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# Population biology of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Anomura: Porcellanidae) in the Southwestern Atlantic

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**ABSTRACT**

A population of the porcelain crab *Pachycheles laevidactylus* was evaluated based on sex ratio, sexual dimorphism, reproductive intensity, relative growth and sexual maturity. The porcelain crabs were identified, sexed and measured as follows: carapace (*CL*, length; *CW*, width), chelar propodus (*PL*, length; *PH*, height) and abdomen (*AL*, length; $AW_2$ and $AW_5$, the width of the 2nd and 5th abdominal somite, respectively). For the 1,109 specimens analyzed, the sex ratio was 1:1, but contrasted in some seasons. Females were significantly larger than males, and ovigerous females were recorded in all seasons, with greater intensity in autumn and winter. In males, the biometric ratios of the major chelar propodus (*PHxCL* and *PLxCL*) showed positive allometry regarding body size, with a reduction in the allometry rate after puberty. The same occurred with females for the biometric ratios of the abdomen ($AW_2xCL$ and $AW_5xCL$). Males attain morphological sexual maturity at 3.48 mm *CL*, earlier than females, which occurred at 5.00 mm *CL*. In this study, *P. laevidactylus* matured with a larger size than reported for others analyzed in the temperate zone. It is the first study addressing aspects of the population biology of *P. laevidactylus* in a region with a subtropical climate.

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## Introduction

The family Porcellanidae is one of the most diverse and common families of rocky shore crustaceans (Haig 1960; Veloso and Melo 1993; Werding et al. 2003). Members of Porcellanidae are collectively known as 'porcelain crabs' due to their small size and delicate body (Haig 1960). Porcellanidae has 29 genera currently described (WoRMS 2022b), and the genus *Pachycheles* is one of the largest. It contains 48 species and is the second most speciose genera of the family after *Petrolisthes* (WoRMS 2022a). Species in *Pachycheles* are commonly found living under stones (e.g. *P. setimanus*) or on reefs constructed by annelid worms and corals (e.g. *P. chacei* and *P. holosericus*) throughout the intertidal and subtidal zones in both temperate and tropical coasts (Haig 1960).

Overall, natural history studies have been important in helping to understand the origin and evolution of crustaceans as symbionts and their relationship with their host partners (Baeza 2015). In particular, the close ecological relationship between host and guest generates a series of morphological and behavioural adaptations that lead to the evolution via natural selection of the species involved in the relationship (Stillman 2002). For instance, a study conducted on the porcelain crab *P. monilifer* compared the reproductive performance of females collected from two different hosts, demonstrating that the reproductive traits of symbionts are modified depending on the host (Leone and Mantelatto 2015). Considering the above, information on the natural history of symbiotic species inhabiting different hosts may be relevant to understand how the porcelain crabs' population and reproductive biology adjust under different ecological conditions.

*Pachycheles laevidactylus* Ortmann, 1892, is one of the most emblematic porcelain crabs of the Brazilian coast. It is known for its close symbiotic association with different host species, e.g. the mytilid clam *Brachidontes rodriguezii* (see Camiolo and Luppi 2016); the annelid worm *Phragmatopoma caudata* (see Pinheiro and Fransozo 1995; Horch and Terossi 2022a, 2022b). This species is distributed along the southwestern Atlantic, from the state of Pernambuco, northeastern Brazil, to Mar del Plata,

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northern Argentina, encompassing warm and temperate waters (Pinheiro and Fransozo 1995; Camiolo and Luppi 2016; Horch and Terossi 2022a, 2022b). Most studies have focused on the population and reproductive biology from temperate latitudes of *P. laevidactylus* (Bremec and Cazzaniga 1984; Camiolo and Luppi 2016; Horch and Terossi 2022a, 2022b). On the other hand, a pair of studies were conducted in warm waters. They reported valuable information regarding the fecundity of two populations of *P. laevidactylus* (=*P. haigae*, junior synonym) of Brazil, one from the southeast region (Pinheiro and Fransozo 1995) and another from the northeast region (Ogawa and Rocha 1976). Considering that the Brazilian coast has a large geographical extension (~8000 km) and that the life-history traits (e.g. sex ratio, sexual dimorphism, size at sexual maturity, growth, among others) of a species are differentially affected throughout its geographic distribution (see Rivadeneira et al. 2010), the implementation of new studies in unexplored areas can help us understand the individual adaptations to different environmental conditions.

Considering all the host in which *P. laevidactylus* has already been found, the species stands out as the most frequent decapod crab in the sand reefs of *P. caudata*, verified in southern region of Brazil (Horch and Terossi 2022a, 2022b). This colonial annelid builds complex sandstone galleries from sediment particles that are cemented together by a mucoprotein (Zhao et al. 2005; Lane-Medeiros et al. 2021), creating a biogenic microhabitat with a great diversity and numerous interspecific and intraspecific interactions among individuals (Ataide et al. 2014; Lane-Medeiros et al. 2021).

Thus, in this study, we are interested in examining the sex ratio, sexual dimorphism, reproductive intensity and growth pattern of the porcelain crab *P. laevidactylus* from southeastern region of Brazil. This information will provide insight into the life-history traits of this species in an unexplored area, comparing our results with those from other *P. laevidactylus* populations to improve our understanding of the individual and population response to the latitudinal level.

## Material and methods

### Sampling of crabs and measurements

Specimens of *Pachycheles laevidactylus* were collected bimonthly during low tides between July 1990 and

