



Size-Normalized Fecundity Reveals Reversed Geographic Patterns in the Porcelain Crab *Pachycheles laevidactylus* (Crustacea: Decapoda: Porcellanidae)

Esli E. D. Mosna^{1,2} · Amanda P. Horch³ · Mariana Terossi³ · Marcelo A. A. Pinheiro^{1,2}

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Abstract

Fecundity in pleocyemate crustaceans is defined as the number of eggs produced per spawning event and is strongly dependent on female body size, which can limit direct comparisons among populations. To address this limitation, we evaluated geographic variation in fecundity in the porcellanid crab *Pachycheles laevidactylus* along the southwestern Atlantic, comparing populations from Ubatuba (UB: southeastern Brazil) and Torres and Tramandaí (TO and TR: southern Brazil) based on both absolute average fecundity (F) and size-normalized fecundity (F'). Ovigerous females were measured for carapace length (CL), and egg number (EN) was quantified for each individual. Carapace length and absolute fecundity followed the same pattern among localities (TR>TO>UB). However, after removing the effect of body size, this pattern reversed (UB>TO>TR), indicating that the higher fecundity observed in southern populations may have been driven by differences in the population size structure of ovigerous females. Size normalization also resulted in a sharp reduction in variability, with the coefficient of variation decreasing by approximately 50% compared to absolute fecundity. These results demonstrate that population structure can mask underlying differences in reproductive patterns, supporting the use of size-corrected metrics in interpopulation comparisons. This approach provides a more consistent and biologically meaningful framework for assessing geographic variation in decapod crustaceans.

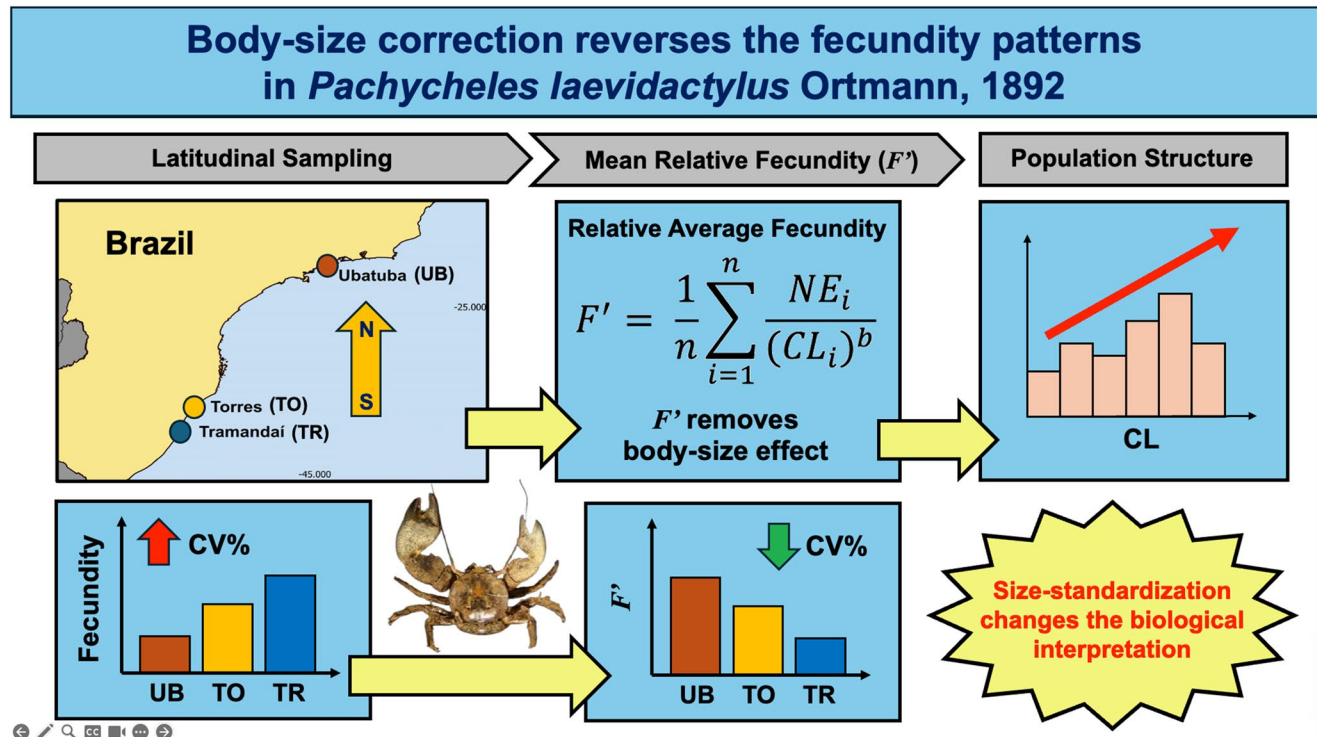
✉ Esli E. D. Mosna
e.mosna@unesp.br

¹ Departamento de Ciências Biológicas Ambientais – Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), Universidade Estadual Paulista (UNESP), IB/Campus do Litoral Paulista (IB/CLP), São Vicente, SP, Brasil

² Programa de Pós-Graduação em Ecologia, Evolução e Biodiversidade (PPG- EcoEvoBio), UNESP IB/Rio Claro, Rio Claro, SP, Brasil

³ Programa de Pós-Graduação em Biologia Animal, Laboratório de Carcinologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brasil

Graphical Abstract



Keywords Anomura · Latitudinal variation · Size-normalized fecundity · Western Atlantic

Introduction

Fecundity is one of the most relevant reproductive metrics in decapod crustaceans and is commonly defined as the number of eggs produced by females per spawning event (Sastry 1983). Fecundity and spawning frequency are species-specific traits that reflect reproductive and ecological strategies (Pinheiro and Fransozo 1995) and are strongly influenced by temperature, food availability, and the body size of ovigerous females (Laptikhovsky 2006; Horsch and Terossi 2022a). These factors must be considered in geographic studies because environmental conditions influence both growth patterns and population structure, often confounding the interpretation of reproductive output.

Latitudinal variation in reproductive traits has been widely reported in marine invertebrates. In decapods, populations from colder regions often exhibit larger body sizes and higher fecundity, whereas those from warmer environments tend to mature earlier and at smaller body sizes (Clarke 1987; Lardies and Castilla 2001; Brante et al. 2004; Gonz  lez et al. 2016). However, these comparisons are generally based on raw fecundity values, which integrate both reproductive allocation and population size structure. Consequently, differences attributed to environmental gradients

may reflect shifts in size distribution rather than true variations in reproductive investment.

In pleocyemate crustaceans, fecundity estimates are based on a power function relating the number of eggs (NE) to body size, represented in porcellanids by carapace length (CL), because this relationship is often curvilinear (Pinheiro and Fransozo 1995). However, linear models have also been applied in some cases (Patel et al. 2024; Hamasaki et al. 2025), although they may not adequately capture the allometric nature of this relationship.

