan 1999). Research on the development of seed production has achieved significant progress in South-East Asia in recent years (Quinitio et al. 2001, Allan and Fielder 2003, Quinitio et al. 2007, Quinitio and Estepa 2011). However, no effort has been made in the WIO region to produce seed in hatcheries because farming is mainly small scale. Therefore, the assumption is that there are sufficient numbers of seed crabs in the wild to meet the growing industry. However, this assumption may not hold for long because of overexploitation of the resource by artisanal fishers using such traditional capture methods as hook sticks, pots, traps and seine-nets, as in South-East Asia (Motoh 1983, Angell 1992, Kosuge 2001).

Currently, artisanal fishers in the WIO can meet the demand from tourist hotels, private homes and export markets, which is growing rapidly (Barnes et al. 2002, ACDI-VOCA 2005, Richmond et al. 2006, Mirera 2009, 2011). However, being unregulated, the fishery is vulnerable and there are indications of a significant decrease in wild populations (Francis and Bryceson 2001). Such a decline will have direct negative impacts on recruitment and seed availability and the behaviour of the industry in the region, as observed in other parts of the world (Takeuchi 2000, Hamasaki et al. 2002).

Because of limited knowledge on the availability of juvenile mud crabs from the wild and their behaviour in culture conditions, most culture initiatives in the WIO grow small subadults to market size over short periods. In South-East Asia, lean crabs which have reached market size are cultured to gain weight in a process referred to as ‘fattening’. In the WIO, crab culture is small scale and is mainly carried out in individual cages to minimise cannibalism and aggression (fighting). However, survival is low and growth slow in such culture systems (Mirera 2011). Recent initiatives have therefore been taken to develop small-scale, grow-out systems in ponds and pens, where small juvenile crabs are farmed for longer to attain market size, similar to the system used in South-East Asia (Mwaluma 2002, Mirera 2009, Mirera and Mtile 2009).

Globally, the factors affecting survival in crab culture are cannibalism, moulting, salinity and temperature fluctuations, feed, shelter and stocking density (Trino et al. 1999, Ruscoe et al. 2004, Holme et al. 2007, Mann et al. 2007, Rodriguez et al. 2007, Mirera 2009, Quinitio and Estepa 2011). Some of these mortality-associated factors have been addressed in South-East Asia and survival is currently between 50% and 70% per growth cycle in various culture systems (pens, cages and ponds).
However, aggression and cannibalism, which are ranked as the main causes of low survival in semi-intensive and intensive culture systems, still remain a challenge (Quinitio et al. 2001, Williams and Primavera 2001, Allan and Fielder 2003, Mann and Paterson 2003, Paterson et al. 2007). Research in South-East Asia has used hatchery-produced seed crabs that are of similar size at stocking, which reduces cannibalism (Parkes et al. 2011). However, there is little information on how the interactions between different size classes of crabs in culture systems influence cannibalism. Information on different size-class interactions is essential to improve culture success in the WIO, where seed supply is from the wild and there are many size classes being stocked (Mirera 2009, Mirera and Mitile 2009).

Cannibalism of juvenile portunid crabs is at its greatest when the cannibalising crabs are large enough to kill other crabs in intermoult with hard exoskeletons (Moksnes et al. 1997, 1998, Marshall et al. 2005). To avoid high rates of cannibalism in crab aquaculture, therefore, it is critical to ensure that the sizes of crabs are kept similar in pens to preclude this type of cannibalism.

The aim of the present study was to investigate how size-class differences affect cannibalism rates of juvenile mud crabs and how cannibalism is influenced by the availability of shelter. The information will hopefully guide farmers on possible size-class combinations to stock and on suitable shelters to use at the farms.

Material and methods

A series of laboratory experiments was carried out at the Kenya Marine and Fisheries Research Institute (KMFRI), Mombasa, Kenya, to assess the interactive effect of size difference and shelter on cannibalism in juvenile mud crabs. As the primary aim was to assess cannibalism on intermoult crabs, we used short experimental trials (48 h) to minimise moulting, and high densities of crabs (75 crabs m⁻²) to enhance cannibalistic interactions between the crabs.