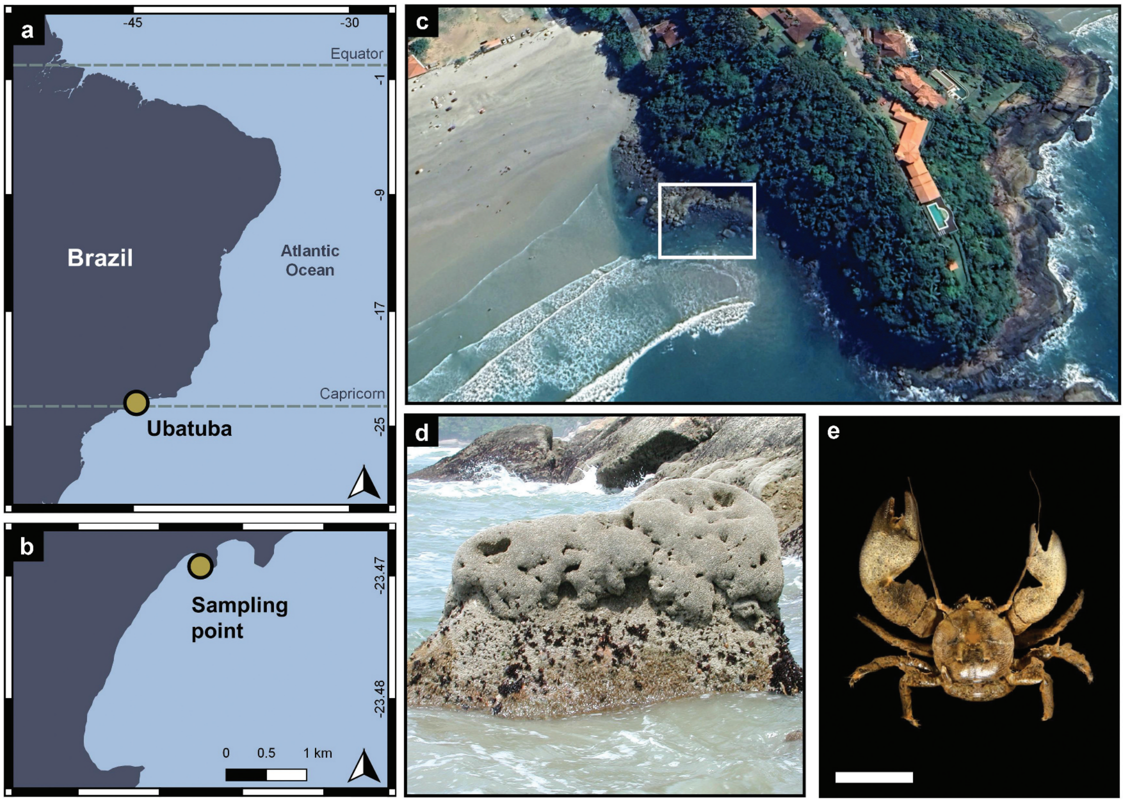

**Figure 1.** (a) Location of the city of Ubatuba, state of São Paulo, Brazil. (b) location of the sampling point, Praia Grande. (c) photograph of the rocky shore in the Praia Grande beach. (d) photograph of the sand reefs of *Phragmatopoma caudata* Krøyer in Mörch, 1863. (e) photograph of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892, scale bar 4 mm. Photographs by Alvaro Migotto (CEBIMar/USP) (d) and Nahuel Emilliano Farias (e).

May 1991 from the rocky shore at Praia Grande (Figure 1a-c) (23°28′1.58″ S45°3′35.07″W), in the city of Ubatuba, on the northern coast of São Paulo State, Brazil (Figure 1a, b). All specimens were found living in annelid worm reefs built by *P. caudata* (Figure 1d), of which *P. laevidactylus* (Figure 1e) is a non-obligate symbiotic species. This species was found preferentially inhabiting sand reefs of *P. caudata* in the study area.

In order to obtain representative samples, we removed the oldest portions of the sandy reef (about 3 kg) during each sampling activity. They were recognized for their greater thickness, intense surface colonization by bryozoans and the presence of tunnels and cavities. The collection of older fragments ensured a representative sample that was not biased towards juvenile individuals that recently settled on the reef. Then, the fragments were placed into individual plastic bags and immediately preserved in alcohol (70%) until further examination at the laboratory.

In the laboratory, each fragment was examined for *P. laevidactylus* specimens. Males have well-developed gonopods (2nd pleomere) and gonopores at the coxae of the 5th pair of pereopods. In contrast, females have three paired setose pleopods (3–5th pleomeres) and gonopores at the base of the 3rd pair of pereopods (Osawa and Mclaughlin 2010). Biometry of each specimen was taken under a stereomicroscope (Zeiss® Stemi® SV-6), as follows: carapace (*CL*, length from the rostrum tip to the posterior margin of the carapace; and *CW*, widest measure between the lateral margins of the carapace); largest chelar propodus (*PL*, length from the tip of manus' finger to the articulation with the carpus; and *PH*, highest height between the margins of the manus); and abdominal somites (*AL*, longest length registered at the middle region from the margin of the 1st abdominal somite to the tip of the telson; $AW_2$ and $AW_5$, corresponding to the widest measure of the 2nd and 5th somites, respectively).

## *Population structure, adult sex ratio, sexual dimorphism and reproductive intensity*

To examine the overall frequency distribution of *P. laevidactylus*, a size-frequency histogram of the *CL* was constructed to each sex and non-sexable with 1 mm size classes, 12 in total (0–12 mm *CL*). The availability of receptive females for reproduction is one of the most influential factors in determining crustacean mating systems because it determines the intensity and direction of competition for sexual partners (Bauer 2004; Hernáez et al. 2021). In order to obtain an approximation of the proportion of receptive females to sexually active males in *P. laevidactylus*, we used the adult sex ratio (*ASR*), of the overall population. Therefore, we calculated the number of males divided by the total number of males and females in the adult phase. Then, the observed *ASR* was tested for deviations from an expected 1:1 sex ratio using a binomial test (Wilson and Hardy 2002). Here we define an adult as all crabs larger than the size at the onset of maturity in males and females, which is explained in detail below.

Furthermore, we calculated the *ASR* during different moments of the study period. This analysis was conducted to test potential differences in sex ratio, considering that temporal alterations of this parameter in natural populations have been correlated with changes in temperature, photoperiod, and food availability (Lardies et al. 2004, and references therein). Therefore, we carried out the collections bimonthly and grouped our data into four climate periods: winter (July and September); spring (November); summer (January and March); and autumn (May).

The occurrence of sexual dimorphism (i.e. the distinct relative difference in body size and chelipeds between the sexes) in *P. laevidactylus* was evaluated by comparing the average of body sizes (*CL* or *CW*) and chelipeds (*PL* or *PH*) between male and female crabs. We used a t-test or Mann-Whitney U test, depending on whether the variances between the compared datasets were homogenous.

The reproduction of *P. laevidactylus* was seasonally evaluated based on the following parameters: proportion of ovigerous females regarding adult females, expressed in percentage (*OF%*); adult sex ratio, obtained by the proportion between adult males and females (*ASR*); and mean size (*CL*) of each sex at each climatic season.

The reproductive potential of the species was compared between the seasons to verify whether a given season presents a prevalence in the frequency of ovigerous females, if there are similar *ASR* values and larger average body sizes (*CL*) for both sexes, as suggested by Pinheiro et al. (2017). The seasonal effect on *OF*% and *ASR* was evaluated by a chi-square test ($\chi^2$) between the climatic seasons. Meanwhile, the mean body size (*CL*) was evaluated as a function of two effects (seasonality and sex) using a two-way ANOVA and the interaction of these effects. If a significant effect between seasonality and sex (F-test) is shown, the means corresponding to each effect will be contrasted by as 'a posteriori' Turkey test, using the 'emmeans' package (Length 2019) developed for the R environment (R Core Team 2021).

