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Population structure and egg production of the seagrass shrimp *Hippolyte kraussiana* Stimpson, 1860 (Decapoda: Hippolytidae) at Inhaca island, Mozambique

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Summary

Hippolyte kraussiana, a poorly known tropical species, was collected from seagrass beds of Inhaca island, Mozambique, in August 2005 during neap/spring and low/high tides by means of a small aluminium trawl fitted with a 1 mm mesh body and cod-end-net. Specimens were identified, sexed, counted and morphometric measurements were made. Ovigerous females were classified as small [carapace length (CL): 1.10–1.35 mm] and large (CL: 1.40–1.80 mm); the embryo mass was staged and counted. Females showed, on average, a much higher density when compared with males (0.064 ± 0.003 and 0.153 ± 0.11 ind.m⁻² for males and females, respectively) and were significantly larger (0.9 ± 0.1 and 1.3 ± 0.1 mm of CL for males and females, respectively). At 1.28 mm of CL at least 50% of the females were found carrying eggs on the pleopods. Average (\pm SD) brood size of small and large ovigerous females were 33 (± 7) and 43 (± 13). The number of embryos decreased significantly over the incubation period for each size-class. Average (\pm SD) brood loss from embryonic stage I to stage IV for small and large female shrimp was 47% (± 12.4) and 58% (± 15.8), respectively. Senescence seems to occur since larger females always had a higher brood loss and negative allometry was recorded. The mean embryo volume in the same development stage was not significantly different among the small and large shrimps, increasing significantly from 0.013 mm³ to 0.022 mm³ (69%) from first to last embryonic stage, respectively. This study intends to give baseline information about egg production and population structure, to contribute to a better knowledge of this little known species.

Key words: *Hippolyte kraussiana*, population structure, fecundity, egg development, brood loss, seagrass, Mozambique

Introduction

Seagrass beds form an important component of tropical and temperate coastal marine ecosystems. These

meadows constitute areas of high productivity, providing habitat, feeding and breeding grounds for a diversity of fauna (Larkum et al., 1989; Heck et al., 1995;

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Vermaat et al., 1997), and supporting important human exploitation (Sheridan, 1997). They sustain a high diversity and abundance of microphytobenthos and microorganisms (Stoner, 1980; Ansari, 1984; Schneider and Mann, 1991; Cariou-Le Gall and Blanchard, 1995) and associated fauna (De Grave, 1999; Schwamborn and Criales, 2000), although data on associated caridean shrimp is generally lacking (De Grave, 1999).

It is known that the caridean shrimps occupy a key position in trophic processes within the seagrasses 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 shown to have a very diverse and sometimes complex reproductive processes (e.g., Bauer, 1986, 1989; Lin and Zang, 2001). 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 (Clarke, 1979; Hines, 1982; King and Butler, 1985). Also, 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 species which support fisheries (Morizur et al., 1981) and detecting population variability in relation to habitat variations (Thessalou-Legaki, 1992).

The genus *Hippolyte* Leach, 1814, comprises more than 30 species occurring all around the world except in extremely cold waters. It is often taxonomically considered a very difficult genus, as many species display considerable variation, particularly in the morphology of the rostrum (Udekem d'Acoz, 1996). Little is known about this genus, particularly the biology of these crustaceans including the seagrass's caridean shrimp *Hippolyte kraussiana*. The species distribution ranges from South Africa to Madagascar and along the Indian Ocean shores (Udekem d'Acoz, 1996).

The East African coast, and more precisely the Inhaca island shores, bear diverse and abundant seagrass meadows (e.g. Bandeira, 1995, 1996, 1997), but few studies have been published either on the associated fauna (e.g. Paula et al., 2001). By increasing the ecological or biological knowledge of species, it becomes possible to construct baseline information, to which future studies can be compared. In this study we intend to increase the knowledge on the biology of an abundant seagrass's species, *Hippolyte kraussiana*. To achieve this goal, population structure, embryo production and brood loss during the incubation period in small and

large sized ovigerous females collected off Inhaca island, Mozambique, will be evaluated.