Experimental set-up

Local fishers were hired to collect juvenile crabs from the nearby mangrove intertidal flat during low spring tides. Crab collection took approximately 3 h and transport to the laboratory another hour. Sorting was done in the field, hard-shelled healthy crabs (active and feeding) with intact appendages being packed in plastic buckets with clean, wet sand, covered with mangrove leaves and transported to the laboratory. At the laboratory the juveniles were sorted according to size class (see below), placed in 50-litre aquaria with sand at a density of approximately 30 crabs m⁻² and acclimatised for at least 24 h before use in the experiment. Crabs were fed sardine during acclimatisation. Although communal acclimatisation may introduce superior/inferior behavioural traits in crabs (Bergman and Moore 2005, Parkes et al. 2011, Beattie et al. 2012), the effect should be same in all treatments because the acclimatisation was standard for all size classes. Crabs were measured (internal carapace width, ICW, and carapace length, CL) at the start of the experiment, to enable identification of individual crabs at the end of trials that included the effects of moulting. Only healthy crabs (active and feeding) with intact appendages were used in the experiments.

The tests were carried out in small, circular, static tanks (bottom area 0.03 m²; 10 litres) with 20 mm of sieved (1000 μm) beach sand, filled with natural surface seawater from Tudor Creek. Tanks were covered with black polythene sheeting to minimise disturbance. The tanks were provided with mild aeration throughout the experimental period. Water was maintained at room temperature (27–28 °C) and at an average salinity of 32 (SD 1.20). The tanks were arranged in a fully randomised design on vertical metal racks in two parallel rows on one side of the room. The trials were conducted for 48 h (day and night) and the experiment spread over a period of two months.

Treatments

In all experimental treatments, four crabs per tank were assessed (equivalent to ~75 crabs m⁻²), either four crabs of the same size class (control treatment) or one of a larger size class (referred to as the ‘prey crab’) and three smaller crabs of the same size class (referred to as ‘predator crab’). We used several prey crabs in each tank to increase the chances of detecting differences in the rates of cannibalism between treatments. Cannibalistic interactions between four size classes of juvenile mud crabs (A: 21–30 mm, B: 31–40 mm, C: 41–50 mm, D: 51–70 mm ICW) were tested in all possible combinations in four types of shelter treatments: seaweed (Eucheuma denticulatum), plastic strings (bundles of string locally known as ‘kakabans’), bamboo tubes, and sand substratum without any extra shelter (all treatments had sand on the bottom of the container). The number of size combinations tested differed between different size classes; i.e. the smallest size class (A) was assessed in four size combinations, including the control treatment with same size (AA) and three treatments with one larger predator crab (AB, AC, AD), the second size class was assessed in three size combinations (BB, BC, BD), the third in two (CC, CD) and the largest size class (D) only with crabs of the same size (DD, i.e. control treatment). In total, 40 different treatment combinations were assessed with five replicates for each treatment. A total of 800 crabs was used in the experiments.

Substrata were selected based on their potential to provide shelter from cannibalism and on their availability to crab farmers. Red algae (Eucheuma denticulatum) for the experiment were obtained from community farms along the southern coast of Kenya. Four branches 200–300 mm long with a total weight of 250 g were used for the shelter. The shelter made of plastic strings was cut from sacks into pieces 400 mm long, with about 200 strings tied at the centre in a bundle. The bottom ends of the seaweeds and plastic strings were buried in the sand. Dried bamboo tubes were cut into pieces 105 mm long and with 40 mm internal diameter and three pieces were placed horizontally on the bottom of each tank.