### Relative growth and size at morphological maturity

All biometric relationships were submitted to regression analyses adjusted by the power function ($Y=aX^b$) (Huxley 1950; Hartnoll 1978, 1982) using *CL* as the independent variable (*X*) and the other variables as dependent (*Y*). The coefficient of determination ($R^2$) expresses the adjustment of the equation to the empirical points based on log-transformed biometric relationships ($lnY=lna+blnX$), and the allometric growth was established by constant 'b' (see Somerton 1980). Separately, the slope degree (in degrees), represented by the inverse tangent of the 'b' constant in degrees, was measured and indicated the declivity of the straight line regarding the axis of the abscissas. Data were submitted to the same procedures indicated by Somerton (1980) and Somerton and Macintosh (1983) to identify the size at maturity. The 'segmented' package of 'R' software – Version 2.5.0 (Ihaka and Gentleman 1996) was used to identify a possible inflection point (puberty size) during ontogeny of both sexes, revealing the morphological dimorphism between the developmental stages (juvenile and adult). In each case, the allometric growth rate (*b*) was established as isometric ($b = 1$), positive allometric ($b > 1$), or negative allometric ($b < 1$), using a t-test to verify a possible difference of b-value from the unit ($a = 0.01$). In order to confirm one or two regression lines for the empirical point of each regression analysis, data points were submitted to covariance analysis (ANCOVA), to verify the significance of the contrast between slopes ('b' - constant of each equation), the same with the origin point ('a'- constant of each equation), according to Sokal and Rohlf (2011). Thus, the effect of the covariate (*CL*) and the categorical variable (ontogenetic stages: juvenile and adult) was tested, in addition to the interaction of these two factors on the dependent variables ($PL$, $PH$, $AL$, $AW_2$, $AW_5$). In the case of statistical significance for the interaction of factors (*CL* and ontogenetic phases), it was assumed that the slopes of the mathematical equations differed significantly and, therefore, must be represented separately.

## Results

### Sex ratio, sexual dimorphism and reproductive intensity

A total of 1,109 specimens were retrieved from annelid worm reefs of *P. caudata*, of which 537 were males (48.4%), 527 females (47.5%), and 45 undetermined individuals (4.1%), being all in post-larval stage (juvenile and adult). Non-sexable individuals were recorded only in the first three size classes (1–4 mm *CL*), ranging from 1.6 to 3.1 mm (mean ± SD: 2.4 ± 0.4 mm, $n = 45$), with 27.1% of already sexable individuals in the third size class (2–3 mm *CL*), rising to 97.2% in the next class (3–4 mm *CL*) (Figure 2). The carapace length (*CL*) of male and female crabs ranged from 2.1 to 9.3 mm ( 5.6 ± 1.5 mm, $n = 537$) and from 2.7 to 9.7 mm (5.9 ± 1.5 mm, $n = 527$) in the overall population, respectively (Figure 2). There was a significant difference in body size between both sexes ($t = -2.33$, df = 1061.90, $p = 0.001$), and females, on average, were larger than males. For the two propodus measures used (*PH and PL*), the cheliped size of males (*PH*: 4.6 ± 1.7 mm; *PL*:7.6 ± 2. 9 mm) and females (*PH*: 4.4 ± 1.4; and *PL*: 7.3 ± 2.37) was similar (*PH*: $t = -1.31$, df = 402.21, $p = 0.19$, and *PL*: $t = -1.29$, df = 407.01, $p = 0.20$). The *P. laevidactylus* overall sex ratio did not differ significantly from evenness (males: females = 1.00:0.98; $\chi^2 = 0.09$, df = 1, $p = 0.76$) (Figure 3).

Considering only the sexually mature individuals, the adult sex ratio (*ASR*) differed significantly only in spring ($\chi^2 = 18.63$, $p < 0.0001$) (Figure 4a), with more males ($n = 154$; 63.9%) than females ($n = 87$; 36.1%,) (Table 1a), maintaining similarity between the sexes in the other climatic seasons ($\chi^2 \leq 3.04$, $p \geq 0.08$) (Figure 4a). Ovigerous females represented 71.5% of the total females collected ($n = 377$), with sizes ranging from 5.0 to 9.7 mm *CL*. Ovigerous females comprised more than 54% of the females sampled in the monthly samples, with a similar number ovigerous and non-ovigerous females in spring ($\chi^2 = 1.05$, $p = 0.31$) and a predominance of ovigerous females in the other climatic seasons (*OF* % ≥ 73%; $\chi^2 \geq 36.75$, $p < 0.05$) (Table 1a). Therefore, a *OF*% contrast was confirmed between the climatic seasons ($\chi^2 = 5.99$, $p < 0.001$), with greater intensity in autumn ($n = 48$; 94%) (Figure 4a).

The sizes of *P. laevidactylus* differed between seasons ($F = 52.49$, $p < 0.0001$) and between sexes ($F = 9.87$, $p = 0.002$), despite the absence of the interaction of these two effects ($F = 1.72$, $p = 0.16$) (Table 1b). The smallest size averages for each sex were recorded in spring (males: 5.2 ± 1.6 mm *CL*; females: 5.2 ± 1.4 mm *CL*) and the largest in winter (males: 6.7 ± 1.6 mm *CL*; females: 6.8 ± 1.6 mm *CL*) (Figure 4b). However, size differed between sexes only in summer, when females were larger than males (5.8 ± 1.4 mm *CL* > 5.4 ± 1.3 mm *CL*), while in the other climatic seasons the size did not differ between sexes.

### Relative growth and sexual maturity

The relative growth pattern in the *CWxCL* relationship (Table 2) indicates a positive allometry for both males ($b = 1.03$) and females ($b = 1.07$).