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. The climate is characterized by hot, wet (September–March) and warm, dry (April–September) seasons (Bandeira, 1995). On the west coast of Inhaca there is a dense population of the seagrass *Thalassodendron ciliatum* (Forskål), which dominates the seagrass assemblage that includes patches of *Halodule uninervis* (Forskål). In the southern bay, the flat sides of the channel between Ponta Torres and Saco mangrove are covered with seagrass species dominated by *Thalassia hemprichii* (Ehrenb.) and *Halodule wrightii* Ashers. The third main association of seagrasses occurs on the island's southern banks, between the island and Machangulo peninsula, and it is dominated by the southern species *Zostera capensis* Setchell (Paula et al., 2001).

This study was performed in the southern bay of Inhaca island, called Saco. The bay covers an area of 15.4 km², is surrounded by a diverse mangrove community (De Boer, 2000) and is classified as a Mozambiquean natural reserve a status implemented in the island that limits sampling to a minimum.

Sampling

The data presented here were obtained as a bycatch of a penaeid shrimp sampling program that University of Eduardo Mondlane conducted at the extensive seagrass bed that occupies subtidal areas of Saco. Samples were taken during a complete lunar cycle, in August 2005, for three consecutive days during both neap and spring tides. Each day, eight trawls were performed along each pre-fixed 50 m long transect 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 4 extra kilograms of lead to ensure bottom settling.

Population structure, maturation and morphometrics

Shrimp samples were preserved in buffered 4% formaldehyde diluted with seawater, and returned to the laboratory for examination. The specimens were identified, sex determined (by investigating the presence

(male) or absence (female) of an appendix masculina on the second pair of pleopods) and counted. Carapace length (CL) was measured from the posterior margin of the eye orbit to the posterior mid-dorsal margin of the carapace, under a stereo microscope with a calibrated micrometer eyepiece to the nearest 0.02 mm.

Size of mature females was determined according to the criteria used by Kensler (1967) and Aiken and Waddy (1980) regarding the presence of attached eggs. The proportion of mature females by size was fitted to a logistic equation, Eq. (1):

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

with the logarithmic transformation given by Eq. (2):

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

where P is the predicted mature proportion, and a and b the estimated coefficients of the logistic equation. The estimation of parameters of this equation was made by correlation analysis of variables P and CL after linearization. Size at sexual maturity (CL_{50}), corresponding to a proportion of 50% sexually mature females, was estimated as the negative ratio of the coefficient [$CL_{50} = -(a/b)$] by substituting $P = 0.5$ in Eq. (1).

Fecundity, egg development and egg loss

Ovigerous females were classified as small (CL: 1.10–1.35 mm) and large (CL: 1.40–1.80 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. After sampling, for every egg stage, 10 eggs from each of the 10 randomly chosen females of each size class, were selected and their length (L) and width (W) measured under a stereo microscope with a calibrated micrometer eyepiece to the nearest 0.01 mm. Embryo volume (V) (mm^3) was calculated using the formula for oblate spheroids $V = 1/6 (\pi W^2 L)$ used by several authors (e.g., Calado and Narciso, 2003). Direct egg counting was performed. The differences between brood 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. Morphometric relations (SL/CL and TL/CL) were examined using linear regression analysis (Sokal and Rohlf, 1995).

To compare egg number and volume at each stage, a one-way ANOVA was used for each female size group. When ANOVA assumptions, homogeneity of variances and normal distribution of residuals, were not met, the data was transformed (log or square root) and tested again. 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 significant treatment effect. Sex ratio was compared and tested with a χ^2 test. All the results were considered statistically significant at $p < 0.05$ level (Sokal and Rohlf, 1995).

For egg stage I (fecundity) and IV (potential fertility), relationship between number of embryos and animal size (CL) was examined using linear regression analysis (Sokal and Rohlf, 1995). The confidence limits of linear regression slopes were estimated and compared with an expected slope of 3, since the number of embryos approximates a volume, to assess the existence of isometry (see Bauer, 1991). In allometric analysis with log-transformed measures, where y is a volume and x is a linear measure, a slope of 3 indicates isometry, significantly < 3 negative allometry, and significantly > 3 positive allometry.