At the start of each trial, the predator crab (if present) was placed in experimental tanks 30 min before introducing prey crabs. The larger crabs were used only once as predators but could be used as prey crabs in their respective size classes after undergoing an additional acclimatisation for
at least 24 h. During the 48 h trials, crabs were monitored daily and any mortality or moult was noted. At the end of each experimental run, all shelters were carefully removed to avoid loss of the experimental specimens. Water and sand were sieved through a 500 μm sieve to retrieve crabs, moult shells, broken shells and crab remains. Morphometric measurements (ICW, CL) were taken for whole moult shells and live crabs were checked for cannibalistic scars (broken carapace), moultling and loss of appendages. Simultaneously, the presence of dead and uneaten crabs, live crabs, moulted crabs and moult, shells as well as evidence of damaged crabs, were noted.

**Statistical analyses**

All data were tested for homoscedasticity with Cochran’s C-test (Sokal and Rohlf 1981) and, if found to be heteroscedastic, were square-root transformed before the ANOVA was performed. All data for the percentage of cannibalised crabs were square-root transformed to homogenise the variance. A posteriori multiple comparisons were carried out with the Student Newman Keuls (SNK) procedure.

To test for the effects of shelter and crab size differences on cannibalistic interactions, a series of ANOVAs was carried out. As the experimental design was not orthogonal, the effect of prey size and predator size was tested in separate sets of two-way ANOVA. In all analyses, the percentage of cannibalised crabs (the percentage of prey eaten) and the percentage limb loss of prey crabs (the percentage of surviving crabs missing one or more appendages) were tested as dependent variables. Limb loss of predator crabs was negligible and not included in the analyses. To assess the combined effect (shelter and size), we also carried out analysis on the total percentage of crabs cannibalised or missing a limb. The percentage of crabs found dead and uneaten, and the percentage of prey crabs that moulted, were also analysed as dependent variables to establish whether factors other than cannibalism affected survival, and if moult rate was being influenced by experimental treatments.

The overall effects of predator presence and shelter were tested in a two-factor ANOVA model using predator treatments (control, predator size classes B–D) and shelter treatments (4 levels) as fixed independent variables. Each prey size class (size classes A–C) was also tested in three separate series of analyses using the same two-factor ANOVA model. The overall effect of prey size (size classes A–D) was tested in a one-factor ANOVA model using all data. To assess cannibalistic interactions only within crab size classes, prey size and shelter were analysed as independent variables using only data from the control treatments, in a separate series of analyses.

**Results**

**Experimental conditions**

All crabs used in the experiment were accounted for at the end of each trial. In five of the predator treatment combinations (4.1% of the treatments), the predator was dead at the end of the trials, so those data were excluded from the analyses because the predatory aspect was lost in the treatment. In 7.5% of the predator treatment combinations, the predator crab had moulted and these data were included in the analyses because there was predation in some of the trials. In total, 3.8% of the prey crabs were found dead and uneaten at the end of the trials; their individual data were not used in the analysis. The reason for the mortality was unclear, but it did not differ significantly (p > 0.05) between treatments in any analyses (Tables 1 and 2) and should not have affected the cannibalism results. On average, 4.3% of the prey crabs had moulted at the end of the trial. The percentage of prey crabs that moulted did not differ significantly (p > 0.05) between predator treatments. However, the percentage of prey crabs that moulted was significantly higher in sand substratum than in the other substrata when analysing data from all experimental units (Table 1, Figure 1). The substratum pattern in moult crabs was indicated for each prey size class, although the difference was not significant when analysing the data separately by size class (Table 2). A similar result was found when analysing the control data separately, where the moult rate was significantly higher in sand than in the bamboo treatment (Table 2, Figure 3, SNK-test, p < 0.05).

**Cannibalistic interaction**

Overall, cannibalistic interactions increased with predator size, decreased with prey size and were fewer in the substratum that provided shelter. However, the effect of predator presence and shelter differed between prey size classes.