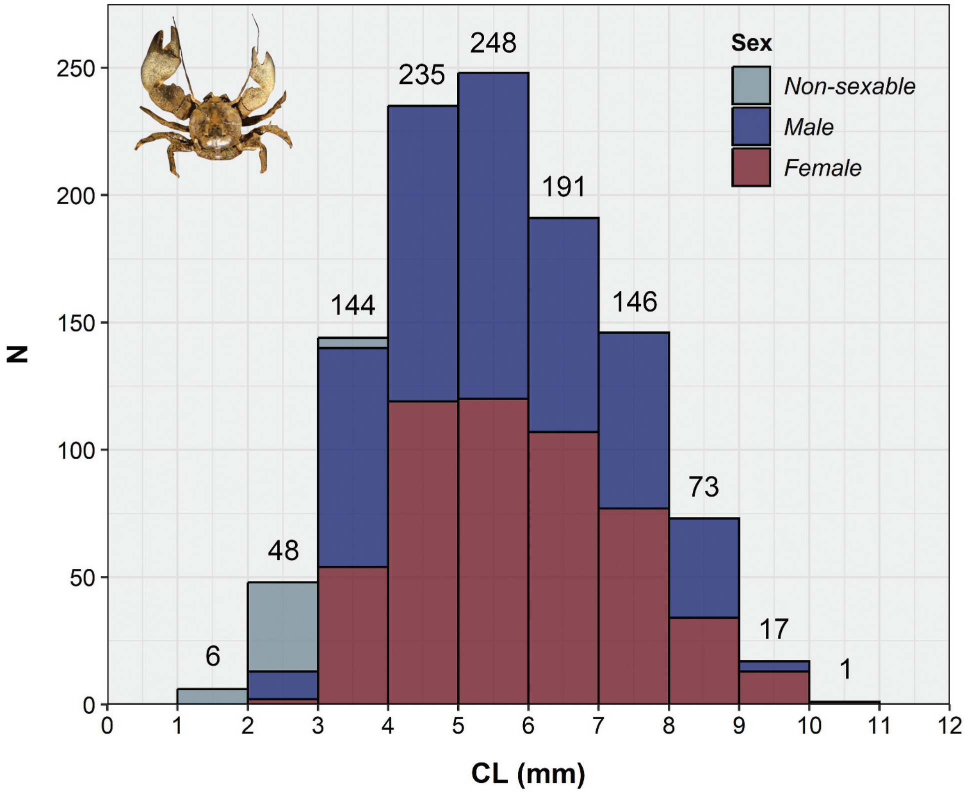

**Figure 2.** Size-frequency histogram of *Pachycheles laevidactylus* Ortmann, 1982 by size class (*CL*, carapace length) of males (blue), females (red) and non-sexable (grey) individuals. Values in the top of each bar indicate the number of individuals sampled for each size class.

The propodus ratios (*PH*x*CL* and *PL*x*CL*) show positive allometry, regardless of sex (Table 2). However, only for males, this relationship generated two equations (juvenile and adult phases) with a reduction in the model declivity, expressed by the growth constant (b), after the puberty moult (*PH*: difference in 0.42, with a reduction of 22.8°; and *PL*: difference in 0.28, with a reduction of 15.6°). Furthermore, in males, the intercept point between the equations of the *PL*x*CL* relationship occurred at 3.48 mm *CL* (Figure 5), while in females, there was no inflection point.

The biometric relationships of the abdomen ($AW_2$x*CL* and $AW_5$x*CL*) indicate a difference in relative growth between the sexes. For males, the allometry level did not change along the ontogeny. However, an antagonistic growth was verified regarding the analysed somite, with positive allometry for $AW_2$x*CL* and negative allometry for $AW_5$x*CL* (b = 1.05 and 0.98, respectively; Table 2). For females, these two somites grew in positive allometry, with a reduction in the growth constant (b) when the juvenile phase was compared to the adult phase for both relationships, although more expressively for $AW_5$ than $AW_2$ (b-value difference: 0.33 = 18.3°; and 0.23 or 13°, respectively). Furthermore, the size of morphological sexual maturity was similar between these biometric relationships, with an inflection point between the regression lines for the phases at 5.00 mm *CL* (Figure 6).

The ANCOVA showed a significant effect of ontogenetic phases on carapace length (*CL*) for each dependent variable used in males and females (Table 3).

## Discussion

Our study provides valuable information about the life-history traits of *P. laevidactylus* from Ubatuba beach, in the southeast region of Brazil. Very similarly to other studies with the same species on higher latitudes (Argentina, Camiolo and Luppi 2016; and south Brazil; Horch and Terossi 2022a, 2022b), our findings highlighted some biological aspects of *P. laevidactylus* for the first time in a subtropical region, as follows: (1) an unbiased sex ratio; (2) a reverse sexual dimorphism, with males being smaller than females; (3) a continuous reproduction, with higher intensity in winter and autumn; and (4) males mature before females, following the sexual dimorphism. Although from different

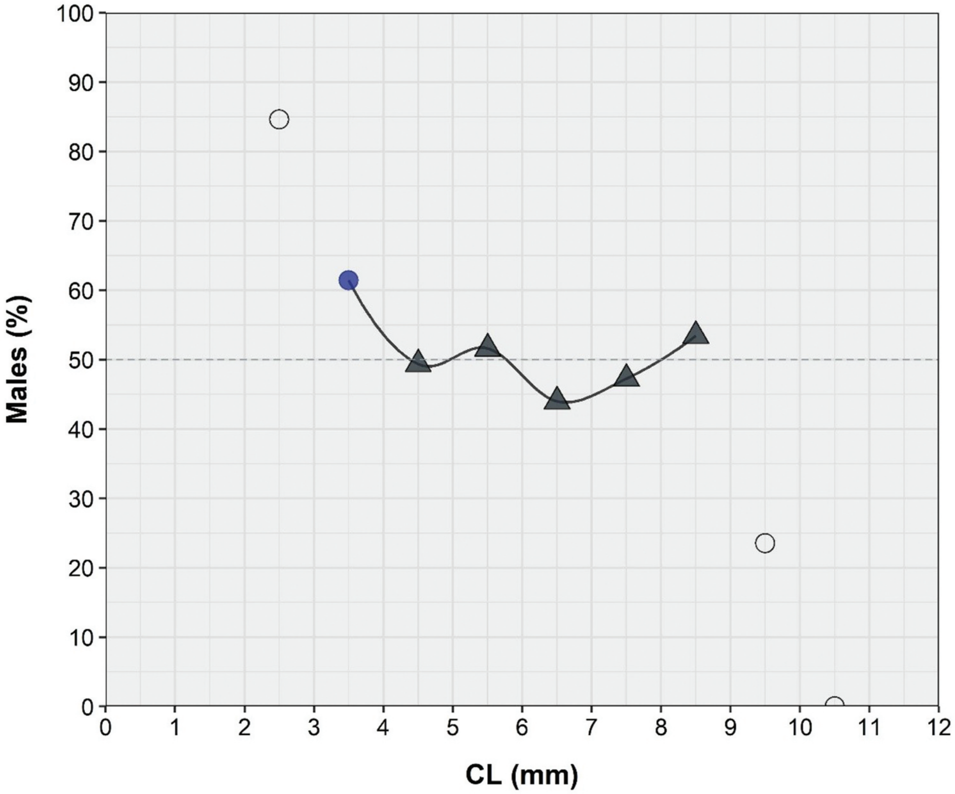

**Figure 3.** Sexual ratio of *Pachycheles laevidactylus* Ortmann, 1892 during ontogeny, considering the size variation of carapace length (*CL*, in millimetres). Where: triangles, sex ratio near 1:1; blue circle, significant difference towards males; white circles, values not applied due to not attaining the minimum value of 20 individuals.

