

New Insights into the Life-history Traits of the Night Shrimp *Processa hemphilli* (Caridea: Processidae) in the Western Atlantic

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We analyzed sexual dimorphism, sex ratio, relative growth, morphological sexual maturity, fecundity, embryo volume, and reproductive output of a population of the night shrimp *Processa hemphilli* from the Southeast coast of Brazil. Sampling was seasonally conducted, from June 2016 to April 2019 in Ubatuba, São Paulo. Our results showed the presence of sexual dimorphism in the body size, with females being larger than males. In addition, there was no difference in the overall sex ratio. However, it was possible to observe a skewed sex ratio to males in the smaller size classes, whereas females were more abundant in the larger size classes. The estimated carapace length at the onset of morphological sexual maturity of females and males was 3.6 mm and 3.2 mm, respectively. The mean fecundity of females was 285 ± 142 embryos (mean \pm SD) embryos and was positively correlated with the carapace length. The embryo volume differed between the developmental stages with a constant increase in volume throughout the development between stages I and III. The mean reproductive output of females was 52.4%. Our results suggest that *P. hemphilli* have a pure search mating system, show sex allocation in the growth of body structures, and that females have high reproductive investment. All of these results represent the first insights into the life-history traits of the species in the western Atlantic and contribute to the knowledge about processid species.

Key words: Decapoda, Relative growth, Mating system, Sexual maturity, Sex allocation.

BACKGROUND

The night shrimp genus *Processa* Leach, 1815 is the largest of the family Processidae Ortmann, 1896 (Bauer 1985 2004; Manning and Chace 1971). These small and nocturnal shrimps are abundant in shallow water habitats like grass flats being at the base of the food chain (Bauer 1985 2004; Bauer and Conner 2012; Rasch and Bauer 2015). Shrimps of this genus are small and have burrowing habits, emerging at night, and thus

avoiding predation by fish or other taxa (Bauer 1985 2004; Manning and Chace 1971).

Processa hemphilli Manning & Chace, 1971 reaches up to 14 mm in total length. It differs from other species of the genus by having chelae only the right side of the first pair of pereopods, while the left ends in a simple dactyl. Other characteristics are a rounded fifth abdominal pleura posterolaterally, an antennal spine and the second pair of pereopods symmetrical with a multiarticulated carpi (Manning and Chace 1971;

Almeida and Bezerra 2011). They live from shallow to 154 m depths, temperatures from 10.6 to 32.0°C and salinity from 29.9 to 38.0. They are widely distributed, being found from North Carolina, in the USA to Buenos Aires, Argentina (Christoffersen 1979; Almeida and Bezerra 2011). Processidae shrimps are a link between primary production and other trophic levels (Bauer 1985 2004), being essential for the balance of the marine ecosystem.

To understand a species' life-history, we need population biology parameters such as sex ratio, growth of body structures, size at onset of morphological sexual maturity, fecundity, embryo volume, and reproductive output (Stearns 2000). Despite the wide distribution and ecological importance of *P. hemphilli*, there are no studies on its general biology. Crustaceans show ontogenetic differences in the growth pattern of certain body structures during development (Hartnoll 1978). The growth pattern of each sex is directly related to its energy allocation strategy and is influenced by physiological processes such as reproduction and growth (Lika and Kooijman 2003). The allocation of resources for reproductive processes may differ between sexes of the same species as a result of different population roles. This process is defined as sex allocation (Charnov 1982).

Growth and reproduction are antagonist processes and represent a typical tradeoff during development (Koene and Ter Maat 2004). Thus, comparing the relative growth between males and females of different species can uncover different energy allocation strategies that maximize reproductive potential (Charnov 1982). The analysis of relative growth of different body structures can also help to understand the mating system of the species. Species with different mating systems may exhibit different energy allocation specific to body structures (Correa and Thiel 2003; Bauer 2004). Reproductive strategies vary widely among crustaceans (Hartnoll 1985). Tradeoffs between age and size at sexual maturity and between reproductive investment and lifespan are common throughout the individual life (Stearns 2000). In addition, reproductive features are modulated by the interaction of intrinsic (phylogenetic component) and extrinsic (environmental component) factors (Hartnoll 1985).

Most studies on marine shrimps carried out on the Southeast coast of Brazil have focused on Penaeidae. Special attention has been given to species of great economic importance, such as those targeted for fishing (Costa et al. 2005 2008; Castro et al. 2005; Carvalho-Batista et al. 2019; Miazaki et al 2021) and some caridean shrimp caught by fisheries (Chacur and Negreiros-Fransozo 1999; Braga et al. 2009; Almeida et al. 2012; Herrera et al. 2017; Pescinelli et

al. 2018). Although processid species are an especially important link in the food chain and trophic net in the coastal areas, there are no studies with *P. hemphilli* on the Southeast coast of Brazil. Hence, we analyzed the sexual dimorphism, sex ratio, relative growth, morphological sexual maturity, fecundity, embryo volume, and reproductive output of *P. hemphilli*. Based on these life-history traits, inferences were made about the mating system of the species.

MATERIALS AND METHODS

Study area and sampling of specimens

Seasonal sampling took place from June 2016 to April 2019 in Ubatuba bay (23°25'–23°27'S; 45°00'–45°03'18"W), Ubatuba, state of São Paulo, Southeast Brazil (Fig. 1). Samples were initially collected both day and night. As no individuals were collected during the day, only night samples were taken thereafter. Individuals were captured at night using a shrimp fishing boat equipped with mini otter-trawl nets (20 mm mesh size, 0.5 mm mesh at the cod end) with a sampling effort of 5 minutes/trawl, at depths from 3 to 5 m at a constant speed of 2.0 knots. The collected material was stored in plastic bags containing seawater and packed in coolers with crushed ice. Samples were taken to the laboratory for measurements and observations and later preserved in 70% ethanol.

