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Reproductive Biology of the Freshwater Shrimp *Atya scabra* (Leach, 1815) (Crustacea: Atyidae) in Ilhéus, Bahia, Brazil

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Alexandre Oliveira Almeida, Emerson Contreira Mossolin, and Joaldo Rocha Luz (2010) Reproductive biology of the freshwater shrimp *Atya scabra* (Leach, 1815) (Crustacea: Atyidae) in Ilhéus, Bahia, Brazil. *Zoological Studies* **49**(2): 243-252. Reproduction and population aspects of the freshwater shrimp *Atya scabra* in the Santana River, city of Ilhéus, state of Bahia, Brazil, were studied from Apr. 2004 to May 2005. During these 14 mo, 3752 individuals were captured, with a sex ratio of 1.01 males for each female. The total number of individuals caught per month ranged 80-532. Males were generally larger than females. The smallest female found (5.40 mm in carapace length and 29.03 mm in total length) was ovigerous, which indicates that only adult individuals were caught. Ovigerous females were found every month, which indicates continuous reproduction and a high index of reproductive activity during the year. The highest reproduction indices were observed in May (94.3%) and Oct. (98.6%) 2004, and Mar. (93.7%) 2005. Fecundity ranged 870-8907 eggs, with a mean of 3811 (±1992.87) eggs per female. The size of the females and their fecundity were positively correlated. The distribution of individuals in length classes by month showed that representatives of smaller classes occurred throughout almost the entire study period. This indicates a constant input of individuals into the population, which corroborates the characterization of the reproductive period as being continuous, and explains the large numbers of ovigerous females found each month. The 2nd abdominal segment is proportionally larger in females than in males, in width, height, and pleural length: these female secondary characteristics are related to an increased incubation area for eggs. http://zoolstud.sinica.edu.tw/Journals/49.2/243.pdf

Key words: Caridea, Camacuto Shrimp, Reproduction, Secondary sexual characters, Freshwater.

Crustaceans, especially members of the order Decapoda (shrimp, crabs, lobsters, etc.) are ecologically and economically important. This interest has prompted scientific studies in many areas, including reproduction. Studies in this area were initially conducted to generate data that could be used in aquiculture, including studies on larval development and gonadal maturation (Verdi 1995). In commercially exploited species, such studies are important to support governmental regulation of fishing, thus preventing the excessive reduction of stocks or adverse impacts on the environment. In addition to practical applications, knowledge about the reproduction of a species is an important element for investigating physiological and ecological aspects (Valenti et al. 1986).

Among species of freshwater shrimp of the family Atyidae, 4 are known in Brazil, 2 of the genus *Potimirim* Holthuis and two of the genus *Atya* Leach (Melo 2003). Only *Atya scabra* (Leach, 1815) is of commercial interest. This species is economically important in parts of

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Mexico (Martínez-Mayén and Román-Contreras 2000) and Venezuela, and in Brazil mostly in the state of Pernambuco (Holthuis 1980) and other states in northern Brazil. Palacios et al. (2008) mentioned that *A. margaritacea* A. Milne-Edwards has an important ecological function of removing sediments and detritus after periods of high input, making this detritus available to higher trophic levels.

In southeastern Bahia, *A. scabra* is one of the resources, together with other freshwater shrimp of the family Palaemonidae, such as *Macrobrachium carcinus* (L.), *M. acanthurus* (Wiegmann), and *M. olfersi* (Wiegmann), exploited by artisanal fishermen. Although it is not the most profitable species, interest in *A. scabra* has been increasing because of reductions in populations of other shrimp of the genus *Macrobrachium* Bate. According to fishermen's reports, the shrimp populations of local rivers have been progressively dropping in recent decades, due to overfishing and contamination, among other factors (Almeida et al. 2008). In the list of species of the Brazilian fauna that are at risk of extinction, *A. scabra* is considered a vulnerable species in 10 Brazilian states, including the state of Bahia (Amaral 2005).

In the Americas, *A. scabra* is distributed from Mexico to Brazil (from the states of Ceará to Rio Grande do Sul), as well as in Cuba, Jamaica, and from Hispaniola to Curaçao. In Africa, it occurs from Liberia to northern Angola and on Annobon and the Cape Verde Is. (Melo 2003). This shrimp usually lives on rocky bottoms of clean shallow streams with a strong current, although adults and young females are also found in backwaters near areas of faster currents. Young shrimp may also be found among underwater roots along stream banks (Darnell 1956, Hobbs and Hart 1982, Rocha and Bueno 2004). The external morphology of this species is adapted to life in this environment: the 1st 2 pairs of pereiopods are modified to capture food, and the 3rd pair is well developed and used for anchoring to the substrate (Bond-Buckup and Buckup 1999).