**Table 1.** Reproductive intensity of *Pachycheles laevidactylus*. (A) variation of the carapace length (*CL*, mm) for each sex, frequency of ovigerous females (*OF* %) as adult sex ratio (*ASR*) in function of climatic seasons. (B) below is the two-way analysis of variance testing the effect of climatic seasons and sex (and their interactions) on *CL*. Where: M, males; F, females; *df*, degrees of freedom; *MS*, mean of squares; *F*-value, Fisher's value; bold values, statistical significance ($p < 0.05$).

| | Male | | Female | | |
|---|---|---|---|---|---|
| Season | *N* | *CL (s±sd)* | *N (OF%)* | *CL (s±sd)* | *ASR* (M:F) |
| **(A)** | | | | | |
| Winter | 94 | 6.7 ± 1.6 | 100 (86%) | 6.8 ± 1.6 | 1:1 |
| Spring | 154 | 5.2 ± 1.6 | 87 (54%) | 5.2 ± 1.4 | **1:0.6** |
| Summer | 216 | 5.4 ± 1.3 | 281 (73%) | 5.8 ± 1.4 | 1:0.8 |
| Autumn | 45 | 5.9 ± 1.1 | 48 (94%) | 6.4 ± 0.9 | 1:1 |
| Total | 509 | 5.6 ± 1.5 | 516 | 5.9 ± 1.5 | 1:1 |

| | *CL* | | | |
|---|---|---|---|---|
| Source of variation | *df* | *MS* | *F*-value | *p*-value |
| **(B)** | | | | |
| Season | 3 | 107.8 | 52.5 | **<0.0001** |
| Sex | 1 | 20.3 | 9.9 | **0.0017** |
| Season*Sex | 3 | 10.6 | 1.7 | 0.16 |
| Residuals | 1056 | 2,172.1 | | |

geographical areas mentioned above, the populations of *P. laevidactylus* showed a very similar structure (Camiolo and Luppi 2016; Horch and Terossi 2022a, 2022b), indicating that the species appears to choose habitats that provide numerous associated advantages, such as shelter from predation, access to food, and to sexual partners, among others.

The unbiased sex ratio in the studied population of *P. laevidactylus*, where an equal proportion of males and females occur, suggests that male competition is weak in

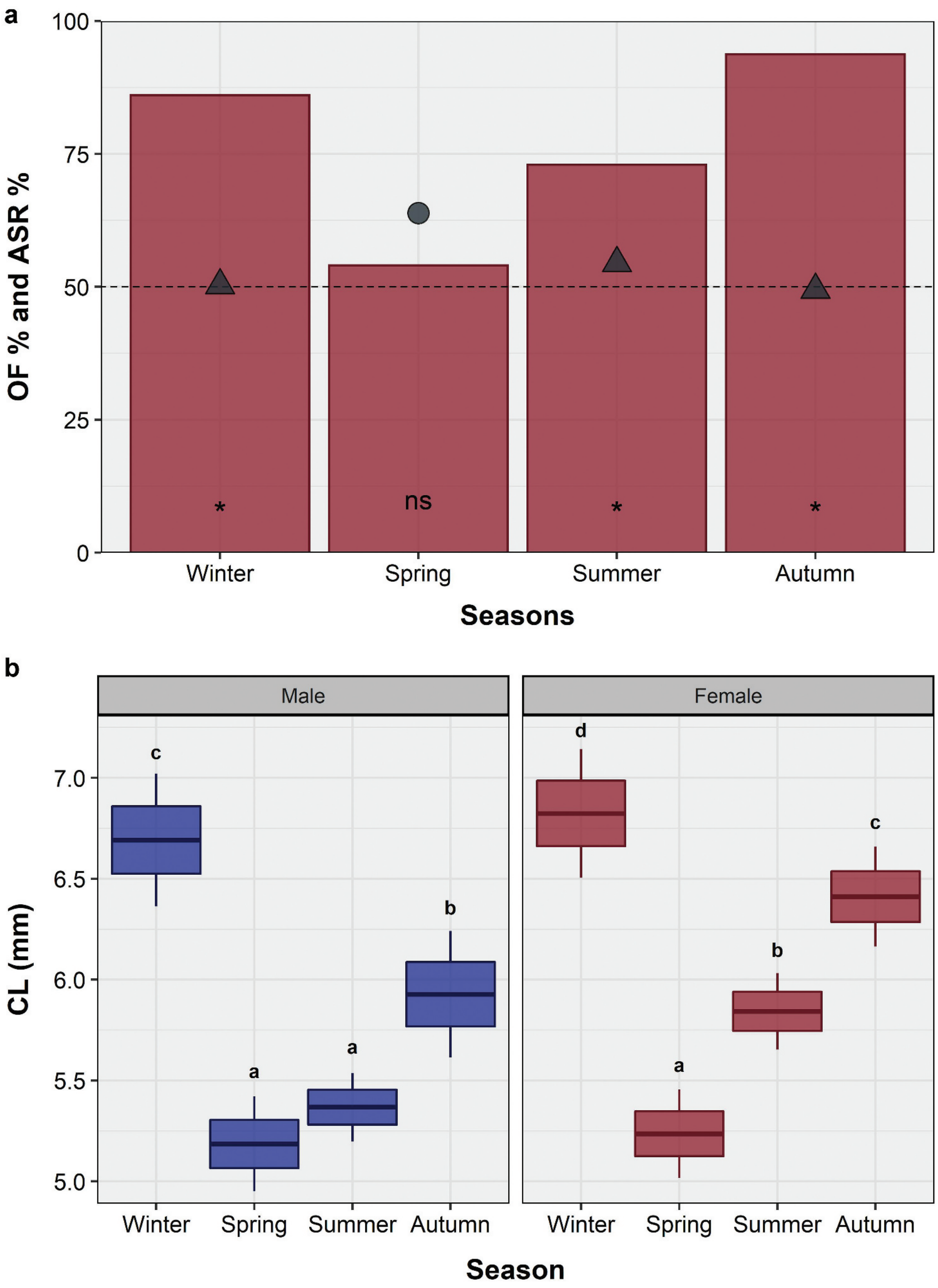

**Figure 4.** Reproductive intensity of *Pachycheles laevidactylus* Ortmann, 1892. (a) frequency of ovigerous females (bars: *OF* %) and adult sex ratio (*ASR*) in each climatic season, and (b) variation of the carapace length (*CL*, in millimeters) of each sex in function of climatic seasons. Where: triangles, similar proportions between sexes; circles, statistic prevalence of males; *, statistic contrast between proportions of ovigerous and not ovigerous females; box, standard error of the mean; horizontal line inside de box, mean; whiskers, confidence interval of the mean at 5%; and distinct letters show significant contrast in mean size of each sex between seasons, based on a two-way ANOVA (see Table 1).