In all, 51 individual crabs were cannibalised, giving an equivalent of 7.5% cannibalism in 48 h for all predatory treatment combinations. When testing the overall effect of predator crab and shelter treatments, the percentage of cannibalised crabs was significantly higher in the sand substratum (on average 15% loss 48 h−1) than in all substrata combined (3–8% loss 48 h−1) in all predator treatments (Table 1, Figure 1). Cannibalism appeared to increase with predator size, from an average of 5% in control treatments to 13% in the presence of predator size class D, but this trend was not significant (Table 1). There was also a trend of decreased cannibalism with increased prey size, from 11% at prey size A to 5% at prey size C, but no significant effect of prey size was found (one-factor ANOVA; df = 3, 191; F = 1.46; p = 0.22).

The percentage of surviving crabs missing one or more limbs followed a pattern similar to that of cannibalism. However, predator treatments had a greater effect than shelter treatments on limb loss. The percentage limb loss increased significantly from an average of 3% in control treatments to 12% in the presence of the larger predator size classes (Table 1, Figure 1), although it was not significantly affected by shelter. Total negative interactions (i.e. the sum of prey crabs cannibalised or missing a limb) showed a significant effect of both shelter and predatory treatment. Sand substratum had a significantly greater degree of negative interaction than the three shelters used. Also predator size class D had a significantly greater percentage of limb loss than the control treatments (Table 1; SNK-test at p < 0.05).

Analyses of each prey size separately demonstrated that cannibalism on the smallest prey crabs was more...
Table 1: Two-factor ANOVA model of square-root transformed data (for all prey sizes) testing the percentage of cannibalised prey crabs $48 \text{ h}^{-1}$, the percentage of live prey crabs missing one or more limbs, the total number of negative interactions (i.e. the sum of prey crabs cannibalised or missing a limb), the percentage of moulting prey crabs, and the percentage of prey crabs found dead and uneaten (mortality), as a function of predator and substratum treatment

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Cannibalism</th>
<th>Limb loss</th>
<th>Total negative interactions</th>
<th>Moult</th>
<th>Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>SS $F$</td>
<td>df</td>
<td>SS $F$</td>
<td>df</td>
</tr>
<tr>
<td>Predator</td>
<td>3</td>
<td>1.11</td>
<td>1.81 (ns)</td>
<td>3</td>
<td>0.30</td>
</tr>
<tr>
<td>Shelter</td>
<td>3</td>
<td>1.85</td>
<td>3.00*</td>
<td>0.90</td>
<td>1.00 (ns)</td>
</tr>
<tr>
<td>Predator $\times$ Shelter</td>
<td>9</td>
<td>1.09</td>
<td>0.80 (ns)</td>
<td>0.10</td>
<td>0.67 (ns)</td>
</tr>
</tbody>
</table>

$^*$ $p < 0.05$; $^** p < 0.01$; (ns) $p > 0.05$

Table 2: Two-factor ANOVA models of square-root transformed data testing the percentage of cannibalised prey crabs $48 \text{ h}^{-1}$, the percentage of live prey crabs missing one or more limbs, the percentage of moulted prey crabs, and the percentage of prey crabs found dead and uneaten (mortality), as a function predator treatment (control, predator size B, C and D) and habitat treatment (sand alone, seaweed, plastic strings and bamboo tubes), for prey size class A (21–30 mm), B (31–40 mm) and C (41–50 mm ICW), and for control treatments without predator crabs