Results

Population structure, maturation and morphometry

A total of 557 individual shrimp (23 males, 204 non-ovigerous females and 330 ovigerous females) were collected. Females showed, on average, a much higher density when compared to males (0.0064 ± 0.004 and $0.153 \pm 0.11 \text{ ind.m}^{-2}$ for males and females, respectively) and were significantly larger (0.9 ± 0.1 and $1.3 \pm 0.1 \text{ mm}$ of CL for males and females, respectively) (Table 1, Fig. 1). The size of 1.28 mm of CL can be considered as the early maturity since at least 50% of females were ovigerous (Fig. 2).

Fecundity, development and egg loss

The number of newly extruded embryos increased significantly with increasing female size (Table 2). The number of embryos decreased over the incubation period for each size-class, and significant differences

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

	Density (m ²)	Carapace length (mm)		
		Average (\pm SD)	Minimum	Maximum
Male	0.006 \pm 0.004 ^a	0.9 \pm 0.1 ^a	8	1
Non-ovigerous female	0.056 \pm 0.040 ^{1,b}	1.2 \pm 0.1 ^{1,b}	9	16
Ovigerous female	0.096 \pm 0.078 ^{2,c}	1.3 \pm 0.1 ^{2,b}	11	18

Table 2. Average (\pm SD) number of embryos during embryonic development for small and large ovigerous female shrimp (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	33 \pm 10 ^{a,1} (N= 40)	26 \pm 8 ^b (N= 27)	22 \pm 7 (N= 13)	18 \pm 8 ^c (N= 10)
Large	47 \pm 13 ^{a,2} (N= 25)	34 \pm 10 ^b (N= 27)	27 \pm 14 (N= 8)	20 \pm 10 ^c (N= 10)

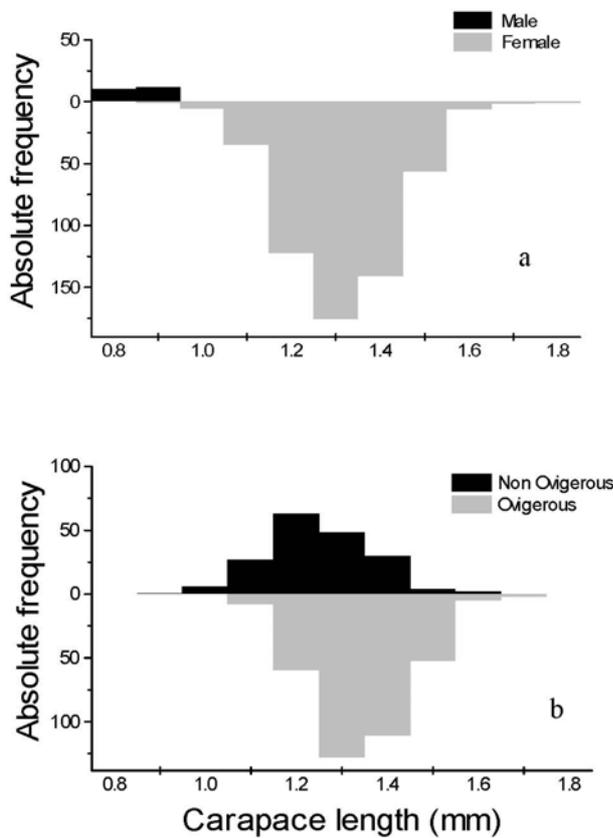


Fig. 1. *Hippolyte kraussiana* population structure. (a) Male and female frequency. (b) Non-ovigerous and ovigerous female frequency.

