



BIOLOGY

Growth, sexual maturity and sexual dimorphism of *Aegla georginae* (Decapoda: Anomura: Aeglidae) in a tributary of the Ibicuí River in southern Brazil

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ABSTRACT. This study aimed to estimate the growth and size at the onset of sexual maturity in a population of *Aegla georginae*. Specimens were sampled from November 2007 to October 2008 in the Perau Creek (Ibicuí-Mirim sub-basin; Uruguay River basin). All captured specimens were sexed, and their cephalothoracic length (CL), minor and larger propodi length (MPL, LPL, respectively), height of major chela (HMQ), and abdomen width (AW) were measured. The lengthwise growth of males and females was evaluated using the Bertalanffy model, and the morphological sexual maturity was evaluated using the REGRANS program. The smallest ovigerous female presented a 10.45 mm CL. Males reached larger sizes than did females, but the growth rate was similar between the sexes. Longevity estimates for males and females were 670 and 736 days, respectively. The best relationship used to infer the size at morphological sexual maturity in males was CLxHMQ (12.78 mm) and in females was CLxAW (10.78 mm). *Aegla georginae* follows a common pattern for aeglids in terms of lifecycle, where sexual dimorphism is associated with the onset of morphological sexual maturity.

KEY WORDS. Age estimative, Bertalanffy, longevity, size at onset maturity.

Species of *Aegla* Leach, 1820 have a lifecycle that is entirely restricted to freshwater environments and is the only taxon of Anomura with this profile (BOND-BUCKUP et al. 2008, FERNANDES et al. 2013). This genus is composed of over 70 described species with distributions restricted to subtropical South America (SANTOS et al. 2013).

Previous studies have contributed to the understanding of the population dynamics (i.e., longevity, recruitment, allometry, growth rates, juvenile cohort) in species such as *Aegla platensis* Schmitt, 1942 (BUENO et al. 2000); *Aegla castro* Schmitt, 1942 (SWIECH-AYOUB & MASUNARI 2001); *Aegla leptodactyla* Buckup & Rossi, 1977 (NORO & BUCKUP 2003); *Aegla jarai* Bond-Buckup & Buckup, 1994 (BOSS et al. 2006); *Aegla longirostri* Bond-Buckup & Buckup, 1994 (SILVA-CASTIGLIONI et al. 2006); *Aegla italacomiensis* Bond-Buckup & Buckup, 1994 (SILVA-GONÇALVES et al. 2009); and *Aegla manuinflata* Bond-Buckup & Santos, 2009 (TREVISAN & SANTOS 2011).

Body growth can be represented by a curve that corresponds to the dimensions of an individual measured over time or, more often, by means of the partial or total population (MARGALEF 1977). This curve is of great importance because it provides information regarding the maximum size, the age when this size is achieved and the growth rate of individuals (VALENTI et al. 1987).

Additionally, data on the growth and the size at onset of sexual maturity are important to understand the reproductive biology and population in aeglids (BUENO & SHIMIZU 2008, COPATTI et al. 2015). According to HARTNOLL (1982, 2001) allometric growth is useful for estimating sexual maturity, because second pleomere width and cheliped dimensions exhibit different growth rates according to the state of maturity. Additionally, the greater cephalothorax width in females and cephalothorax length in males, respectively, can characterise sexual dimor-

phism in aeglids (BARRÍA et al. 2014). Sexual dimorphism in the width of the abdomen is not found in other groups of Anomura (TREVISAN et al. 2012).

In recent years, some studies have investigated aspects of reproductive biology in aeglids, highlighting aspects of gonadal development (SOKOŁOWICZ et al. 2006), macroscopic and histological analyses of the gonads (SOKOŁOWICZ et al. 2007) and morphological, physiological and functional sexual maturity (BUENO & SHIMIZU 2009). Furthermore, VIAU et al. (2006), OLIVEIRA & SANTOS (2011), TREVISAN & SANTOS (2012) and COPATTI et al. (2015) developed studies that focused on the size at the onset of morphological sexual maturity in aeglids based on the relative growth of body parts, demonstrating the importance of morphological variations in sexual maturity.

Considering the importance of body growth and the onset of morphological sexual maturity for understanding aeglid biology, we propose to study these parameters in *Aegla georginae* Santos & Jara, 2013, a threatened species (endangered) of southern Brazil (SANTOS et al. 2013). Additionally, we provide information on differences in size and sexual maturity between the sexes, sexual dimorphism and lifecycle of *A. georginae*.

MATERIAL AND METHODS

Field investigations were conducted in the Perau Creek, Jaguari, RS, Brazil (29°29'13"S, 54°42'42.6"W), a second-order river located in the Jaguari River micro-basin. The stretch of stream in the study is located on the southern boundary of the Atlantic, a region of ecotone with the Pampa biome. The Jaguari River microbasin belongs to the Ibicuí River sub-basin, corresponding to the largest sub-basin of the Uruguay River. The Jaguari River has its mouth in the upper Ibicuí River, and its tributaries are fast streams, creating valleys with rocky outcrops (COPATTI et al. 2009).