this porcelain crab species. This result agrees with the pattern expected by Fisher's theory, where natural selection favours an equal frequency between the sexes (Fisher 1930) and suggests the existence of weak competition for mates in *P. laevidactylus* and other porcelain crab species. Such a pattern has already been observed for other populations of the same species (Bremec and Cazzaniga 1984; Horch and Terossi 2022a) and in other porcelain crab species [e.g. *Pachycheles chubutensis* (Bremec and Cazzaniga 1984); *P. monilifer* (Fransozo and Bertini 2001); and *Petrolisthes armatus* (Miranda and Mantellato 2009; Pinheiro et al. 2017)]. The similar sex ratio can also indicate the absence of deaths during male confrontations. After all, if deaths did occur, the

**Table 2.** Relative growth of *Pachycheles laevidactylus*. Equations obtained by regression analysis using power function (and logarithmized equation), with dependent variables based on carapace width (*CW*), propodus of the greater chelae (*PH*, propodus height; and *PL*, propodus length) and abdomen (*AL*, total length; $AW_2$, width of the 2nd somite; and $AW_5$, width of the 5th somite) in function of the independent variable (*CL*, carapace length). Where: S/P, sex/ontogenetic phase (NS, not sexed; M, males; F, females; JM, juvenile males; AM, adult males; JF, juvenile females; and AF, adult females); N, amostral number; $R^2$, determination coefficient; A, allometric degree (0, isometry; +, positive allometry; and –, negative allometry).

| Biometric Relationships | S/P | N | Power Function ($Y=aX^b$) | Linearized Equation ($\ln Y=\ln a+b\ln X$) | $R^2$ | A |
|---|---|---|---|---|---|---|
| | NS | 36 | $CW = 0.90CL^{1.05}$ | $\ln CW = -0.10 + 1.05\ln CL$ | 0.97 | 0 |
| *CW*x*CL* | M | 252 | $CW = 0.94CL^{1.03}$ | $\ln CW = -0.07 + 1.03\ln CL$ | 0.99 | + |
| | F | 233 | $CW = 0.90CL^{1.07}$ | $\ln CW = -0.10 + 1.07\ln CL$ | 0.98 | + |
| | NS | 28 | $PH = 0.33CL^{1.46}$ | $\ln PH = -1.11 + 1.46\ln CL$ | 0.84 | + |
| *PH*x*CL* | JM | 42 | $PH = 0.33CL^{1.59}$ | $\ln PH = -1.11 + 1.59\ln CL$ | 0.77 | + |
| | AM | 179 | $PH = 0.66CL^{1.17}$ | $\ln PH = -0.42 + 1.17\ln CL$ | 0.95 | + |
| | F | 184 | $PH = 0.60CL^{1.10}$ | $\ln PH = -0.50 + 1.10\ln CL$ | 0.93 | + |
| *PL*x*CL* | NS | 29 | $PL = 0.80CL^{1.13}$ | $\ln PL = -0.22 + 1.13\ln CL$ | 0.89 | 0 |
| | JM | 31 | $PL = 0.65CL^{1.48}$ | $\ln PL = -0.43 + 1.48\ln CL$ | 0.85 | + |
| | AM | 189 | $PL = 0.76CL^{1.20}$ | $\ln PL = -0.28 + 1.20\ln CL$ | 0.98 | + |
| | F | 190 | $PL = 0.89CL^{1.17}$ | $\ln PL = -0.12 + 1.17\ln CL$ | 0.97 | + |
| *AL*x*CL* | NS | 28 | $AL = 0.98CL^{0.95}$ | $\ln AL = -0.02 + 0.95\ln CL$ | 0.93 | 0 |
| | M | 181 | $AL = 0.82CL^{1.12}$ | $\ln AL = -0.19 + 1.12\ln CL$ | 0.99 | + |
| | F | 228 | $AL = 0.65CL^{1.36}$ | $\ln AL = -0.44 + 1.36\ln CL$ | 0.97 | + |
| | NS | 30 | $AW_2 = 0.56CL^{1.05}$ | $\ln AW_2 = -0.57 + 1.05\ln CL$ | 0.94 | 0 |
| $AW_2$x*CL* | M | 180 | $AW_2 = 0.58CL^{1.05}$ | $\ln AW_2 = -0.55 + 1.05\ln CL$ | 0.99 | + |
| | JF | 93 | $AW_2 = 0.38CL^{1.39}$ | $\ln AW_2 = -0.98 + 1.39\ln CL$ | 0.84 | + |
| | AF | 133 | $AW_2 = 0.79CL^{1.16}$ | $\ln AW_2 = -0.23 + 1.16\ln CL$ | 0.92 | + |
| | NS | 30 | $AW_5 = 0.55CL^{1.07}$ | $\ln AW_5 = -0.60 + 1.07\ln CL$ | 0.94 | 0 |
| $AW_5$x*CL* | M | 183 | $AW_5 = 0.61CL^{0.98}$ | $\ln AW_5 = -0.49 + 0.98\ln CL$ | 0.99 | – |
| | JF | 94 | $AW_5 = 0.33CL^{1.51}$ | $\ln AW_5 = -1.12 + 1.5\ln CL$ | 0.85 | + |
| | AF | 139 | $AW_5 = 0.71CL^{1.18}$ | $\ln AW_5 = -0.34 + 1.18nCL$ | 0.91 | + |

female sex should be predominant (Baeza and Thiel 2007). Differential predation pressures or agonistic confrontations can lead to different mortality rates between the sexes (Miranda and Mantellato 2009), generating population selection and the predominance of one sex over the other. These populations pressures are unknown for porcellanids, including *P. laevidactylus*. However, their cryptic habit and aggregate distribution during ontogeny can reduce the mortality rate due to predation (see *Allopetrolisthes punctatus* by Cruz and Retamal 2018) and promote a an unbiased sex ratio.

