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Population structure, fecundity and embryo loss of the sea grass shrimp *Latreutes pymoeus* (Decapoda: Hippolytidae) at Inhaca Island, Mozambique

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Latreutes pymoeus is a poorly studied tropical and sub-tropical shrimp species that mainly lives on sea grass beds. Samples were collected from sea grass beds of Inhaca Island, Mozambique, during August 2005 at neap/spring and low/high tides. Specimens were identified, sexed, counted and morphometric measurements were made. Ovigerous females were classified as small (carapace length (CL): 2.7–3.2 mm), medium (CL: 3.3–3.8 mm) and large (CL: 3.9–4.4 mm). Embryo masses were carefully removed from the pleopods with forceps, eggs staged and counted. On average, about 20% more males were found than females (0.64 ± 0.25 and 0.56 ± 0.28 ind m^{-2} , respectively), but males were significantly smaller (2.25 ± 0.32 and 2.60 ± 0.47 mm CL for males and females, respectively). At 3.1 mm CL at least 50% of the females found carried embryos in the pleopods. Average (\pm SD) brood size increased significantly with female length (76 ± 18 , 133 ± 64 and 205 ± 61 , for small, medium and large ovigerous females). The number of embryos decreased significantly over the incubation period for each size-class of the shrimp. Brood loss from embryonic Stage I to Stage IV for small, medium and large shrimp were 19.8%, 36.5% and 41.8%, respectively. Although an increase in brood loss was observed with increasing shrimp size, senescence did not seem to occur since larger shrimps carried a higher number of embryos and negative allometry was not recorded. Mean embryo volume, in the same development stage, was not significantly different among the small, medium and large shrimp, increasing significantly from 0.014 mm^3 to 0.029 mm^3 from the first to last embryonic stages.

INTRODUCTION

Sea grass beds are an important component of tropical and temperate marine ecosystems. These meadows constitute areas of high productivity, providing habitat, feeding and breeding grounds for a diversity of fauna (e.g. Heck et al., 1995), and generally supporting important human exploitation (Sheridan, 1997). They sustain a high diversity and abundance of microphytobenthos and micro-organisms (e.g. Schneider & Mann, 1991) and associated fauna (e.g. Brouns & Hejls, 1985), although data on associated caridean shrimps are scarce (De Grave, 1999).

Caridean shrimps occupy a key position in trophic processes within sea grass systems by exerting a strong influence on the structure and dynamics of the lower trophic levels of the system, as well as by transferring a major portion of their relatively high productivity to higher consumers (Howard, 1984). Caridean shrimps have already been shown to have very diverse and sometimes complex reproduction processes (e.g. Bauer, 1986, 1989). Decapod crustaceans' reproductive output is considered one of the most determinant factors of their life history pattern. Interspecific comparisons of reproductive output have provided much of the basis for theoretical considerations of life history strategies (e.g. King & Butler, 1985). On the other hand, intraspecific variations of the reproductive output have been considered as prominent

decapod population characteristics. For instance, they have been used in defining stock units in exploited species (Morizur et al., 1981), in detecting population variability in relation to habitat variations (Thessalou-Legaki, 1992), and in studying the reproductive biology of species (Somerton & Meyers, 1983).

Latreutes pymoeus occurs from the Red Sea and East Africa to Australia and Japan, extending to the central Pacific, and is usually associated with sea grasses and/or seaweeds. However, most studies on this species have focused on its taxonomy (De Grave, 1999).

In this study we contribute to the knowledge of the biology of one of the most abundant caridean species of sea grass beds of Inhaca Island, Mozambique. The East African coast, and more precisely the shores of Inhaca Island, support diverse and abundant sea grass meadows (e.g. Bandeira, 1995), but few studies have been published either on their ecological function or associated fauna (e.g. Paula et al., 2001). By increasing the ecological knowledge, as well as the biology of the species, it is possible to construct baseline information for future comparative studies. The main goal of this study is to evaluate the population structure, embryo production and brood loss during the incubation period in small, medium and large sized ovigerous females of *Latreutes pymoeus* collected off Inhaca Island, Mozambique.

