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Spawning Characteristics of the South African Mudcrab *Scylla serrata* (Forskål) in Captivity

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Abstract

Scylla serrata is a potential aquaculture species in Southern Africa. Information about its reproductive biology is required as a prerequisite to establishing hatchery technology. Adult female *S. serrata* were caught in the Umlalazi estuary on the subtropical east coast of South Africa and kept in captivity to observe and record spawning characteristics. Data collected included crab size and mass, time in captivity prior to spawning, fecundity per batch, relative fecundity, individual egg mass and size, size of zoea 1 larvae, incubation time, and hatch success rate. Of the 119 crabs kept in captivity 83% spawned in the maturation system—most within 40 d of capture. The crabs were highly fecund (mean relative fecundity per batch = 10,655 ± 4,069 eggs/g female) and the majority of the batches hatched within 288 h (12 d) at 27 C. Spawning in captivity occurred throughout the year, with a peak in late winter/early spring. This differs slightly from records of ovarian maturity stages of the crabs in the wild. A pattern of synchronous spawning was recorded where the females were observed to extrude their eggs in groups, commonly within 3 d of one another, separated by long periods of inactivity, suggesting an exogenous spawning cue. A total of 1,374,488 zoea larvae were obtained per kg of female per month. This means that if sufficient mature females can be caught from the wild, these could be used for stocking hatchery operations. The crabs were easy to maintain, mature, and spawn in captivity. This will facilitate future domestication which will eventually reduce the need for wild caught broodstock. The spawning characteristics of South African *S. serrata* fit in well with those observed for the genus throughout its distribution implying that ecological and fisheries management could be similar.

Scylla serrata is a large, commercially important, brackish water, carnivorous crab, distributed throughout the Indo-Pacific region (Brock 1960; Tamura 1970; Hill 1975; Heasman and Fielder 1977). The species is a candidate for aquaculture in Southern Africa, but a major bottleneck to the establishment of mudcrab farming worldwide is the dependence on wild caught juveniles (Williams and Primavera 2001). Hatchery techniques thus need to be developed for the species in the region. An essential component of hatchery production is the establishment of a broodstock that can produce a predictable supply of fertilized eggs (Wickins and Lee 2002). A thorough understanding of the reproductive biology of the species is thus required. Despite a renewed research effort worldwide (Wickins and Lee 2002), driven in part by dwindling natural fisheries for this species (Le Vay 2001), little has been published in the primary literature about the spawning characteristics of *S. serrata*. In addition, much of

the work that was published before Keenan et al.'s (1998) revision of the genus leaves some doubt as to the precise species from which data were collected.

South African mudcrabs are known to mate and undergo ovarian maturation in estuaries (Hill 1975, 1994; Robertson and Kruger 1994). They then migrate offshore to spawn on the continental shelf. Fertilized eggs attach to the pleopods where they are incubated. Hatched larvae are released into the ocean (Hill 1975; Heasman and Fielder 1983; Hill 1994; Le Vay 2001). Berried females are caught sporadically in offshore trawl nets and are extremely rare in estuaries. Observations on spawning behavior and data of egg production and hatching are therefore scant. The only information on reproduction of *S. serrata* in South Africa are seasonal ovarian maturation indices of crabs in the wild and some anecdotal data on spawning in captivity (Robertson and Kruger 1994).

The aim of the research was to gather information about the spawning characteristics of wild-caught *S. serrata* in captivity. This information will be used as a basis for husbandry practice and to establish hatchery techniques that will contribute to the eventual domestication of the species. The information can also be used as a component for conserving the wild population or managing the fishery (Caddy 1989; Koslow 1992). In order to achieve this, mature females were caught from the wild and maintained in our research facility on the subtropical east coast of South Africa (Rhodes University Mudcrab Hatchery at Mtunzini Prawn Farm).