In Brazil, *A. scabra* lives in rivers that are directly or indirectly connected to the Atlantic Ocean, which is explained by their life cycle which includes larval stages that depend on brackish water in estuaries. Its larval development was studied by Abrunhosa and Moura (1988), who described 11 planktotrophic larval stages. In Brazil, only 1 study examined its reproductive biology (Galvão and Bueno 2000) in a river in the city of São Sebastião, state of São Paulo.

Based on this information, the evident lack of knowledge about the biology of many freshwater decapod carideans is worrisome, because of the intense fishing exploitation and subsequent changes in their habitats. The objective of this study was to examine populational and reproductive aspects of *A. scabra* in a river in southeastern Bahia, to determine aspects of its reproduction, including the breeding season, fecundity, sex ratio, recruitment, secondary characters, and the size at sexual maturity of females.

MATERIAL AND METHODS

The study area was a 30 m stretch of the Santana River, in the city of Ilhéus, Bahia (14° 51'16.8"S; 039°05'58.6"W) (Fig. 1). This river is still relatively unaffected by human influences compared to the main river of the basin, the Cachoeira River. The city of Ilhéus has a tropical climate, with humid and semi-humid weather, and mean annual temperatures varying 22-25°C. Rainfall is regular, with abundant rains in annual amounts exceeding 1000 mm, which can reach 2700 mm in areas near the seashore (Faria-Filho and Araujo 2003). Data on mean monthly rainfall and air temperature given here (Fig. 2) were provided by SBIL/INFRAERO - Ilhéus, Bahia.

Sampling of *A. scabra* was carried out each month with the help of hand nets (with a mesh size of 14 mm), from Apr. 2004 to May 2005, for a total of 14 collections. Samples were always taken in the morning, in a part of the river with a fast current and no tidal influence. The shrimp were easily obtained up to depths of 40 cm, by turning over rocks in the riverbed, and among roots of the aquatic macrophyte *Mourera* Aublet (Podostemaceae), which is very common in areas with a strong current (Almeida et al. 2008). Voucher specimens were deposited in the Crustacean Collection of the Museu de Zoologia, Universidade Estadual de Santa Cruz, Ilhéus, Bahia (MZUESC nos. 357, 359, and 512), and in the Crustacean Collection of the Biology Department of the Faculty of Philosophy, Science and Languages of the Ribeirão Preto campus of the University of São Paulo (CCDB/FFCLRP/USP), Ribeirão Preto, São Paulo (CCDB no. 2178).

The standard sampling effort lasted 1 h; usually 3 and sometimes 4 people took the samples. In the field, captured animals were separated and sexed based on the presence or absence of the appendix masculina on the 2nd pair of pleopods (according to Galvão and Bueno 2000). The total length (TL) (the distance between the tip of the rostrum and the posterior margin of the telson) and the carapace length (CL) (the distance between the postorbital margin and posterior margin of the carapace) were measured with digital calipers (to 0.01 mm precision). The ovigerous or non-ovigerous condition of females was also noted. After the sex was checked and the specimens measured, a subsample was brought to the laboratory for studies on fecundity and secondary sexual characters (see below). The remaining shrimp were released at the collection local.

Fecundity was determined by counting the total number of eggs of 30 ovigerous females. Individuals were randomly chosen (5 in each month in the 1st 6 mo) that carried eggs in the initial developmental stages (characterized by homogeneous distribution of the vitellus, without visible appendices or developed eyes). The use of females with eggs in the initial developmental stages was aimed at avoiding potential egg loss, as noted by Balasundaram and Pandian (1982) and Anger and Moreira (1998). The egg mass was completely removed from the pleopods with a small brush, and the eggs were placed in Petri dishes for counting under a stereoscopic microscope. Pearson's linear regression was used to assess the correlation between CL and the number of eggs.

For the study of secondary sexual characters related to female maturity, the following parameters were used: CL and CW, carapace width (measured at the level of the 3rd pereiopod) as independent variables; and ML, length of the merus of pereiopod 3; ASW, 2nd abdominal segment width; PH, height of the pleura of the 2nd abdominal segment; and PW, width of the pleura of the 2nd abdominal segment as dependent variables. The following relationships were studied in males and females through linear regression analyses: 1) CL × ML; 2) CL × ASW; 3) CL × PH; 4) CL × PW; 5) CW × ML; 6) CW × ASW; 7) CW × PH; and 8) CW × PW.