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Cannibalism</th>
<th>Limb loss</th>
<th>Moult</th>
<th>Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>SS $F$</td>
<td>df</td>
<td>SS $F$</td>
</tr>
<tr>
<td>Prey size A</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>3</td>
<td>3.29</td>
<td>4.46**</td>
<td>0.17</td>
</tr>
<tr>
<td>Shelter</td>
<td>3</td>
<td>0.09</td>
<td>0.12 (ns)</td>
<td>0.06</td>
</tr>
<tr>
<td>Predator $\times$ Shelter</td>
<td>9</td>
<td>2.60</td>
<td>1.17 (ns)</td>
<td>0.32</td>
</tr>
<tr>
<td>Prey size B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>2</td>
<td>0.15</td>
<td>0.40 (ns)</td>
<td>0.06</td>
</tr>
<tr>
<td>Shelter</td>
<td>3</td>
<td>1.04</td>
<td>1.90 (ns)</td>
<td>0.01</td>
</tr>
<tr>
<td>Predator $\times$ Shelter</td>
<td>6</td>
<td>0.74</td>
<td>0.67 (ns)</td>
<td>0.01</td>
</tr>
<tr>
<td>Prey size C</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>1</td>
<td>0.05</td>
<td>0.41 (ns)</td>
<td>0.10</td>
</tr>
<tr>
<td>Shelter</td>
<td>3</td>
<td>2.08</td>
<td>5.66**</td>
<td>0.06</td>
</tr>
<tr>
<td>Predator $\times$ Shelter</td>
<td>3</td>
<td>0.13</td>
<td>0.38 (ns)</td>
<td>0.15</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prey size</td>
<td>3</td>
<td>0.30</td>
<td>0.64 (ns)</td>
<td>0.02</td>
</tr>
<tr>
<td>Shelter</td>
<td>3</td>
<td>1.56</td>
<td>4.44**</td>
<td>0.01</td>
</tr>
<tr>
<td>Predator $\times$ Shelter</td>
<td>9</td>
<td>1.33</td>
<td>1.26 (ns)</td>
<td>0.10</td>
</tr>
</tbody>
</table>

$^{**} p < 0.01$, (ns) $p > 0.05$; $^1$ Data heteroscedastic despite transformation

influenced by the size of larger predatory crabs, whereas cannibalism on the larger prey crabs was more affected by the shelter available (Figure 2). Cannibalism on size class A was heavily affected by predatory treatment and increased significantly from 2% in control treatments to 27% in the presence of predator size class D (Table 2, Figure 2). In contrast, cannibalism on size class A was not significantly influenced by the type of shelter, although there was a trend of more cannibalism in sand than where bamboo shelter was available. The percentage of size class A missing a limb appeared to increase from 1% in control treatments to 14% in the presence of predator size class D, but no statistical difference could be detected (Table 2).

Cannibalism of size class B was less affected by the presence of larger predatory crabs (cannibalism and limb loss varied between 4% and 9% and 4% and 11% respectively). There was a trend of greater cannibalism in the sand treatment (13%) relative to bamboo, where there was no cannibalism (Figure 2). However, no significant effects were found on either cannibalism or limb loss (Table 2). Cannibalism of size class C was significantly greater in the sand treatment (20%) than in the shelter treatment (0–2%), whereas no significant effect of predator treatment was found (Table 2, Figure 2). In contrast, limb loss appeared to increase from 3% in the control treatment to 12% in the predator treatments, a difference that was borderline significant ($p = 0.056$), whereas no clear effect of shelter was observed (Table 2).

Analyses of data from control treatments (same size class of crabs) showed significantly more cannibalism in the sand substratum (on average 11%) than on other substrata (0–3%). Although no significant effect of prey size was found (Table 2), a trend of less cannibalism in the smallest size class (on average 1.8%) than in the larger size class (5–8%) was observed. This difference was most apparent in sand where cannibalism in the control treatments was zero for size class A, but 20% for the larger size classes (Table 2, Figure 3).
In grow-out aquaculture of portunid crabs, cannibalism often constitutes the biggest cause of mortality, resulting in loss of up to 90% (Rodriguez et al. 2001, Allan and Fielder 2003, Mirera 2009, Shelley and Lovatelli 2011). Two approaches to decrease the rates of cannibalism in culture have recently been suggested: (1) to size-grade the crabs (e.g. nursery culture methods with regular sorting to separate small crabs from larger ones and hence decrease predation on smaller crabs [Marshall et al. 2005, Rodriguez et al. 2005, Parkes et al. 2011]); (2) to provide structurally complex habitats that provide shelter from cannibalism for smaller prey crabs and moulting crabs (Hutchinson 1999, Marshall et al. 2005, Mann et al. 2007, Ut et al. 2007, Parkes et al. 2011, Beattie et al. 2012).