Among anomuran crabs, the family Porcellanidae Haworth, 1825 is among the most diverse, with species distributed from tropical to temperate marine zones, where they inhabit subtidal rocky shores or live in symbiotic association with other marine invertebrates (Haig 1960; Veloso and Melo 1993; Werding et al. 2003; Leone and Mantelatto 2015). *Pachycheles* Stimpson, 1858 comprises 48 species and is the second-largest genus in Porcellanidae (WoRMS, 2026). *Pachycheles laevidactylus* Ortmann, 1892, is widely distributed along the southwestern Atlantic, from northeastern Brazil to northern Argentina (Boschi 1963; Ogawa and Rocha 1976; Camiolo and Luppi 2016). This species exhibits high symbiotic plasticity and occurs in mussel beds of *Brachidontes rodriguezii* (d'Orbigny, 1842) (Camiolo and

Luppi 2016) and in sandy aggregations built by the annelid *Phragmatopoma caudata* Krøyer in Mörch, 1863, (Horch and Terossi 2022a).

Previous studies had documented considerable geographic variation in population and reproductive parameters for *Pachycheles laevidactylus* along the Southwest Atlantic (Ogawa and Rocha 1976; Pinheiro and Fransozo 1995; Camiolo and Luppi 2016; Horch and Terossi 2022a; b). In this context, populations from southern, and consequently colder, locations exhibit larger body sizes, as well as a higher absolute egg production (Camiolo and Luppi 2016; Horch and Terossi 2022a; b), while lower fecundity was recorded for warmer populations within the species' distribution (Pinheiro and Fransozo 1995). This geographic variation in size is consistent with Bergmann's rule, originally developed for endothermic organisms, but previously adapted for marine crustaceans and other ectothermic organisms (Jaramillo et al. 2017; Johnson et al. 2019). Considering that the size of ovigerous females is positively correlated with egg production, comparisons between populations in different locations can generate differences in absolute fecundity (Hines et al. 1982). In this sense, mathematical procedures become necessary, aiming to remove the effect of body size on reproductive effort (Pinheiro and Terceiro 2000).

This study aimed to evaluate the geographic variation in fecundity of the porcelain crab *Pachycheles laevidactylus*, removing the effect of female body size. We compared populations from southeastern (Ubatuba) and southern Brazil (Torres and Tramandaí) using both absolute and size-normalized fecundity. Since the southern populations are composed of larger ovigerous females and fecundity increases significantly with female body size, we hypothesized that differences in female size structure contribute substantially to the higher absolute fecundity observed in these populations.

Consequently, after considering body size, we predicted that the observed geographic hierarchy for absolute fecundity would be reduced or reversed, revealing size-specific egg production differences among the sampled populations.

Material & Methods

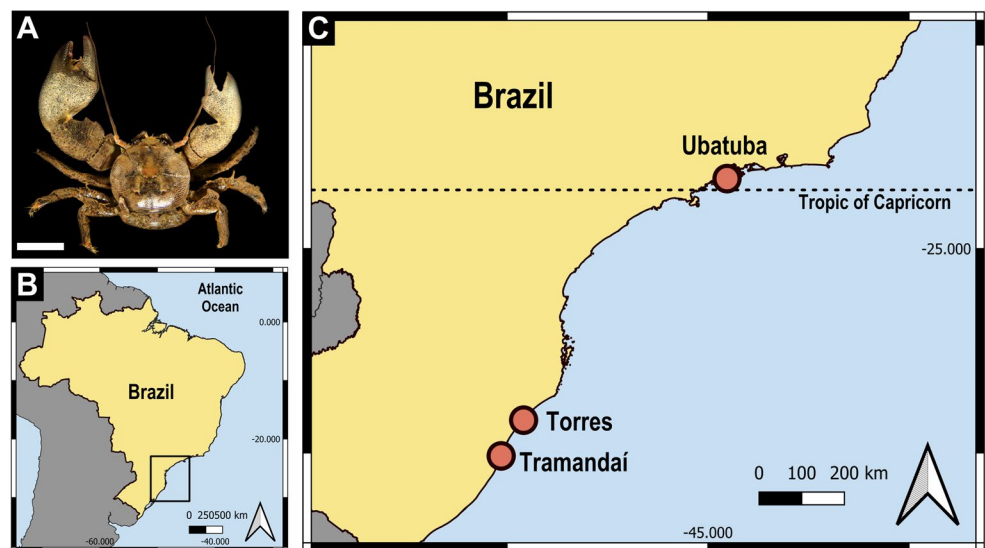
Study Area and Sampling

Ovigerous females of *Pachycheles laevidactylus* (Fig. 1A), associated with sandy aggregations produced by the annelid *Phragmatopoma caudata*, were collected from three distinct localities (Fig. 1B, C): **Ubatuba (UB)**, at Praia Grande (23°28'1.58" S, 45°3'35.07" W), located on the northern coast of the state of São Paulo (subtropical region); **Torres (TO)**, at Prainha (29°20'20.9" S, 49°43'23.0" W); and **Tramandaí (TR)**, at Fishing Platform (30°00'16.7" S, 50°07'49.2" W), both located on the northern coast of the state of Rio Grande do Sul (temperate region).

Specimens were collected during periods of low tidal amplitude. In Ubatuba, sampling was conducted between July 1990 and May 1991, whereas in Torres and Tramandaí, sampling was carried out between November 2018 and August 2019.

At each locality, sandy aggregations were inspected in situ, and the oldest portions (~3 kg), identified by their greater thickness, were selectively removed. These fragments were placed in individual plastic bags for subsequent sorting and analysis. In the laboratory, the material was frozen at -14 °C for approximately 1 h to cryo-anesthetize the porcelain crabs. The samples were then transferred to plastic trays, and the aggregations were carefully fragmented and rinsed with water to separate the animals.

Fig. 1 Studied species and sampling areas. (A) Adult specimen of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892; scale bar: 4 mm (photograph by Nahuel Emilliano Farias). (B) Geographic localities of the study area along the Brazilian coast. (C) Sampling sites (Ubatuba, Torres, and Tramandaí) in the southwestern Atlantic



Subsequently, the specimens were examined under a stereomicroscope to ensure accurate identification based on the diagnostic characters defined by Ferreira and Mello (2016). Ovigerous females were then separated for further analysis.

Fecundity Analysis

Each individual was subjected to biometric analysis by measuring carapace length (CL), defined as the distance from the tip of the rostrum to the posterior margin of the carapace, using a stereomicroscope (Axiolab®, Zeiss®) connected to a computer-based image analysis system (KS-300®, Zeiss®), with a precision of 0.01 mm.