MATERIALS AND METHODS

Study area

Inhaca is a small island (42 km²) situated in southern Mozambique, East Africa (26°S 33°E). The island is positioned in a transitional region of tropical to warm subtropical conditions and constitutes a barrier between Maputo Bay and the Indian Ocean. Its climate is characterized by hot, wet (September–March) and warm, dry (April–September) seasons (Bandeira, 1995).

This study was performed in the southern bay of Inhaca Island, called Saco. The bay covers an area of 15.4 km² and it is surrounded by a diverse mangrove community (De Boer, 2000). Sampling was conducted at the extensive sea grass bed, dominated by *Thalassia hemprichii* (Ehrenb.) and *Halodule wrightii* Ashers, that occupies subtidal areas of Saco Bay (Paula et al., 2001). Tides are semidiurnal, with more than 3 m tidal amplitude during the spring-tide period.

Sampling

Inhaca Island is a Mozambiquean natural reserve therefore sampling had to be reduced to a minimum. The data presented here were the by-catch resulting from some sampling the University of Eduardo Mondlane was carrying out at Saco Bay. One month is not sufficient to characterize a species; however, this study only intends to be a preliminary work, presenting baseline information, especially when nothing is known regarding *Latreutes pymoetus*. Samples were taken during a complete lunar cycle at low and spring tides, during August 2005. Each day, eight trawls were performed along pre-fixed 50 m long transects parallel to the mangrove fringe, by means of an aluminium 1-m wide beam trawl (1×0.25 m mouth aperture) fitted with a 1-mm mesh body and cod-end-net, equipped with an extra 4 kg of lead to ensure bottom settling.

Population structure and maturation

Shrimps were preserved in buffered 4% formaldehyde diluted with seawater, and taken to the laboratory for examination. Specimens were identified, counted and their sex determined (by investigating the presence (male) or absence (female) of an appendix masculina on the second pair pleopod). Morphometric measurements were taken under a binocular microscope with a calibrated micrometer eyepiece, to the nearest 0.02 mm: carapace length (CL), from the posterior margin of the eye orbit to the posterior

mid-dorsal margin of the carapace; standard length (SL), from the posterior margin of the orbit to the tip of the telson; and total length (TL), from the tip of the rostrum to the tip of the telson.

According to the criteria used by Kensler (1967) and Aiken & Waddy (1980), female maturation size was determined by calculating the size which corresponded to 50% of ovigerous females. The proportion of mature females by size was fitted to a logistic equation:

$$P = \frac{1}{1 - e^{-(a+b \times CL)}} \quad (1)$$

With the logarithmic transformation given by:

$$\ln\left(\frac{1-P}{P}\right) = a + b \times CL \quad (2)$$

where 'P' is the predicted mature proportion, 'a' and 'b' the estimated coefficients of the logistic equation ('a' as the y-intercept value and 'b' as the slope value), and CL the carapace length. The estimation of parameters of this equation was made by correlation analysis of variables of P and CL after linearization. Size at sexual maturity (CL₅₀), corresponding to a proportion of 50% sexually mature females, was estimated as the negative of the ratio of the coefficient (CL₅₀ = -(a/b)) by substituting P=0.5 in eqn 1.

Fecundity, egg development and egg loss

For a better understanding of the effect of female size on several reproductive characteristics, ovigerous females were divided into three non-contiguous size-classes with the same interval: small (CL: 2.7–3.2 mm), medium (CL: 3.3–3.8 mm) and large (CL: 3.9–4.4 mm). The embryo mass was carefully removed from the pleopods with forceps and staged according to Bauer (1986): Stage I, early embryos with no visible blastoderm; Stage II, blastoderm distinct with half yolk, no eye development; Stage III, embryos with eyes, abdomen not free from cephalothorax; Stage IV, embryos near to hatching, little or no yolk, large eyes, abdomen free from the cephalothorax. Right after sampling, for every egg stage of each size-class, ten embryos from each of ten randomly chosen females were selected and their length (L) and width (W) measured under a microscope with a calibrated micrometer eyepiece to the nearest 0.001 mm. Embryo volume (V) (mm³) was calculated using the formula for oblate spheroids V=1/6 (πW²L). Direct egg counting was used in the present work. Differences between brood

Table 1. Average (±SD) density (absolute and relative) and average, maximum and minimum carapace length of total males and females, as well as ovigerous and non-ovigerous females. Within columns, different superscript letters represent significant differences between males and females (total), while different superscript numbers represent significant differences between ovigerous and non-ovigerous females (P<0.05).