Males of *P. laevidactylus* were, on average, smaller than females (*CL*), while both sexes had similar cheliped sizes. Males with a smaller size than females are a pattern already reported for *P. laevidactylus*, as described by Horch and Terossi (2022a), in another population on the Brazilian coast. The same occurs with the congeners *P. natalensis* and *P. tomentosus* (Ahmed and Mustaquim 1974). However, there are cases where the inverse pattern occurs, with males being larger than females, as Fransozo and Bertini (2001) pointed out for the congener crab *P. monilifer* and other porcelanids such as: *Porcellana platycheles*, by (Smaldon 1972); *Petrolisthes* spp. [*P. boscii* and *Petrolisthes rufescens*, according to Ahmed and Mustaquim (1974); *P. laevigatus*, by Lardies et al. (2004); and *P. armatus*, evaluated by Miranda and Mantellato (2009) and Pinheiro et al. (2017)]. Reverse sexual dimorphism (RSD) is expected in species where males compete for females using exploration tactics and do not interact agonistically with other males but only search for receptive females (Baeza and Thiel 2007). In these cases, an intrasexual selection favours smaller males, which occurs for *P. laevidactylus* in the present study and is confirmed for studies carried in temperate climate zones for this species (Camiolo and Luppi 2016; Horch and Terossi 2022a).

The reproductive season of Pleocyemata crustaceans is defined by the months of developed gonads and/or the presence of ovigerous females (Pinheiro and Terceiro 2000), where in many cases the reproduction tends to be continuous in tropical and subtropical regions due to greater thermal stability and photoperiod (Wenner et al. 1974; Pinheiro and Fransozo 2002). Previous studies on *P. laevidactylus* indicate its reproduction is continuous throughout an annual cycle (Horch and Terossi 2022a). This fact was also confirmed for other Porcellanidae, as follows: *Petrolisthes politus* according to Scelzo (1985); *P. elongatus* by Jones (1977); and *P. armatus* (Miranda and Mantellato 2009; Pinheiro et al. 2017).

The presence of ovigerous females throughout the year guarantees a constant supply of larvae, the same for juvenile recruitment, which is an essential characteristic for the maintenance and stability of a population (Miranda and Mantellato 2009). According

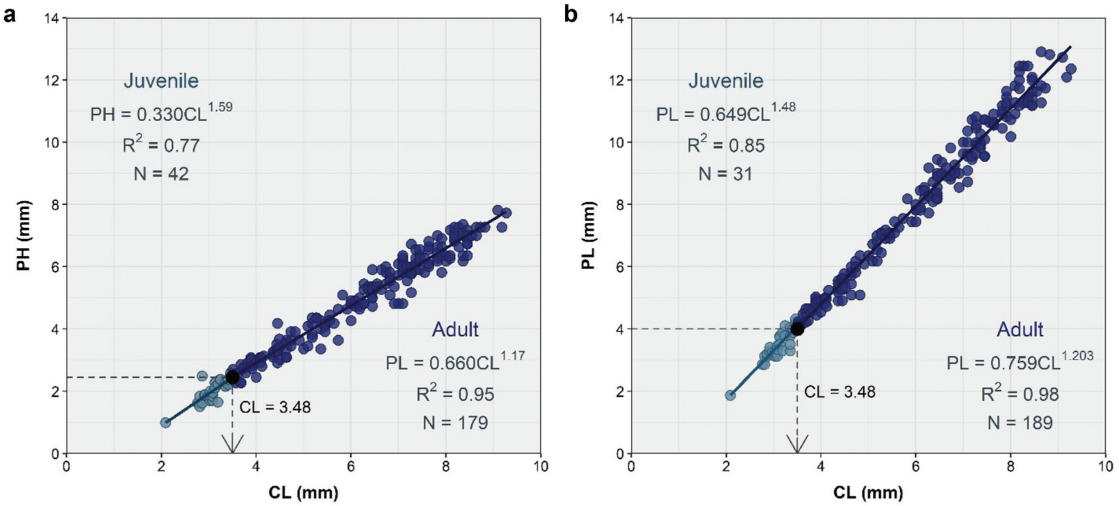

**Figure 5.** Biometric relationship *PHxCL* and *PLxCL* for males of *Pachycheles laevidactylus* Ortmann, 1892. Highest height between the margins of the manus (*PH*), evolving propodus length (*PL*) and carapace length (*CL*), both in millimetres. Body size values were used to estimate morphological maturity. Where: light and dark blue colour dots are related to juveniles and adults, respectively, with an arrow indicating the size estimated at morphological maturity.

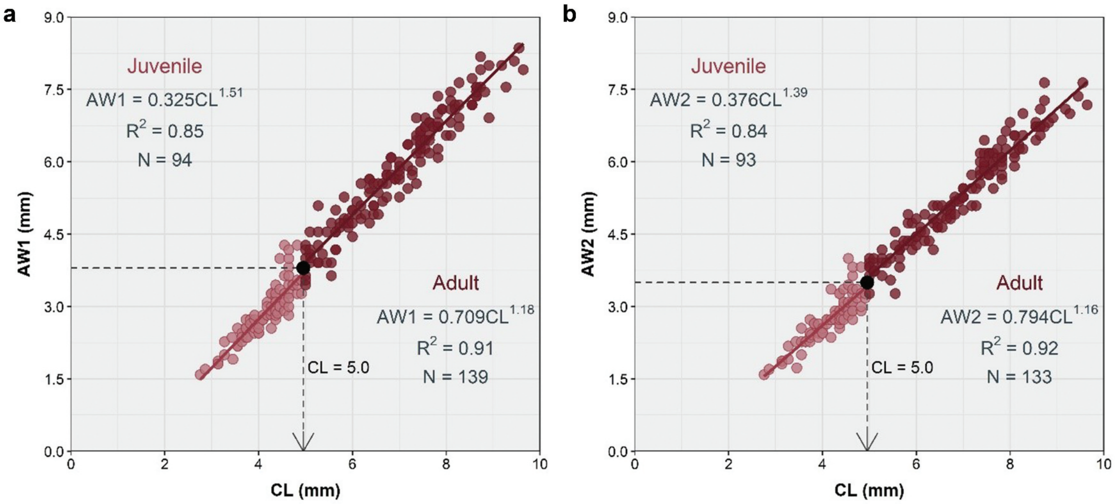

**Figure 6.** Biometric relationships $AW_1$*xCL* and $AW_2$*xCL* for females of *Pachycheles laevidactylus* Ortmann, 1892. Evolving abdominal width ($AW_1$, 5th somite; and $AW_2$, 2nd somite) and carapace length (*CL*), both in millimetres. Body size values were used to estimate morphological maturity. Where: light and dark red colour dots are related to juveniles and adults, respectively, with an arrow indicating the size estimated at morphological maturity.

to Pinheiro et al. (2017), a subtropical area in southeastern Brazil registered the highest proportion of ovigerous females of *Petrolisthes armatus* in the spring and summer months, coinciding with the rise in temperature, precipitation, and photoperiod. Furthermore, even if reproduction is continuous, the intensity can vary according to the proportion of ovigerous females and their reproductive potential (fecundity). Regarding *P. laevidactylus* in this study, the largest ovigerous females were registered mainly in autumn and winter. Meanwhile, the smallest sizes (*CL*) and possibly the recruitment occur in the spring and summer months, the opposite of what was reported in the above-mentioned study.