Individuals used for these measurements were captured in Mar. and Apr. 2004. To compare the measurements obtained for males and females, the covariance analysis technique according to Snedecor and Cochran (1967) was applied. The residual mean squares were compared by the bilateral *F*-test. Taking into consideration the relative homogeneity in the residual variances, the regression coefficients, i.e., the measurement slopes (b) were compared, again using the *F*-test. If the null hypothesis was rejected ($p < 0.01$ and $p < 0.05$), the analysis was concluded by identifying

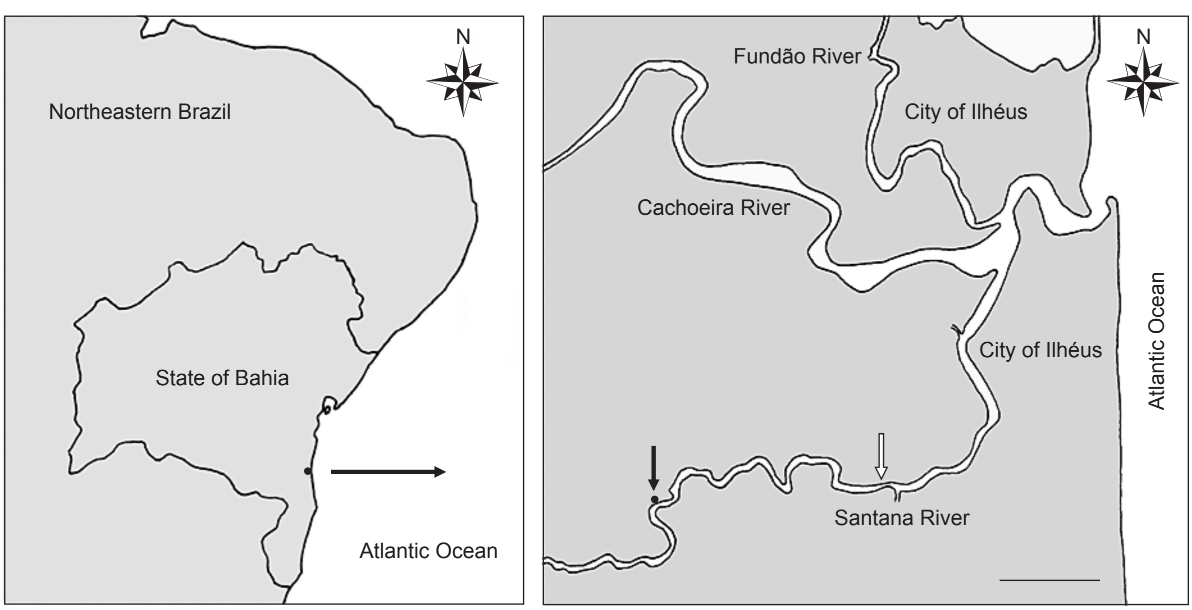

Fig. 1. Map showing the location of the study area in the Santana River, Ilhéus, Bahia, Brazil. The solid arrow indicates the collection site (14°51'16.8"S; 39°05'58.6"W). The white arrow indicates the limit of tidal influence. Scale bar = 1.8 km.

a significant difference between sexes according to the relationship studied. If the null hypothesis was accepted, the regression constants were compared, that is, the measurement elevation (a).

RESULTS AND DISCUSSION

Sex ratio

During 14 mo of sampling, 3752 individuals were captured, including 1885 males and 1867 females, resulting in a (M: F) sex ratio of 1.01 males for each female. Males predominated in 7 mo, and females predominated in the other 7 mo; the ratio varied between 0.56 (July 2004) and 2.54 (Sept. 2004).

The few population studies on species of *Atya* have generally reported a preponderance of males over females. According to Martínez-Mayén and Román-Contreras (2000), it is possible that male predominance is an intrinsic characteristic of species of this genus. When Darnell (1956) studied a population of *A. scabra* in Mexico, he found an apparent predominance of males over females, although this was not statistically significant (only 28 males and 18 females were collected). Even with a small number of individuals, Darnell considered that the sex ratio to be directly related to the environments in which juveniles, males, and females were found (some near the river margin and others in rapids). Covich et al. (2003), who studied *A. lanipes* Holthuis, from Puerto Rico, followed the same reasoning, in which an increased water volume due to rain may have influenced the riverbed at the sampling point, thus generating observed variations in the sex ratio.