Results from the present study suggest that cannibalistic interactions between juvenile mud crabs are strongly influenced by both the difference in size between the crabs and the availability of shelter. However, the response of prey crabs to experimental treatments was very size-specific. Cannibalism on the smallest size class (20–30 mm ICW) increased 10-fold in the presence of the...
largest predatory crabs (51–70 mm) relative to the control treatments. Shelter had less influence on controlling cannibalism in that size class. In contrast, cannibalism on larger prey crabs (31–50 mm CW) was less influenced by the presence of larger predators but decreased by >50% in the presence of shelters rather than a simple sand substratum. The results suggest that size-grading and shelter could both be important in minimising cannibalism in grow-out aquaculture but that size-grading is particularly important for smaller crabs, whereas shelter is more important for the larger size classes.

**Effects of crab size**

In brachyuran crabs, the relative difference in size between predator and prey crabs is important in influencing the rates of cannibalism. When crabs are of similar size, cannibalism on intermoult crabs is minimal, although it is greater in newly moulted, soft, defenceless crabs. However, above a critical size difference, cannibalism can affect hard intermoult prey crabs, usually resulting in rates of cannibalism that are much greater (Kurhara et al. 1988, Moksnes et al. 1997, Fernández 1999, Moksnes 2004). To address this situation, size-grading is practised in nursery culture of mud crabs to increase the survival rates of juveniles (Cerezo 2001, Rodriguez et al. 2005, Mann et al. 2007). Therefore, culture of mud crabs needs to aim to separate crabs of different sizes prior to stocking as well as during culture, to preclude cannibalism on hard intermoult crabs.

In the present study, the effect of relative size differences on cannibalism was demonstrated in the smallest prey size class (20–30 mm). In control treatments, where the relative size difference between prey and predator was <50%, cannibalism was low (<2% 48 h⁻¹), but it increased with increasing size difference to 27% mortality 48 h⁻¹ in the presence of the largest predators, in which there was a mean size difference of ~140%. High rates of cannibalism on smaller crabs by larger ones (40–50 mm ICW) suggested that hard shelled (intermoult) crabs of the smallest size class (A 20–30 mm ICW) were preyed upon at a mean size difference of 80% between prey and predator. The findings suggest that the critical size difference between prey and predator is between 50% and 80% for that prey size, and that juvenile mud crabs 20–30 mm ICW have to be separated from crabs >40 mm ICW to decrease cannibalism. This is consistent with the findings of Rodriguez et al. (2007) on the preference of farmers in South-East Asia for crab >43 mm ICW to ensure faster growth and reduced mortality.

In larger prey sizes (31–50 mm ICW), the rates of cannibalism did not increase in the presence of larger predators, suggesting that cannibalism was mainly of newly moulted crabs. The low rate of cannibalism on hard, intermoult crabs could in part be explained by the smaller mean size difference between prey and predator crabs in these treatments (28–70%) compared with that in the smallest size class, but also that a greater size difference is required to allow cannibalism on hard crabs by the larger prey crabs. Although the presence of larger predatory crabs did not increase the rates of cannibalism for the 31–50 mm ICW prey size class, the percentage limb loss did increase by an average of four times in treatments with the largest predator size relative to the control treatments. The findings therefore support the belief that agonistic interactions may be manifest in limb loss where size differences are small. This implies that size-grading crabs between 31 and 70 mm CW may have only small effects on cannibalism and survival, but it could decrease the number of incidents of limb loss that impact crab quality.