Margins of the study stretch show remnants of the original deciduous forest interspersed with grass patches, with low anthropic use in the surrounding lands. The river bottom is mainly stony but also consists of sand, gravel, clay, and leaves. The river has an average width of 3 m and a depth of 15-45 cm.

Physiochemical parameters of the water were measured monthly. Dissolved oxygen (6.00-8.55 mg.L⁻¹ O₂) and temperature (10.0-22.5°C) were measured using a YSI oximeter (model Y5512), pH (6.0-7.5) was measured using the pH meter Quimis (model 400.A), and alkalinity (24-3545 mg.L⁻¹ CaCO₃), hardness (15-20 45 mg.L⁻¹ CaCO₃), and total ammonia (0.01-0.08 N-NH₃) were monitored using a water analysis kit (Alfakit, Florianópolis, Brazil).

Monthly samplings were performed from November 2007 to October 2008 in a section of the stream that is approximately 30 m in length. Specimens were captured using 25 plastic traps with beef liver randomly set along the sampling zone, and all traps were set late in the afternoon and checked for aeglid individuals the following morning. An additional effort (30 min) was conducted with a hand net (Surber sampler, 0.1 m² area,

250 µm mesh net) by two researchers for each monthly sampling. Specimens were collected according to permits granted by appropriate agencies (SISBIO process 14180-1).

The following body dimensions of individuals were measured using a digital caliper to the nearest 0.01 mm: cephalothorax length (CL) (from the tip of the rostrum to the posterior margin of the cephalothorax); cephalothorax width (CW) (distance between the bases of the epibranchial spines); second abdominal somite width (AW); minor propodus length (MPL); larger propodus length (LPL); and height of major chela (HMQ) (Fig. 1). After the measurements, the specimens were returned to the collection location.

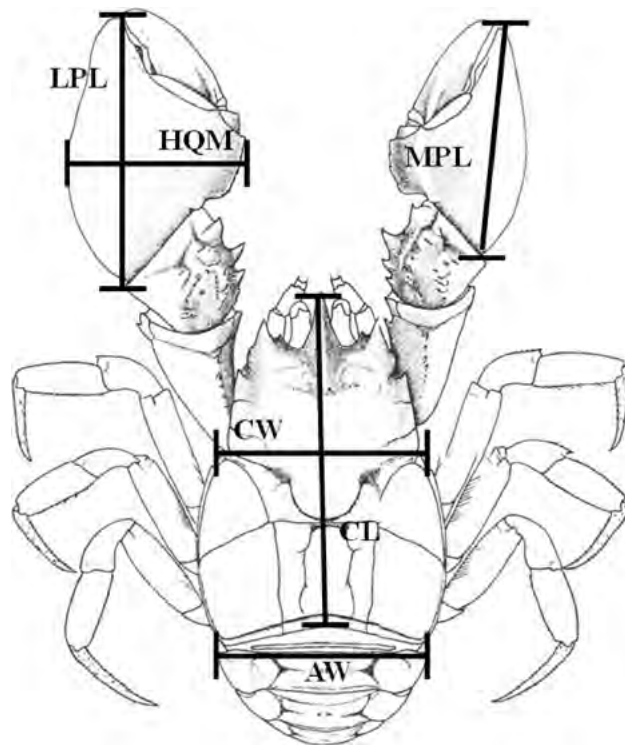


Figure 1. *Aegla georginae* body dimensions. CL, cephalothorax length; CW, cephalothorax width; AW: second abdominal somite width; MPL, minor propodus length; LPL, larger propodus length; HMQ: height of the major chela. Adapted from SANTOS et al. (2013).

Analysis of the growth in length of *A. georginae* was performed based on the distribution of the absolute frequencies of size class intervals of 1.00 mm CL, equivalent to one fourth of the standard deviation calculated for the total sample examined. Individuals with less than 3.00 mm CL were considered unsexed juveniles because their pleopods and genital pores were too undeveloped to provide reliable identification of the animals' sex and were added to both sexes in the analysis of the frequency distribution of size classes.

The increase in length was estimated separately in males and females by means of the displacement of the modal frequencies obtained during the sampling of each month, in accordance with the size class frequency distributions (MACDONALD 1987). Modal values of the CL frequency distribution were calculated according to SPIEGEL (1979): $\text{Mode} = L_1 + [\Delta_1/\Delta_1 + \Delta_2] C$, where: L_1 = the inferior limit of the modal class; Δ_1 = excess of modal frequency/inferior class; Δ_2 = excess of modal frequency/superior class and; C = the amplitude of the modal class interval. BERTALANFFY'S (1938) model was used for the CL curve growth: $C_t = L_\infty [1 - e^{-k(t-t_0)}]$, where: C_t = median CL of aeglids at age t (mm); L_∞ = maximum mean cephalothorax length, in mm; k = age-specific growth rate; e = natural logarithms; t = age in days, and t_0 = the parameter related t_0 the size of the aeglids at birth. The growth curves obtained for males and females were linearised using the method ALLEN (1976) proposed, and those of males and females were compared using a covariance analysis (ANCOVA; $\alpha = 5\%$) (ZAR 1996).

