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Reproduction, growth and longevity of the endemic South American crab *Aegla marginata* (Decapoda: Anomura: Aeglidae)

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ABSTRACT

Reproduction, growth and longevity of *Aegla marginata* sampled with traps in Intervalas State Park (Brazil) from October 2013 to December 2014 are described. Male and female carapace lengths (CL) ranged in size from 5.50 to 20.00 mm and 5.20 to 19.67 mm, respectively. Functional sexual maturity was determined at a CL of 9.28 mm. The main reproductive period occurred during colder seasons (autumn and winter, March–August). Egg number varied between 40 and 146 (mean \pm SD; 95 ± 31.5), with an average reproductive output of 10.8% of the female weight, a value close to that found in other anomurans, enough to guarantee the success of this species during embryonic development. Fecundity increased with animal size (ANCOVA, $p < 0.05$), which allows an animal to produce more eggs, maximising reproductive efficiency, according to its size. Sex ratio was skewed towards males (Chi-Square, $p < 0.05$), especially during the reproductive period, in which females tended to exhibit cryptic behaviour when incubating eggs. The number of females and males was similar in the months before reproduction, suggesting that females were more active looking for food to store energy for the next reproductive period, and/or were looking for mates. The longevity of 2.43 (males) and 2.49 (females) years (Von Bertalanffy method) corroborate other studies that estimated a longevity of 2 to 3.3 years for *Aegla* spp. We conclude that *A. marginata* has seasonal reproduction and recruitment. All the information gathered here should be useful to future studies with other populations of *A. marginata* outside protected areas.

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Fecundity; reproductive periodicity; sex ratio; latitudinal variation; life span

Introduction

The Aeglidae Dana, 1852 (Crustacea: Anomura) contains only one extant genus, *Aegla* Leach, 1820 (Pérez-Losada et al. 2004), which is represented by over 75 species that are exclusively adapted to freshwater environments, according to the checklist of McLaughlin et al. (2010) and recent descriptions (Santos et al. 2012, 2013, 2014, 2015). The geographic distribution of aeglids is restricted to the South American Neotropical region, ranging from the south of Minas Gerais state (Brazil) to the island of Duque de York (Chile) (Bond-Buckup & Buckup 1994; Santos et al. 2012).

The aeglid's freshwater habitat (lotic and lentic environments) has been degraded in recent decades, resulting in changes in water quality, riverbed homogenisation, an increase in the amount of sediment, artificial eutrophication and a decrease in natural habitats and microhabitats. These perturbations are responsible for the alteration and loss of aquatic biodiversity in general (Cortes et al. 1998; Goulart & Callisto 2003). According to the conservation status of Brazilian fauna (Chico Mendes Institute for Biodiversity Conservation – ICMBio – regulatory ordinance

No. 444/2014 and 445/2014), 26 species of crustaceans are currently under threat, represented by 25 species (96%) in the genus *Aegla*, and one mangrove crab *Cardisoma guanhumi* Latreille, 1828. Thus, aeglid species represent all freshwater crustacean species that are currently under any type of threat.

Aegla marginata Bond-Buckup & Buckup 1994 occurs in Brazil from the southern region of São Paulo state (approx. 24°12'S and 48°03'W) to the north-west region of Santa Catarina state (approx. 26°18'S and 48°50'W) (Bond-Buckup & Buckup 1994). This species is not threatened; however, population biology studies do not exist to provide preservation status information throughout its wide geographic distribution. Recently, Trevisan et al. (2012) used a geometric morphometric approach to confirm the presence of sexual dimorphism in *A. marginata*.

Population biology studies of *Aegla* have been conducted in the last decade (Bueno & Shimizu 2008; Rocha et al. 2010; Cohen et al. 2011; Bueno et al. 2014), which has helped to understand population dynamics and has provided information on population size estimates (Bueno et al. 2014). All these studies have considerable importance

for the conservation of these species (Pérez-Losada et al. 2009).

In general, it is proposed that the genus *Aegla* originated from a marine ancestor from the cold waters of the South Pacific (Feldmann 1984; Pérez-Losada et al. 2004) and any pattern of reproduction in cold temperate regions could be a reflection of its marine ancestry. In addition, the reproductive pattern of *Aegla* spp. varies with latitude, i.e. species living in cold temperate regions (e.g. *Aegla uruguayana* Schmitt, 1942 – latitude 34°14'S) (Viau et al. 2006) reproduce throughout the whole year, whereas species that inhabit subtropical regions (e.g. *Aegla franca* Schmitt, 1942 – latitude 20°18') (Bueno & Shimizu 2008) demonstrate seasonal reproduction (Tudge 2003; Bueno & Shimizu 2008). This is opposite to the paradigm of latitudinal trends in life-history traits for marine crustaceans, as in many other invertebrates (Thorson 1950; Sastry 1983), including caridean (Bauer 2004) and penaeoidean shrimp (Bauer 1992; Castilho et al. 2007), i.e. a tendency towards continuous reproduction throughout the year in tropical and subtropical regions and seasonal reproduction at higher latitudes. These differences might reflect life-history adaptations in relation to the variability of water temperature and food resource availability (plankton production) of each latitudinal gradient.

Based on latitudinal trends, subtropical aeglid species generally demonstrate a yearly reproductive peak of four to six months, which coincides with colder seasons (autumn–winter) (April–September) (López 1965; Rocha et al. 2010; Cohen et al. 2011; Grabowski et al. 2013). This short reproductive period might have implications for the conservation of *Aegla* spp., because it causes difficulties in population recovery if their habitat is under the effects of environmental degradation owing to anthropogenic factors.

The objective of this study was to analyse reproduction, growth and longevity of *A. marginata* in Intervalles State Park, São Paulo state, Brazil. Moreover, the patterns found for *A. marginata* were compared with the latitudinal trend proposed for aeglids, to evaluate whether this species corroborates the pattern found for congeneric species.

Material and methods

Samples

Animals were sampled monthly in the Mirante das Antas stream (24°16'S and 48°24'W) in the Intervalles State Park (ISP), São Paulo state, Brazil, from October 2013 to December 2014. Sixteen baited (with fish-flavoured dry cat food) plastic traps were randomly placed into the stream according to the methodology of Rocha and Bueno (2004), during twilight. Traps were inspected the following

morning, because *Aegla* spp. typically exhibit a nocturnal exploratory behaviour (Sokolowicz et al. 2007; Bueno & Shimizu 2008). Environmental parameters (air temperature and rainfall) were obtained from measurements taken daily by the ISP.