Materials and Methods

Broodstock Capture

Mature female crabs were caught from February 2000 to August 2001 using hoop-and-bag traps in the Umlalazi estuary (31°47'E, 28°57'S) on the subtropical east coast of South Africa. The traps were not size selective, and mature males and im-

mature females were returned to the water immediately. As the Umlalazi estuary is a proclaimed estuarine sanctuary we were also required to return the mature females unharmed to this estuary on completion of our observations. Water temperatures in the estuaries ranged from 17 to 22 C in winter and from 22 to 30 C in summer. Females were identified as being sexually mature by their wide, dark, U-shaped abdomens fringed with setae (Warner 1977; Heasman 1980; Barnes 1987; Robertson and Kruger 1994). Fishing was conducted only during daylight hours. Traps were checked at 15-min intervals and the crabs were removed and transported to our facility in a 200-L plastic bin covered with a wet hessian sack. Catch per unit effort (CPUE) was calculated for mature females as: $(nc/t)/nt$ where: nc = number of crabs caught; t = soak time in hours; nt = number of traps, and expressed as crabs per trap hour (Robertson 1989).

The animals were disinfected against bacteria and fungi by bathing them overnight in an aerated seawater bath containing 100-ppm malachite green and 100-ppm formalin (Castille and Lawrence 1989; Hamasaki and Haitai 1993). Size was recorded (carapace width in mm and weight in grams), and each crab was numbered by engraving the carapace using a jeweller's engraver.

Broodstock Conditioning

The crabs were maintained in a recirculating system at a density not exceeding 1.5 animals/m². No male crabs were introduced into the spawning system, as the females were presumed to have mated in the wild and thus were carrying spermatophores (Robertson and Kruger 1994). The 12-m³ maturation tank (4 × 3 m) had a concrete bottom that was painted black, and water depth was maintained at 1 m. Nine round plastic bins (40 cm in diameter, 15 cm in height) filled with beach sand were placed on the bottom of the tank to facilitate spawning. Twelve shelters in the form of

roof tiles raised on plastic pipes were placed on the bottom of the tank to reduce cannibalism and stress. Water was recirculated through a 600-L biological trickle filter at a rate of 1L/sec. Prior to reaching the trickling filter the water was passed through a nylon stocking to collect particulate waste. The stocking was cleaned daily and replaced once a month. Approximately 1 m³ of the water was replaced daily with fresh seawater at a salinity of 30–32 ppt, pumped from a beach well point and filtered to 1 μm. Light was subdued (1–3 lx, Lutron LX-105 light meter, Taiwan) by painting the fluorescent lamp covers green and photoperiod was maintained at a constant 14 L:10 d cycle. The system was indoors but temperature was not controlled, and varied from 19 C in winter to 25 C in summer. Crabs were fed to satiation on a feeding tray, twice per day with squid (*Loligo* sp.), shrimp (*Fenneropenaeus indicus*), mussels (*Perna perna*), or fish roe (assorted species) on successive days. Uneaten food was removed daily and the tank bottom was vacuumed once a week.

Spawning, Incubation, and Hatching

Crabs that spawned (extruded eggs) were easily detected by shining a torch into the tank and turning over the artificial shelters. Berried females were netted out of the maturation tank as soon as they were observed and placed into 60-L glass observation aquaria provided with an external 15-L airlift biological sand filter. The aquaria were filled with seawater from the main recirculating system, and once the crabs had been introduced, the water was heated with a 150-W submerged aquarium heater to 27 C over 24 h. The crabs were not fed after extruding their eggs, but the aquaria were siphoned daily to remove feces and dropped eggs. Dropped eggs were examined under a microscope and were commonly found to be infected with fungi, polychaet, or nematode worms. Females were then treated with 1-ppm and 10-ppm formalin for 24 h. If after treatment the female continued to

drop large quantities of eggs, she was considered unsuitable for further work and immediately returned to the estuary of origin.

Once a berried crab was judged to be a suitable hatchery candidate, it was moved to a covered 600-L fiberglass, cylindro-conical incubation tank. A window was provided in the side of the tank for observing the female. The tank was filled with filtered (1 μm), UV sterilized seawater. The water was recirculated through an 80-L biological airlift filter and then passed through a UV sterilizer at a rate of 1.7 L/min. Water was drained from the tank into the filter through a 0.3-mm outlet screen to prevent loss of hatching zoea. A sheet of perforated PVC placed at the bottom of the cylindrical portion of the tank provided the crabs with a flat substratum that allowed dropped eggs and feces to sink into the conical tank bottom from where they could be removed by opening a valve.