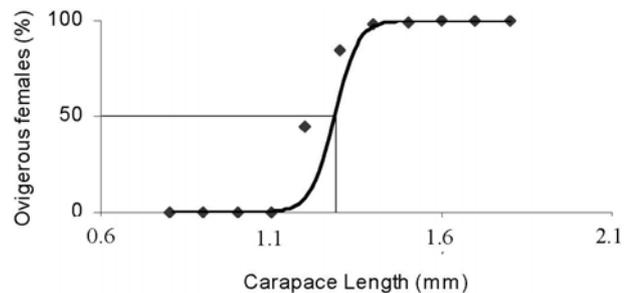


Fig. 2. Logistic function fitting the cumulative proportion of *Hippolyte kraussiana* ovigerous females.

were found between early and late embryonic stages (Table 2). Brood loss from embryonic stage I to stage IV for small and large shrimp was 47% and 58%, respectively.

There is a linear relationship between log (embryo number) and log (CL) (Fig. 3):

- Egg stage I: $\log(\text{embryo number}) = 3.2618 \log(\text{CL}) + 2.5934$ ($r = 0.70, P < 0.001$)
- Egg stage IV: $\log(\text{embryo number}) = 1.9627 \log(\text{CL}) + 2.1443$ ($r = 0.56, P < 0.05$)

Significant differences were found between slopes of both regressions ($P < 0.05$). Considering only the second regression (egg stage IV) and because 95% confidence limits on b include $b < 3$, the increase in brood size with female size can be described as negatively allometric.

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

Size	Embryonic stage			
	I	II	III	IV
Small	0.013 \pm 0.001 ^a	0.015 \pm 0.001 ^b	0.018 \pm 0.002 ^c	0.022 \pm 0.002 ^d
Large	0.013 \pm 0.001 ^a	0.015 \pm 0.001 ^b	0.017 \pm 0.002 ^c	0.021 \pm 0.002 ^d

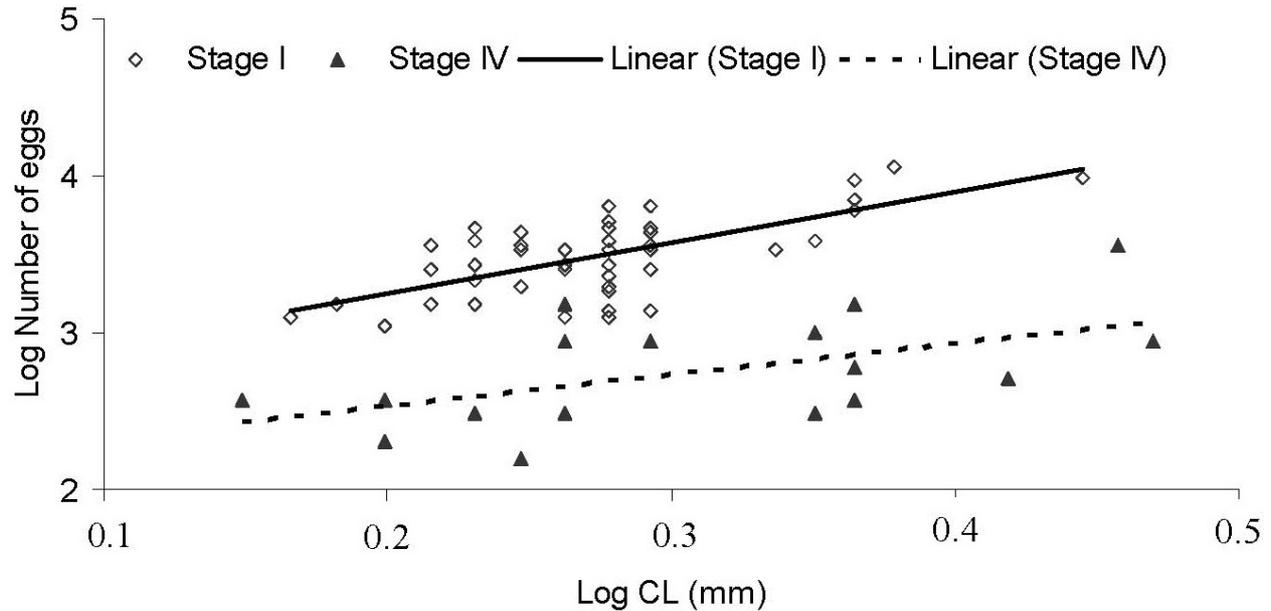


Fig. 3. Relationship between the number of newly extruded eggs (fecundity) or number of eggs at stage IV (potential fertility) and *Hippolyte kraussiana* female size (CL, carapace length).