Carapace length (CL, mm) was measured *in situ* from the post-orbital margin to the posterior margin of the carapace (Bueno & Shimizu 2008). Following all observations and measurements, the animals were released back into the stream, except the ovigerous females that were fixed and transported to the laboratory to evaluate reproductive output and fecundity.

Animals were also measured from the tip of the rostrum to the posterior margin of the carapace (CLR) (Bueno & Shimizu 2008), to compare values with those of other studies that used this dimension (Bahamonde & López 1961; López 1965; Rodrigues & Hebling 1978; Jara 1989; Swiech-Ayoub & Masunari 2001; Fransozo et al. 2003; Viau et al. 2006). The relationships between CLR (dependent variables) and the CL (independent variable) were analysed using linear regressions and the coefficient of determination (R^2), to find equations for each sex (Zar 2010).

Reproductive period

Females were identified in the field by the presence of well-developed pleopods and by the gonopore position on the coxa of the third pereopod pair. Males were identified by the lack of pleopods, a structure that they do not possess throughout their whole life-cycle (Bueno & Shimizu 2008). Recruitment was evaluated by the observation of specimens in the population with a CL less than 5 mm. Because of the difficulty in identifying the sex *in situ* of these animals, they were not sexed and were classified as juveniles.

The reproductive period was determined by observation of ovigerous females (= females with embryos attached to the pleopods) in the population throughout the sampled months (Bueno & Shimizu 2008; Grabowski et al. 2013). Females with well-developed gonads were macroscopically evaluated to determinate their developmental stage as proposed by Bueno and Shimizu (2008). Females with mature gonads were identified as stages 2, 3 and 4. The first stage was eliminated, because it indicates that these females are not reproducing (Bueno & Shimizu 2008). According to these authors, mature gonads are characterised by strong red posterior lobes in the form of two parallel stripes (for *A. marginata*, we observed a strong orange colouration of the gonads), with at least one of them reaching or passing the second pereopod pair (stage 2), a further posterior lobe reaching the third pereopod pair (stage 3), and at least one of the posterior



Figure 1. Embryonic developmental stages in *Aegla marginata* sampled in Intervales State Park (São Paulo). (I) Initial stage; (II) Intermediate stage and (III) Final stage.

lobes reaching the fourth pereopod pair, indicating imminent oviposition (stage 4).

To evaluate senescence in females, we undertook an exploratory analysis of graphs with ovigerous females and females with well-developed gonads (DE) distributed by size-classes. Senescence is a mechanism in which that we observe a decline in survival and reproductive performance with increase of age (Charlesworth 1993). The pattern of degenerative changes after the first reproduction, i.e. changes in structure, physiology and behaviour (Vogt 2014). These changes can be related to somatic structures, mutation accumulation and this can be reflected into physiology of reproduction (Charlesworth 1993; Vogt 2014).

Cross-correlation analysis was used to identify a possible correlation between the reproductive period of the female and the monthly temperature variation or the monthly rainfall. Significant relationships are those with an association coefficient equal to 1, which are classified as perfect; between 0.99 and 0.70, the association is classified as strong, 0.69–0.40 moderate; and 0.4–0.1 weak (for more details, see Grabowski et al. 2014 and Castilho et al. 2015).

Sex ratio

Only active individuals tend to be caught in traps, and therefore, do not represent the actual sex ratio, because samples will predominantly contain males, because they are more active than females. However, the use of traps will provide information concerning the temporal scale of individual activity, especially for females during the reproductive period. The sex ratio was calculated based on the ratio of females/males, and values > 1 indicated sex ratio female-biased and values < 1 indicated male-biased. Therefore, the sex ratio was temporally tested, with the aim of investigating the activity of females in periods before and during reproduction, to evaluate whether any significant difference existed between the monthly number of males and females, a Chi-Square test (Zar 2010) was performed.

Reproductive output and fecundity

Ovigerous females were fixed and transported to the laboratory, and the carapace length was measured. The eggs were carefully removed and counted with a manual counter. Llodra (2002) defined fecundity as the total number of offspring (oocytes, eggs, embryos, larvae or juveniles) produced by a female over a certain period of time; here, we use the number of eggs as the measure of fecundity. For each female, 15 eggs were randomly isolated and photographed using the imaging system of the ZEISS Stemi V6 stereomicroscope, which enabled the minor and major axis of the eggs to be measured, to calculate the egg volume (EV), according to the following formula:

$$EV = \frac{1}{6(a \times b \times \pi)}$$

where a represents the minor axis and b , the major egg axis (Turner & Lawrence 1979).

The eggs were categorised into three embryonic developmental stages (Figure 1) proposed by Bueno and Shimizu (2008): stage 1 (initial), embryos showing no sign of development of compound eyes and the yolk occupying more than 80% of the egg volume; stage 2 (intermediate), embryos with signs of compound-eye development and the yolk occupying 50% to 80% of the egg volume and stage 3 (final), having clearly recognisable embryos and the yolk occupying less than 50% of the egg volume.

We used only females that contained embryos in stage 1 for fecundity and reproductive output analyses, because crustaceans tend to lose eggs during their incubation (Bueno & Shimizu 2008; Hernáez & Wehrmann 2011).

After the eggs were counted, the eggs and corresponding females were dried for 48 h at 60 °C to obtain the dry mass (Terossi et al. 2010). For the reproductive output (RO) calculation, an equation based on the dry mass of the eggs in the initial stage and that of females without eggs was used (Clarke et al. 1991):

$$RO = \left(\frac{\text{Total Egg Dry Weight}}{\text{Corresponding Female Dry Weight}} \right) \times 100$$

For the subsequent analyses, all variables were log-transformed and we used eggs from all three developmental stages.

A covariance analysis (ANCOVA) was applied to the number of eggs vs. CL (using embryonic development stage as a co-variable), to estimate potential egg loss during the incubation period (Hernández & Wehrtmann 2011).

To detect the relationship between egg volume and the embryonic development stage or female size (Hernández & Wehrtmann 2011), an ANCOVA test was applied, using CL as a co-variable.

Functional maturity

According to López-Greco and Rodríguez (1999), small ovigerous females can be considered the 'minimum functional maturity size', because the CL50 value corresponds with the 'population functional maturity size'.

For functional maturity analysis, we used ovigerous females and those with developed gonads during the highest peak (winter) of the reproductive period (Bueno & Shimizu 2008). Functional maturity was defined as the mean size at which 50% (CL50) of females are reproducing during the reproductive period, which was obtained from the interpolation of the equation obtained from logistic regression (Pagano & Gauvreau 2006; Rocha et al. 2010) of the gonad development stage (immature 0, mature 1) vs. the CL data-set. Males were excluded from the maturity analysis because mating experiments were not performed, and 'mating scars' on males were not observed.