Wild-caught crabs were added to the main maturation tank to maintain the stocking density after crabs that had spawned had been removed. Once hatching had taken place, the crabs were returned to their estuary of origin.

Measurement of Parameters

Fecundity in the text refers to the numbers of eggs extruded per female per batch and was estimated as follows: berried crabs were weighed shortly after the extrusion of eggs and reweighed after the larvae had hatched. This gave the total mass of the eggs. Four crabs starved for the 12-d incubation lost $1.14 \pm 0.80\%$ of their body weight. This was considered negligible and was therefore not included in further calculations. Total egg mass was calculated as:

$$\text{Total egg mass} = \text{mass of crab at extrusion} \\ - \text{mass of crab after hatch.}$$

Subsamples of at least 300 eggs were removed from the egg bolus as soon as possible after extrusion using sterilized forceps, weighed, and counted in three replicates under a dissecting microscope. This provided

an estimate of individual egg mass, whereupon fecundity was estimated by dividing total egg mass by individual egg mass. To validate this method, the total number of eggs produced by two females was counted and compared to these estimates.

Egg diameter and larval size (distance between the lateral spine tips) were measured under a compound microscope using a graduated eyepiece at 40 times magnification.

Hatching success was calculated as follows: after hatching in the 600-L tank, the larvae were mixed well by vigorous aeration. Nine 50-mL samples were scooped out of the tank at different depths. The larvae in each sample were counted, and an average was calculated as the density of larvae per 50 mL, allowing for the estimation of the number of larvae in the 600-L tank. Hatching success (%) was calculated by:

$$(\text{Number of larvae hatched} / \text{Number of eggs extruded}) \times 100.$$

Statistics

A regression model was fitted to the data to determine the relationship between variables using SPSS 11.0.1 (2001, SPSS, Belgium) software. Data was then checked for normality, linearity, and homoscedacity, and a residual plot was done. Pearson's coefficient was used to examine correlation between variates. Linear, quadratic cubic and power curve estimates were used to determine best fit (Sokal and Rohlf 1995). Data are presented as mean \pm standard deviation.

Results

Female Broodstock Capture

Monthly catch per unit effort (CPUE) was not related to season. A total of 119 crabs were caught. CPUE ranged from 0.05 in July and August to 0.16 mature female crabs per trap hour in March and June (Fig. 1). The monthly CPUE averaged over the 19-mo sampling period was 0.10 ± 0.04 mature female crabs per trap hour. No traps

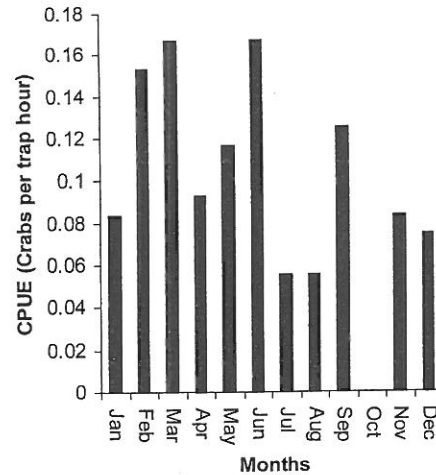


FIGURE 1. Monthly catch per unit effort averaged from data collected over a 19-mo period for mature female *S. serrata* caught in the subtropical Umlalazi estuary, South Africa (N = 119).

were deployed in October 2000 due to extreme weather conditions. Carapace width (CW) of mature females ranged between 90–200 mm, with 91% of the females being larger than 120-mm and smaller than 170-mm CW (Fig. 2).

There was a highly significant correlation ($P = 0.0001$) between CW and mass. The relationship was best expressed as $CW = 0.0014 \cdot \text{Mass}^{2.56}$ ($N = 119$, Pearson's correlation coefficient = 0.91) (Fig. 3).

Spawning Characteristics

Table 1 summarizes the spawning parameters of the crabs that spawned over the 19-mo period. Of the 119 crabs stocked into the system, 98 (82.6%) spawned. Cannibalism of newly molted crabs was the only cause of mortality. Only four crabs were lost as a result of this as low molting frequency among mature crabs, and high rates of feeding reduced cannibalism to very low levels.