Relative growth patterns of males and females, according to the characteristics of the growth model for each sex, were assessed after an initial adjustment of dispersion points using REGRANS software (PEZZUTO 1993). We used the power equation $y = ax^b$ to describe the relative growth of *A. georginae*. Equation was linearised ($\log y = \log a + b \log x$), and the cephalothorax length (CL) was used as the independent variable (x), related to the other bodily dimensions, which were the dependent variables (y). For this analysis, we used only the dimensions of chelipeds for males and the abdomen for females because these dimensions are considered secondary sexual characteristics in pleocyemate decapods; moreover, development of these structures is associated with a shift between phases in the lifecycle (HARTNOLL 1982).

The coefficient of allometric growth (b) of the equation expresses the analogy between the parts evaluated. We used a Student's t -test to verify whether the growth was positive or negative allometric (statistically above or below 1.00, respectively) or isometric growth (statistically similar to 1.00). Furthermore, the intercept of the linear growth of male and female juveniles and adults was evaluated. These analyses were performed using an analysis of covariance (ANCOVA) with a confidence interval of 95% (SOKAL & ROHLF 1979).

For assessment of sexual dimorphism, the animals were divided into four categories according to size at morphological sexual maturity (see Results): juvenile males, adult males, juvenile females, and adult females. All measurements taken in the field were log-transformed to normalise the data. All aeglids measurements were standardised by applying the formula $Y_i^* = Y_i (X/X_i)^b$, where: Y_i^* = standardised measurement of the length of specimen i ; Y_i = measurement of the dimension of the specimen to be standardised; X_i = cephalothorax length of specimen i ; X = mean value of CL of specimens examined; and b = exponent of the allometric equation $Y = ax^b$. An ANOVA was used to compare all dimension measures of various categories (ZAR 1996).

RESULTS

A total of 1774 individuals were measured: 1259 males, 512 females and three non-sexed juveniles. CL of the males and females, ranged from 3.11 to 26.00 mm and from 3.73 to 22.36 mm, respectively. We recorded 119 ovigerous females, with 112 reaching this phase during autumn (60, 39 and 13 in March, April and May, respectively). In addition, between June and September, one or two ovigerous females were recorded per month. CL of the ovigerous female ranged from 10.45 to 19.38 mm.

Recruiting was detected beginning in March 2008, at the end of the summer season. However, juveniles were sampled in all seasons of the year for both sexes, according to the distribution of absolute frequencies of CL (Figs. 2-3).

Regarding the sexual dimorphism of *A. georginae*, no significant differences were observed between the bodily dimensions of male and female juveniles ($p > 0.05$); however, significant differences were found between male and female adults ($p < 0.05$). All dimensions of adult males were higher than those of adult females ($p < 0.05$).

The estimated value of the average maximum cephalothorax size (L_∞) through the growth curve was 26.57 and 21.71 mm for males and females, respectively (Figs. 4-5). These values are close to the record for the largest animals found in field: 26.00 and 21.90 mm CL for males and females, respectively. Males reached greater CL than did females, but the growth rate was similar between the sexes ($k = 0.0064$ and 0.0080 for males and females, respectively). Longevity estimated through the analyses of the growth curve was higher in females (736 days) than in males (670 days).

Analyses of body relationships of *A. georginae* showed that the measures of chelipeds in males and AW in females are effective for estimating the size of the onset of morphological sexual maturity (Figs. 6-9). Evaluations of elevations and intercepts of the linear models of juvenile and adult males allowed for the estimation of the inflection point at 12.78 mm for the CLxHMQ relationship. In females, the CLxAW relationship showed an inflection point at 10.78 mm (Table 1). These relationships indicate morphological sexual maturity because they have values that approach the size of the smallest ovigerous female found in field (10.45 mm CL). So, *A. georginae* adult females can become ovigerous in March (beginning of the reproductive period), regardless of their CL.

During the ontogeny of *A. georginae*, relationship between the body parts had different allometric coefficients. In males, all the relationships of cheliped dimensions showed positive allometry. In females, in turn, the CLxAW relationship showed positive allometry for adults, while in juveniles allometry was negative (Table 1). In all male and female data groups, secondary sexual characteristics showed different growth patterns before and after the onset of morphological sexual maturity because the values of the intercepts (a) and slopes (b) were different according to ANCOVA ($p < 0.01$) (Table 2).