Growth and longevity

Growth analysis was performed separately for males and females, using the von Bertalanffy growth model (1938). For this analysis, we used modal progression, which correlates age with animal size (Simões et al. 2013). For this, animals were placed into 1-mm CL size classes (as used by other studies on *Aegla* – Bueno & Shimizu 2008; Rocha et al. 2010) for each sampled month and the modal values were determined for each CL frequency using the PeakFit 4.0 program (Simões et al. 2013). Superimposed modal peaks were discarded, because they represented non-real age groups. The modal values were then plotted onto a scatter graph against time, from which it was possible to identify growth cohorts (Simões et al. 2013). From these cohorts, three growth parameters were obtained using 'Solver', a Microsoft Excel supplement: (1) CL_{∞} : the size reached by the individual if it were to grow indefinitely; (2) k : growth coefficient, a rate related to the time in which asymptotic length is reached and (3) t_0 : the theoretical age that the organism has when its size is zero. These parameters were generated from the von Bertalanffy growth

model (1938): $CL_t = CL_{\infty} (1 - e^{-k(t-t_0)})$, where CL_t corresponds to the CL at age ' t '.

The growth and longevity results of Noro and Buckup (2003) for *A. leptodactyla* Buckup & Rossi, 1977 were used as seed values, as they showed similar values to those observed in the field for *A. marginata*. Therefore, similar to Simões et al. (2013) the criterion used to validate the growth of a cohort was the similarity to seed values. The ages obtained over time (in days) for each cohort were corrected, based on the time interval between samples and the t_0 value obtained. Finally, the cohort data were pooled and mean curves were constructed for each sex. Subsequently, the results obtained from male and female growth curves were submitted to the ' F ' test for comparison (Cerrato 1990). Longevity was estimated by the inverse formula of von Bertalanffy (1938) with an adaption suggested by D'Incao and Fonseca (1999), being $t_0 = 0$ and $CL_t/CL_{\infty} = 0.99$. Hence, the equation is given by: $t_{\max} = 0 - (1/k) \ln[1 - (CL/CL_{\infty})]$.

Results

Samples

We sampled a total of 1325 males and 877 females. The CL measurements for males varied from 5.50 to 20.00 mm, whereas that for females ranged from 5.20 to 19.67 mm. The relationship between CL and CLR was provided by the function $CLR = 1.11CL + 0.56$ ($r^2 = 0.98$) for males, and for females by the function $CLR = 1.10CL + 0.75$ ($r^2 = 0.96$).

Reproductive period and functional maturity

In total, 32 ovigerous females were recorded in 8 out of the 15 months studied, in two reproductive periods. In 2013, a less intense reproductive period during spring (October–December) was observed, and in 2014, two reproductive peaks were observed: one intense period during the autumn and winter (May to September) and a less intense period in December, when we captured only one ovigerous female (Figures 2 and 3).

Cross-correlation identified a strong negative relationship ($r > -0.7$) between temperature and the frequency of ovigerous females. This relationship was significant, with a time lag 0 ($r = -0.812$) and a time lag in the previous month ($r = -0.659$) (Figure 4). No significant relationship ($p > 0.05$) was observed between the frequency of ovigerous females and rainfall. Significant relationships only are graphically represented.

Females with mature gonads were recorded in April, May and June 2014. The smallest and the largest ovigerous female measured 8.6 mm CL, and 17.9 mm CL, respectively. The functional maturity (CL50) for females was estimated to be 9.28 mm CL.

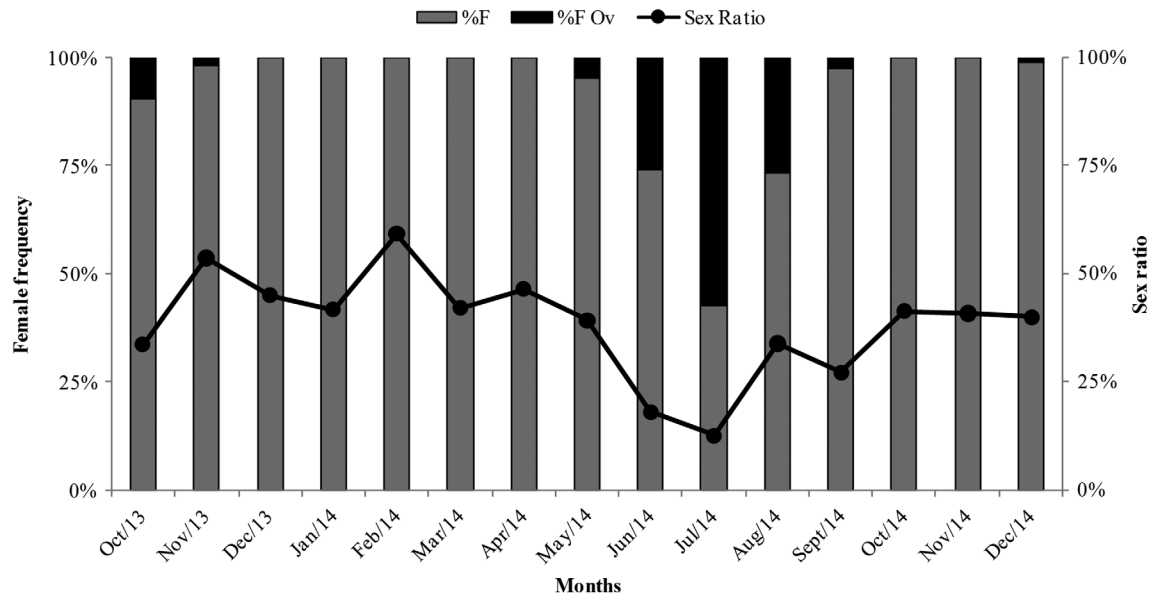


Figure 2. *Aegla marginata*. Female frequency discriminating non-ovigerous (F) and ovigerous (F Ov).

Notes: The line represents sex ratio calculated by number of females divided by monthly total number of specimens (male + female) multiplied by 100 to obtain the % value and therefore > 50% the ratio is skewed towards females and < 50% of the ratio is skewed towards males.