Berried crabs did not bury themselves in the sand of the spawning bins and were often observed sitting on top of the shelters

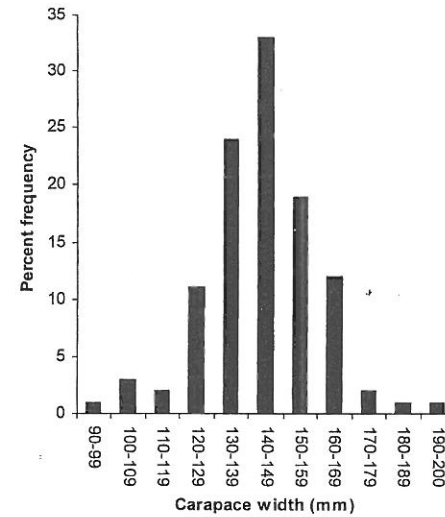


FIGURE 2. Size frequency distribution of mature female *S. serrata* caught in the subtropical Umlalazi estuary, South Africa (N = 119).

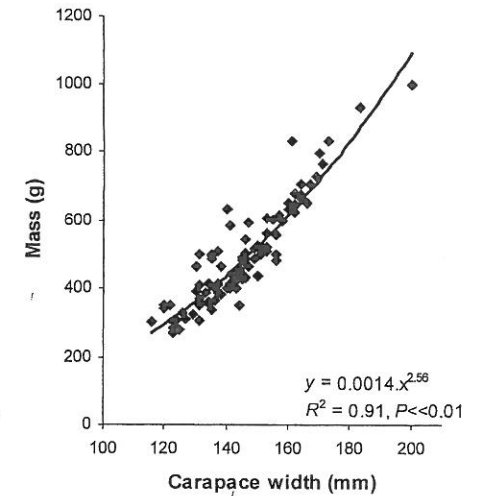


FIGURE 3. Relationship between carapace width and mass for mature female *S. serrata* caught in the subtropical Umlalazi estuary, South Africa (N = 119).

or swimming in the water column. The majority of the crabs (62%) spawned within 40 d of being stocked into the system. There was no relationship between time to spawn (days in captivity) and season of the year. Fecundity was correlated to carapace width ($R^2 = 0.18$, $y = 0.0515x - 2.4036$,

$p = 0.026$) although this correlation was weak as some smaller crabs produced large batches and some large crabs produced small batches of eggs (Fig. 4).

The difference between the calculated estimates of egg number and actual egg number of the two females was found to be less than 2% ($\pm 100,000$ eggs). Average fecun-

TABLE 1. Spawning characteristics of 98 female *S. serrata* spawned over a 19-mo period in KwaZulu-Natal, South Africa.

Parameter	Minimum	Median	Maximum	Mean (standard deviation)	N
CW of crabs that spawned (mm)	116	146	200	145 (14)	69
Mass of crabs that spawned (g)	270	464	1000	490 (144)	69
Time to spawning (d in captivity)	5	31	112	38 (23)	69
Fecundity: (millions of eggs/female per batch)	2.45	4.73	10.75	5.17 (1.93)	28
Relative fecundity (number of eggs/g of female/batch)	3,825	9,866	25,503	10,655 (4,069)	28
Total egg mass (g of eggs/female per batch)	50	101	250	109.40 (37.45)	28
Calculated mass of individual eggs (μg)	16.23	21.85	31.78	22.00 (3.91)	28
Egg diameter at extrusion (mm)	0.29	0.30	0.33	0.30 (0.01)	28
Egg diameter just prior to hatch (mm)	0.38	0.40	0.41	0.40 (0.01)	28
Incubation time (h at 27 C)	233	288	335	288 (21)	18
Percent hatching	72	84	97	84 (6)	28
Width of Z1 between lateral carapace spines (mm)	0.75	0.81	0.87	0.81 (0.03)	10

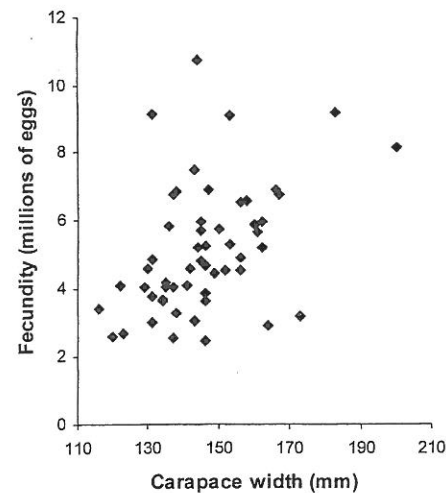


FIGURE 4. Relationship between carapace width (mm) and fecundity (number of eggs per female per batch) for *S. serrata* ($N = 60$).