The structure of ovigerous females in size-class distribution, grouped into 1-mm body-size (CL) classes in each locality, was used to construct frequency histograms for comparison. Additionally, the skewness coefficient (sk) was calculated at each locality, according to the classification proposed by Wegner (2010) and Pinheiro et al. (2022). Accordingly, the distribution of ovigerous females was characterized into three categories: symmetrical ($-0.5 \leq sk \leq 0.5$); positively skewed ($sk > 0.5$), with a prevalence of the smallest individuals; and negatively skewed ($sk < -0.5$), with the presence of the largest individuals. The intensity of skewness was also evaluated and categorized as slight ($0.5 < |sk| < 1$) or strong ($|sk| \geq 1$).

The eggs of each ovigerous female were carefully removed from the pleon using a fine dissecting needle, and the total number of eggs (NE) was counted under a stereomicroscope using a manual counter. The embryonic stage of each mass of eggs was classified according to the criteria of Pinheiro and Fransozo (1995), based on the embryo-to-yolk ratio and the presence or absence of eye pigmentation, as follows: initial stage, embryo/yolk ratio below 30% and no eye pigmentation; intermediate stage, approximately 50% embryo/yolk ratio and presence of eye pigmentation; and final stage, embryo/yolk ratio above 70% and presence of eye pigmentation. To minimize the potential bias associated with egg loss during embryonic development, only ovigerous females with early-stage egg masses were included in subsequent fecundity analyses.

For fecundity estimation, scatter plots representing the relationship between NE and CL were initially constructed for each locality. Empirical data points were fitted using a power regression model ($Y = a \cdot X^b$), where NE is the number of eggs (dependent variable), CL is carapace length (independent variable), and a and b are constants representing the intercept and slope of the model, respectively. The same data were also log-transformed and subjected to linear regression analysis ($\ln Y = \ln a + b \cdot \ln X$) to linearize the relationship and allow comparison among localities through analysis of covariance (ANCOVA).

Absolute average fecundity (F) of *P. laevidactylus*, based on the $NE \times CL$ relationship, was calculated for each locality, with subsequent removal of the size effect in each case to estimate size-normalized fecundity (F'), corresponding to the relative average fecundity proposed by Pinheiro and Terceiro (2000). Although this parameter represents a mean value, it is hereafter expressed simply as F' for clarity and consistency throughout the text., as represented by the following formula:

$$F' = \frac{1}{n} \sum_{i=1}^n \frac{NE_i}{(CL_i)^b}$$

In this expression, F' represents the size-normalized fecundity, n is the number of ovigerous females at each locality, NE_i is the number of eggs counted in the i -th female, b is the exponent of the fitted power function to the relationship $NE \times CL$, and CL_i is the carapace length of the i -th female.

Statistical Analysis

Shapiro–Wilk normality and Levene’s homoscedasticity tests were applied to carapace length (CL , mm), fecundity (NE , units), and size-normalized fecundity (F') across the three localities.

If the data met parametric assumptions, means were compared using a one-way ANOVA followed by Tukey’s post hoc test. For non-parametric data, medians were used as measures of central tendency and compared using a Kruskal–Wallis (KW) test, followed by multiple comparisons with Dunn’s test (Zar 1999).

The coefficient of variation (CV , in %), expressed by the formula $CV = (SD/mean) \times 100$, was also calculated to compare the variability of the two main reproductive variables (F and F') at each locality. This approach allows direct assessment of variability, enabling comparison of CV before and after removing the size effect: CV_F vs. $CV_{F'}$.

All analyses were performed in R (R Core Team 2026).

Results

A total of 580 ovigerous females were analyzed (Table 1), comprising 155 from Ubatuba (CL : 3.3–9.6 mm), 228 from Torres (3.4–12.1 mm), and 197 from Tramandaí (3.3–13.1 mm). The population structure of ovigerous females was approximately symmetrical across all localities (Fig. 2), being slightly positively skewed in Ubatuba and Tramandaí ($sk=0.05$ and 0.43 , respectively), and slightly negatively skewed in Torres ($sk = -0.07$).

Table 1 Summary of carapace length (CL, mm), absolute fecundity ($F=NE$, number of eggs), and relative average fecundity (F' , dimensionless) of *Pachycheles laevidactylus* at each locality. Values are represented as mean ($\bar{x}$) $\pm$ standard deviation (SD), with minimum (Min), maximum (Max), sample size (n), and coefficient of variation (CV , %)

Local	n	CL (mm)		NE (units)		$F' \times 10^{-3}$ (dimensionless)		Max	$\bar{x} \pm s$	CV (%)
		Min	Max	Min	Max	Min	Max			
Ubatuba	155	3.3	9.6	2	964	0.96	21.0	5.6 $\pm$ 3.6		64.3
Torres	228	3.4	12.1	1	2,749	0.04	11.0	2.7 $\pm$ 1.7		63.0
Tramandaí	197	3.3	13.1	1	3,000	0.01	5.7	1.6 $\pm$ 0.96		60.0

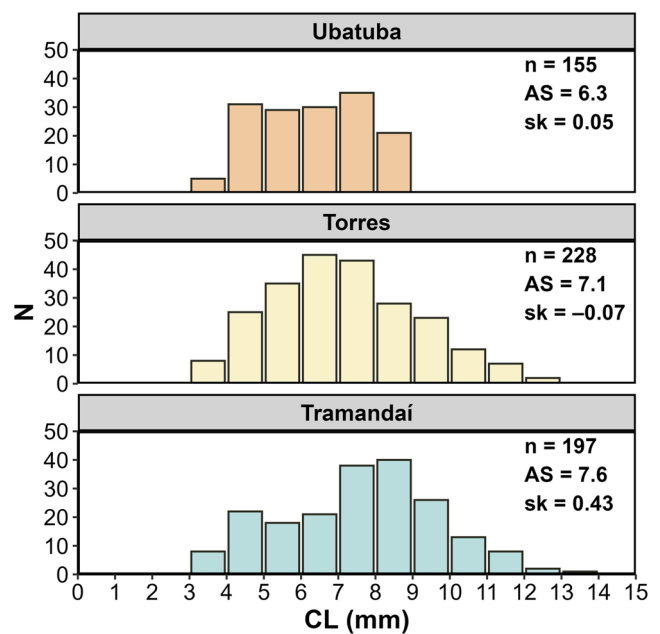
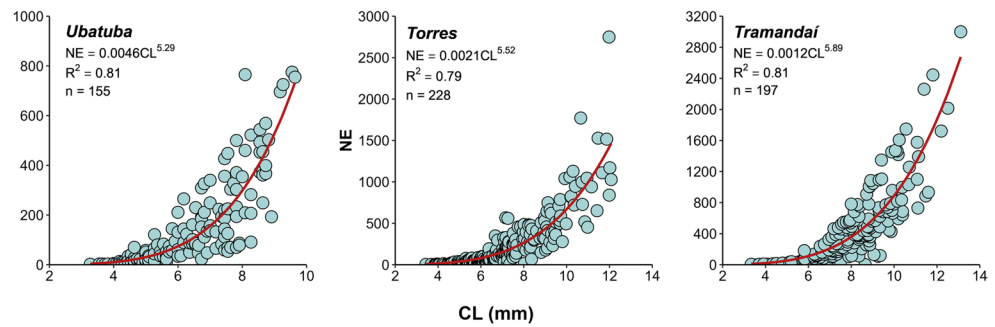