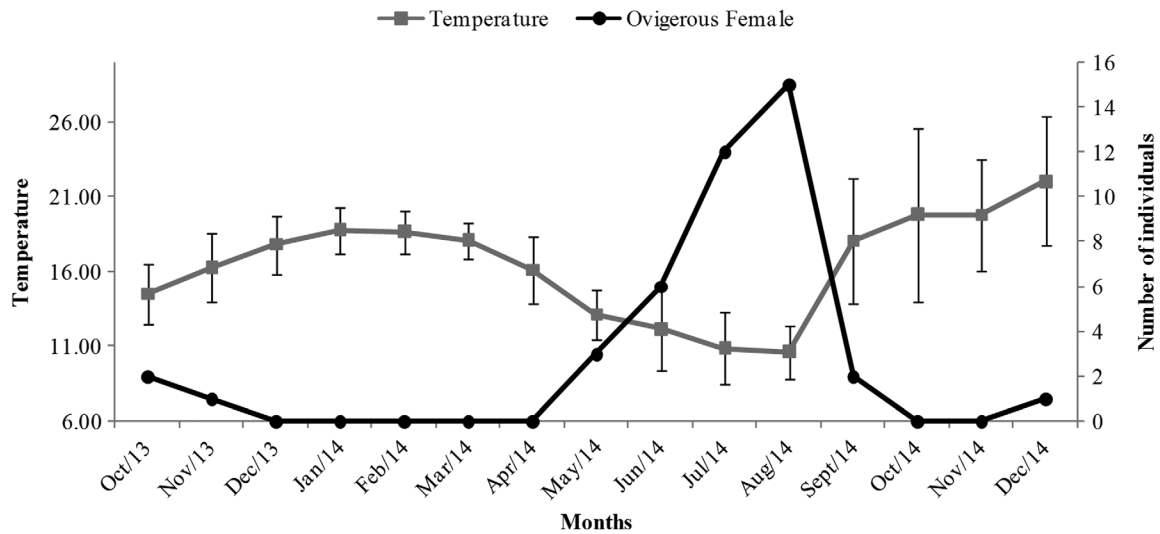


Figure 3. Mean temperature values (\pm SD °C) and number of ovigerous female of *Aegla marginata* captured throughout the sampling months.

Recruitment was observed between December 2013 and September 2014. In subsequent months, it was possible to see the growth of the latter (Figure 5).

Sex ratio

The sex ratio was significant (Chi-square, $p < 0.05$) and was skewed towards males in October 2013 and from May to December in 2014. The sex ratio ($p < 0.05$) was skewed towards females only in February 2014 (Figure 2).

Reproductive output and fecundity

The number of eggs per ovigerous female ranged from 40 to 146 (mean \pm SD; 95 ± 31.5). The reproductive output varied from 2.7% to 20.9% of the females' weight, with a mean of 10.8%. During the embryonic development, a positive relationship was observed between the number of eggs and the size of females (ANCOVA, $F = 9.95$; $p < 0.05$), although no significant egg-loss was observed (ANCOVA, $F = 0.48$; $p > 0.05$).

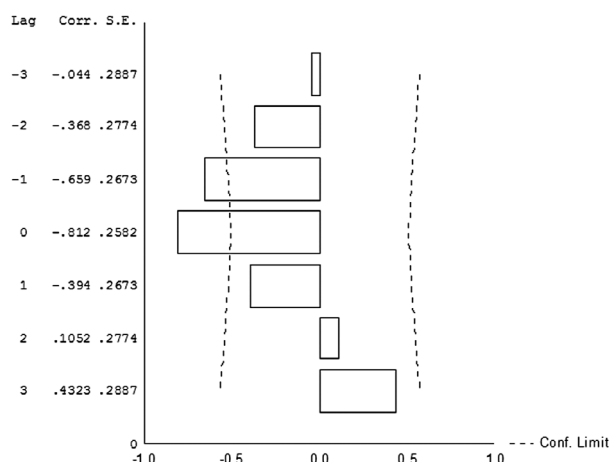


Figure 4. Temporal series analysis (Cross-Correlation) between monthly mean temperature values and ovigerous female number of *Aegla marginata*.

Notes: Horizontal axis is the correlation values. On the vertical axis the labelling represent: (a) lag, the time lag; (b) Corr. = the correlation value and (c) S.E = Standard Error.

Egg volume showed a positive relationship with the size of females (ANCOVA, $F = 41.90$; $p < 0.001$). No difference was observed in the egg volume during embryonic development (ANCOVA, $F = 1.12$; $p > 0.05$) and the mean egg volume was $1.32 \pm 0.29 \text{ mm}^3$ ($\pm \text{SD}$).

Most ovigerous females (71.43%) were abundant in the size class 10.0–12.9 mm CL, whereas females with mature gonads (63.77%) were present in the size class 11.0–13.9 mm CL (Figure 6), indicating possible degenerative changes in the reproductive activity according to age (senescence). Seventeen of the ovigerous females had embryos in the initial stage, 10 in the intermediary stage and five in the final stage.

Growth and longevity

Eight cohorts were selected for males and six for females (Figure 7). A mean growth curve derived from the grouping of cohorts was constructed for each sex (Figure 8). These

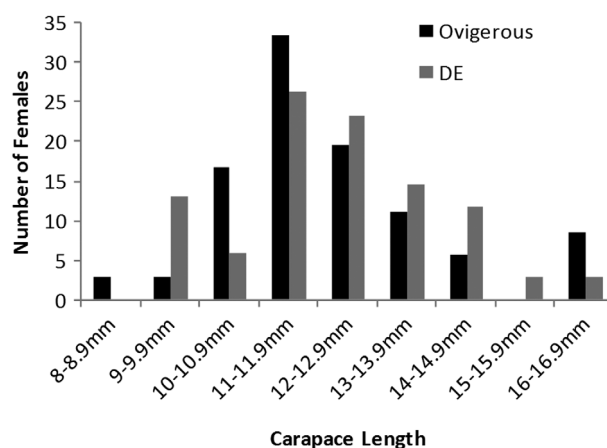


Figure 6. *Aegla marginata*. Number of ovigerous females and females with well-developed gonads (DE) by size classes.

curves were used to determine the growth parameters and longevity. For males, the growth estimate was represented by $CL_{\infty} = 20.66 (1 - e^{-0.0051(t + 0.116)})$, with 2.43 years of longevity ($r^2 = 0.94$). For females, the growth estimate was $CL_{\infty} = 20.04 (1 - e^{-0.005(t + 0.131)})$, with 2.49 years of longevity ($r^2 = 0.95$). The 'F' test result was significant, i.e. the two curves (for males or females) were different (F calculated = $3.14 > F_{\text{critic}} = 2.72$, $p = 0.03$), hence, one curve cannot be used for both sexes (Figure 9).