**Effects of habitat**

In natural populations of brachyuran crabs, cannibalism between juvenile size classes is thought to be a major cause of mortality for small juvenile stages that often aggregate in structurally complex shelters such as seagrass and mussel beds, where predation rates by larger predators are minimised (Fernández et al. 1993, Moksnes et al. 1998, Moksnes and Heck 2006). Providing shelter for juvenile mud crabs at aquaculture farms may therefore have strongly positive effects on their survival. This suggestion has received support in the present study because cannibalism, both within and between size classes, was less for the three shelter treatments (i.e. seaweeds, plastic strings and bamboo tubes) than for the sand substratum without shelter. Although cannibalism did not differ statistically between shelter type, a trend of less cannibalism was observed where bamboo tubes were used as shelter. This
was possibly because bamboo provides greater protection on the seabed than plastic strings or seaweed algae, which provide more shelter within the water column. The tubes may also provide the larger prey sizes of crabs with more effective refuge from cannibalism from predator crabs, as indicated by the lack of cannibalism where bamboo shelters were used for prey size classes B and C (Figure 2). The positive effects of appropriate shelter are consistent with the findings of Ut et al. (2007), who used clam shells and bricks as shelter to increase the survival of juvenile Scylla paramamosain relative to crabs on a simple sand substratum. However, in the present study, the effect of shelter differed between prey sizes.

Cannibalism was on average eight times greater on the sand substratum than where any of the three shelter types were used in the control experiments. This difference was strongly influenced by the larger size classes of crabs, which suffered high rates of cannibalism where there was no shelter (on average 20%), whereas there was zero cannibalism for the smallest size class. The size-specific shelter effect was observed also in the predator treatments, cannibalism being greater with no shelter than where shelter was provided, although this was significant only in the largest prey class (D). Cannibalism on the smallest prey size (A) was similar in all shelter treatments. This result is not consistent with other studies on portunid crabs, however, where the survival of young juvenile stages was many times higher in structurally complex habitats relative to sand or mud habitats (Pile et al. 1996, Moksnes et al. 1997, 1998). The present study used small experimental containers and high densities of crabs (75 crabs m\(^{-2}\)) to enhance agonistic interactions and used primary habitats relative to sand or mud habitats (Pile et al. 1996, Moksnes et al. 1997, 1998). The present study used small experimental containers and high densities of crabs (75 crabs m\(^{-2}\)) to enhance agonistic interactions and hence to determine measurable cannibalism rates within a short period. Although this approach provides comparable relative rates of cannibalism, as well as estimates by size of absolute refuge from cannibalism on intermoult crabs, it may decrease part of the refuge value of shelters and provide greater interactions for bigger crabs because of the limited space. This may be because prey and moult crabs were always within a detectable distance of larger predators in the small experimental containers, so the concealment function of the shelter that is provided in a bigger environment with lower crab densities might have been lost.

The results from the present study may therefore reflect mainly the absolute habitat refuge of the shelter material used, where the prey crab is relatively inaccessible to the predators. This may explain why the bamboo-tube shelter appeared on average to provide a better refuge than the others, as discussed above. The lack of shelter refuge for the smallest size classes should be interpreted with caution, however, because the shelters may provide greater refuge from cannibalism in nature and at lower crab densities in aquaculture systems. However, despite this potential artefact that may have decreased the differences in the efficacy of the shelters provide, cannibalism did decrease and survival increased by an average of 60% in the three shelter types relative to the tests with no shelter. This effect of shelter is consistent with previous studies on juvenile portunid crabs carried out in aquaculture systems in which an increase in survival of ~50% is common when shelters are provided (Mann and Paterson 2003, Marshall et al. 2005, Mann et al. 2007, Ut et al. 2007).

The densities of the crabs used in the experiments were higher than the stocking densities normally used in grow-out pond culture of mud crabs using wild crabs between 40 and 80 mm ICW (Mann et al. 2007, Rodriguez et al. 2007), but similar to the densities used in nursery cultures where mud crab megalopae are grown to ~25 mm ICW (Rodriguez et al. 2001). Although our resulting absolute rates should not be compared with the mortality rates at farms with lower stocking densities, they do provide relative rates of cannibalism to be compared between shelter types, and also provide estimates of absolute refuge by size from cannibalism.