dity was 5.17 ± 1.93 million eggs per mature female, within the size range 116- to 200-mm CW. Mean relative fecundity was $10,655 \pm 4,069$ eggs/g of female. The mean mass of individual eggs was $22.00 \pm 3.91 \mu\text{g}$ ($N = 28$).

During the incubation period the eggs increased in size from 0.30 ± 0.01 mm at extrusion to 0.39 ± 0.01 mm just prior to hatching ($N = 28$) (Fig. 5). The mean incubation period from extrusion to hatching at a constant temperature of 27 C was 288 ± 21 hours ($N = 37$). There was a significant correlation between egg diameter and incubation time at 27 C ($p < 0.001$). The relationship was best expressed by $y = 0.299 + 0.002x + 0.001x^2$ (Pearson's correlation coefficient = 0.85), where $y = h$ from extrusion and $x =$ egg diameter in μm . This allows for the prediction of time to hatch depending on egg size at 27 C. There was little variation in the size of the zoea larvae at hatching (mean 0.81 ± 0.03 mm, range 0.75–0.87 mm, $N = 10$). Mean hatch rate (proportion of Z1 larvae hatching from extruded eggs) was $84 \pm 6\%$ ($N = 28$).

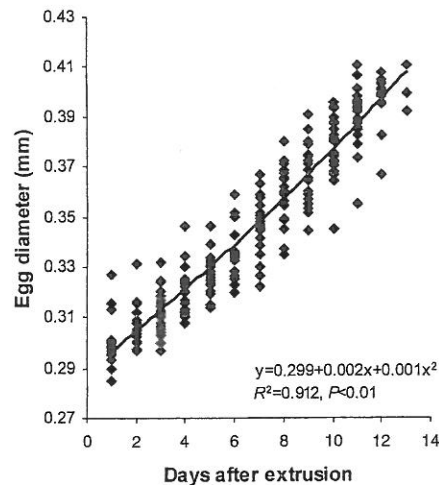


FIGURE 5. Relationship between incubation time (h) and egg diameter at 27 C for *S. serrata* ($N = 37$).

All berried females lost a proportion of their eggs during the incubation period, but the amount varied considerably between individuals: the mass of eggs dropped per batch ranged from 0.6 to 22.0%, (average = $6.5 \pm 6.0\%$, $N = 28$) of the total mass of eggs extruded. Dropped eggs were examined under a microscope, and $85 \pm 5\%$ were fertilized but were found to be infested with fungus and polychaet worms. In most cases eggs were lost as a result of females grooming the bolus.

Spawning Patterns

The crabs extruded eggs during all months of the year, with a peak during July and August (Fig. 6).

Most crabs were observed to spawn within a few days of one another, separated by periods ranging from 10 to 41 d during which no crabs spawned (Fig. 7).

Discussion

Sexual Maturity and Catch Data

Catch per unit effort was lowest during the winter months of July and August; fig-