All specimens captured were identified according to specific keys (Almeida and Bezerra 2011), measured in relation to carapace length (CL) and the sex was identified according to the presence (males) or absence (female) of appendix masculina in the endopods of the second pair of pleopods (Bauer 2004).

Population parameters

Homoscedasticity (Levene) and normality (Shapiro-Wilk) tests were performed as prerequisites for statistical tests (Zar 1996). Specimens were grouped into 0.5 mm CW class intervals. Mann-Whitney test (0.05) was used to see if there was a difference between male and female body size. Chi-square test with a significance level of 5% (Sokal and Rohlf 1995) was used in each size class to determine whether the sex ratio followed a 1:1 ratio. Size classes with fewer than 20 specimens were excluded from this analysis.

Relative growth and morphological sexual maturity

Morphological analyses were conducted under

a stereomicroscope (0.01 mm) based on the following measurements: carapace length (CL), second pleuron length (SPL), propodus length of first and second pereopods (PrL), carpus length of first and second pereopods (CaL), merus of first and second pereopods

(ML), appendix interna length (AIL), and appendix masculina length (AML) (Fig. 2).

Relative growth was obtained from morphometric data, using the allometric equation $y = ax^b$ in the linearized version ($\log y = \log a + b \log x$), where y is

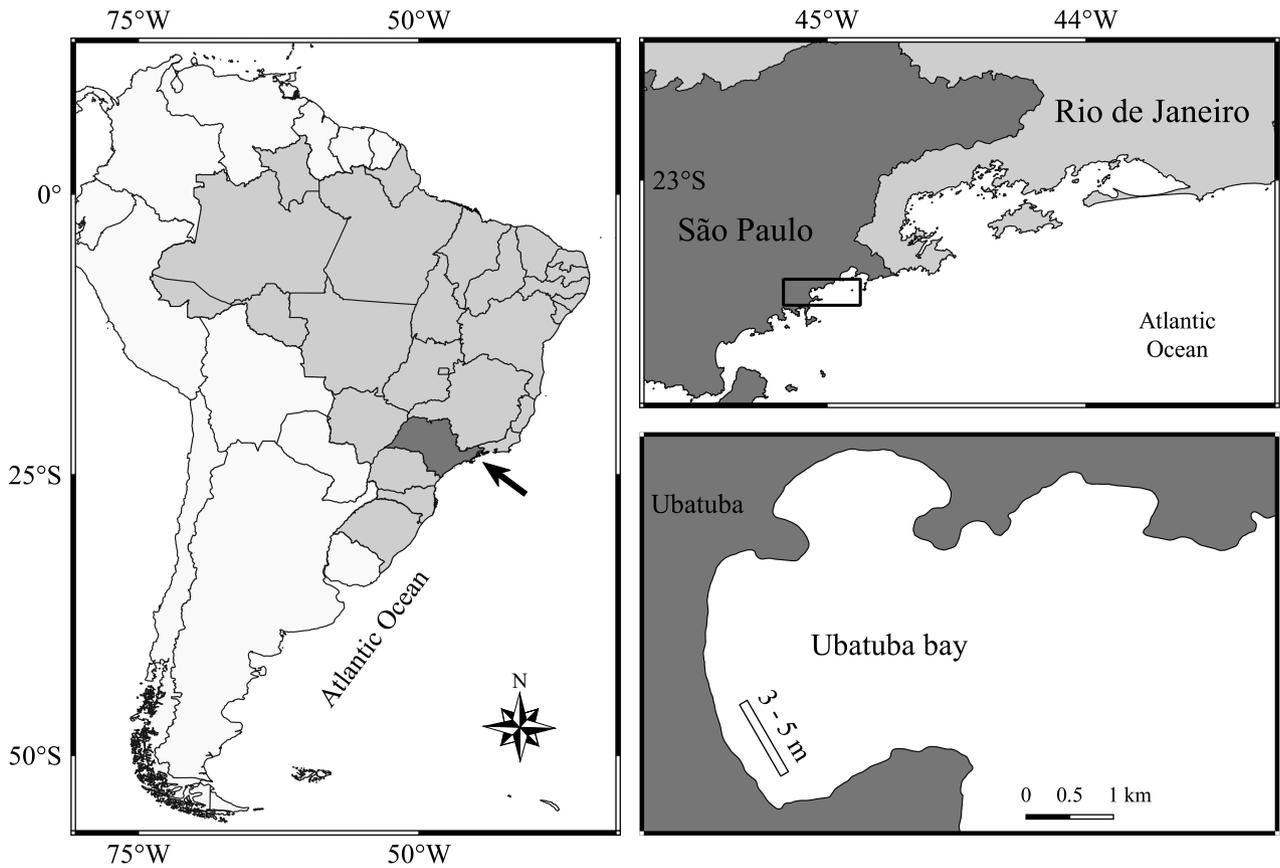


Fig. 1. Location of the study area, Ubatuba bay, São Paulo, south-eastern Brazil.