The average volume of embryos at the same stage was not significantly different among the small and large female shrimp sampled. Embryo volume significantly increased 69% from 0.013 mm³ to 0.022 mm³ from embryonic stages I to IV, respectively (Table 3).

Discussion

Population structure

In many gonochoristic carideans, males are smaller than females (Bauer, 1996). Large size is advantageous to females because egg production shows a high positive correlation with body size in carideans and other decapods (Bauer, 1991). Males, on the other hand, can produce sufficient numbers of the energetically inexpensive sperm at small body size to fertilize the spawn of the large females. Where studied, males of such species do not guard nor defend reproducing females, instead expending energy in searching for and contacting many females in order to meet and mate with

a receptive one (“pure searching” mating tactic; Wickler and Seibt, 1981; see also Bauer, 1996). In fact, small males are also more cryptic, an advantage for escaping predation and, additionally, put less energy into growth (Bauer, 1996). A female, however, must grow to a greater size in order to produce the large, energetically-expensive, vitellogenic oocytes (Bauer, 2000).

Furthermore, although most species of decapod crustaceans have separate sexes, sex change from male to female is not uncommon, especially in some families of caridean shrimps. Protandry has been reported in 37 decapod species, most of which are carideans (Bauer, 2000). A well documented case of protandry in the Caridea is present in several *Pandalus* species such as *Pandalus platyceros* Brandt, 1851 and *Pandalus hypsinotus* Brandt, 1851 (Butler, 1980), i.e., all individuals function first as males and then become females as they increase in size and age. In protandric carideans, the transformation is marked externally by loss of the appendices masculinae (shown to be copulatory structures by Bauer, 1976) and by modi-

fications in the endopods of first pleopods (Dohrn, 1950; Butler, 1980; Charniaux-Cotton, 1975).

The absence of larger males and the absence of females in the size range obtained for males in this study suggest simple protandry. Further studies are necessary to completely validate this hypothesis, namely data concerning morphology of gonads and appendages. The low density of males can be explained by its likely escape through the net, given their small size (less than 1 mm).

Maturation

Breeding patterns in crustaceans are a result of a trade-off between environmental factors and reproductive processes (Flores and Paula, 2002). It is assumed that in subtropical and tropical environments, reproduction is commonly continuous because environmental conditions are permanently favourable for gonad development, feeding and larval release, whereas in temperate regions it is often restricted to a few months (Emmerson, 1994; Ituarte et al., 2004).

Gonad maturation is mainly influenced by temperature, but other parameters such as light, food availability, salinity and tidal periodicity seem to be the most prominent factors controlling reproduction in crustaceans (Giese and Kanatani, 1987; Meusy and Payen, 1988). In a similar study, Bauer (1989) analysed species of the same genus that presented a percentage of ovigerous females higher than 40%. If females were producing successive broods without interruption, one might expect that values for ovigerous female abundance would be consistently high. However, laboratory observations have shown that 1–4 days can pass between hatching of one brood and oviposition of the next (Bauer, 1989); thus discrete observations have to be treated with caution.

Age or size at sexual maturity is by itself a valuable parameter in defining life-history traits (Stearns, 1976), which varies considerably in a number of decapod species, either according to habitat productivity (Conde and Díaz, 1992), latitude (Hines, 1989) or shelter availability (Beck, 1995). In previous studies with *Hippolyte curacaoensis* Schmitt, 1924, Bauer (1989) set the size of female maturity, defined as the size of smallest ovigerous female observed, as 1.70 mm CL. In our work, the smallest ovigerous female was 1.14 mm in CL, smaller than observed for related species.