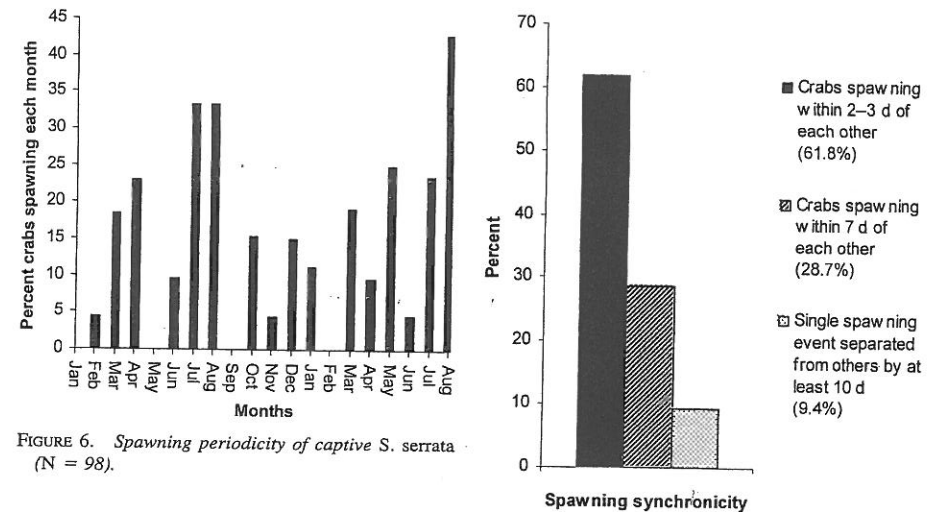


FIGURE 6. Spawning periodicity of captive *S. serrata* ($N = 98$).

ures for these months were less than half those recorded in March and June and lower than the average yearly CPUE (Fig. 1). This coincided with the period during which the highest proportion of females spawned in the laboratory (Fig. 6). Female crabs with ripe ovaries leave estuaries in order to extrude their eggs at sea (Heasman and Fielder 1983; Hill 1994; Le Vay 2001). Low CPUE during these months could therefore have been a consequence of a lower relative abundance of mature females in the estuaries. Similar reasoning was used by Mann et al. (1999) to explain lower than expected Gonado-Somatic Index (GSI) values of mature females caught in Moreton Bay (Australia) during the period corresponding to high spawning activity of the crabs in captivity. More data is, however, required to substantiate this suggestion, particularly as Robertson (1989) suggested that CPUE is a poor index of abundance. While the CPUE of mature females was relatively low, it was consistent and an adequate number of crabs were caught to provide a regular supply of broodstock for hatchery purposes.

Although crabs as small as 90-mm CW were identified as mature according to their external morphology, the smallest crab

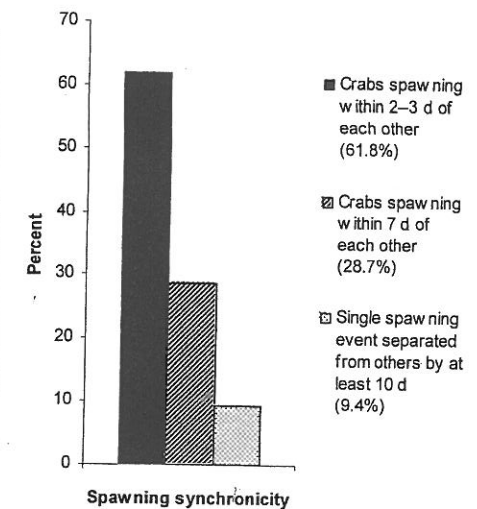


FIGURE 7. Group spawning pattern of captive female *S. serrata* over 19 mo ($N = 98$).

which spawned in the system was 116-mm CW, thus corroborating suggestions by Ong (1966), Marichamy and Rajapackiam (1992), and Robertson and Kruger (1994) that female *S. serrata* do not necessarily attain true functional maturity at the same size they attain morphological maturity. For practical hatchery purposes, where space is a limiting factor, only crabs larger than 115-mm CW should be used.

Fecundity

Fecundity in most crab genera generally increases with size (Prasad and Neelakantan 1989; Norman and Jones 1993; Haddon 1994; Lardies and Wehrmann 1996; Mantelatto and Fransozo 1997). Although this trend was observed for mudcrabs in this study, high variability within size classes resulted in a poor correlation between CW and fecundity. Mudcrabs are known to be able to fertilize more than one batch of eggs (usually 2 to 3) from a single mating (Ong 1966; Heasman et al. 1985; Millamena and Quintio 2000; Djunaidah et al. 2001). As is the case for other brachyurans (Gardner 1997), it has been found that fecundity in

TABLE 2. Fecundity and reproductive output of female *Scylla* species from different locations.