Discussion

The main reproductive period during the autumn–winter seasons identified for *A. marginata* was similar to that of *A. schmitti* Hobbs III, 1979 – another species living at a similar latitude ($25^{\circ}29'S$) (Table 1). The reproductive pattern found for aeglids (Bueno & Shimizu 2008; Cohen et al. 2011) is different to that of other freshwater decapods, which have a reduced reproductive rate in the south of South America (Vogt 2014). *Aegla* spp. that inhabit colder regions (near the southern limit of their distribution: Isla Madre de Dios in Chile) tend to have continuous reproduction, because

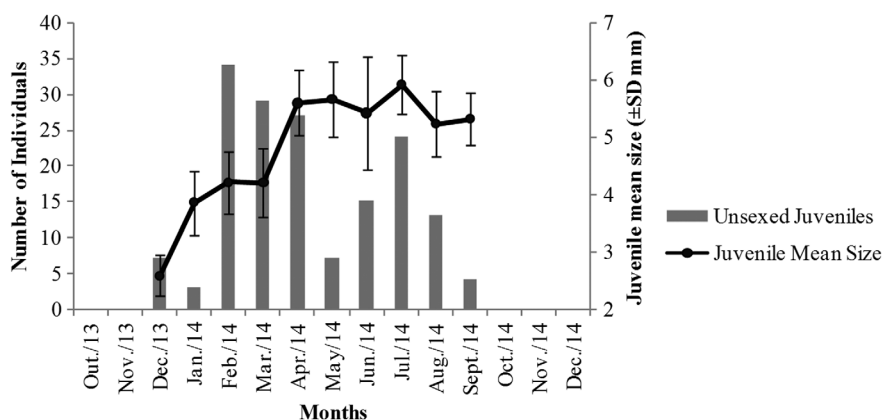


Figure 5. *Aegla marginata*. Mean size ($\pm \text{SD mm}$) and number of unsexed juveniles throughout the sampling period.

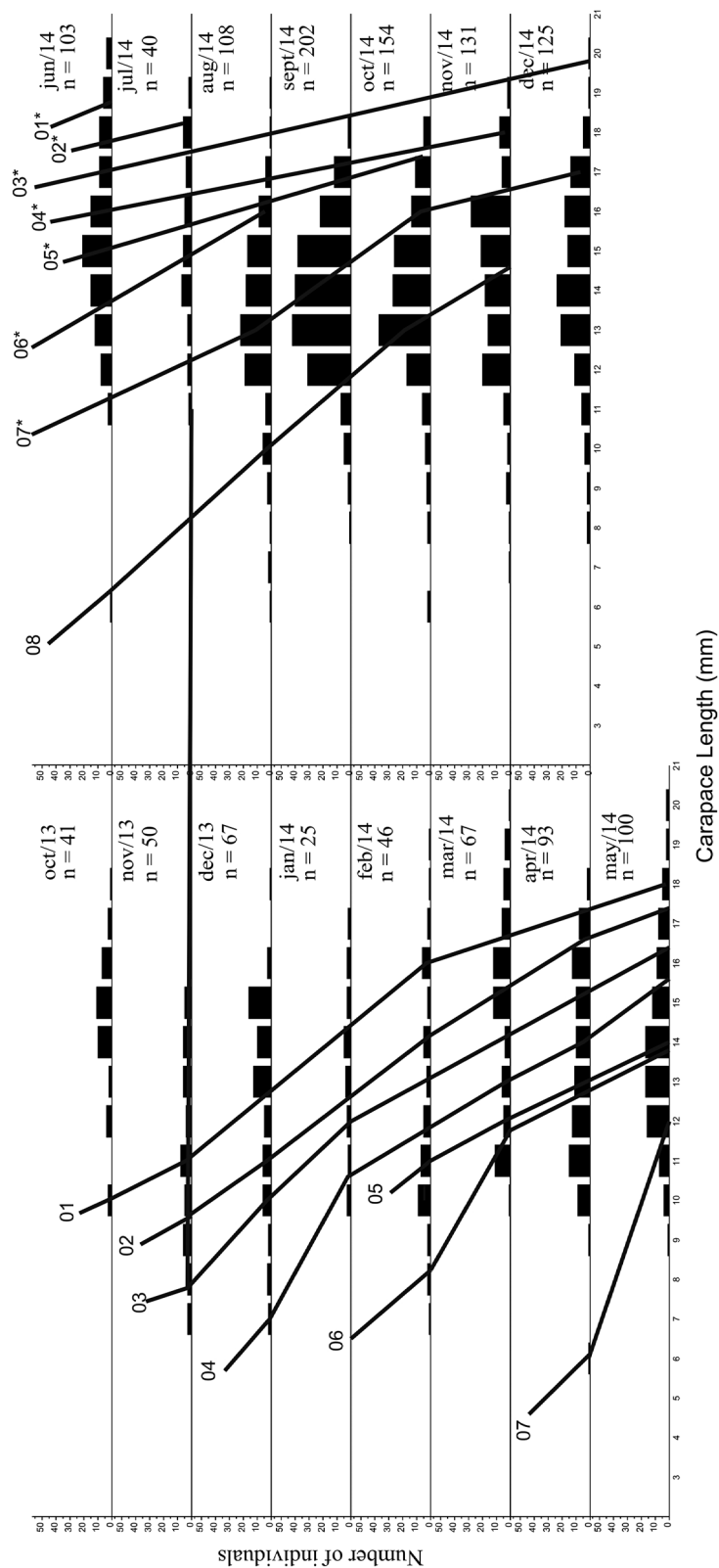


Figure 7. *Aegla marginata*. Carapace length frequency histograms of males sampled from September 2013 to December 2014. Notes: Lines represent the observed cohorts during the study period that describes individual growth. Numbers followed by * indicate cohort continuation.