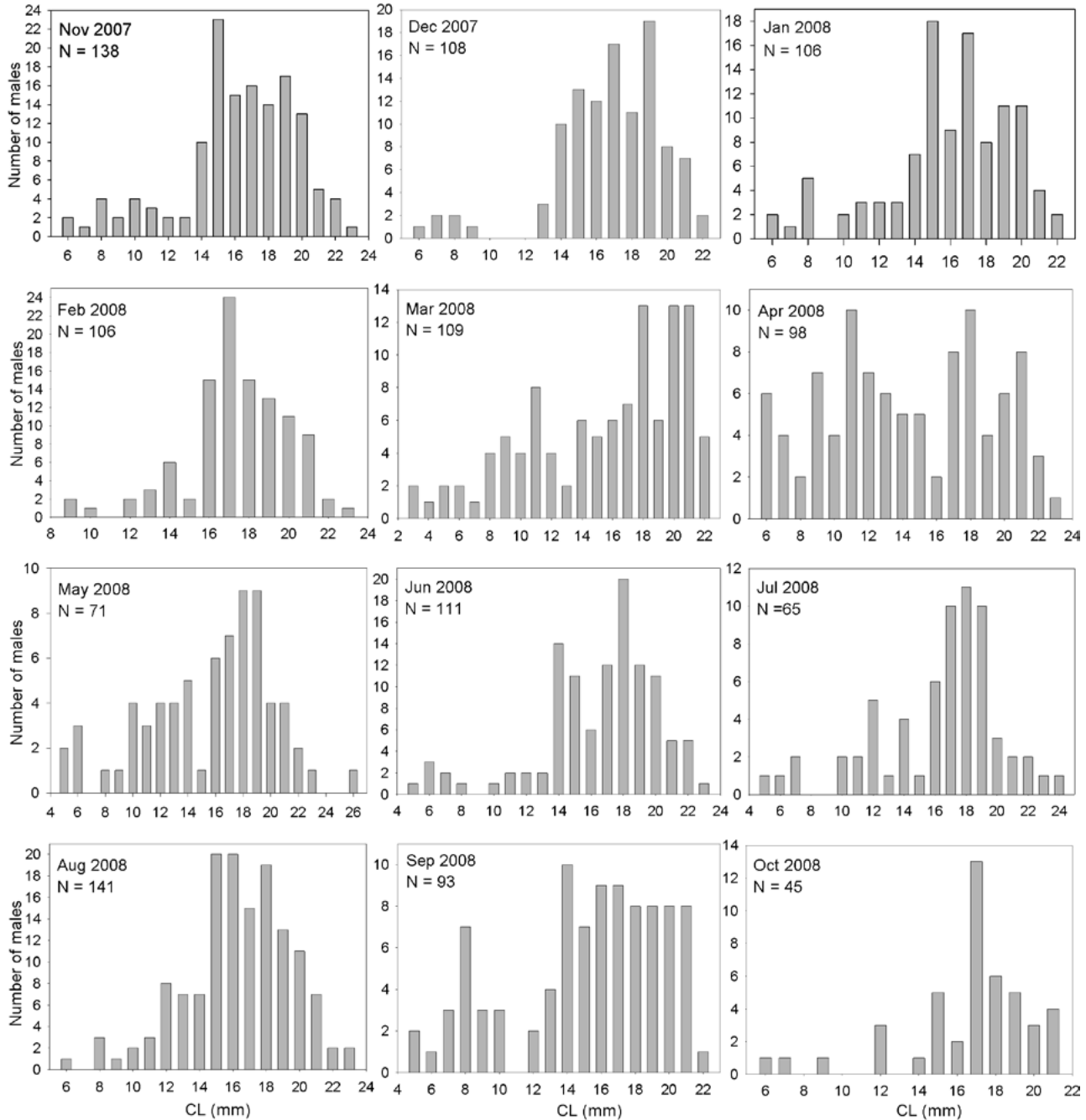


Figure 2. Absolute frequency distribution of cephalothoracic length (CL) (mm) classes of *Aegla georginae* males, Perau Creek, Ibicuí Basin, Brazil.

DISCUSSION

The impact of seasonality on recruitment and reproduction in aeglids is not yet clear. For example, flood pressure could severely affect juveniles since they are more susceptible to being

washed-out to less favourable areas (BUENO et al. 2014). Possibly, regional and latitudinal factors are involved, and those from rivers at low latitudinal regions have shown a marked seasonal reproductive pattern (BUENO & SHIMIZU 2008, BUENO et al. 2014).