Species	Crab size: CW (mm) mass (g)	Fecundity (average number of eggs/female per batch × 10 ⁶)	Reproductive output (number of eggs/batch per g female)	Geographical location	Reference
<i>Scylla</i> sp. (described as <i>tranquebarica</i>)	129–175 300–690	2.1–4.0	153–433	India	Srinivasagam et al. 2000
<i>Scylla</i> sp. (described as <i>serrata</i>)	85–137 98–340	0.1–2.3	168–265	India	Srinivasagam et al. 2000
<i>Scylla</i> sp.	117–140 N/A	1.5–2	N/A	India	Marichamy and Raja- packiam 1992
<i>S. serrata</i>	N/A N/A	1.5–3	N/A	Sri Lanka	Jyamanna and Jinadasa 1993
<i>S. serrata</i>	164–170 744–820	0.4–8.4	543–11,531	Australia	Mann et al. 1999
<i>Scylla</i> (described as <i>ser- rata</i>)	N/A 350–520	0.8–2	N/A	Malaysia	Bin Jamari 1992
<i>S. paramamosain</i>	N/A 200–300	0.6–3.0	N/A	Vietnam	Hai et al. 2001
<i>S. paramamosain</i>	69–169 170–790	0.05–1.8 (Z1 larvae)	N/A	Vietnam	Dat 1999
<i>S. serrata</i>	N/A 350–400	1.2–1.6	2,319–5,262	Philippines	Millamena and Bang- caya 2001
<i>S. serrata</i>	130–174 313–950	0.4–5.2 (Z1 larvae)	N/A	Philippines	Quinitio et al. 2001
<i>Scylla</i> sp.	N/A 200–300	2.7–3.3	N/A	Indonesia	Djunaidah et al. 2001
<i>S. serrata</i>	120–170 270–1,000	2.5–10.8	3,825–25,503	South Africa	This study

S. serrata usually decreases with each subsequent batch of eggs (Ong 1966). Since females were used for only a single spawning in this study, the smaller egg mass produced by some of the larger females may have been the second or third batch from a single molt and mating, while large batches produced by some of the smaller females may have been a first spawning. This may explain the poor correlation between crab size and batch size. Table 2 lists observed fecundity data of *Scylla* species. The number of eggs per batch and relative fecundity of South African crabs was high compared to the range recorded in Australasia (Bin Jamari 1992; Marichamy and Rajapackiam 1992; Jyamanna and Jinadasa 1993; Dat 1999; Mann et al. 1999; Srinivasagam et al. 2000; Djunaidah et al. 2001; Hai et al.

2001; Millamena and Bangcaya 2001; Quinitio et al. 2001).

Seasonality of Spawning

Patterns of seasonal reproductive activity of mudcrabs worldwide were reviewed by Le Vay (2001). Maturation and spawning of *Scylla* both in the wild and in captivity has been observed year-round. There are some seasonal peaks, though these differ according to climate and latitude. In this study the peak spawning period in captivity over the 19-mo period was in late winter (July and August). This coincided with the seasonal rise in sea surface temperature and mirrored the peak in spawning for *Sesarma meinerti*, another large estuarine crab in the region (Emmerson 1994). This did not, however, fit well with the incidence of mature ovaries

in February, May, and October found by Robertson and Kruger (1994) for the same population, or their suggestion that spawning probably occurred from late spring to early autumn. It should, however, be noted that Robertson and Kruger (1994) recorded high variability in GSI values. This gives substance to the suggestion by Heasman et al. (1985) that GSI values were not a good indicator of spawning periodicity for mudcrab. The true situation could, however, have been confused by the fact that the animals in this study were brought into artificial conditions that may have provided cues different to those that the crabs might have experienced in the wild. Mudcrabs are known to be able to maintain ovarian maturity for extended periods before spawning (Heasman et al. 1985). The introduction of the females to captive conditions may have induced them to spawn earlier than in the wild. In contrast to the studies by Mann et al. (1999) and Nghia et al. (2001), who found a strong correlation between the time taken to spawn in captivity and season, we made no such observations. Only long-term studies of spawning and recruitment will clear up the discrepancy of whether mudcrabs in South Africa have a distinct spawning season.

Synchronicity of Spawning

Spawning synchronicity is common amongst crustaceans (Olive 1992) and is often associated with food abundance, resulting in optimum egg quality. It also ensures that larvae encounter optimal conditions for growth (photoperiod and temperature) and favorable dispersion of the larvae (currents) (Olive 1992; Emmerson 1994; Greco and Rodriguez 1999).