Fig. 2 Size-frequency distribution of ovigerous females of *Pachycheles laevidactylus* by carapace length (CL, mm) at each locality. Values shown are sample size (n), average size (AS), and skewness coefficient (sk)

The number of eggs per female in Ubatuba ranged from 2 to 964 (Table 1), with a mean of 155 ± 178 eggs and a high coefficient of variation ($CV=114.8\%$). A strong and significant positive correlation was observed between NE and CL ($\rho=0.88$; $p<0.001$), with a good fit to the power function $NE = 0.0046 \cdot CL^{5.29}$ ($R^2=0.81$) (Fig. 3). In Torres, NE ranged from 1 to 2,749 eggs (254 ± 351 eggs), with an even higher CV (138.2%). A similarly strong positive correlation with CL was also observed ($\rho=0.91$; $p<0.001$), with a good fit to the function $NE = 0.0021 \cdot CL^{5.52}$ ($R^2=0.79$). In Tramandaí, NE ranged from 1 to 3,000 eggs (431 ± 497 eggs), also with high variability ($CV=115.3\%$), and showed a strong positive relationship with CL ($\rho=0.89$; $p<0.001$), and a good fit to the function $NE = 0.0012 \cdot CL^{5.89}$ ($R^2=0.81$). Across all localities, absolute fecundity (F) of *P. laevidactylus* exhibited consistently high variability, with CV values ranging from 114.8% to 138.2%.

Size-normalized fecundity (F') in Ubatuba ranged from $0.96 \cdot 10^{-3}$ to $21.0 \cdot 10^{-3}$ ($5.6 \pm 3.6 \cdot 10^{-3}$), with a markedly lower variation ($CV=64.3\%$) than that observed for NE . In Torres ($0.04 \cdot 10^{-3}$ to $11.0 \cdot 10^{-3}$; $2.7 \pm 1.7 \cdot 10^{-3}$) and Tramandaí ($0.01 \cdot 10^{-3}$ to $5.7 \cdot 10^{-3}$; $1.6 \pm 0.96 \cdot 10^{-3}$), the same reduction in variability was observed ($CV=63.0\%$ and 60.0% , respectively). Overall, the variability of F' was substantially lower than that of NE , ranging from 60.0% to 64.3%, corresponding to an average reduction of 50.8% in CV after removing the effect of size.

Fig. 3 Relationship between fecundity (NE , number of eggs) and carapace length (CL , mm) in *Pachycheles laevidactylus* for each locality. Lines represent fitted power functions describing the fecundity-size relationship



When fitted to a linear regression model, fecundity in *P. laevidactylus* differed significantly among localities ($F=8.2$; $p<0.001$), indicating that individuals from different regions exhibited distinct fecundities at comparable carapace length. Body size ($\ln CL$, covariate) also had a strongly significant effect ($F=2542.1$; $p<0.001$) (Table 2). However, no significant interaction was found between locality and body size ($\ln CL \times \text{Locality}$: $F=1.4$; $p=0.25$), indicating that the slopes of the absolute average fecundity (F) functions did not differ among localities (Fig. 4; Table 2).

The body size (CL) of ovigerous females differed significantly among localities ($KW=33.88$; $p<0.001$) (Fig. 5A), following the hierarchy: **TR>TO>UB**. Absolute average fecundity (F) also differed among localities ($KW=29.29$; $p<0.001$), maintaining the same pattern (Fig. 5B). In contrast, size-normalized fecundity F' showed significant differences as well ($KW=214.92$; $p<0.001$), with the hierarchy reversed: **UB>TO>TR** (Fig. 5C).

To account for the geographic proximity between the two southern localities, an additional pairwise comparison of size-normalized fecundity (F') was performed between Torres and Tramandaí. This parameter differed significantly between these sites (Wilcoxon rank-sum test: $W=32792$; $p<0.001$), indicating substantial within-region variability F' despite their close spatial proximity. In addition, a sensitivity analysis was conducted by pooling Torres and Tramandaí into a single “South” group and comparing the F' of this group with that of the southeastern locality (Ubatuba). This pooled regional comparison also revealed a significant difference ($W=55641$; $p<0.001$), supporting the robustness of the South–Southeast contrast when the southern sites are considered jointly.

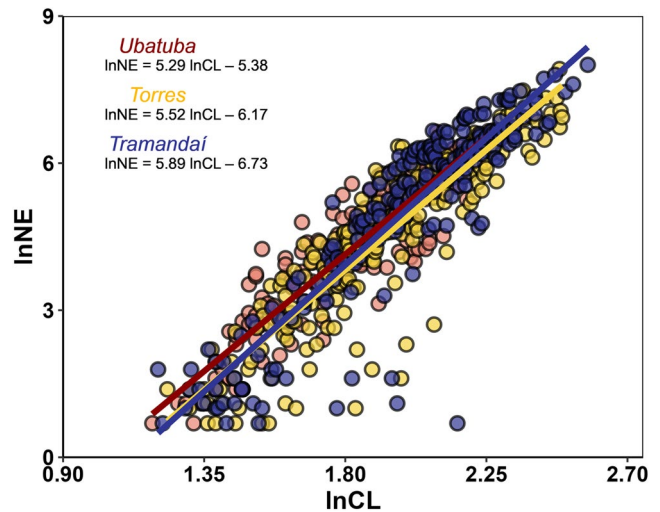


Fig. 4 Log-transformed relationship between fecundity ($\ln NE$) and carapace length ($\ln CL$) in *Pachycheles laevidactylus* across localities. Fitted linear models illustrate differences among intercepts (a), while slopes (b) remain consistent among populations