For a population of *A. margaritacea*, in Mexico, Martínez-Mayén and Román-Contreras (2000) observed a significant deviation in the sex ratio (1.2 M: F). These authors explained the preponderance of males as being a result of the continuous reproduction and possible migration of females toward the river outflow, as occurs in certain species of *Macrobrachium* (Bauer 2004, Bauer and Delahoussaye 2008). Rains increase the river volume and consequently aid in the dispersal of newly hatched larvae toward the estuaries. In another study with *A. margaritacea* in Mexico, Palacios et al. (2008) found a sex ratio of 1.96 M: F; males were more frequent throughout the year, with the exception of the month in which the rains began, when the sex ratio was essentially equal.

In contrast to observations in the studies mentioned above, a higher proportion of females was found in a population of *A. scabra* in Brazil (state of São Paulo) by Galvão and Bueno (2000),

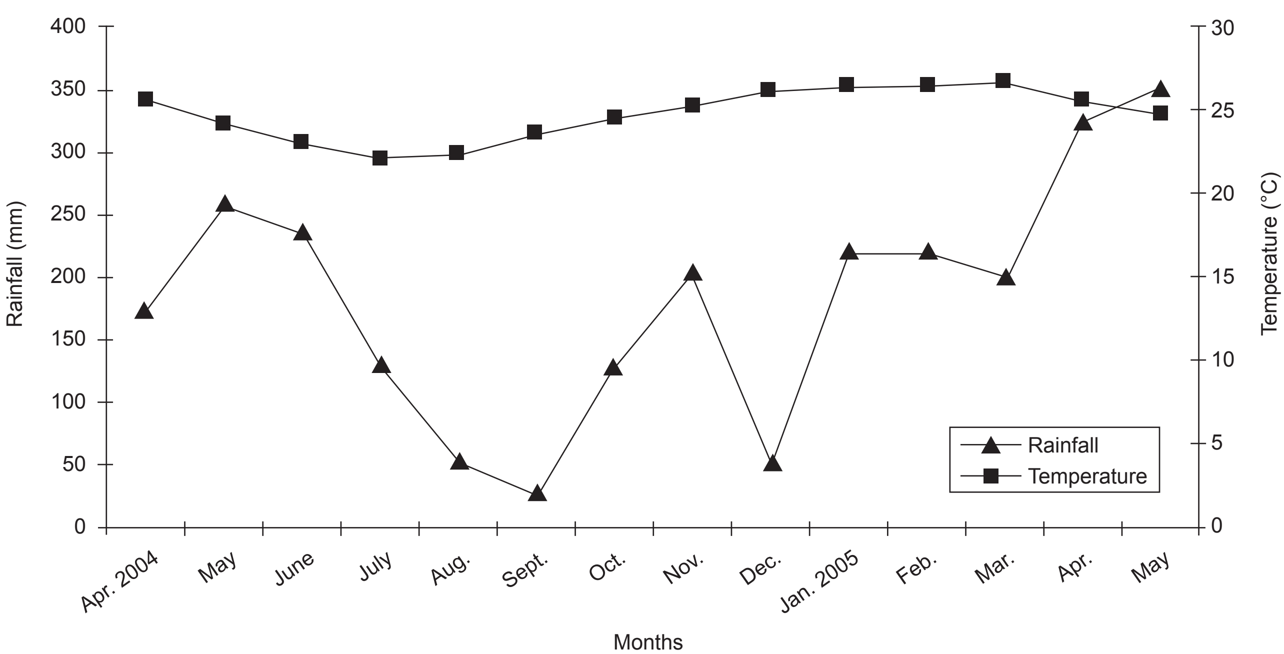

Fig. 2. *Atya scabra*. Relationship between rainfall and temperature from Apr. 2004 to May 2005, Santana River, Ilhéus, Bahia, Brazil.

who collected 1037 individuals and found a ratio of 1 male for 2.32 females (that is, 0.4 M: F). Those authors, however, did not comment on the possible causes for the sex ratio being so skewed in favor of females.

Population structure

The total number of individuals captured per month varied between 80 and 532 animals. Males were generally larger than females. The size of males ranged 5-38.18 mm CL (14.98-88.77 mm TL), while the female size ranged 5.4-23.06 mm CL (29.03-64.4 mm TL). Both the smallest and largest females were ovigerous, which indicates that only adult individuals were caught, an aspect which is further discussed in "Recruitment" and "Secondary sexual characteristics".