	Density		Carapace length		
	Absolute (m ⁻²)	Relative (%)	Average (±SD)	Minimum	Maximum
Male	0.64 ±0.25	54.0 ±20.6	2.2 ±0.3 ^a	1.2	4.0
Female (non-ovigerous)	0.36 ±0.27 ¹	30.0 ±22.0	2.6 ±0.41	1.3	3.9
Female (ovigerous)	0.20 ±0.35 ²	16.0 ±2.9	3.4 ±0.32	2.5	4.4
Females (total)	0.56 ±0.28	46.0 ±23.2	2.9 ±0.6 ^b	1.3	4.4

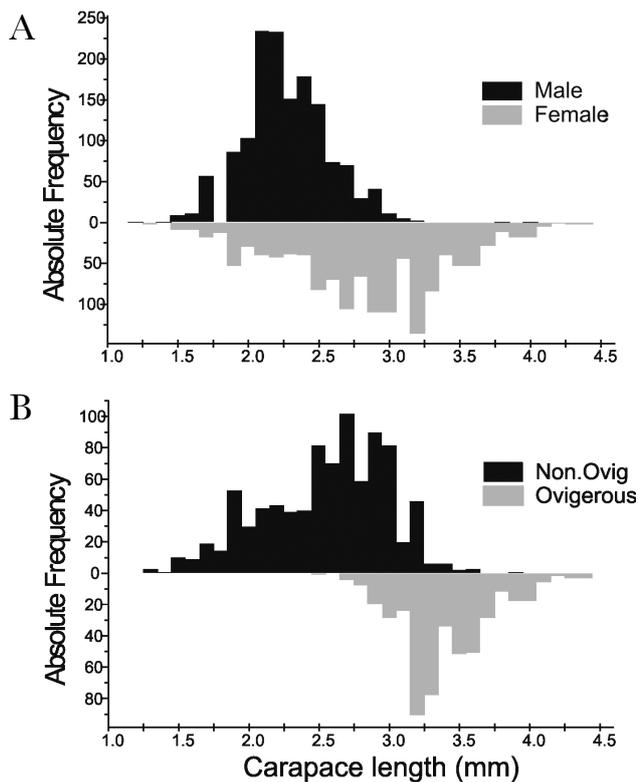


Figure 1. *Latreutes pymoeus* population structure. (A) Male and female frequency; (B) non-ovigerous and ovigerous female frequency.

size and embryo volume at each stage, from different sized animals, were analysed.

Statistical analysis

A Student's *t*-test was used to compare average density and size (CL) between males and females, and between ovigerous and non-ovigerous females. Comparison of morphometric relations (SL/CL and TL/CL) between males and females were examined using linear regression analysis.

A one-way analysis of variance (ANOVA) was used to compare egg number and volume at each stage, between the female size-classes. When ANOVA assumptions, homogeneity of variances and normal distribution of residuals were not met, the data were transformed (log or square root) and tested again. The equivalent non-parametric Kruskal–Wallis test was used when transformation failed to meet the ANOVA assumptions. A Tukey or Dunn multi-comparisons test was used if ANOVA or Kruskal–Wallis, respectively, showed a significant treatment effect. The sex ratio was compared and tested with a χ^2 -test. All the results were considered statistically significant at $P < 0.05$.

For egg Stages I (fecundity) and IV (potential fertility), the relationship between number of embryos and animal size (CL) was examined using linear regression analysis. For both regressions, a standard deviation of 5% of the obtained slope values was calculated. If the interval, slope value $\pm 5\%$, includes 3, since the number of embryos approximates a volume, it is possible to consider the existence of isometry (see Bauer, 1991).