Aegla georginae juveniles were sampled in all seasons of the

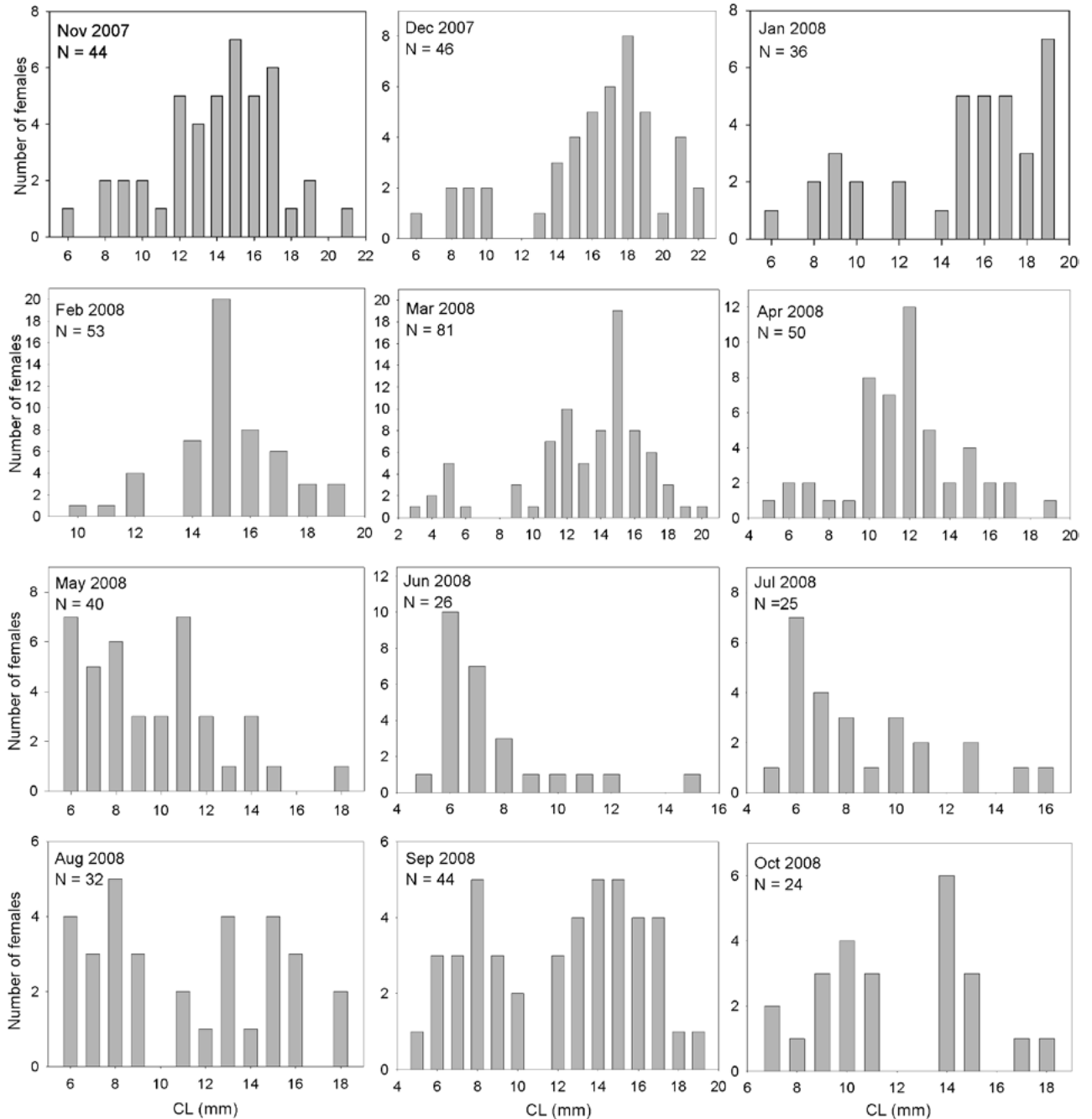


Figure 3. Absolute frequency distribution of cephalothoracic length (CL) (mm) classes of *Aegla georginae* females, Perau Creek, Ibicuí Basin, Brazil.

year, but ovigerous females were more abundant in autumn and juveniles might have originated mainly from spawning occurred during this season. In addition, records of the few ovigerous females during winter and early spring may be viewed as possible isolated cases of late oviposition and also contributing to lower

rates of registered juveniles throughout the year. According to TUDGE (2003), the timing of spawning differs between species and between populations of the same species. Thus, *A. georginae* could potentially breeds from March to September.

The higher concentration of juveniles in March might be

Table 1. Allometric relationships of the populations of *Aegla georginae* in the PerauCreek, Ibicuí Basin, Brazil. (JM) Juvenile males, (AM) adult males, (JF) juvenile females, (AF) adult females, (CL) cephalothorax length, (AW) second abdominal somite width, (MPL) minor propodus length, (LPL) larger propodus length, (HMQ) height of major chela, (+) positive allometry, (–) negative allometry, (*) significant.