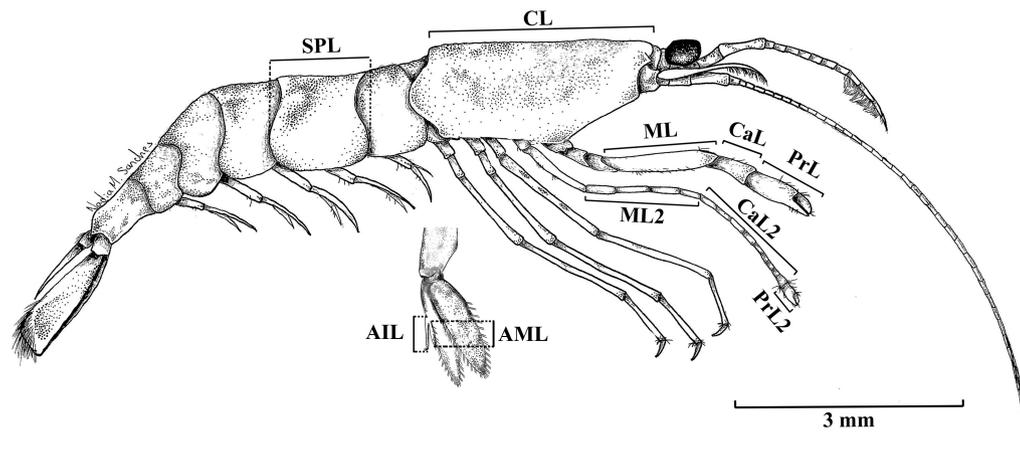


Fig. 2. *Processa hemphilli*, Manning & Chace, 1971. Body dimensions used in the morphometric analyses. Carapace length (CL), second pleuron length (SPL), propodus length of first and second pereopods (PrL), carpus length of first and second pereopods (CaL), merus of first and second pereopods (ML), appendix interna length (AIL), and appendix masculina length (AML). Illustrations by Nádia de Moraes Sanches.

the dependent variable or the dimension studied, x is the independent variable, b is the allometric coefficient of the studied structure, and a is the point at which the straight line intersects the ordinate axis (Hartnoll 1985). A non-hierarchical ‘*K-means* clustering’ analysis was performed on the log-transformed data. In this analysis, data is distributed into a predetermined number of groups. This number of groups is defined by an iterative process that minimizes variance within groups while maximizing variance among them. The result (*K-means*) was refined by discriminant analysis.

The allometric condition b for each structure was analyzed ($b = 1$: isometry; $b < 1$: negative allometry; $b > 1$: positive allometry) using a Student’s t -test (Ho: $b = 1$, $\alpha = 5\%$) (Zar 1996). After the size categories were determined, log-transformed data were used for each category for a covariance analysis (ANCOVA). This analysis tests the angular and linear coefficients between juveniles and adults for each relationship and verifies whether the found groups could be represented by different linear equations. We used the software STATISTICA 7.0 (StatSoft 2004) (Zar 1996) for all analyses. Morphological sexual maturity was estimated based on the relationship between two measurements that showed the highest allometric coefficient between the juvenile and adult stages (*i.e.*, different linear equations). The size of the smallest adult was used to establish the size the species reaches morphological sexual maturity (Sampedro et al. 1999). When there was an overlap in growth lines (juveniles and adults), the L50 method was used to identify the size of morphological sexual maturity. This method indicates the size at which half of the population has matured reproductively. This procedure analyzes the distribution of individuals according to size classes based on CL. Subsequently, the equation of the logistic curve $y = 1/(1 + e^{-r(CL-CL_m)})$ was fitted to the data by the least-squares method (Vazzoler 1996), and the size at morphological maturity was defined by the interpolation point (50%).

Fecundity, embryo volume, and reproductive output

Embryos of each female were carefully removed from the pleopods with a brush and classified according to the stage of embryonic development, following Wehrmann’s (1990) and Oliveira et al. (2018): early stage (I), with no eyes and yolk occupying 75–100% of embryo volume; intermediate stage (II), with vestigial eyes and yolk occupying about 50–75% of embryo volume; and final stage (III), with developed eyes and yolk occupying 25–50% of embryo volume.

To calculate the embryo volume, 15 embryos were randomly selected from each female and measured under a stereomicroscope equipped with an ocular micrometer. The mean embryo volume was calculated using the formula $[v = 1/6 * \pi * (d_1)^2 * d_2]$ where d_1 and d_2 correspond to the longest and shortest diameters, respectively (Bauer 1991). All females with embryos in stage I of development were used for the fecundity analysis. The Spearman correlation ($\alpha = 0.05$) was used to analyze the relationship between female size and fecundity as well as the relationship between female size and embryo volume. Analysis of Covariance (ANCOVA, Zar 1996) was applied to determine the relationship between CL (independent variable) and fecundity (dependent variable), using the embryo developmental stage. Kruskal-Wallis test ($\alpha = 0.05$) was used to determine if there were differences in the volume of embryos between stages of development.

To measure the reproductive output (RO) females and embryo mass were dried at 60°C for 48 h and weighed using an analytical balance (precision 0.0001 g). The RO was calculated according to formula of Clarke et al. (1991): $RO = (\text{Dry weight of the brood mass} / \text{Dry weight of the female without embryos}) \times 100$. Only embryos in the initial stage of development (Stage I) were used to calculate fecundity and RO. Spearman’s correlation was used to analyze the relationship between female size and RO.