The measurements determined here are similar to those reported by Galvão and Bueno (2000) for the same species in São Paulo, in which the smallest ovigerous female was 25.3 mm TL (which was also the smallest female found during the 2 yr of their study), while the largest female was 61.1 mm TL. Males ranged 22.7-89.3 mm TL. In Mexico, males were also larger than females; the largest was 94.5 mm, and the smallest ovigerous female was 39 mm TL (Darnell 1956). Hobbs and Hart (1982) analyzed samples of *A. scabra* from several locations; the largest male from Brazil was 46.3 mm CL, and the largest in Africa was 34.4 mm. The smallest and largest females in Brazil were 7.1 and 29.5 mm CL, respectively, and the largest was also ovigerous.

For *A. margaritacea* in Mexico, the minimum size at maturity observed in females was 32 mm TL (Martínez-Mayén and Román-Contreras 2000). This size greatly differs from that reported by Hobbs and Hart (1982), who found an ovigerous female at around 22 mm TL. Although the former authors found females of different sizes beginning the reproductive process, they commented that females longer than 45 mm TL were more likely to be reproductive. Palacios et al. (2008) considered that all individuals of 15-32 mm were juveniles, and the smallest ovigerous female was 40 mm TL. Males (at 25-96 mm TL) were significantly larger than females, which were 22-65 mm TL.

There is a strong association between sexual dimorphism and the mating system in carideans. Males of species that guard females are often larger in body size than females and/or possess proportionately larger cheliped weapons (e.g., *Macrobrachium* spp.) (Bauer 2004). Although there is no information on the mating system of *A. scabra*, the larger size of males indicates some sort of guarding of females or intrasexual competition involving fighting and pushing. Undoubtedly, a large size and massive chelipeds are advantageous in sequestering females from other males (Bauer 2004).

An aspect that may influence the capture of large-sized individuals is their value as food for humans. In some areas, selective fishing of the largest individuals may directly influence population studies, in which the capture of individuals of all lengths is extremely important (Martínez-Mayén et al. 2000). Although *A. scabra* is used as food and bait by people living along rivers, at least in some basins of southeastern Bahia (Almeida et al. 2008), the artisanal capture of this shrimp was only sporadically observed in the study area.

Reproductive period

Of the 1867 females collected, 1430 (76.6%) were ovigerous, and ovigerous females were found every month. The smallest proportion of total females captured was 51.0% (Jan. 2005). The highest indices were observed in May (94.3%) and Oct. (98.6%) 2004, and Mar. (93.7%) 2005 (Fig. 3). Dissection of females carrying eggs in the final incubation stage or larval-release stage, showed ovaries in advanced vitellogenesis, indicating that these females continuously produce broods (Luz and Almeida, pers. obs.), and therefore are soon ready for a new clutch. Based on these observations, we can characterize the reproductive period as continuous and with a high rate of reproductive activity throughout the year.

Galvão and Bueno (2000) also found ovigerous females in all months of their study of this same species, with peaks of up to 85% in months with the highest temperature and rainfall. In drier and colder months, the authors found only 6% ovigerous females. In Mexico, the same pattern was seen for *A. margaritacea*, which also continuously reproduced with a peak during the rainy season, probably to facilitate larval dispersal (Martínez-Mayén and Román-Contreras 2000). In contrast, Palacios et al. (2008) observed a seasonal reproductive period, with a high index in the beginning of the rainy season.

Similar relationships between the reproductive peaks and months with the highest temperature and rainfall were also observed for other freshwater caridean species in other regions of Brazil (Carvalho et al. 1979, Valenti et al. 1986, Mossolin and Bueno 2002), thus demonstrating a certain general pattern for this group of crustaceans. In the population studied, a relationship between reproductive peaks and high rainfall indices was not clearly observed. If on 1 hand the reproductive peak in May 2004 (94.33% ovigerous females) was related to the increased precipitation, the main peak during the entire study period (Oct. 2004, with 98.6% ovigerous females) was preceded by 3 mo of low rainfall (Figs. 2, 3).

Fecundity

All eggs of 30 females were counted, for a total of 114,349 eggs, and a mean of 3811 (± 1992.87) eggs per female. The female with the fewest eggs had 870 eggs (10.87 mm CL and 33.22 mm TL), and the one with the most eggs carried 8907 (19.36 mm CL and 58.22 mm TL). Figure 4 shows the relationship between the size of each female and the number of eggs carried.

When Darnell (1956) studied a population of this species in Mexico, he found 8000 eggs on 1 female that was 57.5 mm long, and the size and number of eggs were similar to those found in this study. On the other hand, the smallest number found by Darnell (43 mm TL, with 746 eggs) greatly differs from the numbers carried by individuals of a similar size found in this study (for example, 1 female at 43.36 mm TL carried 3327 eggs). Concerning the mean fecundity, Galvão and Bueno (2000) obtained estimates very similar to ours, with 3881 (± 1531) eggs per female, and a range of 324-11,263 eggs.