Although spawning synchronicity of *S. serrata* in captivity (Fig. 7) has not been previously documented, it has been observed in Australia. Pheromones have been shown to affect sexual behavior in crabs (Gleeson 1991). Evidence also exists that hatching eggs release hormones, which influence female crab behavior (Gleeson and

Smith 1984; Kamio et al. 2002; Tankersley et al. 2002). Despite a paucity of evidence in the literature, it is possible that pheromones could be released during spawning that could induce other females to spawn. Researchers in the Philippines have, however, not recorded synchronous spawning in mudcrabs kept in the same system. Also, attempts to induce maturation or spawning with exogenous hormones in decapods such as shrimp, for example, have been largely unsuccessful (Chamberlain 1985). There are two other possible explanations for this phenomenon. Firstly, that changes in conditions in the broodstock maturation system acted as cues to spawning, but were so subtle as to go undetected, and secondly, that mudcrabs caught in the wild have molted, mated, and matured their ovaries with some degree of synchrony. This synchrony was then carried through the captive maturation process, resulting in synchronous spawning. There is also some evidence that the lunar cycle coordinates egg laying and hatching in the lobster *Homarus gammarus*, which has benefits for the larvae (Ferrero et al. 2002). Although Hai et al. (2001) found that spawning in *Scylla* did not follow moon phases, no such correlation was recorded in this study.

There were no obvious correlations between spawning patterns and parameters measured in the broodstock system during this study. If, however, spawning is synchronized by a naturally occurring cue, it could be a useful tool for broodstock management and would be a worthwhile area of research. Whatever the mechanisms behind this phenomenon, the results implied that when using wild-caught females, more than one batch of eggs was usually available for experimental or rearing purposes.

Other Aspects of Spawning

As most of the crabs spawned soon after introduction to the maturation system, it was unnecessary to ablate the eyestalk to induce maturation and spawning, a relatively common practice for mudcrabs (Mann et

al. 1999; Millamena and Quintio 2000; Millamena and Bangcaya 2001). The maturation tank size and stocking densities used in this study allowed for an adequate number of crabs to be held in captivity to ensure a relatively constant supply of viable eggs.

We observed that when berried females could not access the spawning bins due to larger territorial females occupying them, the eggs did not attach well to the pleopods and resulted in a complete loss of the batch. When enough bins were provided, however, the beach sand they contained proved an ideal substrate, negating the need for the (more difficult to maintain) mud-based medium used by Djunaidah et al. (2001).

Hatching in the incubator tank occurred in the morning between 0800 and 1200 h for 94% of the crabs. Incubation time at 27 C corresponded with that observed by Hai et al. (2001) (9–12 d at 25–31 C) and for the majority of batches did not vary by more than 24 h (Table 1). Moreover, the small variance in the increase in egg size from extrusion to hatching between different crabs (Table 1) means that, along with ontogeny of the embryo, time after extrusion and egg diameter could be used as a tool to predict the hatch date. This has important implications for the preparation of the hatchery and enrichment of live food.

Conclusion

The relatively high fecundity and limited seasonality of spawning of South African *S. serrata* may be an adaptation to the variable nature of South African estuaries, of which approximately 70% are closed by barrier sandbars that open intermittently (Bell et al. 2001; Viljoen and Cyrus 2002). The spawning characteristics of South African *S. serrata* are nevertheless comparable to those observed for the genus throughout its distribution. This should be considered when formulating future fisheries management or conservation policies if these are to

be adapted from those established elsewhere.

Using the fecundity data, the average percent hatching success and the percent females that spawn on a monthly basis, a total of 1,374,488 first zoea (Z1) larvae could be expected per kg of female per mo. For practical aquaculture purposes, maintaining a relatively small number of female broodstock (approximately 20 animals in this study) under the correct artificial conditions could ensure a regular, year-round supply of eggs for supplying a hatchery. The comparatively high fecundity of the crabs means that relatively few individuals need to be caught from the wild for stocking commercial hatcheries, as opposed to penaeid shrimp, for example (Wickins and Lee 2002). The crabs spawned easily with little requirement for special diets or environmental manipulation. The life cycle has also been closed in captivity (Quintio et al. 2001). This implies that domestication of the broodstock will not be difficult, which could reduce the dependence on wild-caught broodstock in the future.

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