Variable	Category	Inflection point (mm CL)	Intercept (a)	Declivity (b)	Linear equation $\text{Log } y = \log_a + b \log_x$	R ²	All	t test (b = 1)
AW	FJ	10.78	0.18	0.98	$\text{LogAW} = 0.18 + 0.98 \log \text{CL}$	0.91	–	38.62*
	AF		0.25	1.08	$\text{LogAW} = 0.25 + 1.08 \log \text{CL}$	0.92	+	59.76*
MPL	JM	14.54	0.47	1.12	$\log \text{MPL} = 0.47 + 1.12 \log \text{CL}$	0.93	+	51.36*
	AM		0.95	1.55	$\log \text{MPL} = 0.95 + 1.55 \log \text{CL}$	0.88	+	51.33*
LPL	JM	13.90	0.42	1.12	$\log \text{LPL} = 0.42 + 1.12 \log \text{CL}$	0.92	+	47.67*
	AM		1.06	1.69	$\log \text{LPL} = 1.06 + 1.69 \log \text{CL}$	0.82	+	60.43*
HMQ	JM	12.78	0.89	1.33	$\log \text{HMQ} = -0.05 + 1.33 \log \text{CL}$	0.95	+	34.02*
	AM		1.45	1.84	$\log \text{HMQ} = 0.16 + 1.84 \log \text{CL}$	0.95	+	67.12*

Table 2. Summary of comparisons between the straight lines of *Aegla georginae* juveniles and adults in the Perau Creek, Ibicuí Basin, Brazil. (M) Male, (F) female, (CL) cephalothorax length, (AW) second abdominal somite width, (MPL) minor propodus length, (LPL) larger propodus length, (HMQ) height of major chela.

Sex	Relationship	F Intercept	F slope	α Intercept	α slope
M	CL X MPL	356.60	2832.27	<0.0001	<0.0001
M	CL X LPL	523.50	360.00	<0.0001	<0.0001
M	CL X HMQ	162.70	166.86	<0.0100	<0.0100
F	CL X AW	5.87	9.47	0.0100	<0.0100

related to the intense reproductive peak of this species during this period. This pattern is consistent with previous studies, in which aeglids have a single pulse of recruitment per year, as described for *Aegla laevis laevis* Latreille, 1818 (BAHAMONDE & LOPEZ 1961); *Aegla paulensis* Schmitt, 1942 (LOPEZ 1965); *Aegla perobae* Hebling & Rodriguez, 1977 (RODRIGUES & HEBLING 1978); *A. platensis* (BUENO et al. 2000); *A. leptodactyla* (NORO & BUCKUP 2003); *A. jarai* (BOSS JR et al. 2006); and *A. longirostri* (SILVA-CASTIGLIONI et al. 2006). In contrast, recruitment throughout the year was described by TREVISAN & SANTOS (2011) for *A. manuinflata*, CHIQUETTO-MACHADO et al. (2015) for *A. schmitti* Hobbs, 1978 and COPATTI et al. (2015) for three sympatric aeglids, *A. platensis*, *Aegla grisella* Bond-Buckup & Buckup, 1994 and *Aegla ludwigi* Santos & Jara, 2013.

In this study, we verified that asymptotic growth differs between the sexes and *Aegla georginae* males reached larger sizes than did females. The larger size of males compared to females is a common dimorphic trait in pleocyemate decapods (HARTNOLL 1974). The size of males might be advantageous during potential intraspecific competition for reproduction (AYRES-PERES et al. 2011, GRABOWSKI et al. 2013). According to SIQUEIRA et al. (2013), female preference for larger males may be one factor related to the evolution of sexual dimorphism.

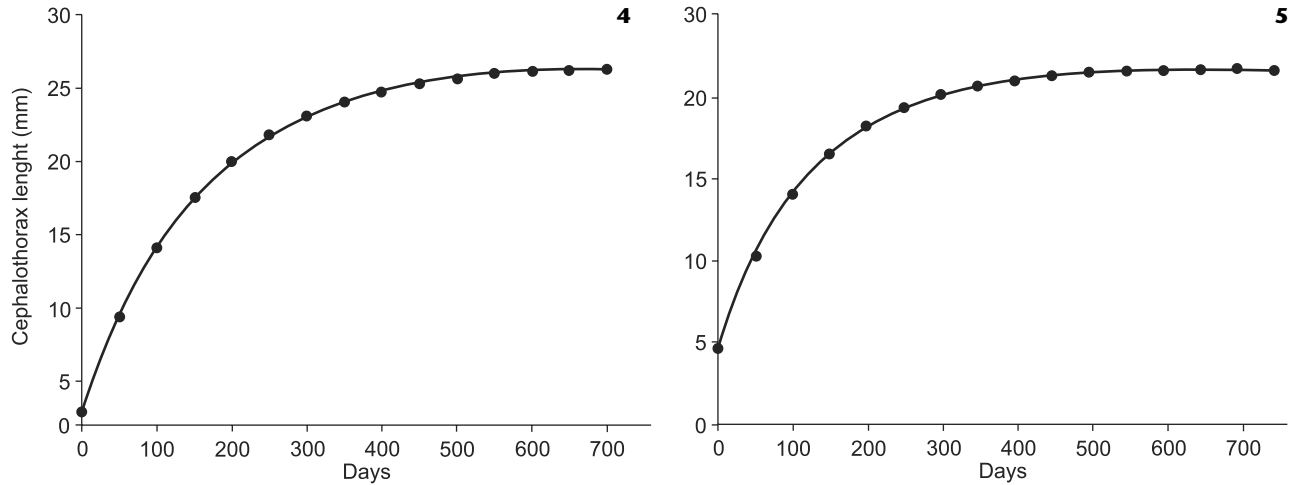
Furthermore, this pattern was also observed for *A. laevis laevis* (BAHAMONDE & LOPEZ 1961); *A. paulensis* (LOPEZ 1965); *A. perobae* (RODRIGUES & HEBLING 1978); *A. platensis* (BUENO &