RESULTS

Population parameters

A total of 451 individuals were sampled: 225 females (49.9%) (180 ovigerous) and 226 males (50.1%). The CL of females ranged from 2.2 to 5.5 mm (mean \pm SD of 4.0 ± 1.36 mm). Male CL ranged from 2.0 to 5.0 mm (mean \pm SD, 3.3 ± 1.55 mm). Size data was not normally distributed (Shapiro-Wilk, $P < 0.05$). There was a significant difference between the mean sizes of males and females (Mann-Whitney test $P < 0.05$) with males being smaller.

The size-frequency distribution showed a greater concentration of males in smaller classes (3.0 to 4.0 mm CL). Females were more frequent in the larger classes (3.5 to 5.5 mm CL) (Fig. 3A). Ovigerous females were more abundant in the classes 4 to 5 mm CL (Fig. 3A). The overall sex ratio was 1:0.99 and did not differ statistically from the expected 1:1 ($P = 0.96$). There was a significant difference in abundance, in which males were predominant up to 3.5 mm CL. From this size onwards, females were more abundant (Fig. 3B).

Relative growth and morphological sexual maturity

All growth equations for different morphological structures differed significantly between juveniles and adults in either slopes or intercepts (ANCOVA, $P < 0.05$) (Table 1). All calculated growth equations between juveniles and adults showed negative allometry with the exception of the following relationships: SPL vs. CL for females, CaL2 vs. CL for females, and ML1 vs. CL for males (Table 2). The relationships that best demonstrated changes in the growth pattern between juveniles and adults were SPL vs. CL for females, and CaL2 vs. CL for males. The CL at morphological sexual maturity was 3.6 mm for females and 3.2 mm for males (Figs. 4 and 5).

Fecundity, embryo volume, and reproductive output

A total of 89 females with embryos at different

stages of development were analyzed: stage I ($N = 23$), stage II ($N = 24$) and stage III ($N = 42$) (Table 3). There was a positive correlation between CL and number of embryos (Spearman's correlation, $P < 0.05$). There was a proportional increase in embryo number according to female size (Fig. 6A). Mean fecundity was 265 ± 141 embryos (mean \pm SD) (min-max, 22–592). There was no difference between the developmental stages for the correlation fecundity/female size CL (ANCOVA, $P > 0.05$). Meanwhile, the mean embryo volume differed significantly between developmental stages (Kruskal-Wallis/Dunn, $P < 0.05$), (Fig. 6B). embryo volume increased throughout the development: $0.001\text{--}0.028\text{ mm}^3$ (mean \pm SD, 0.022 ± 0.006) in stage I, $0.026\text{--}0.028\text{ mm}^3$ (mean \pm SD, 0.027 ± 0.001) in stage II, and $0.026\text{--}0.050\text{ mm}^3$ (mean \pm SD, 0.032 ± 0.007) in stage III.

The mean reproductive output of females was $52.4 \pm 20.2\%$. There was no significant correlation between mean RO and size of female (Spearman's correlation, $P > 0.05$).

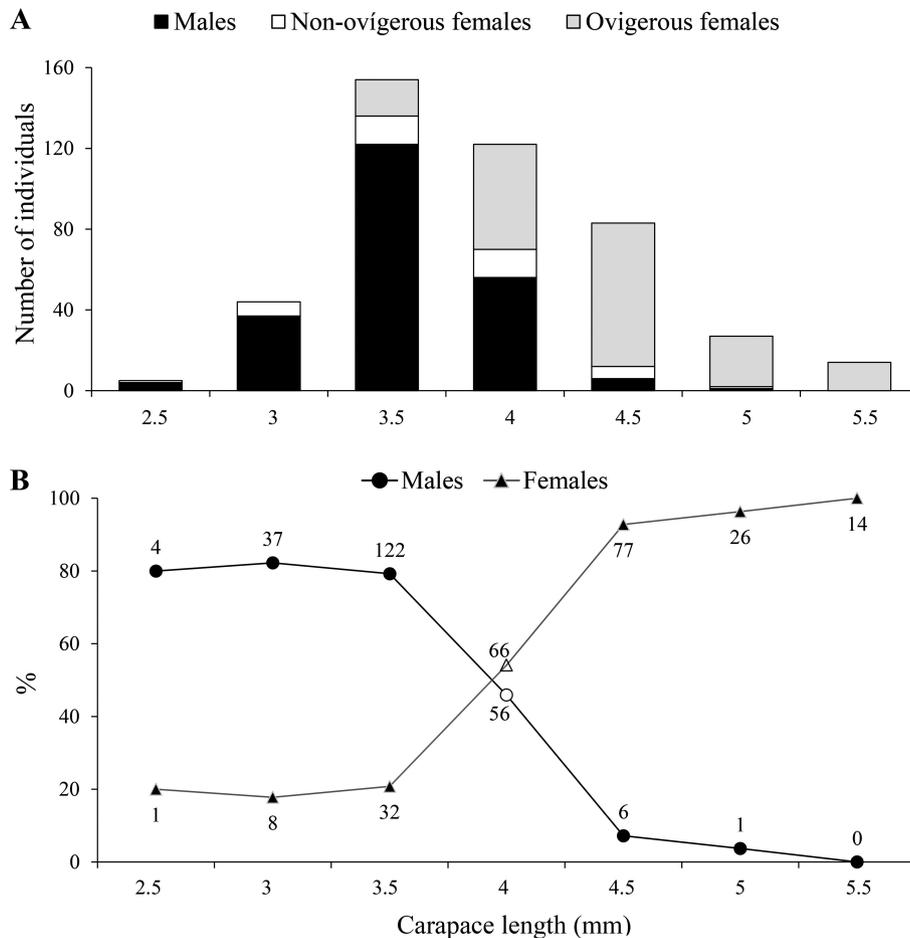


Fig. 3. *Processa hemphilli*, Manning & Chace, 1971. (A) Size-frequency distribution of males and females. Class interval of 0.5 mm (CW). (B) Size-frequency variation on the proportion of males and females. Significant differences from the proportion 1:1 are identified by filled markers.