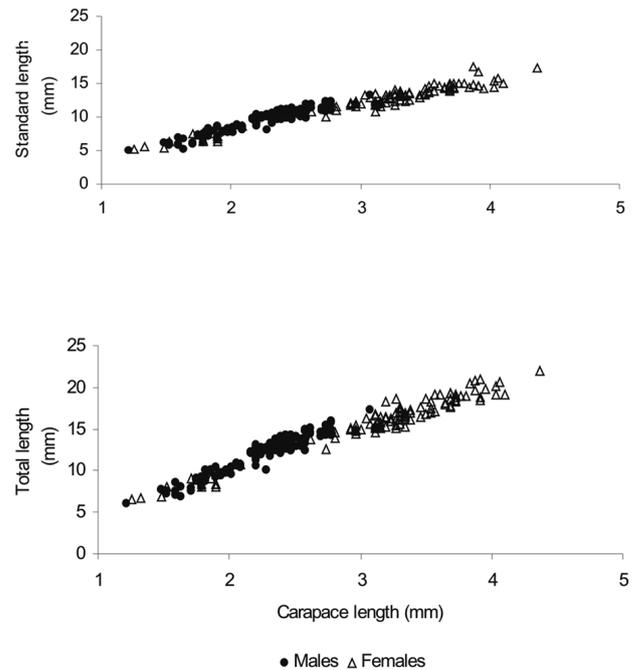


Figure 2. *Latreutes pymoeus* morphometric regressions (standard length vs carapace length; total length vs carapace length) for males and females.

RESULTS

Population structure and maturation

A total of 2889 shrimps (1536 males, 870 non-ovigerous females and 483 ovigerous females) was collected. There was no significant difference between male and female absolute density, and total density reached values a little higher than 1 shrimp m^{-2} . A significant difference was only observed between ovigerous and non-ovigerous females, with non-ovigerous females representing almost 65% of total female density (Table 1). Males were significantly smaller than females, especially when compared with ovigerous females (Table 1 and Figure 1). There were few male specimens smaller than the smallest female shrimp and while smaller shrimps could be either males or non-ovigerous females, larger shrimps were usually ovigerous females (Figure 1).

Figure 2 shows the morphometric relations in males and females (SL/CL and TL/CL) and significant differences were found between both regressions of males and females. With increasing CL, males tend to increase SL and TL more rapidly when compared with females, showing a significant higher slope value (Figure 2):

Linear regression of males:

$$SL = 4.4419CL - 0.5204 \quad (R^2 = 0.89); \quad TL = 5.8983CL - 1.3213 \quad (R^2 = 0.90)$$

Linear regression of females:

$$SL = 3.8428CL + 0.3271 \quad (R^2 = 0.95); \quad TL = 5.0694CL - 0.1702 \quad (R^2 = 0.95)$$

The smallest ovigerous female was 2.5 mm in CL (Table 1) and when females' CL reached 3.1 mm, at least 50% of them were ovigerous (Figure 3).

Fecundity, egg development and egg loss

The number of newly extruded embryos increased significantly with increasing female size (Table 2). The

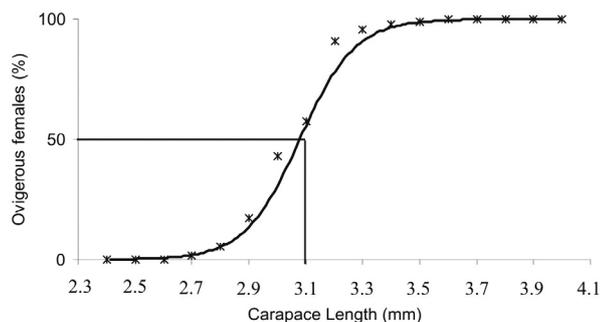


Figure 3. Logistic function fitting the cumulative proportion of *Latreutes pymoeus* ovigerous females. $P = \frac{1}{1 - e^{-(a+b \cdot CL)}}$, where a= 31.92 and b= -10.40 (R²=0.97).

Table 2. Average (\pm SD) number of embryos during embryonic development for small, medium and large ovigerous female shrimps (N, number of sampled ovigerous females). Different superscript letters within rows and different superscript numbers within columns represent significant differences (P<0.05).