BOND-BUCKUP 2000); *A. castro* (SWIECH-AYOUB & MASUNARI 2001); *A. leptodactyla* (NORO & BUCKUP 2003); *A. longirostri* (COLPO et al. 2005); *Aegla fransiscana* Buckup & Rossi, 1977 (SILVA-GONÇALVES et al. 2006); *A. itacolomiensis* (SILVA-GONÇALVES et al. 2009); *A. manuinflata* (TREVISAN & SANTOS 2012); *Aegla parana* Schmitt, 1942 (GRABOWSKI et al. 2013); and *A. platensis* and *A. grisella* (COPATTI et al. 2015), which corroborate our observations. On the other hand, *A. platensis* appears to be an exception, where females showed a larger asymptotic size than did males (BUENO et al. 2000, DALOSTO et al. 2014).

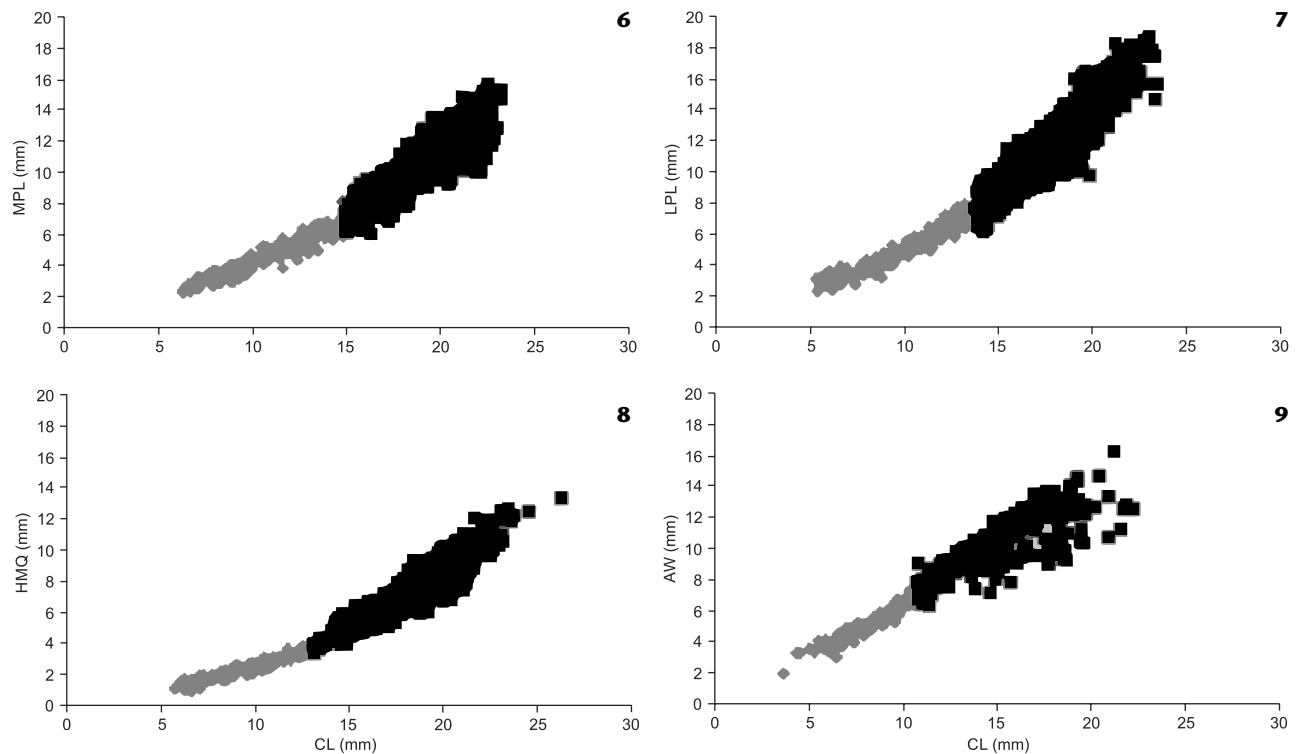
Females invest a significant amount of energy in reproductive functions and do not molt during egg incubation, whereas males do not have this limitation, reaching larger sizes compared to females (HARTNOLL 1974). Moreover, reduction in growth can be related to stress resulting from egg laying (SWIECH-AYOUB & MASUNARI 2001). In females, a tradeoff between energy and growth is given, where the energy supply devoted to reproduction does not allow for a level of growth that is similar to that of males.