DISCUSSION

This study provides details on the life-history of the night shrimp *Processa hemphilli* in Southeast Brazil. We found sexual dimorphism regarding body size in which females were larger than males. Although there was no difference in the overall sex ratio, we observed a skewed sex ratio with a higher abundance of

males in smaller size classes and a higher abundance of females in larger size classes. This different distribution in size classes is in line with the estimated size for sexual maturity where males reach sexual maturity in smaller sizes. These traits point to the pure search mating system that is shown in many caridean species. Dimorphism in size can be attributed to the mating system and selective sexual pressures (Correa and Thiel

Table 1. *Processa hemphilli*, Manning & Chace, 1971. Results of analysis of covariance (ANCOVA) between juveniles and adults of males and females for each relationship

Relationships	Factors	Par. (Log)	F	P
CL vs. PrL1	Females (J vs. A)	a	10.947	0.001*
		b	1.946	0.165
	Males (J vs. A)	a	25.513	0.000*
		b	0.987	0.322
CL vs. CaL1	Females (J vs. A)	a	78.367	0.000*
		b	0.166	0.684
	Males (J vs. A)	a	76.514	0.000*
		b	2.946	0.087
CL vs. ML1	Females (J vs. A)	a	67.612	0.000*
		b	0.209	0.648
	Males (J vs. A)	a	33.142	0.000*
		b	1.487	0.224
CL vs. PrL2	Females (J vs. A)	a	41.098	0.000*
		b	0.969	0.326
	Males (J vs. A)	a	213.668	0.000*
		b	1.438	0.232
CL vs. CaL2	Females (J vs. A)	-	-	-
		b	7.101	0.008*
	Males (J vs. A)	-	-	-
		b	15.656	0.000*
CL vs. ML2	Females (J vs. A)	-	-	-
		b	64.881	0.000*
	Males (J vs. A)	a	26.776	0.000*
		b	1.866	0.173
CL vs. SPL	Females (J vs. A)	-	-	-
		b	4.855	0.029*
	Males (J vs. A)	a	36.440	0.000*
		b	0.248	0.619
CL vs. AIL	Females (J vs. A)	a	25.604	0.000*
		b	1.924	0.168
	Males (J vs. A)	a	84.046	0.000*
		b	0.132	0.718
CL vs. AML	Males (J vs. A)	-	-	-
		b	4.678	0.032*

Second pleuron length (SPL), propodus length of first and second pereopods (PrL), carpus length of first and second pereopods (CaL), merus of first and second pereopods (ML), appendix interna length (AIL), and appendix masculina length (AML); Par = parameter; F = statistic values; P = significance *Significant difference P < 0.05).

2003; Bauer 2004). In the pure search mating system, small, cryptic, and agile males have greater reproductive success than bigger ones (Andersson 1994; Correa and Thiel 2003; Bauer 2004).

There are a few explanations for the size difference between the sexes in this type of system. One is the possibility of partial protandry (sex change male to female), strongly suggested by the sudden change in

Table 2. *Processa hemphilli*, Manning & Chace, 1971. Analysis of morphometric data using the carapace length (CL) as an independent variable

Relationship	Sex	N	<i>a</i>	<i>b</i>	<i>r</i> ²	T (b = 1)	<i>P</i>	Allometry
CL vs. PrL1	JF	42	-0.345	0.771	0.583	2.234	< 0.001	-
	AF	124	-0.336	0.788	0.511	2.775	< 0.001	-
	JM	48	-0.299	0.616	0.446	3.330	< 0.001	-
	AM	116	-0.260	0.589	0.414	5.634	< 0.001	-
CL vs. CaL1	JF	57	-0.661	0.802	0.564	1.746	< 0.001	-
	AF	111	-0.657	0.901	0.503	0.993	< 0.001	-
	JM	70	-0.710	0.892	0.455	0.881	< 0.001	-
	AM	74	-0.561	0.685	0.405	3.208	< 0.001	-
CL vs. ML1	JF	58	-0.167	0.783	0.524	1.882	< 0.001	-
	AF	109	-0.118	0.784	0.460	2.444	< 0.001	-
	JM	25	-0.168	0.762	0.430	2.729	0.206	-
	AM	121	-0.314	1.020	0.490	0.052	< 0.001	0
CL vs. PrL2	JF	45	-0.698	0.675	0.570	2.690	0.045	-
	AF	102	-0.654	0.620	0.475	4.8888	< 0.001	-
	JM	36	-0.627	0.513	0.403	7.018	0.280	-
	AM	101	-0.165	0.528	0.460	5.811	0.513	-
CL vs. CaL2	JF	54	-0.063	0.616	0.539	4.330	< 0.001	-
	AF	103	0.122	0.800	0.563	2.583	< 0.001	-
	JM	62	-0.397	1.284	0.609	2.133	< 0.001	+
	AM	104	-0.199	0.901	0.537	1.000	< 0.001	-
CL vs. ML2	JF	50	-0.243	0.642	0.528	3.192	0.026	-
	AF	106	-0.382	0.931	0.606	0.874	< 0.001	-
	JM	61	-0.237	0.626	0.505	4.584	< 0.001	-
	AM	100	-0.361	0.835	0.551	1.546	< 0.001	-
CL vs. SPL	JF	53	-0.402	1.412	0.490	-1.856	< 0.001	+
	AF	124	-0.187	1.033	0.536	-0.327	< 0.001	0
	JM	48	-0.153	0.815	0.508	1.460	< 0.001	-
	AM	135	-0.112	0.774	0.520	3.000	< 0.001	-
CL vs. AIL	JF	33	-0.683	0.440	0.464	4.979	< 0.001	-
	AF	85	-0.818	0.764	0.520	2.448	< 0.001	-
	JM	17	-0.965	0.817	0.514	1.005	0.777	-
	AM	21	-0.323	0.277	0.405	6.225	0.865	-
CL vs. AML	JM	54	-0.556	0.665	0.517	3.180	0.009	-
	AM	88	-0.494	0.599	0.510	5.163	< 0.001	-