For *A. margaritacea* in Mexico, Martínez-Mayén and Román-Contreras (2000) observed a relationship between the number of eggs and female size, in which the smallest (32 mm TL) ovigerous female carried 1504 eggs, and the largest (66 mm TL) carried 16,200 eggs. Palacios et al. (2008) studied the fecundity of females at 43-59 mm TL, and reported a range of 1860-22,400 eggs. Galvão and Bueno (2000) also mentioned the relationship between size and number of eggs carried, but comparison of their numbers with those found in this study is difficult because they did not report the size of the females sampled. This problem is common in related scientific articles. Extreme care should be taken when comparing amounts, because differences may be related to different methods, environmental aspects, genetic variations of populations, missing eggs, etc.

Even with these differences, all investigators who studied atyid shrimp found certain features in common, such as the transport of many small-sized eggs (Anger et al. 2002), the total elimination of mature eggs (total spawning), and the concomitant development of ovaries and eggs, thus suggesting the ability to perform successive spawnings (Galvão and Bueno 2000; Luz and Almeida, pers. obs.). A similar ability to continuously reproduce is possessed by shrimp of other groups, such as *M. olfersi* (Mossolin and Bueno 2002).

Recruitment

While the distribution of individuals by length classes was observed each month, lower size classes occurred throughout almost the entire period. This observation indicates that there is a constant entrance of individuals into the population, which corroborates the characterization of the reproductive period as being continuous and also explains the high proportions of ovigerous females every month. Although it is possible to consider this to be continuous recruitment, a graphical presentation was impeded by the small size of individuals caught, because all of them were mature enough to be considered adults (see “Population structure”).

The absence of young individuals did not prevent the analysis of other aspects examined here. Darnell (1956), Villalobos (1959), Galvão and Bueno (2000), and Martínez-Mayén and Román-Contreras (2000) explained this absence through behavioral characteristics, i.e., size segregation related to several microenvironments of the river. The stretches of river used in our study and also by the authors mentioned above probably did not cover the area where the juveniles live, next to the river outflow. Another possibility is that the mesh size of the hand net used in the sampling (= 14 mm) was too large to retain small juveniles.

Secondary sexual characteristics

Completely developed appendices masculinae were observed in all males captured, and they were therefore considered adults. Although it is not possible to confirm that the individuals were sexually mature, Martínez-Mayén