Discussion

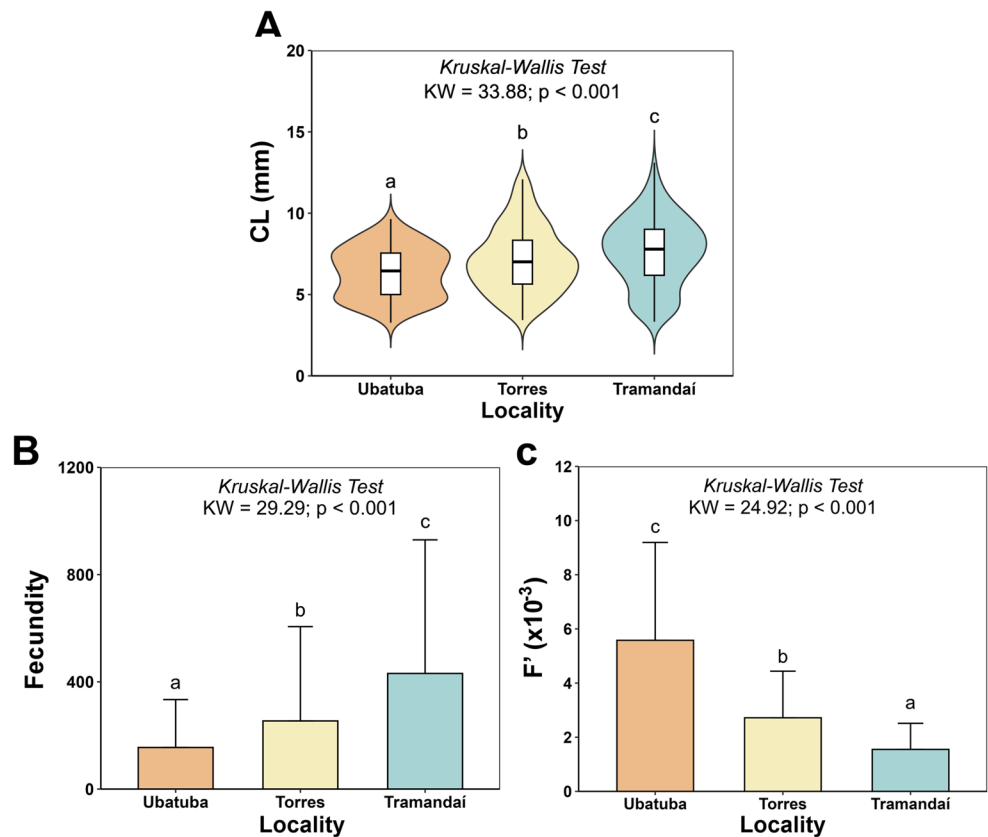
This study evaluates geographic variation in fecundity in *Pachycheles laevidactylus* by separating the effects of female body size from size-independent reproductive output across populations from southern and southeastern Brazil.

As reported in previous studies, ovigerous females of *Pachycheles laevidactylus* from colder regions exhibited larger body sizes and higher absolute fecundity (Camilo and Luppi 2016; Horch and Terossi 2022b; Mosna et al. 2023) than those from Ubatuba, reinforcing the well-established positive relationship between female size and

Table 2 Analysis of covariance (ANCOVA) testing the effects of carapace length ($\ln CL$, log-transformed values) and locality, on absolute fecundity ($\ln NE$, log-transformed values) in *Pachycheles laevidactylus*. Values correspond to log-transformed variables. df =degrees of freedom; MS =mean square; F -value= F -statistic. Bold values indicate statistical significance ($p<0.05$)

Source of Variation	$\ln NE$			
	df	MS	F -value	p -value
$\ln CL$	1	1466.2	2542.1	<0.001
Locality	2	4.7	8.2	<0.001
$\ln CL \times \text{Locality}$	2	0.8	1.4	0.25
Residuals	574	0.6		

Fig. 5 Population and reproductive traits of *Pachycheles laevidactylus* at each locality. **(A)** Carapace length (CL); **(B)** Absolute average fecundity ($F = NE$, number of eggs); and **(C)** Size-normalized fecundity ($F' \times 10^{-3}$), excluding the effect of body size. Boxplots represent the median (horizontal line), interquartile range (box), and $1.5 \times \text{IQR}$ (whiskers). Violin plots indicate kernel density distribution. Bars represent mean values $\pm$ standard error. Distinct letters associated with bars indicate statistically significant differences among localities ($p < 0.05$)



fecundity (Patel et al. 2024). This relationship reflects fundamental growth constraints in decapod crustaceans, in which body size results from the cumulative outcome of successive molting events and ultimately determines the upper limit of reproductive output (Hartnoll 1982). This size-dependent pattern is also consistent with observations in other anomurans, such as *Aegla marginata*, in which fecundity increases significantly with body size as a strategy to maximize reproductive efficiency according to individual growth conditions (Silva et al. 2016). However, this pattern changed drastically after controlling for body size, with Ubatuba showing the highest size-normalized fecundity. This inversion is biologically significant, as it demonstrates that the higher egg production observed in Torres and Tramandaí may be influenced by the size structure of ovigerous females (Pinheiro and Terceiro 2000), masking underlying differences in fecundity between populations.

Reproduction in crustaceans is influenced by multiple abiotic drivers, including temperature (Pinheiro et al. 2017; Horch and Terossi 2022a), photoperiod (Bouchon et al. 1992; Wang et al. 2025), precipitation (Craveiro et al. 2019; Aviz et al. 2024), and, in more terrestrial species, air exposure and humidity (Marin and Tiunov 2023). Latitude integrates much of this environmental variability and is therefore a major source of geographic variation in life-history traits (Bauer 1989; Vergamini and Mantelatto 2008;

Hernández et al. 2012). For *P. laevidactylus*, previous studies have shown that populations from colder regions tend to attain larger sizes and higher absolute fecundity (Ogawa and Rocha 1976; Pinheiro and Fransozo 1995; Horch and Terossi 2022a), a pattern consistent with the temperature-size rule for ectotherms (Frizot et al. 2025). In warmer environments, individuals generally mature earlier and become ovigerous at smaller sizes, whereas in colder environments growth is slower but maturity is reached at larger sizes (Hines 1989).

In this context, the contrasting patterns observed for absolute fecundity (F) and size-normalized fecundity (F') highlight that these metrics capture different biological dimensions. Absolute fecundity reflects total brood production as a function of the size structure of ovigerous females, whereas size-normalized fecundity isolates reproductive production after removing the effect of body size (Hines 1982; Pinheiro and Terceiro 2000; Griffen et al. 2024). Such differences can be interpreted within a life-history framework, in which organisms optimize reproductive output through trade-offs between growth and reproduction, adjusting energy allocation according to local environmental conditions (Hartnoll and Gould 1988). Thus, the observed inversion between southern and southeastern populations emerges only after accounting for size, revealing differences that would otherwise remain obscured.