Fecundity and brood loss

The production of eggs requires an optimal allocation of energy into growth and reproduction for maximizing parental fitness (Llodra, 2002). Tempera-

ture has been identified as the main abiotic factor influencing the reproductive activity (Pinheiro and Fransozo, 2002). Other authors have pointed out the importance of photoperiod (Giese and Kanatani, 1987), intertidal zonation (Emmerson, 1994), rainfall (Litulo, 2004), salinity, tidal and lunar periodicity (Emmerson, 1994) as primary modulators of breeding, growth and egg production.

While fecundity may give us an idea of the species reproductive potential, brood loss influence the real reproductive output and subsequent offspring. Therefore, it should be considered a factor in models of fecundity-per-recruitment (Morizur et al., 1981; Campbell, 1985), since it varies considerably among decapods. Brood size within species of decapods is related to body size. The analyzed specimens are very small, thus brood size is constrained by body size. Flexibility is thus primarily introduced by the dependent variables, egg size and number. The options open to small crustaceans are, therefore, more limited than those available to larger animals. According to Mauchline (1988), there may be a minimum viable size of egg. Consequently, the potential number of eggs that small crustaceans can produce within a single brood is limited. As in other studies dealing with caridean species (e.g., Corey and Reid, 1991; Pandian, 1994), it was also found that brood size is predominantly determined by female size.

Hippolyte zostericola (Smith, 1873), for instance, presented a much higher fecundity (147); however it is a larger species, ranging 1.92–3.36 mm in CL, while *Hippolyte nicholsoni* Chace, 1972 with a CL range of 0.64–1.44 mm only showed a mean fecundity of 25 eggs (Corey and Reid, 1991). Bauer (1991) set an embryo volume of 0.005 mm³ for *H. curacaoensis* in contrast to the 0.013 mm³ for *H. kraussiana*, which may explain the larger number of embryos per brood presented by the former species. Therefore the larger size of embryos obtained in this study suggests some kind of abbreviated development.

A comparison between size classes shows that larger females produce a higher amount of eggs, as expected from the allometric relation. However, due to the higher relative brood loss in larger females, when comparing the number of embryos in late developmental stage, a negative allometry is possible to observe (Bauer, 1991). As a result, we can conclude that senescence seems to occur since the largest shrimp in the sampled population always presented fewer embryos in late development stage (IV) resulting in larger brood loss.

There are numerous reports of brood loss in crustaceans, whether dependent or not on parental size, such as egg loss at oviposition, aborted development, mechanical losses due to abrasion with the substratum or/and by trawling, maternal cannibalism, embryo

predation and parasitism (reviewed by Kuris, 1991). The brood loss reported in the present work for the *Hippolyte kraussiana* (47–58%) are within the range reported by Kuris (1991) for decapod crustaceans and by Oh and Hartnoll (1999) for caridean shrimps (12–74%).

Among caridean decapods, variations in egg size are accompanied by changes in the stage of development at which the larvae hatch (Wear, 1974; Pandian, 1994). The increase of volume, during incubation period, is 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 and George, 1984). This egg swelling is generally attributed 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., Corey and Reid, 1991; Lardies and Wehrtmann, 2001). As a result, with an increase of egg number, as observed in larger females, an increase in egg volume during egg development can lead to higher brood loss.

In the present study the average volume of embryos in the same development stage was not significantly different among the small and large shrimp collected, as in other studies (e.g., Calado and Narciso, 2003). Nonetheless, until brood loss is also studied in other *Hippolyte* species it is not possible to know if this pattern is specific to the studied species or is a common feature in the genus.

The population structure and the reproductive characteristics studied referred to a single season. To better understand the species reproductive dynamics, further studies should focus on periodic samples over a complete seasonal cycle. This study only addressed a comparison of egg number between size classes and egg stages. Future studies should also address the biochemical composition of different sized *H. kraussiana* in different periods of the reproductive season, since similar embryo volumes recorded may be unrelated to their lipid content, and consequently embryos produced by different sized shrimp in different seasons may result in newly hatched larvae with varying lipid reserves, which is known to affect embryo, larvae and juvenile growth and survival.

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