Relative growth studies are relevant tools to estimate the size at morphological maturity, where the growth pattern depends on the sex and ontogenetic phase (juvenile or adult) of the species (Hartnoll 1982). This fact is not common in anomuran crabs, where there is a great variation among the sizes at morphological maturity, with the limitation of fewer studies on representatives of the Infraorder Anomura (Miranda and Mantellato 2010; Pinheiro et al. 2017) when compared

**Table 3.** Summary of covariance analysis, testing the effect of ontogenetic phase (juvenile and adult) and carapace length (*CL*) of *Pachycheles laevidactylus*, in function of the secondary sexual characters of males (*PL*, propodus length of the greater chelae) and females ($AW_2$, abdominal width of 2nd somite; and $AW_5$ abdominal width of 5th somite). Where: *df*, degrees of freedom; *SQ*, sum of squares; and *F*, Fisher's value.

| Sex | Dependent Variable | Variation Source | *df* | *SQ* | *F** |
|---|---|---|---|---|---|
| Male | *PL* | *CL* | 1 | 39.08 | **16793.26** |
| | | Phase | 1 | 0.01 | **5.32** |
| | | *CL*×Phase | 1 | 0.02 | **9.34** |
| | | Residuals | 216 | 0.50 | – |
| Female | $AW_2$ | *CL* | 1 | 30.77 | **7291.91** |
| | | Phase | 1 | 0.050 | **11.82** |
| | | *CL*×Phase | 1 | 0.030 | **7.03** |
| | | Residuals | 221 | 0.933 | – |
| Female | $AW_5$ | *CL* | 1 | 35.67 | **7247.97** |
| | | Phase | 1 | 0.06 | **11.73** |
| | | *CL*×Phase | 1 | 0.009 | **17.84** |
| | | Residuals | 229 | 1.13 | – |

*F-values presented in bold font have 5% statistical significance ($P < 0.05$).

to the Infraorder Brachyura, which holds the pioneering studies on morphological maturity (Hartnoll 1974, 1978, 1982, 2001).

In males of true crabs (Infraorder Brachyura), chelipeds are important secondary sexual characters, as they are used in behaviours related to courtship, selection, and manipulation of female for mating (see Pinheiro and Fransozo 1993; Pinheiro and Hattori 2006). Knowledge of the reproductive behaviour of *P. laevidactylus* is still scarce, especially regarding the interactions of males with other males or females. However, the positive allometry reduction verified in measurements registered in larger chela after pubertal moult indicates that this structure may not be used for this purpose, or even that agonistic interactions do not occur between males of *P. laevidactylus*. A reduction in the allometric rate of the greater chela has been previously reported for males of *P. laevidactylus* (Camiolo and Luppi 2016; Horch and Terossi 2022a), which is opposite to that observed in male brachyurans, which show an increase in the positive allometry rate after the pubertal moult (see *Arenaeus cribrarius* by Pinheiro and Fransozo 1993, and *Ucides cordatus* by; Pinheiro and Hattori 2006).

For *P. laevidactylus* females, both abdominal ratios showed positive allometry in the entire ontogeny, but with a reduction in the growth rate after the puberty moult, differing from the peculiar pattern that occur in brachyuran crabs of isometry or negative allometry in adult females (Pinheiro and Hattori 2006; Pardal-Souza and Pinheiro 2013). As in other Pleocyemata, the abdomen in females of 'non-brachyuran crabs' (*e.g.*, Porcellanidae) has a similar role as in true crabs (Infraorder Brachyura): it protects the egg mass attached to the bristles of pleopodal endopods during incubation (Pinheiro and Fransozo 1993). However, the allometric reduction of the abdomen in porcelain crabs can be explained by the swimming potential of the juveniles, which is minimized in the adults, when these animals are predominantly benthic and live associated with rock crevices, cavities of annelid worm reefs or in association with other animals (Pinheiro et al. 2017; Horch and Terossi 2022a).

Chelae and abdomen measurements have been used before to determine the size at sexual maturity of males and females, respectively (Pinheiro and Fransozo 1993; Miranda and Mantellato 2010). Some authors establish the percentage of estimated size for the maturity of each species in relation to the maximum size obtained in the field (see Pinheiro et al. 2017). Knowing that the largest size recorded for *P. laevidactylus* in this study was 9.7 mm *CL*, the percentage of maturity size corresponded to 36.1% and 54.6% of the maximum size for males and females, respectively. In the south of Brazil, the largest size recorded for *P. laevidactylus* was 15.1 mm *CW* (Horch and Terossi 2022a), with a percentage of maturity size corresponding to 34.3% and 35.5%, for males and females, respectively, after converting *CW* to *CL*, using the authors' equation. *Pachycheles laevidactylus* specimens in this temperate climate zone are larger and reach the maturity size before individuals in the subtropical climate zone represented here. In Argentina (another temperate climate zone), Camiolo and Luppi (2016) recorded a morphological maturity of 4.4 mm *CW* for *P. laevidactylus*, a value below that found in Rio Grande do Sul (Horch and Terossi 2022a) and for females in this study. This condition is antagonistic to previous patterns reported for decapods (Castilho et al. 2007; Hirose et al. 2013), where in warmer environments reproduction begins earlier than in colder environments (Blackburn et al. 1999; Blanckenhorn and Demont 2004). However, it is not antagonistic in cases where the inverse pattern occurs (Terossi et al. 2010). This variation may be related to abiotic and biotic factors other than temperature, such as latitude, salinity, habitat, food availability, competition, and predation risk (Hirose et al. 2013; Horch and Terossi 2022a). Here we address the relationship between maturity sizes and different climatic zones, where again, *P. laevidactylus* does not follow this relationship's usual pattern as also seen in Horch and Terossi (2022a).

During its life history, *P. laevidactylus* is conditioned by numerous factors, be it the latitude or the different hosts that the species inhabits [e.g. *Brachidontes rodriguezzi* (see Camiolo and Luppi 2016); *Phragmatopoma caudata* (see Pinheiro and Fransozo 1995; Horch and Terossi 2022a, 2022b). Thus, it is difficult to point out which factor affects the population parameters of *P. laevidactylus*. Until now, the differences observed here in relation to the previous studies (Camiolo and Luppi 2016; Horch and Terossi 2022a) apparently are regulated by the environmental differences belonging to the latitudinal gradient. In the future, it becomes necessary to elaborate more studies aiming to elucidate such questions, mainly addressing the species associated with different hosts in the same latitude.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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