Size	Embryonic stage			
	I	II	III	IV
Small	76 \pm 18 ^{a,1} (N=23)	75 \pm 19 (N=30)	63 \pm 23 (N=26)	61 \pm 21 ^b (N=20)
Medium	133 \pm 64 ^{a,2} (N=23)	131 \pm 43 ^a (N=30)	89 \pm 30 ^b (N=28)	85 \pm 33 ^b (N=20)
Large	205 \pm 61 ^{a,3} (N=21)	171 \pm 52 (N=21)	120 \pm 54 ^b (N=10)	119 \pm 68 ^b (N=10)

number of embryos decreased over the incubation period for each size-class, and significant differences were found between early and late embryonic stages (Table 2). Brood loss from embryonic Stage I to Stage IV for small, medium and large shrimps was 19.8%, 36.5% and 41.8%, respectively, which indicates a higher embryo loss in larger females.

There was a linear relationship between log (embryo number) and log (CL) (Figure 4):

Egg Stage I: $\log(\text{embryo number}) = 3.694 \log(\text{CL}) + 0.300$ ($r^2 = 0.84$, $P < 0.01$, $N = 67$)

Egg Stage IV: $\log(\text{embryo number}) = 3.112 \log(\text{CL}) + 0.516$ ($r^2 = 0.63$, $P < 0.01$, $N = 50$).

Table 3. Average (\pm SD) embryo volume during embryonic development for small, medium and large ovigerous female shrimps. Different superscript letters within rows represent significant differences (P<0.05).

Size	Embryonic stage			
	I	II	III	IV
Small	0.014 \pm 0.002 ^a	0.016 \pm 0.002 ^b	0.022 \pm 0.002 ^c	0.029 \pm 0.002 ^d
Medium	0.014 \pm 0.002 ^a	0.016 \pm 0.002 ^b	0.022 \pm 0.002 ^c	0.028 \pm 0.002 ^d
Large	0.014 \pm 0.002 ^a	0.015 \pm 0.002 ^b	0.021 \pm 0.002 ^c	0.028 \pm 0.002 ^d

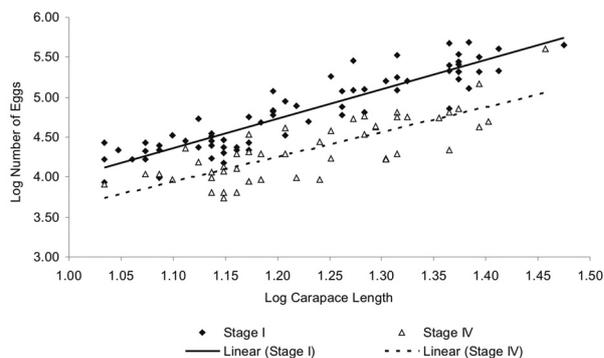


Figure 4. Relationship between Ln number of newly extruded embryos (fecundity) or number of embryos at Stage IV (potential fertility) and *Latreutes pymoeus* female size (Ln CL – carapace length).

Significant differences were found between both regressions' slopes, demonstrating also a differential embryo loss between shrimp size-classes, with higher losses in bigger shrimps. Considering the second regression, because the 95% confidence limits on 'b' include b=3, the increase in brood size (egg Stage IV) with female size can be described as isometric. For the first regression (egg Stage I), the same relation can be described as positively allometric.

The average volume of embryos at the same stage was not significantly different among the small, medium and large female shrimp sampled. Embryo volume significantly increased from 0.014 mm³ to 0.029 mm³ (100%) at embryonic Stages I and IV, respectively (Table 3).

DISCUSSION

Population structure and maturation

The high variability in shrimp density found during the sampling period reflected the high degree of patchiness, both spatially and temporally (even for a short period of time), that shrimp may display (e.g. Omori, 1974). Other studies on penaeid shrimps collected at Saco Bay (e.g. Dall et al., 1990), also reported this density variation, namely due to immigration and emigration in large numbers, from coastal areas during spring tides. Consequently the availability of shrimps can change markedly over short periods of time.