Temperature is often considered a key driver of the reproductive process in decapod crustaceans (Laptikhovsky 2006). However, reproductive investment involves a trade-off between egg number and egg size, and the present study focuses exclusively on fecundity expressed as egg number. Trade-offs between these traits have been documented in decapod crustaceans, including porcelain crabs, in which variation in fecundity may occur together with changes in egg volume and reproductive output (Hamasaki et al. 2021). Therefore, although the inversion observed here remains valid for the number of eggs normalized by size, its interpretation should be taken with caution, considering the absence of egg size for a general understanding of latitudinal patterns. Even so, the pattern observed here is consistent with previous studies, where lower fecundity is reported in tropical and subtropical regions (Ogawa and Rocha 1976; Pinheiro and Fransozo 1995) and higher fecundity in temperate zones (Horch and Terossi 2022a). Porcellanids generally exhibit low tolerance to elevated temperatures (Stillman and Somero 2000; Stillman 2004), and warmer conditions may shift energy investment toward metabolism and somatic maintenance at the expense of reproduction (Diaz 1980; Pinheiro and Fransozo 1995). Thus, even in species with continuous reproduction, such as *P. laevidactylus*, reproductive peaks tend to occur during colder seasons (Mosna et al. 2023), resulting in a seasonal-continuous reproduction (Pinheiro and Fransozo 2002; Vergamini and Mantelatto 2008). Comparable environmental modulation has been documented for brachyurans such as *Callinectes sapidus*, in which temperature and salinity gradients directly influence growth, reproductive timing, and fecundity, leading to spatially structured population patterns (Marchessaux et al. 2023).

Food availability is another key factor influencing reproduction output in decapod crustaceans, as it determines how energy is allocated between growth and reproduction (Sastri 1983; Conti et al. 2024; Qiao et al. 2024). Along the Brazilian coast, marine primary productivity tends to increase toward temperate regions, such as Torres and Tramandaí, where nutrient availability and phytoplankton production are higher (Chavez et al. 2011), compared to subtropical areas, such as Ubatuba. As a filter-feeding species, *P. laevidactylus* depends largely on plankton and benthic food sources (Zimba et al. 2016; Horch and Terossi 2022b). This greater availability of food resources may contribute to the higher absolute fecundity in southern populations, although it does not necessarily translate into higher size-standardized reproductive allocation.

Interpopulation differences in reproductive allocation are reinforced by the ANCOVA results, which indicate significant effects of body size and locality on fecundity, while the absence of interaction ($\ln CL \times \text{Locality}$) suggests that the

size-fecundity relationship is consistent across populations. This suggests that differences among localities are primarily associated with shifts in intercept (i.e., fecundity level), rather than changes in the scaling relationship itself, indicating conserved allometric scaling among populations. Thus, differences between localities are primarily associated with changes in the intercept, or expected fecundity for a comparable body size, and not with changes in the scaling relationship itself. This result indicates that differences in egg count related to locality remain detectable even after considering female body size, although current data do not allow these differences to be directly attributed to variation in reproductive energy investment.

A second key result of this study is the marked reduction in variability after removing the effect of body size. The coefficient of variation decreased from approximately 114.8–138.2% in absolute fecundity to 60.0–64.3% in F' , corresponding to a reduction of about 50%. This substantial decrease demonstrates that a large proportion of the observed variability in fecundity is attributable to differences in body size among ovigerous females. Thus, F' provides a measure of fecundity that is less size-dependent and more comparable across localities. By reducing the variation associated with female body size, this approach helps to distinguish differences in egg count that are not simply attributable to population size structure. Again, these results should be interpreted with caution, not inferring that the reduced variability is evidence of differences in total reproductive investment, since egg size, energy investment, and other factors were not quantified.

At the same time, an important limitation must be considered: the Ubatuba samples were collected in 1990–1991, whereas the southern populations were sampled in 2018–2019. These datasets were generated independently and were not originally designed for direct comparison. Given that coastal systems may undergo substantial changes over decadal scales, particularly under ongoing climate warming and increasing anthropogenic pressure, the present analysis does not fully disentangle spatial from temporal effects (Vasconcellos et al. 2023). Spatial replication is also a relevant limitation, considering that southeastern Brazil is represented by one locality, while two localities were sampled for southern Brazil. Therefore, the observed differences should be interpreted cautiously as interpopulation patterns, recognizing that some of the variation may also reflect long-term environmental changes (Martinez et al. 2022).

The use of size-normalized fecundity (F') removes the size effect, enabling more consistent comparisons among populations by reducing the influence of population structure (Pinheiro and Terceiro 2000). This approach is conceptually analogous to indices such as Fulton's condition factor (Le Cren 1951; Ricker 1975; Carvalho-Souza et al. 2023), in

which size effects are similarly controlled. The present results reinforce the value of this approach, as both the inversion in fecundity patterns and the reduction in variability became evident only after applying size standardization. More broadly, these findings highlight the importance of incorporating size-corrected metrics in comparative reproductive studies, particularly when evaluating geographic variation.

Overall, the patterns observed here reinforce the idea that reproductive output in brachyuran and anomuran crabs arises from the interaction between growth dynamics and environmental constraints, with organisms adjusting their reproductive strategies through trade-offs that maximize lifetime reproductive success across different ecological conditions (Hartnoll 1982).

Future Directions

Future research should integrate egg size and offspring quality metrics to provide a more comprehensive evaluation of reproductive investment, particularly in relation to environmental gradients such as temperature and productivity.

In addition, studies conducted under standardized temporal frameworks are needed to disentangle spatial from long-term environmental effects, especially in the context of ongoing climate change.

Experimental and physiological approaches may also help clarify how energy is partitioned between growth and reproduction under contrasting environmental conditions, thereby improving our understanding of the mechanisms underlying reproductive plasticity in porcellanid crabs. The authors declare that they have no financial, professional, or personal conflicts of interest that could have inappropriately influenced the content of this work.

Conclusions

This study demonstrates that apparent geographic patterns in the fecundity of *Pachycheles laevidactylus* are strongly influenced by population size structure. While absolute fecundity increased toward southern localities, this pattern reversed after controlling for body size, revealing that the Ubatuba population exhibited higher size-normalized fecundity than the two southern localities.

These findings indicate that differences in fecundity among populations are not solely driven by environmental gradients but are largely mediated by variation in the size distribution of ovigerous females. As a result, analyses

based exclusively on absolute fecundity may lead to misleading interpretations of reproductive patterns across geographic scales.

The marked reduction in variability following size normalization further reinforces the importance of accounting for body size when comparing reproductive traits. This approach provides a more consistent and biologically meaningful assessment of reproductive allocation.