The moulting rate of juvenile crabs was also affected by the presence of shelter, being greater in the no-shelter tests than where shelter was provided in both control and predatory treatments. This result was unexpected and not consistent with other studies of portunid crabs that show greater rates of moult in habitats that provide shelter from predators relative to suboptimal substrata such as open sand, where the moult is delayed (Moksnes et al. 1997, 2003). However, the moult pattern observed was likely not a result of cannibalism removing moulting individuals because that should have produced the opposite pattern (see Figure 1).

**Implications for the culture of mud crabs**

Cannibalism constitutes a major source of mortality in mud crab culture but is poorly understood globally (Allan and Fielder 2003, Mann and Paterson 2003, Mann et al. 2007, Ut et al. 2007, Mirera 2009, Shelley and Lovatelli 2011). Results from the present study suggest that both size-grading and the provision of suitable shelter can decrease the rates of cannibalism in grow-out culture of mud crabs. To avoid high rates of cannibalism on hard intermoult crabs, this study suggests that the relative size difference between crabs reared together should be small, i.e. all animals should be within 20% of each other by length. This is particularly important if small (<30 mm ICW) juvenile seed crabs are used. In South-East Asia, juvenile seed crabs >40 mm ICW are preferred by farmers because they need less time to reach commercial size relative to smaller seed crabs. However, because the natural mortality of juvenile portunid crabs is many times higher in small newly settled crabs than in larger ones (Pile et al. 1996, Moksnes et al. 1998) and is often density-dependent (Moksnes et al. 1997, Moksnes 2004), the impact on the fished population will be minimised and aquaculture more sustainable if the smallest juvenile crabs available are used. To avoid exceeding the critical size difference at which cannibalism starts, it is important to stock each culture with crabs of similar size. However, because of the great differences in the growth rates of individual crabs (Mann et al. 2007) and the heavy dependence on a wild supply, continuous size-grading of crabs would likely still be required during their culture. According to the results presented here, size-grading would also decrease limb loss, which has negative effects on growth, as well as the quality of the crabs and their market value when one or both chelipeds...
are lost (Juanes and Smith 1995, Paterson et al. 2007, Mirera and Mtile 2009). Continuous loss of chelipeds even from juvenile crabs leads to a disproportional cheliped to body size ratio that will impact the market value in terms of wet weight.

Rates of cannibalism could be reduced further by providing shelters that reduce the encounter rates of crabs in addition to providing shelter to small or moulting crabs. The results here suggest that shelter is particularly important in reducing cannibalism in the more aggressive larger size classes of mud crabs. In this study and in others (e.g. Ut et al. 2007), several types of shelter reduced cannibalism notably, suggesting that farmers could use several locally available substrata as shelter for the crabs, including seaweeds (*Gracilariopsis*) and bamboo (Trino et al. 1999). In the present study, the commercial red alga *Eucheuma denticulatum*, which is easily obtained from local seaweed farms, reduced cannibalism by ~50% relative to that which occurred where there was no shelter. However, there is a need first to establish whether that species can flourish in the brackish water ponds used for mud crab aquaculture, in similar manner to other seaweed species such as *Gracilariopsis* spp. and *Caulerpa* spp. (Trino et al. 1999, Putra et al. 2013). If so, the alga itself might produce extra income for the farmers of mud crabs.

Acknowledgements — This research was funded by the Western Indian Ocean Marine Science Association (WIOMSA), Marine Science for Management (MASMA), through a project entitled ‘Small-scale mariculture of mud crabs (*Scylla serrata*) in East Africa’. We thank the Kenya Marine and Fisheries Research Institute (KMFRI) where the laboratory work was done and Linnaeus University, Sweden, for the PhD scholarship and provision of library services in the writing-up process of the manuscript. We also thank the internship students at KMFRI, Venny Mwainge and Emily Wafula, and laboratory technicians Justus Wakili and Mwendwa Mbaruka, for their support, as well as the artisanal crab fishers who provided the juvenile crabs for the experiment (Abdallah Mtile and Dickson Mwamure).

References