Second pleuron length (SPL), propodus length of first and second pereopods (PrL), carpus length of first and second pereopods (CaL), merus of first and second pereopods (ML), appendix interna length (AIL), and appendix masculina length (AML); JM = juvenile males; AM = adult males; JF = juvenile female; AF = adult female; *b* = allometric coefficient; *a* = intercept; *r*² = determination coefficient; T = statistic values; *P* = significance; + = positive allometry; 0 = isometry; - = negative allometry.

Table 3. *Processa hemphilli* Manning & Chace, 1971. Mean fecundity (number of embryos) by developmental stages

Stage	Number of females	CL (mm) min-max	Fecundity Mean ± SD
I	23	3.34–5.20	265 ± 141
II	24	3.42–5.13	257 ± 117
III	42	3.26–5.33	250 ± 142

CL = carapace length.

the preponderance of males at small sizes and females at larger sizes. Population size-frequency distributions consisting of small males and larger females is evidence indicating or confirming protandry (Bauer 2004; Anker et al. 2009). However, the observation of the development of female primary and secondary sexual characteristics and females with vestiges of male external or internal structures is fundamental in confirming protandry (Bauer 2004; Anker et al. 2009). The same population size-frequency distributions were also recorded by Noël (1973 1976) for *Processa edulis* (Risso, 1816) and the author attributes it to sex change. However, Bauer and Conner (2012) also showed similar size-frequency distribution for *Processa riveroi* RB Manning & Chace, 1971 and *Processa bermudensis* (Rankin, 1900) but found no morphological evidence for sex change. Therefore, there is no consensus on the presence of protandry in *Processa* species.

Other explanation for the size difference between

the sexes is an extremely high cost for males to defend themselves when facing many competitors. Moreover, copulation is restricted to brief encounters to avoid conspicuousness to predators, which also favor smaller individuals (Correa and Thiel 2003). Males do not have high energy investment in the growth of body structures since there is no dispute over sexual partners. In this mating system, the species is under an intense sexual selection leading to a sexual dimorphism with smaller males (Andersson 1994; Correa and Thiel 2003). In sexual systems such as monogamy, e.g., genus *Alpheus* (Costa-Souza et al. 2022) or in mate guarding (Hamasaki et al. 2020) the opposite is observed: that is, a high energy investment in the growth of body structures.

We observed a tradeoff between growth and reproduction in which the females invest more energy in the growth of second pleuron during the juvenile phase. The positive allometry during the juvenile stage is a strategy that may increase reproductive