Overall, this study highlights that population structure can obscure underlying reproductive patterns and demonstrates that size-normalized metrics provide a more robust framework for evaluating interpopulation variation in decapod crustaceans.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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References

- Aviz D, Petracco M, Carmona PA, Santos CRM (2024) Influence of environmental patterns on the population structure and secondary production of the fiddler crab *Uca maracoani* (Latreille) in the Amazon mangroves. *Mar Env Res* 199:106603. <https://doi.org/10.1016/j.marenvres.2024.106603>
- Bauer RT (1989) Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a tropical seagrass meadow. *J Exp Mar Biol Ecol* 127:175–187
- Boschi EE (1963) Sobre dos especies de *Pachycheles* de la Argentina (Crustacea, Anomura). *Neotropica* 9:31–37
- Bouchon D, Souty-Grosset C, Mocquard JP, Chentoufi A, Juchault P (1992) Photoperiodism and seasonal breeding in aquatic and terrestrial Eumalacostraca. *Invertebr Reprod Dev* 22:203–212. <https://doi.org/10.1080/07924259.1992.9672273>
- Brante A, Cifuentes S, Otto-Portner H, Arntz W, Fernández F (2004) Latitudinal comparisons of reproductive traits in five Brachyuran species along the Chilean coast. *Rev Chil Hist Nat* 77:15–27
- Camiolo MD, Luppi TA (2016) Hábitat y historia de vida de *Pachycheles laevidactylus* (Crustacea, Anomura, Porcellanidae) en el intermareal rocoso de Mar del Plata, Argentina. *Iheringia, Sér. Zool.* 106:e2016015. <https://doi.org/10.1590/1678-4766e2016015>
- Carvalho-Souza GF, Medeiros DV, Silva RA, González-Ortegón E (2023) Width/length–weight relationships and condition factor of seven decapod crustaceans in a Brazilian tropical estuary. *Reg Stud Mar Sci* 60:102880. <https://doi.org/10.1016/j.rsma.2023.102880>
- Chavez FP, Messié M, Pennington JT (2011) Marine primary production in relation to climate variability and change. *Annu Rev Mar Sci* 3:227–260. <https://doi.org/10.1146/annurev.marine.010908.163917>
- Clarke A (1987) Temperature, latitude and reproductive effort. *Mar Ecol Prog Ser* 38:89–99. <https://doi.org/10.3354/meps038089>
- Conti F, Pulido-Rodríguez LF, Chemello G, Cattaneo N, Resente M, Parisi G, Olivetto I, Zaranionello M (2024) The role of dietary fatty acids in modulating blue crab (*Callinectes sapidus*) physiology, reproduction, and quality traits in captivity. *Animals (Basel)* 14:3304. <https://doi.org/10.3390/ani14223304>
- Craveiro C, Peixoto S, Silva EF, Eduardo LN, Lira AS, Castro-Neto H, Frédou FL, Soares R (2019) Reproductive dynamics of the white shrimp *Litopenaeus schmitti* (Burkenroad 1936) in a beach seine fishery in northeastern Brazil. *Invertebr Reprod Dev* 63:111–121. <https://doi.org/10.1080/07924259.2019.1575923>
- Diaz H (1980) The mole crab *Emerita talpoida* (Say): a case of changing life history pattern. *Ecol Monogr* 50:437–456
- Ferreira LAA, Melo GAS (2016) Porcelain crabs from Brazil (Crustacea: Decapoda: Anomura: Porcellanidae). *Zootaxa* 4092:175–194. <https://doi.org/10.11646/zootaxa.4092.2.2>
- Frizot N, Bec A, Koussoroplis AM (2025) Ectotherm size- and age-at-maturity in a warmer, variable and resource-poor world. *Ecol Lett* 28(12):e70273. <https://doi.org/10.1111/ele.70273>
- González JA, Pajuelo JG, Triay-Portella R, Ruiz-Díaz R, Delgado J, Góis AR, Martins A (2016) Latitudinal patterns in the life-history traits of three isolated Atlantic populations of the deep-water shrimp *Plesionika edwardsii* (Decapoda, Pandalidae). *Deep-Sea Res Part I Oceanogr Res Pap* 117:28–38. <https://doi.org/10.1016/j.dsr.2016.09.004>
- Griffen BD, Bolander M, Fletcher LS (2024) Factors influencing variation in reproduction in invasive species: a case study of the Asian shore crab *Hemigrapsus sanguineus*. *Biol Invasions* 26:3243–3255. <https://doi.org/10.1007/s10530-024-03382-7>
- Haig J (1960) The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. *Allan Hancock Pac Exped* 24:1–440
- Hamasaki K, Ishii M, Dan S (2021) Seasonal variability in fecundity and egg size in the porcellanid crab *Petrolisthes japonicus* (Decapoda: Anomura: Porcellanidae). *Crustacean Res* 50:17–27. https://doi.org/10.18353/crustacea.50.0_17
- Hamasaki K, Su Z, Dan S (2025) Effects of cheliped autotomy on female reproductive performance in the porcellanid crab *Petrolisthes japonicus* (De Haan, 1849) (Decapoda: Anomura: Porcellanidae) under laboratory conditions. *J Crust Biol* 45:ruaf006. <https://doi.org/10.1093/jcibi/ruaf006>
- Hartnoll RG (1982) Growth. In: Bliss, D.E. (Ed.), *The Biology of Crustacea, Embryology, Morphology, and Genetics*. Academic Press, New York, 2: 111–196
- Hartnoll RG, Gould P (1988) Brachyuran life history strategies and the optimisation of egg production. *Symp Zool Soc Lond* 59:1–9
- Hernández P, Villegas-Jiménez E, Villalobos-Rojas F, Wehrtmann IS (2012) Reproductive biology of the ghost shrimp *Lepidophthalmus bocourti* (A. Milne-Edwards, 1870) (Decapoda: Axiidea: Callianassidae): a tropical species with a seasonal reproduction. *Mar Biol Res* 8:635–643. <https://doi.org/10.1080/17451000.2011.653369>
- Hines AH (1982) Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar Biol* 69:309–320
- Hines AH (1989) Geographic variation in size at maturity in brachyuran crabs. *Bull Mar Sci* 45(2):356–368
- Horch A, Terossi M (2022a) Egg production in the porcellanid crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda: Anomura: Porcellanidae) in southern Brazil. *J Crustac Biol* 42(1):ruac020. <https://doi.org/10.1093/jcibi/ruac020>
- Horch A, Terossi M (2022b) Population structure, maturity and relative growth of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda, Porcellanidae) in a temperate zone. *Mar Ecol* 42(1):e12693. <https://doi.org/10.1111/maec.12693>
- Jaramillo E, Dugan JE, Hubbard DM, Contreras H, Duarte C, Acuña E, Schoeman DS (2017) Macroscale patterns in body size of intertidal crustaceans provide insights on climate change effects. *PLoS One* 12(5):e0177116. <https://doi.org/10.1371/journal.pone.0177116>
- Johnson DS, Crowley C, Longmire K, Nelson J, Williams B, Wittyngham S (2019) The fiddler crab, *Minuca pugnax*, follows Bergmann's rule. *Ecol Evol* 9(24):14489–14497. <https://doi.org/10.1002/ece3.5883>
- Laptikhovskiy V (2006) Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Mar Ecol* 27:7–14. <https://doi.org/10.1111/j.1439-0485.2006.00077.x>
- Lardies M, Castilla J (2001) Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. *Mar Biol* 139:1125–1133. <https://doi.org/10.1007/s002270100661>
- Le Cren ED (1951) The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J Anim Ecol* 20:201–219
- Leone IC, Mantelatto FL (2015) Maternal investment in egg production: Substrate- and population-specific effects on offspring performance of the symbiotic crab *Pachycheles monilifer* (Anomura: Porcellanidae). *J Exp Mar Biol Eco* 464:18–25. <https://doi.org/10.1016/j.jembe.2014.12.002>
- Marchessaux G, Gjoni V, Sarà G (2023) Environmental drivers of size-based population structure, sexual maturity and fecundity: a study of the invasive blue crab *Callinectes sapidus* (Rathbun, 1896) in the Mediterranean Sea. *PLoS One* 18:e0289611. <https://doi.org/10.1371/journal.pone.0289611>
- Marin IN, Tiunov AV (2023) Terrestrial crustaceans (Arthropoda, Crustacea): taxonomic diversity, terrestrial adaptations, and ecological functions. *ZK* 1169:95–162. <https://doi.org/10.3897/zook.1169.97812>
- Martínez AS, Underwood T, Christofolletti RA, Pardo A, Fortuna MA, Marcelo-Silva J, Morais GC, Lana PC (2022) Reviewing the effects of contamination on the biota of Brazilian coastal