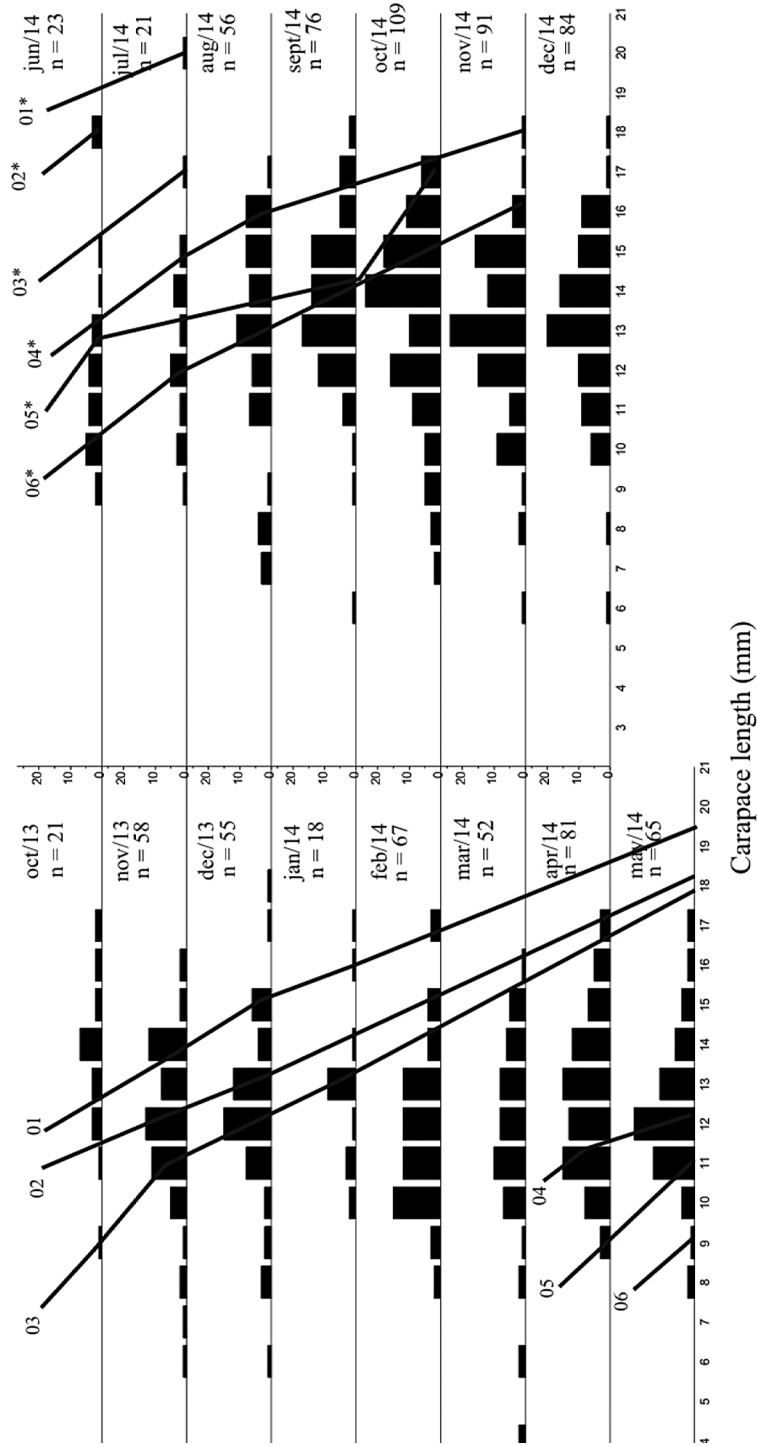


Figure 8. *Aegla marginata*. Carapace length frequency histograms of females sampled from September 2013 to December 2014.

Notes: Lines represent the observed cohorts during the study period that describes individual growth. Numbers followed by * indicate cohort continuation.

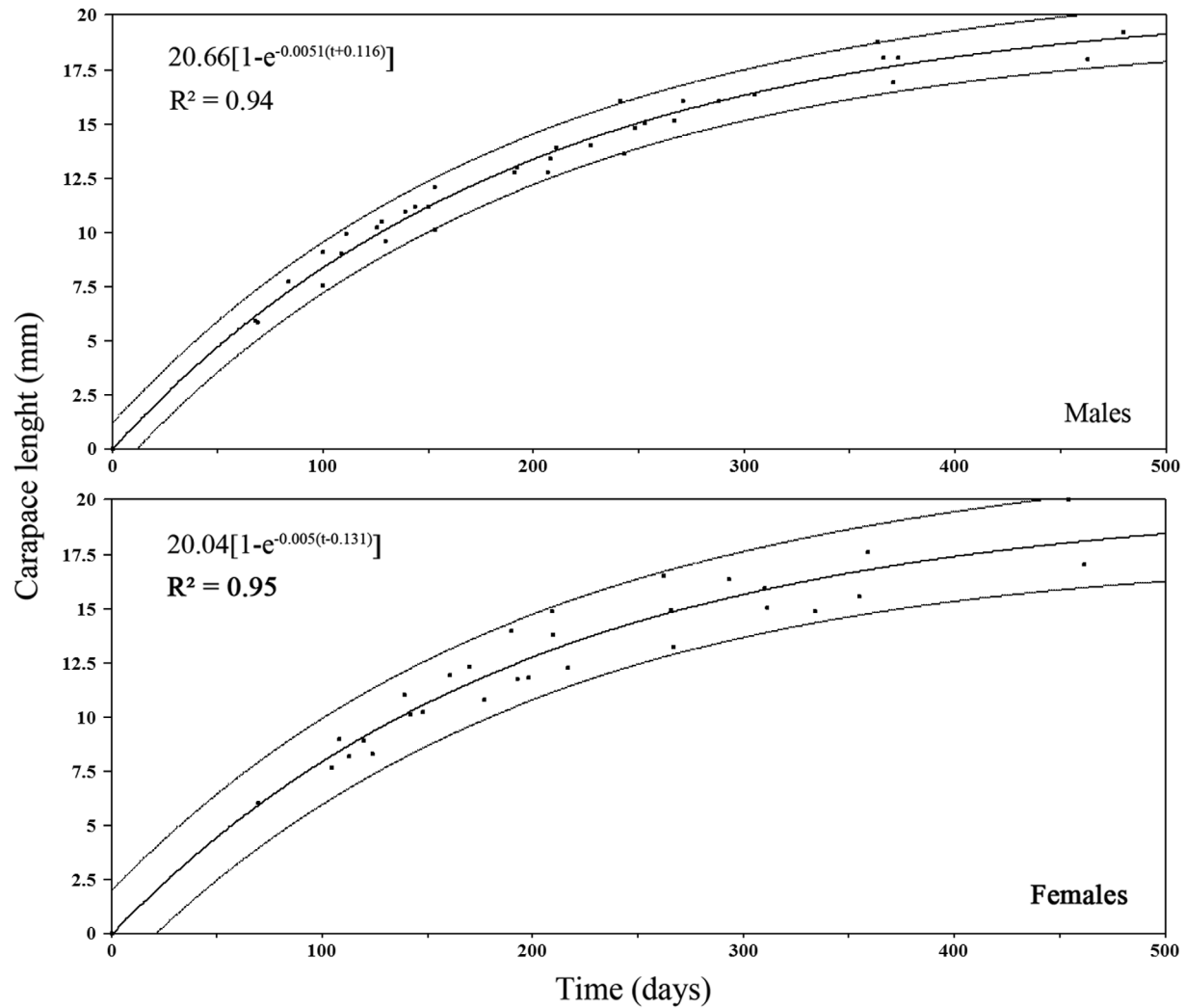


Figure 9. *Aegla marginata*. Mean growth curve (middle line) estimated for males and females of the sampling region from September 2013 to December 2015 based on the Von Bertalanffy growth model.
Note: Outside curves: confidence interval (95%).