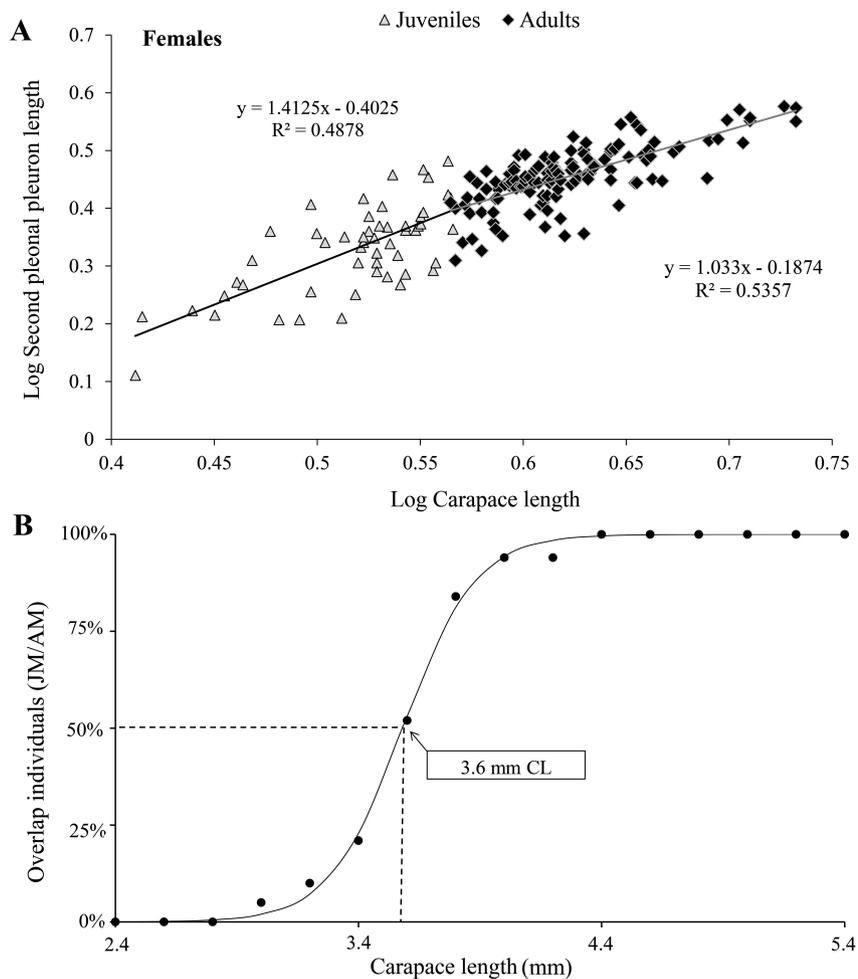


Fig. 4. *Processa hemphilli*, Manning & Chace, 1971. (A) Estimated size at morphological sexual maturity for females. (B) The estimated sizes correspond to the CL of the adjusting the logistic regression of overlapping juveniles and adults, indicating the size in which females are morphologically mature.

performance in females. After reaching sexual maturity, energy allocation can be allocated to the gonadal development, embryo production, and maintenance of embryos. In caridean females, the size of the second pleuron is recognized as an important adaptation since this structure is crucial for embryo incubation (Bauer 2004). Thus, the energy direction for the growth of this structure is one of the factors that influence reproductive success.

The energy investment of males showed positive allometric growth of the carpus of the second pereopod. Meanwhile, the first pereopod showed negative allometry. The first pereopod is more robust compared to the second one in this species. These results reinforce that *P. hemphilli* has a pure search mating system. In addition to being smaller than females, males also have small chelipeds, to which low energy is invested for the development (Bauer and Abdalla 2001; Bauer 2004).

The energy allocation of males to the carpus of

the second pereopod before reaching morphological sexual maturity may be related to a possible function of these appendices during copulation. The second pereopod in *Processa* is long, slender, and shows merus and carpus subdivided into articles. This is considered a taxonomic character in the identification of species, mostly in relation to morphology and number of articles showed in the merus and carpus (Manning and Chace 1971). The carpus of *Processa hemphilli* is subdivided into 10 articles (Manning and Chace 1971). The multi-articulate composition of the carpus makes this segment extremely flexible and has great importance for cleaning its cephalic region, including the gills (Bauer 2004). Although not observed or discussed in the literature, another hypothesis would be the use of the second pereopod to touch the genital openings of the females before copulation. Instead, they constantly roam, searching for receptive females and copulating quickly (Bauer 2004). Considering that females are larger than

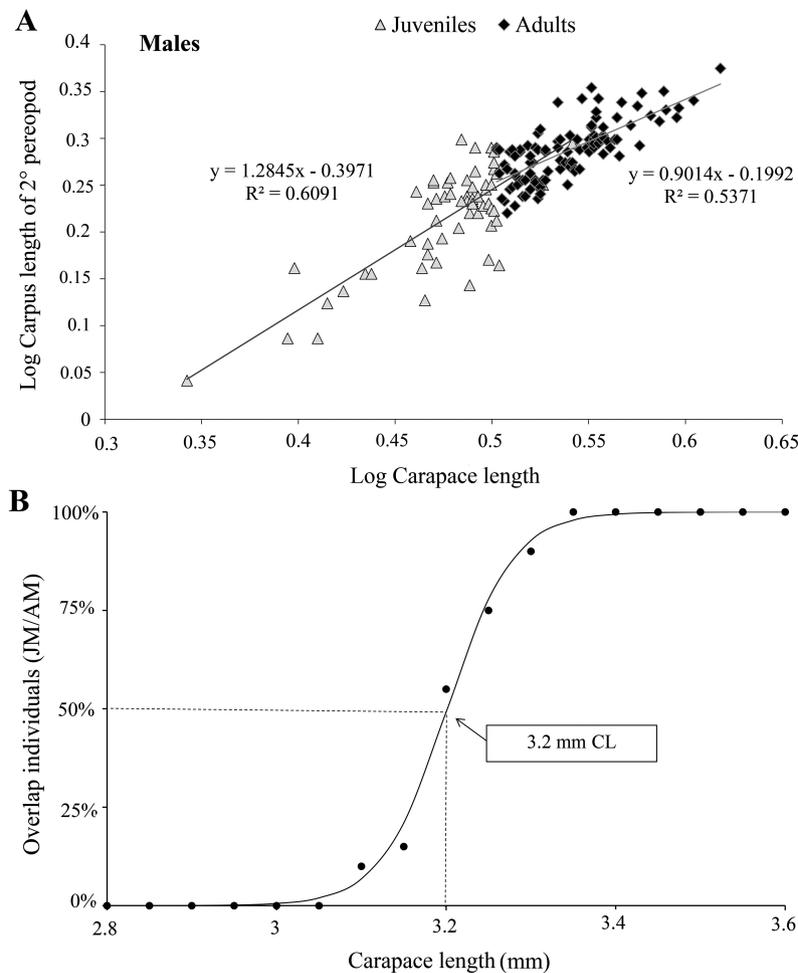


Fig. 5. *Processa hemphilli*, Manning & Chace, 1971. (A) Estimated size at morphological sexual maturity for males. (B) The estimated sizes correspond to the CL of the adjusting the logistic regression of overlapping juveniles and adults, indicating the size in which males are morphologically mature.

males, the energy allocation to the growth of the second pereopod can optimize the touch and copulation process. Thus, the investment in the growth of the articulated carpus can reduce the interaction time between males and females prior to effective copulation. Immediately after the copulation, males move on searching for another reproductive female (Bauer 2004).