- ecosystems: Scientific challenges for a developing country in a changing world. *Sci Tot Env* 803:150097. <https://doi.org/10.1016/j.scitotenv.2021.150097>
- Mosna EED, João MCA, Hernáez P, Ferreira LAA, Noori A, Pinheiro MAA (2023) Population biology of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Anomura: Porcellanidae) in the Southwestern Atlantic. *Invertebr Reprod Dev* 67(3–4):79–91. <https://doi.org/10.1080/07924259.2023.2277950>
- Ogawa E, Rocha C (1976) Sobre a fecundidade de crustáceos decápodos marinhos do estado do Ceará. *Brasil Arq Ciên Mar* 16(2):101–104
- Patel N, Patel KJ, Patel A, Ali D, Alarifi S, Tivedi JN (2024) Unveiling the population structure and breeding patterns of *Petrolisthes bosonii* (Audouin, 1826) a common intertidal inhabitant of Shivrajpur, Saurashtra Coast, Gujarat. *Front Mar Sci* 11:1438129. <https://doi.org/10.3389/fmars.2024.1438129>
- Pinheiro MAA, Fransozo A (1995) Fecundidade de *Pachycheles haigae* Rodrigues da Costa, 1960 (Crustacea, Anomura, Porcellanidae) em Ubatuba (SP). *Brasil Rev Bras Biol* 55(4):623–631
- Pinheiro MAA, Fransozo A (2002) Reproduction of the speckled swimming crab *Arenaeus cribrarius* (Brachyura: Portunidae) on the Brazilian coast near 23°30' S. *J Crustac Biol* 22:416–428
- Pinheiro MAA, Terceiro OL (2000) Fecundity and reproductive output of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Brachyura, Portunidae). *Crustaceana* 73(9):1121–1137
- Pinheiro MAA, João MCA, Leme MHA, Matsunaga AMF, Rio JPP, Hernáez P (2017) Insights of the life history in the porcellanid crab *Petrolisthes armatus* (Gibbes, 1850) (Crustacea: Anomura: Porcellanidae) from the Southwestern Atlantic coast. *Invertebr Reprod Dev* 61(2):78–89. <https://doi.org/10.1080/07924259.2017.1285818>
- Pinheiro MMA, Souza FVB, Boos H, Duarte LFPA (2022) Cytotoxicity, genotoxicity, and impact on populations of the mangrove sentinel species, *Ucides cordatus* (Linnaeus, 1763) (Brachyura, Ocypodidae) after an environmental disaster at Cubatão, São Paulo, Brazil. *Nauplius* 30:e2022025. <https://doi.org/10.1590/2358-2936e2022025>
- Qiao H, Jiang S, Fu H (2024) Molecular advance on reproduction and fertility of aquatic animals. *IJMS* 25:11610. <https://doi.org/10.3390/ijms252111610>
- R Core Team (2026) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191:1–382
- Sastry AN (1983) Ecological aspects of reproduction. In: Vernberg FJ, Vernberg WB (eds) *The Biology of Crustacea. Environmental adaptations*, vol 8. Academic, New York, pp 179–270
- Silva AR, Wolf MR, Castilho AL (2016) Reproduction, growth and longevity of the endemic South American crab *Aegla marginata* (Decapoda: Anomura: Aegliidae). *Invert Reprod Dev* 60:1–15. <https://doi.org/10.1080/07924259.2016.1140088>
- Stillman JH (2004) A comparative analysis of plasticity of thermal limits in porcelain crabs across latitudinal and intertidal zone clines. *Int Congr Ser* 1275:267–274
- Stillman JH, Somero GN (2000) A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus *Petrolisthes*: influences of latitude, vertical zonation, acclimation, and phylogeny. *Physiol Biochem Zool* 73:200–208
- Vasconcellos FC, Souza JN, Dereczynsky CP, Luiz-Silva FP, Parise CK (2023) Warming trends of southwestern Atlantic SST and the summer's warmest SST's impact on South American climate. *Int J Climatol* 43(12):5604–5619. <https://doi.org/10.1002/joc.8163>
- Veloso VG, Melo GAS (1993) Taxonomia e distribuição da família Porcellanidae (Crustacea, Decapoda, Anomura) no litoral brasileiro. *Iheringia Sér Zool* 75:171–186
- Vergamini FG, Mantelatto FL (2008) Continuous reproduction and recruitment in the narrowback mud crab *Panopeus americanus* (Brachyura, Panopeidae) in a remnant human-impacted mangrove area. *Invertebr Reprod Dev* 51:1–10. <https://doi.org/10.1080/07924259.2008.9652251>
- Wang L, Hu M, Cai L, Wang Y, Guan T, Zhu C, Wang H, Wang G, Li J (2025) Effects of light intensity and light duration on growth performance and ovarian development in red swamp crayfish *Procambarus clarkii* (Girard, 1852). *Aquacult Int* 33:54. <https://doi.org/10.1007/s10499-024-01748-1>
- Wegner T (2010) *Applied Business Statistics: Methods and Excel Based Applications*, 2nd ed. Juta and Co. Ltd., Cape Town, p 625
- Werdinger B, Hiller A, Lemaitre R (2003) Geographic and depth distributional patterns of western Atlantic Porcellanidae (Crustacea: Decapoda: Anomura), with an updated list of species. *Mem Mus Vic* 60(1):79–85
- WoRMS – World Register of Marine Species (2026) Porcellanidae Haworth, 1825. Accessed at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106734>. Accessed on: April 16th, 2026
- Zar JH (1999) *Biostatistical Analysis*, 4th ed. Prentice Hall, New York
- Zimba PV, Hill EM, Withers K (2016) Benthic microalgae serve as the major food resource for porcelain crabs (*Petrolisthes* spp.) in oyster reefs: Digestive track content and pigment evidence. *J Exp Mar Biol Ecol* 483:53–58. <https://doi.org/10.1016/j.jembe.2016.06.005>

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