In many gonochoristic carideans, males are smaller than females (Bauer, 1996). Males can produce sufficient numbers of the energetically inexpensive sperm at small body size to

fertilize the egg mass of the largest females. Males of such species do not guard nor defend reproducing females, and thus large body size is not selected for (Bauer, 1996). In fact, small males have an advantage for escaping predation. Females, on the other hand, with increasing body size, can produce larger broods of energetically expensive, larger embryos (Bauer, 1991).

A large percentage of ovigerous females is expected throughout the year, as was already observed by Bauer (1989), on species of the same genus, that presented a percentage of ovigerous females higher than 40% permanently. If instead of counting the number of ovigerous females we take into consideration the maturation of the gonads, we suspect that the number of mature females in the population would be much higher, especially because it has been shown that, for *Latreutes* species, 1–4 days can pass between hatching of one brood and oviposition of the next (Bauer, 1989). It is generally agreed that the inclusion of other criteria, such as the ovarian condition, provides a better estimation of size at maturation (e.g. Kensler, 1967).

In previous studies on *Latreutes parvulus* and *L. fucorum*, Bauer (1989) set the size of female maturity, defined as the size of smallest ovigerous female observed, between 1.6 and 1.8 mm CL, respectively. In our work, the smallest ovigerous female was much larger (2.4 mm CL).

Fecundity, development and egg loss

Breeding patterns in crustaceans are a result of both environmental conditions and trade-off between growth and reproductive processes (Anger, 2001). While several studies have addressed shrimp fecundity, only a few have addressed, in detail, embryo production and brood loss for the whole size range in a particular species (e.g. Calado & Narciso, 2003). While fecundity may indicate a species reproductive potential, brood loss can influence the real reproductive output as well as subsequent recruitment, and therefore should be considered a factor in models of fecundity-per-recruitment (Morizur et al., 1981).

In this study, it was demonstrated that within the species, brood size was determined predominantly by female size, as is usual for caridean shrimps. Larger females produced a higher number of newly extruded embryos than expected from the allometric relation. However, due to the higher percentage of brood loss in larger females, when comparing the number of embryos, in late developmental stage, an isometric relation can be observed. As a result, we can conclude that senescence does not seem to occur in *L. pymoeus*, with the largest shrimps in the sampled population always producing more embryos, as expected in 'r-selected' species. Additionally, if senescence occurred in the sampled population, negative allometry rather than isometry should have been recorded, as expected in 'k-selected' species (see Bauer, 1991).

Brood loss in decapods may be induced by numerous factors: aborted development, mechanical loss due to abrasion, maternal cannibalism, embryo predation and parasitism (see Kuris, 1991 for a review). The brood loss reported in the present study for *Latreutes pymoeus* (19–42%) is within the range reported by Kuris (1991) for decapod crustaceans and by Oh & Hartnoll (1999) for caridean shrimps (12–74%).

During incubation in decapods, an increase in egg length and volume is a general pattern (Wear, 1974). While embryos of *L. pymoeus*, at all stages, were smaller in volume than the majority of the caridean shrimps, the volume increment (100% of initial embryo volume) in all shrimp size-classes is within the range described for other caridean shrimp species (e.g. Lardies & Wehrtmann, 2001). As in other carideans, such as *Lysmata seticaudata* (e.g. Calado & Narciso, 2003) the average volume of embryos at the same stage was not significantly different among the small, medium and large shrimps collected. The increase in embryo volume during the incubation period is known to be mainly a consequence of the increase in water content, either by water uptake to the embryo or retention of metabolic water resulting from respiration (Amsler & George, 1984). This egg swelling is generally considered as a cause of brood loss, since the physical space available under the abdomen for embryo attachment is a limiting factor for embryo production in decapods (e.g. Lardies & Wehrtmann, 2001). As a result, with an increase in egg numbers, as observed in larger females, an increase in egg volume during egg development can lead to a higher percentage of brood loss.

This study only addressed a comparison of brood size across female dimensions and egg stages over a one-month period. To better understand the population structure and reproductive dynamics of this species, future studies should focus on periodic samples over a one or two year period.

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