In terms of longevity, females tend to live slightly longer than do males (DA SILVA et al. 2016). Males demonstrate aggressive playing behavior (AYRES-PERES et al. 2011, COHEN et al. 2011, TREVISAN & SANTOS 2014) and remain exposed for a longer period of time on the surface to feed, dispute and court females and thus would be exposed to predation and environmental adversity, reducing their lifespans (SILVA-CASTIGLIONI et al. 2006, SILVA-GONÇALVES et al. 2009). Under laboratory conditions, males tend to show higher levels of locomotor activity, frequently moving from one place to another (TEODÓSIO & MASUNARI, 2009); hence they might be under greater risk of predation than are females, which could shorten their lifespan. Indeed, *A. georginae* females (736 days) presented superior longevity compared to males (670 days). Greater longevity for females was also reported by SILVA-CASTIGLIONI et al. (2006) for *A. longirostri*, SILVA-GONÇALVES et al. (2009) for *A. itacolomiensis* and CHIQUETTO-MACHADO et al. (2015) for *A. schmitti*.

On the other hand, BAHAMONDE & LOPEZ (1961) and TREVISAN & SANTOS (2011) observed superior longevity for males compared



Figures 4-5. Growth curve of cephalothoracic length (CL) (mm) in *Aegla georginae* males (4) and females (5), Perau Creek, Ibicuí Basin, Brazil. The following equations were fitted to the date: A: $Ct = 26.57[1 - e^{-0.0064(t+18.14)}]$ ($n = 1259$; $r = 0.93$); B: $Ct = 21.71[1 - e^{-0.008(t+30.25)}]$ ($n = 512$; $r = 0.94$). Where Ct = cephalothorax length in the time t; t = time in days.



Figures 6-9. Dispersion diagrams that analyse the morphological sexual maturity of *Aegla georginae* in Perau Creek, Ibicuí Basin, Brazil. (6-8) Males: (6) CLxMPL, $n = 972$; (7) CLxLPL, $n = 951$; (8) CLxHMQ, $n = 915$; (9) females, CLxAW, $n = 976$. Dark points = adults, Grey points = juveniles.

to females for *A. laevis* and *A. manuinflata*, respectively. A variety of patterns for the longevity of aeglids available in the literature (BAHAMONDE & LOPEZ 1961, SILVA-CASTIGLIONI et al. 2006,

SILVA-GONÇALVES et al. 2009, TREVISAN & SANTOS 2011) shows that the lifecycle of males and females depends on the relationship of physiological systems with external factors.

In addition to longevity, size at the onset of sexual maturity in aeglids can vary in both males and females. Secondary sexual characteristics are those directly related to mating or hatching eggs (COPATTI et al. 2015). Thus, the use of chelae in males occurs in cohort rituals, fighting for females, mating and in the place of establishment (AYRES-PERES et al. 2011, COHEN et al. 2011, PALAORO et al. 2014). Allometric growth of the chelipeds is generally positive in males and is highly variable in females (TREVISAN et al. 2012).

Likewise, in females, in turn, the CLxAW relationship showed negative allometry in juveniles and positive allometry in adults. In females, the size of the abdomen increases when they are sexually mature, in addition to being a secondary sexual characteristic (HARTNOLL 1982, 2001). In females, increased AW can be attributed to adaptation for reproductive functions, like internal space for the ovaries during the gonadal cycle, and for parental care of embryos and juveniles under the pleon (SOKOLOVICZ et al. 2006, 2007).

COLPO et al. (2005), VIAU et al. (2006), TREVISAN & SANTOS (2012) and COPATTI et al. (2015) found that AW in females and propodus chelae in males showed a change in the growth rate from juvenile to adult for *A. longirostri*, *Aegla uruguayana* Schmitt, 1942, *A. manuiinflata* and tree sympatric aeglids (*A. platensis*, *A. grisella* and *A. ludwigi*), respectively. These findings are in agreement with our data.

In conclusion, *A. georginae* follows a common pattern for aeglids in terms of lifecycle, growth and sexual maturity, where males are larger compared to females and AW (in females) and chelipeds (in males) are key secondary sexual characteristics defining the onset of morphological sexual maturity. Our results indicate that morphological differences are associated with sex, because sexual dimorphism is associated with the onset of morphological sexual maturity. The onset of sexual maturity of *A. georginae* is estimated as the point at which changes occur in all dimensions of the animal's body, since male and female juveniles grow similarly up to the point of reaching the adult phase (HARTNOLL 1982). Additionally, considering that *A. georginae* is a threatened species and has only recently been described, aspects of its biology such as the short reproductive period may be related to difficulties in population recovery. This knowledge is useful for its preservation and understanding its life history.

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