Table 1. Reproductive period of *Aegla* spp. in different latitudes (lower to higher).

Species	Latitude (S)	Reproductive Period (months)	References
<i>A. franca</i>	20°18'	May–August (4)	Bueno and Shimizu (2008)
<i>A. perobae</i>	22°37'	April–August (5)	Bueno et al. (2014)
<i>A. perobae</i>	22°33'	April–October (7)	Rodrigues and Hebling (1978)
<i>A. castro</i>	23°08'	May–June (2)	Fransozo et al. (2003)
<i>A. paulensis</i>	23°27'	March–July, possibly August (5–6)	Cohen et al. (2011)
<i>A. paulensis</i>	23°47'	May–possibly June–October (2–6)	López (1965)
<i>A. marginata</i>	24°16'	May–December (8)	Present study
<i>A. schmitti</i>	24°31'	April–December (9)	Chiquetto-Machado et al. (Forthcoming)
<i>A. strinatii</i>	24°38'	May–September (5)	Rocha et al. (2010)
<i>A. parana</i>	25°05'	April–August (5)	Grabowski et al. (2013)
<i>A. schmitti</i>	25°29'	April–November (8)	Teodósio and Masunari (2009)
<i>A. castro</i>	25°5'	May–October (6)	Swiech-Ayoub and Masunari (2001)
<i>A. platensis</i>	27°25'	January–December (12)	Dalosto et al. (2014)
<i>A. leptodactyla</i>	28°38'	April–September (6)	Noro and Buckup (2002)
<i>A. longirostri</i>	29°24'	July–March (9)	Colpo et al. (2005)
<i>A. franciscana</i>	29°26'	June–October (5)	Gonçalves et al. (2006)
<i>A. platensis</i>	29°46'	January–December (12)	Bueno and Bond-Buckup (2000)
<i>A. laevis</i>	33°42'	March–October (8)	Bahamonde and López (1961)
<i>A. uruguayana</i>	34°14'	January–December (12)	Viau et al. (2006)
<i>A. denticulata lacustris</i>	40°49'	March–October (8)	Jara (1989)

Source: Adapted from Bueno and Shimizu (2008).

an optimal temperature is maintained all-year-round, whereas species that inhabit subtropical regions (near the northern limit of their distribution: southwest Brazil) tend to show seasonal reproduction (Bueno & Shimizu 2008).

Orton (1920) proposed that marine invertebrates reproduce throughout the whole year in near-tropical regions, owing to the maintenance of a warm water temperature. Therefore, since aeglid species showed a negative correlation with temperature, we assume that the maintenance of cold water temperatures found in freshwater environments in cold temperate regions is the optimal temperature that can sustain continuous reproduction. Thus, cold temperature regions may have the optimal temperature for *Aegla* species because this genus probably evolved from a marine ancestor from the cold waters of the South Pacific (Feldmann 1984; Pérez-Losada et al. 2004).

Recruitment is usually observed during spring in aeglids (Bueno & Bond-Buckup 2000; Dalosto et al. 2014). However, the first juveniles observed by us in the population had a CL of 3 mm or more and were sampled in late 2013, when the summer started. The tiny, newly hatched individuals from spring were probably not captured by our sampling method, because the small holes present in the trap allowed the escape of very small individuals. The higher concentration of juveniles from February to April 2014 might be related to the intense reproductive peak of this species during the winter from the previous year, which might explain the larger juvenile size observed. Gonçalves et al. (2006) also reported recruitment during the summer for *A. franciscana* Buckup & Rossi, 1977, where caught juveniles were similar in size (5 mm CL) to those in this study. Furthermore, newly hatched individuals were not caught in spring by these authors, which corroborate our observations.

During the reproductive period, the sex ratio was skewed towards males, owing to behavioural differences. In this period, females bearing eggs display cryptic behaviour, remaining for a long time in shelters (Cohen et al. 2011) and therefore, they are not caught as often as males, because this trap method captures the active individuals.

In April and May, active females with developed gonads predominated in the population. This peak observed during the months prior to reproduction suggests that these animals are searching for food to store energy for the next reproductive period, when they will show cryptic behaviour. Vogt (2014) suggested that this trade-off allows the females to invest energy into the production of eggs with a special yolk that allows the offspring to hatch in the juvenile form, instead of investing energy into itself.

Few studies exist concerning aspects of egg production in *Aegla* spp. and comparisons with the literature must be made with caution, since different methodologies have been used in these studies (López 1965; Burns 1972; Jara 1977; Noro & Buckup 2002; Lizardo-Daudt & Bond-Buckup 2003; Gonçalves et al. 2006; Bueno & Shimizu 2008; Rocha et al. 2010). A clear latitudinal pattern for fecundity and egg size exists, in which animals at higher latitudes produce more eggs that are small, whereas fewer but larger eggs are produced at lower latitudes (Table 2).

A latitudinal trend in egg number and size might also be related to the origin of the group, because aeglids probably colonised inland waters about 75 mya, originating in the Pacific Ocean (Pérez-Losada et al. 2004). According to these authors, species closer to the Pacific that are distributed in the south of South America are more primitive than other species. Therefore, the trend towards more eggs of a smaller size for species at higher latitudes might be an evolutionary trait of its marine ancestors, because marine

Table 2. Compilation of fecundity and egg size data, smaller ovigerous females (CL = carapace length without rostrum, CLR = carapace length with rostrum) by latitude in different aeglids species.

Species	Latitude (S)	Fecundity (number of eggs)	Smaller Ovigerous Female (mm)	Mean egg size (\pm SD mm)	References
<i>A. franca</i>	20°18'	57–193	12.06(CL)	1.34 \pm 0.11	Bueno and Shimizu (2008)
<i>A. perobae</i>	22°33'	–	11.8 (CLR)	1.336	Rodrigues and Hebling (1978)
<i>A. paulensis</i>	23°47'	64–113	11.5(CLR)	1.299 \pm 0.006	López (1965)
<i>A. marginata</i>	24°16'	42–146	8.60(CL)	1.32 \pm 0.29	Present study
<i>A. schmitti</i>	24°31'	–	14.14 (CL)	–	Chiquetto-Machado et al. (Forthcoming)
<i>A. strinati</i>	24°38'	1–325	15.63(CL)	–	Rocha et al. (2010)
<i>A. leptodactyla</i>	28°38'	115–368	14.09(CL)	–	Noro and Buckup (2002)
<i>A. franciscana</i>	29°26'	28–210	9.19(?)	1.35	Gonçalves et al. (2006)
<i>A. laevis laevis</i>	33°42'	120–400	12.5(CLR)	1.075	Bahamonde and López (1961)
<i>A. rostrata</i>	39°46'	699–1043	–	1.2 \pm 0.003	Jara (1977)

Source: Adapted from Bueno and Shimizu (2008).

decapod crustaceans tend to have more eggs that are smaller (Vogt 2013).