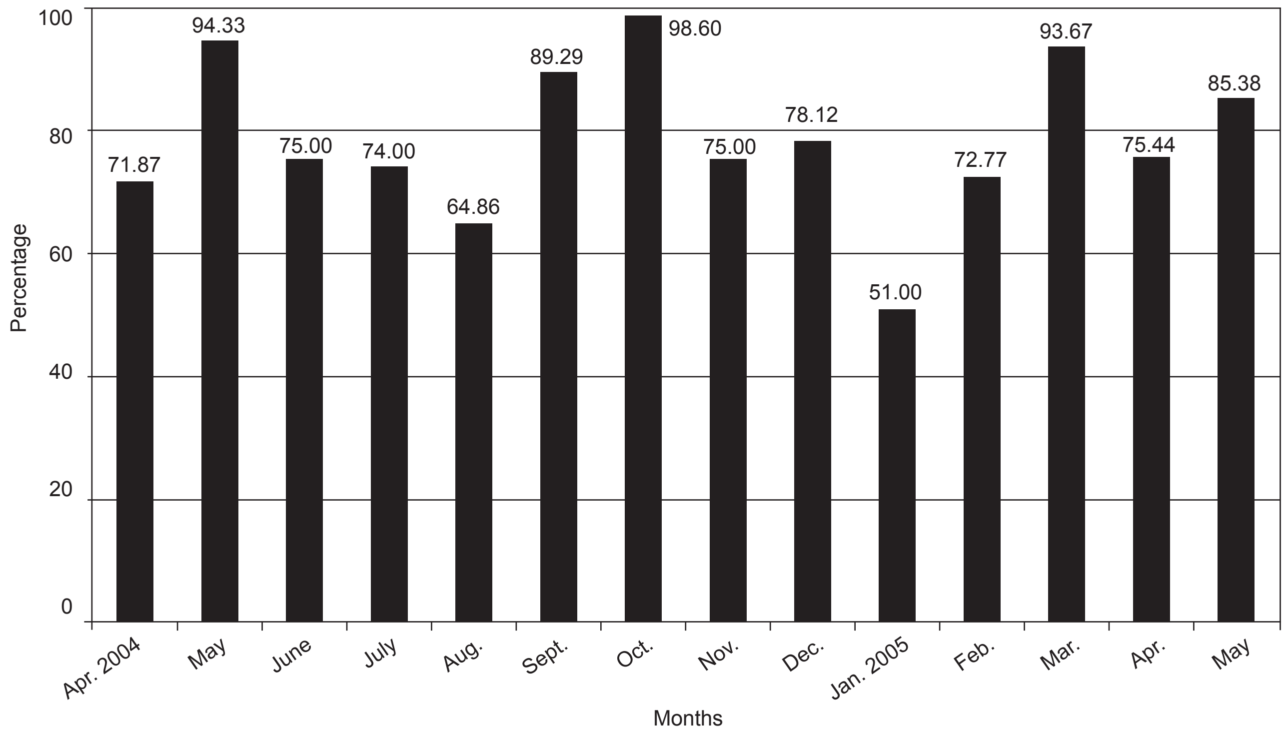

Fig. 3. *Atya scabra*. Percentage of ovigerous females collected from Apr. 2004 to May 2005, Santana River, Ilhéus, Bahia, Brazil.

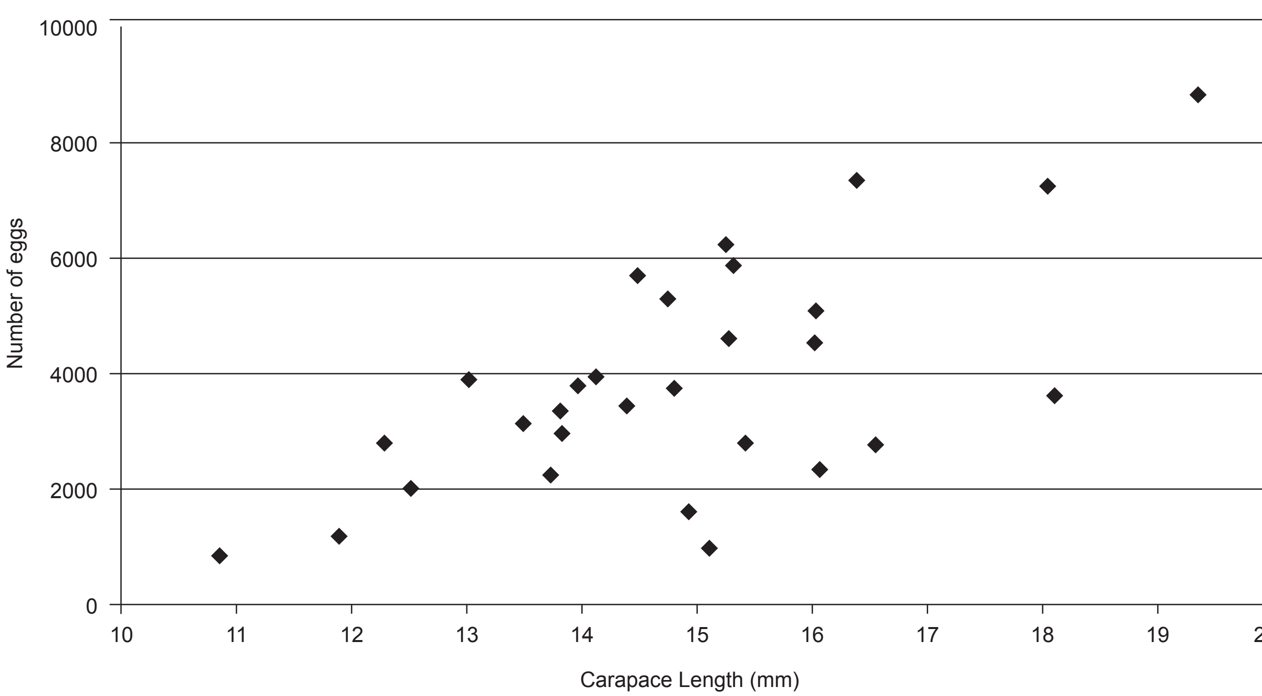

Fig. 4. *Atya scabra*. Relationship between the number of eggs carried and the size of females sampled from Apr. 2004 to May 2005, Santana River, Ilhéus, Bahia, Brazil.

and Román-Contreras (2000) assumed that males of *A. margaritacea* were sexually mature when they reached the same size as mature females, considering that the appendix masculina was completely developed.