The positive correlation between the carapace length and the number of embryos indicates that body size influences embryo production in *P. hemphilli*. This result shows that size is considered the main factor determining the fecundity of the species as larger females showed higher fecundity. The area available for incubation and accommodation of embryos in the abdomen increases with body growth, enabling higher embryo production (Bauer 1991; Ghizelli-Fraga et al. 2021). This relationship between female size and fecundity can be observed for other species of Caridea (Bauer 2004).

The constant increase in embryo volume throughout the development between stages I and III is related to osmotic regulation. Higher water absorption during this embryo development stage facilitates larval hatching (e.g., Pavanelli et al. 2008; Pescinelli et al. 2017 2021; Oliveira et al. 2018; Ghizelli-Fraga et al. 2021). Thus, this increase in embryo volume increases reproductive success.

Although not significantly statistically different, we observed a decrease in mean fecundity (loss of embryos) throughout embryonic development. The decrease of mean fecundity in advanced embryo development stages can be related to the increase in an embryo's volume and consequent space limitation in the female's abdomen (Corey and Reid 1991; Wehrtmann and Lardies 1999). Other factors may also contribute to embryo loss in crustaceans, such as mechanical stress and abrasion, presence of diseases and parasites, maternal cannibalism and predation

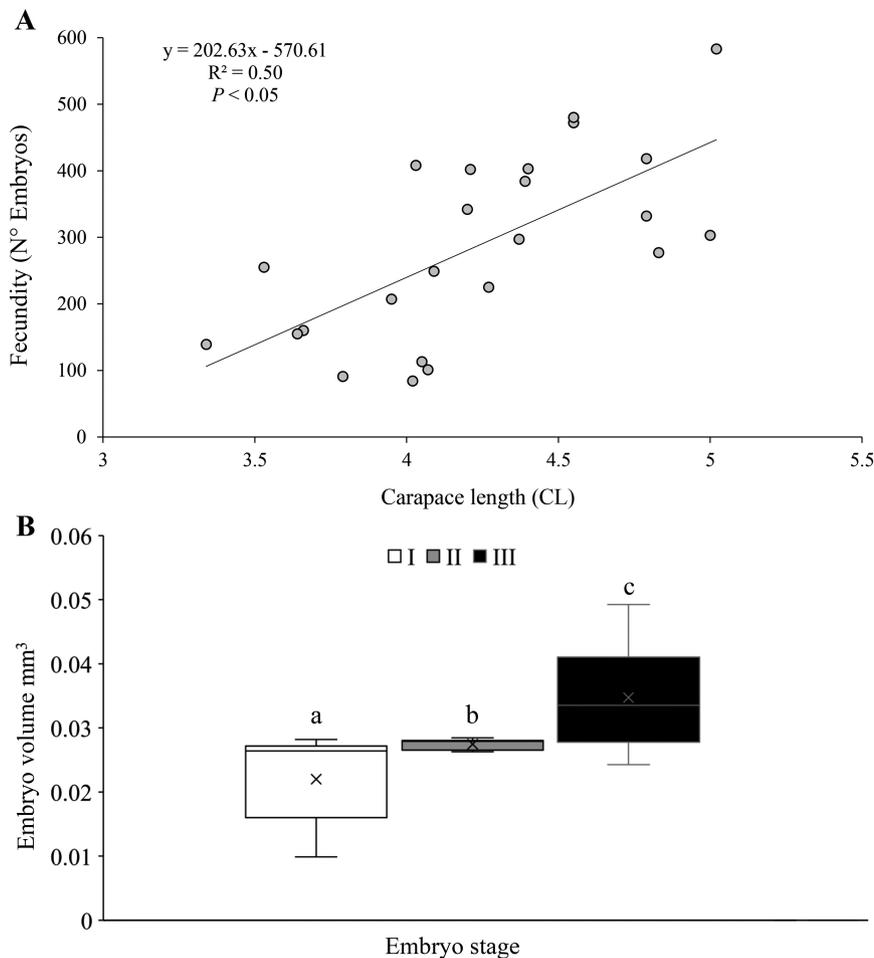


Fig. 6. *Processa hemphilli* Manning & Chace, 1971. (A) Correlation between carapace length and the fecundity of females with embryos in development stage I. (B) Comparison of embryo volume at the early (I), intermediate (II), and final stage of development (III). Minimum, maximum (whiskers), median (horizontal lines) and mean (x). Different letters indicate significant differences among embryo stages.

(Balasundaram and Pandian 1982; Kuris 1991). A similar pattern of reduction in mean fecundity among embryo development stages was observed in the alpheid shrimp *Salmones carvalhoi* Anker, 2007 from Ilha de Itamaracá, Pernambuco (Oliveira et al. 2018).

The high reproductive output of females adds to the energy allocation for the growth of the second pleuron still in the juvenile stage. The negative allometric growth of other body structures indicates that *P. hemphilli* devotes considerable energy to reproduction during its cycle of life. Shrimps of the genus *Processa* have a short life cycle of about one year (Company and Sardá 1999). Thus, the high reproductive investment may be a strategy of *P. hemphilli* that maximizes its contribution of offspring to the next generation in the ecosystem in which it occurs.

CONCLUSIONS

Sexual dimorphism in the body size, males smaller than females, lower size of morphological sexual maturity in males, direct energy investment toward the growth of different body structures in both sexes, and lack of investments in weaponry indicates that *P. hemphilli* demonstrates a pure searching mate system. Moreover, the species has a high investment in reproduction, mainly in females that allocate considerable energy on reproductive output.

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