In addition to the parental care observed in aeglids (López-Greco et al. 2004), the fecundity of aeglids aims to maximise reproductive efficiency – traits that have allowed freshwater colonisation (Vogt 2013). These observed characteristics are included in the k-strategy because of the lower number of offspring with a high survival rate (Vogt 2014).

A positive relationship between the number of eggs and animal size has also been described for *A. leptodactyla* Buckup & Rossi, 1977 (Noro & Buckup 2002); *A. franciscana* Buckup & Rossi, 1977 (Gonçalves et al. 2006) and *A. franca* Schmitt, 1942 (Bueno & Shimizu 2008). Therefore, the positive allometric growth of the abdomen of *A. marginata* (authors' unpublished data) allows more eggs to be produced, maximising reproductive efficiency.

Extended brood care in decapods is an exclusive adaptation to life in a freshwater environment and includes carrying and cleaning the eggs, as well as caring for early post-hatching life stages (Vogt 2014). In our study, no significant egg loss was observed during embryonic development. Martin and Felgenhauer (1986) studied grooming behaviour in *A. platensis* Schmitt, 1942 and *A. uruguayana* Schmitt, 1942. This behaviour by females, which use the fifth pereopod pair, serves to clean solid particles and remove organisms from the egg mass. Probably, constant egg cleaning, the closed abdominal chamber and the long periods in sheltered environments with a low water current, ensure that the females do not lose eggs during their incubation.

Some studies have shown that egg volume increased during embryogenesis (Bueno & Shimizu 2008; Rocha et al. 2010). Verdi (1985) and Lizardo-Daudt and Bond-Buckup (2003) found no differences in egg volume during development, which agrees with the data in our study. To address this question, future histological studies are required that focus on egg production and development in aeglids.

The low number of ovigerous females and females with developed gonads of large sizes (>14 mm) is indicative of less intense reproduction of *A. marginata* with age.

Natural selection possibly favours individuals during their first reproductive cycle (Charlesworth 1993; Rocha et al. 2010). We suggest that senescence occurs in *A. marginata*, where adult females show a decrease in survival and reproduction efficiency as they age (Charlesworth 1993). Senescence is related to changes in the structure, physiology and behaviour of organisms, and these degenerative changes start after the first reproductive cycle (Vogt 2014). We suggest that *A. marginata* shows a gradual senescence (Finch 1994); in this type of senescence, the species show a decrease in reproductive efficiency in the second reproductive season – a similar pattern to that observed in *A. strinatii* Türkay, 1972 (Rocha et al. 2010).

The mean reproductive output of 10.8% of body weight found for *A. marginata* is close to the value found for other anomurans, which ranged from 3 to 10% (Lardies & Wehrtmann 1996; Hernáez & Palma 2003; Hernáez & Wehrtmann 2011). Although these values appear to be relatively low, the amount of energy expended in reproduction is sufficient to guarantee the success of these species during embryonic development (Hernáez & Wehrtmann 2011).

The size of the largest male (20.00 mm CL) and female (19.67 mm CL) was similar to the value obtained for the maximum individual size (CL_{∞}) based on the Von Bertalanffy growth model: 20.66 and 20.04 mm CL for males and females, respectively.

Compared to other aeglid species, no clear latitudinal trend in growth and longevity was observed (Table 3). However, in most species, males are slightly larger than females, except for *A. platensis* (Bueno & Bond-Buckup 2000), where females are larger than males. In *A. platensis*, Bueno and Bond-Buckup (2000) propose that growth difference occurs because few larger males were caught and in *A. manuinflata*, Trevisan and Santos (2011) related the difference in longevity to a higher female mortality rate during the incubation period.

In terms of longevity, females tend to live slightly longer than males, except for *A. manuinflata* (Trevisan & Santos 2011). The values of CL_{∞} , k , t_0 and longevity found for males and females of *A. marginata* are similar, probably because

Table 3. Compilation by latitude of growth and longevity data in aeglids species. CL_{∞} in mm. Longevity in years.

Species	Latitude (S)	CL_{∞} ♂ (mm)	Long. ♂ (years)	CL_{∞} ♀	Long. ♀ (years)	References
<i>A. paulensis</i>	23°27'	21.25	2.82	16.52	3.35	Cohen et al. (2011)
<i>A. marginata</i>	24°16'	20.66	2.43	20.04	2.49	Present study
<i>A. schmitti</i>	24°31'	28.35	2.84	21.69	3.20	Chiquetto-Machado et al. (Forthcoming)
<i>A. castro</i>	25°05'	–	2	–	2	Swiech-Ayoub and Masunari (2001)
<i>A. jarai</i>	27°7'	25.11	2	23.56	2	Boos Jr. et al. 2006;
<i>A. leptodactyla</i>	28°38'	19.83	–	18.96	–	Noro and Buckup (2003)
<i>A. longirostri</i>	29°	27.9	1.9	21.45	2	Silva-Castiglioni et al. (2006)
<i>A. itacolomiensis</i>	29°33'	23.21	2.2	19.49	2.5	Silva-Gonçalves et al. (2009)
<i>A. manuinflata</i>	29°37'	28	3	25.13	2.5	Trevisan and Santos (2011)
<i>A. platensis</i>	29°46'	17.39	2.5	19.12	2.5	Bueno and Bond-Buckup (2000)
<i>A. laevis laevis</i>	33°	–	3	–	3	Bahamonde and López (1961)

they inhabit the same environmental conditions, including temperature, which underlies the similar growth (Trevisan & Santos 2011). Males tend to be larger than females due to different energy allocations, because they invest energy into ontogenetic growth, whereas females invest most energy into reproduction (Silva-Gonçalves et al. 2009).

In summary, our data show that the growth pattern of *A. marginata* in the ISP is similar for males and females and a seasonal reproductive peak is followed by a seasonal recruitment peak. This study was performed within a conservation unit of natural rainforest; however, the conservation status of other populations of *A. marginata* outside the ISP remains unknown, therefore, comparative studies between populations with the aim of conservation are required, since in Brazil, 25 species of *Aegla* are currently already under some type of threat.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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