Concerning the study of secondary sexual characteristics related to female maturity, 5 of the 8 relationships studied had relatively homogeneous residual variances, and we therefore compared their coefficients and regression constants (Table 1). In the relationships of CL with ASW, CL with PW and CW with PW, the measurements did not differ in terms of slope, but highly significantly differed when the elevations were compared. The slopes in the relationships of CL with PH and CW with PH significantly differed ($0.01 < p < 0.05$). In both cases, differences between the regressions for males and females were also highly significant compared to the elevations. These results indicate that the 2nd abdominal segment is proportionately larger in females than in males in relation to its width, height, and pleural width, which would thus represent secondary female sexual characteristics related to an increased area for egg incubation in females.

In *A. margaritacea* from Mexico, Martínez-Mayén et al. (2000) considered the relative growth between parts of the male body to be allometric, which produced a distinct sexual dimorphism. Females grew less during the rainy season, and males grew at a similar rate throughout the year.

Female caridean shrimp have special abdominal characters related to incubation, retention, and embryo incubation. The expansion of the pleura, notably in the 1st 3 abdominal segments, in addition to extending the space where embryos are kept, also protects them during the incubation period. Other alterations occur in the 1st 3 pairs of pleopods, including increases in the basipodite width and coxopodite length, and the presence of ovigerous setae. These characteristics are often partly or completely lost in non-ovigerous females (Bauer 2004). Darnell (1956) and Galvão and Bueno (2000) observed that males of *A. scabra* reach a larger mean body size than females. Females, in turn, have a relatively larger abdomen than males, which is related to the increased egg incubation area and consequently to fecundity.

Pleurae of the 2nd abdominal segment of females are significantly more developed than those of males. Once they are acquired, these secondary sexual characters are retained between 1 reproductive phase and another, as females in the study area are apparently continuously producing broods (as detailed in the “Reproductive period” section). These observations are in accordance with those of Galvão and Bueno (2000) for an *A. scabra* population at São Sebastião, Brazil, in addition to other freshwater carideans (Carvalho-Pinheiro 1983, Mossolin and Bueno 2002). Consequently, it can be assumed that in the population studied, once the secondary sexual characters are acquired, they are retained for the

Table 1. *Atya scabra*. Comparison of secondary sexual characteristics of males and females sampled in the Santana River, Ilhéus, Bahia, Brazil, by means of a covariance analysis. The relationships in bold indicate heterogeneous variances

	Males					Females					Males × Females		
Relationship	*n*	A	B	*r*	*F*	*n*	A	B	*r*	*F*	*F* (comparison of residual variances)	*F* (comparison of slopes; b)	*F* (comparison of elevations; a)
CL/ML	31	- 3.0686	0.8807	0.91	148.5961	38	0.5607	0.6489	0.936	254.3671**	**9.2512****	-	-
CL/ASW	31	0.1148	0.459	0.9667	414.0205**	38	0.102	0.5262	0.9573	395.0868**	2.1305 *	3.1902 NS	49.036**
CL/PH	31	1.2057	0.2739	0.9635	376.0593**	38	1.1775	0.3744	0.7805	56.1215**	0.2343 NS	4.5838*	68.322**
CL/PW	31	2.6018	0.3514	0.9434	234.7565**	38	2.687	0.4792	0.7087	36.3281**	0.2441 NS	2.9078 NS	49.5741**
CW/ML	31	-2.688	1.7644	0.9143	147.7578**	38	- 0.3135	1.3161	0.9469	312.2015**	**11.1459****	-	-
CW/ASW	31	0.3672	0.9146	0.9609	349.3113**	38	- 0.5093	1.0555	0.9578	399.9599**	**2.5233****	-	-
CW/PH	31	1.4484	0.537	0.9424	230.3771**	38	0.8197	0.7417	0.7712	52.8475**	0.3529 NS	4.2228*	37.1158**
CW/PW	31	2.8802	0.6919	0.9269	176.9787**	38	2.1199	0.9634	0.7108	36.759**	0.3144 NS	3.136 NS	30.3392**

CL, carapace length; CW, carapace width; ML, length of merus of pereiopod 3; ASW, width of 2nd abdominal segment; PH, height of pleura of 2nd abdominal segment; PW, width of pleura of 2nd abdominal segment; *n*, number of individuals; a, regression constant; b, regression coefficient; *r*, determination coefficient; *F*, calculated *F* value (*F* calc); NS, not significant; probability > 0.05; *, probability between 0.05 and 0.01; **, probability ≤ 0.01).

remainder of the life of the female.

It is expected that this information may help when implementing measures aimed at regulating fishing by pertinent governmental organizations, in order to guarantee the sustainable exploitation of this species as a fishery resource in this region, by preventing excessive reduction of the population.

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