



Reproductive potential of the endangered land crab, *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Brachyura: Gecarcinidae), from Trindade Island, Brazil

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ABSTRACT

An analysis of reproductive potential can elucidate significant aspects of the population biology and evolution of brachyuran crabs, providing a crucial baseline for conservation efforts concerning endangered species. *Johngarthia lagostoma* is an endemic species to Atlantic Oceanic islands (Rocas Atoll, Fernando de Noronha, Ascension, and Trindade), and it is classified as endangered (EN) in Brazilian territory according to IUCN criteria. Until now, the reproductive potential of this species has only been described for the Ascension Island population. Therefore, we assessed the reproductive effort and fecundity of *J. lagostoma* on Trindade Island. A total of 43 ovigerous females in the final stage of embryonic development were analyzed. Their egg masses were removed, weighed, and counted using a volumetric method. The carapace width ranged from 55.3 to 100.1 mm (mean \pm standard deviation: 75.2 ± 13.1 mm). It exhibited a good fit and positive correlation with the egg weight and fecundity data but a poor fit and negative correlation with reproductive effort. The contrasting results of fecundity ($82,938 \pm 43,673$ eggs) and reproductive effort (10.5 ± 1.5 %) recorded for *J. lagostoma* reveal a well-established population on Trindade Island compared to Ascension Island. These observations provide valuable information for proposing more effective management strategies for this endangered species across these Atlantic oceanic islands.

KEYWORDS

Conservation, Decapoda, fecundity, oceanic island, reproductive effort.

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INTRODUCTION

Reproductive potential refers to the capacity of a population of a species to reproduce under optimal environmental conditions (Ramírez-Llodra, 2002). This parameter is closely linked to fecundity, which measures the number of eggs produced per spawning or life cycle (Sastry, 1983). In decapod crustaceans, reproductive parameters like these are commonly estimated using mathematical models, to characterize possible patterns between different groups, to better understand the dynamics and evolution of their populations (Sastry, 1983). Consequently, such evaluations are crucial to support conservation efforts across diverse taxonomic groups (Ramírez-Llodra, 2002; González-Pisani and López-Greco, 2014).

The infraorder Brachyura is of great ecological importance in continental and island coastal environments (Alexander, 1979; Perger et al., 2013). Within the group, the family Gecarcinidae MacLeay, 1838 shows the highest degree of adaptation to a terrestrial lifestyle (Wolfe et al., 2022; Marin and Tiunov, 2023). These crabs are the most abundant arthropods on oceanic islands, playing a key role in nutrient cycling (Liu and Jeng, 2007). During reproduction, they exhibit distinctive migrations from vegetated areas to sandy beaches, often covering distances exceeding 5 km (see Hicks, 1985).

There are records of two gecarcinid species in Brazilian territory (Melo, 1996): 1) *Cardisoma guanhumi* Latreille, 1825, which has a broad coastal distribution across the entire Brazilian mainland, from the state of Ceará to São Paulo; and 2) *Johngarthia lagostoma* (H. Milne Edwards, 1837), found only on four oceanic islands worldwide, three of which are in Brazil (Rocas Atoll, Fernando de Noronha, and Trindade islands), with the fourth belonging to the United Kingdom (Ascension Island). Due to their extremely limited distribution, little is known about the biology of these species. Studies on *J. lagostoma* conducted by Hartnoll et al. (2006; 2009; 2010) on Ascension Island have associated its reproductive season with months

of high rainfall (January to May). Additionally, Rodríguez-Rey et al. (2016) evaluated global populations of *J. lagostoma*, confirming three distinct genetic units: one represented by Rocas Atoll with Fernando de Noronha Island, another by Ascension Island, and a third (more isolated) by Trindade Island. Copulatory behavior, size at sexual maturity, and population structure have been reported for Trindade Island (João et al., 2021; 2022; 2023a). Meanwhile, Hartnoll et al. (2010) established the reproductive potential of *J. lagostoma* for Ascension Island, determined by average fecundity and reproductive effort. Some of these reproductive parameters have been previously evaluated for other gecarcinids of the genera *Cardisoma* Berthold, 1827, *Epigrapsus* Heller, 1862, *Gecarcinus* Leach, 1814, and *Gecarcoidea* H. Milne Edwards, 1837 (see Gifford, 1962; Liu and Jeng, 2005; Hartnoll et al., 2007; Liu and Jeng, 2007; Vásquez-Lopez and Ramírez-Pérez, 2015). *Johngarthia lagostoma*, studied by Hartnoll et al. (2010) solely on Ascension Island, also falls within this group.

According to IUCN criteria, *J. lagostoma* is categorized as ‘Endangered’ (EN) in Brazil, due to its restricted geographic distribution and growing anthropogenic activity on some oceanic islands (Pinheiro et al., 2016; MMA, 2022). Of the three Brazilian islands where it is found, the population on Trindade Island deserves particular attention due to its designation as a pristine environment with minimal anthropogenic impacts (Hartnoll et al., 2006; João et al., 2021), as well as its genetic isolation, as previously mentioned. Therefore, data on *J. lagostoma* on Trindade Island (Pinheiro et al., 2016; João et al., 2021; 2022; 2023a; 2023b), can serve as a baseline for comparisons with Ascension Island (Hartnoll et al., 2006; 2009; 2010), and other oceanic islands that lack studies on this species.

This study assesses the reproductive potential of *J. lagostoma* on Trindade Island (Brazil), one of the species’ few strongholds worldwide, based on estimates of fecundity and reproductive effort. We hypothesize a positive relationship between these metrics and the size of females on Trindade Island.

MATERIALS AND METHODS

Study area and ovigerous female sampling

Individuals of *Johngarthia lagostoma* were sampled on Trindade Island (20°51'S 29°30.8'W), a volcanic island in the Atlantic Ocean, approximately 1,200 km off the Brazilian coast (Fig. 1A, B). The island has a small size (~13 km²) and is part of the

submarine chain Vitória-Trindade (Fig. 1C). It is inhabited solely by the Brazilian navy and rotating research personnel (about 40 people). *Johngarthia lagostoma* individuals are distributed across the island, with resident sites in hills up to 600 m altitude and migrating to reproductive sites on sandy beaches, where reproduction occurs (João et al., 2023a).

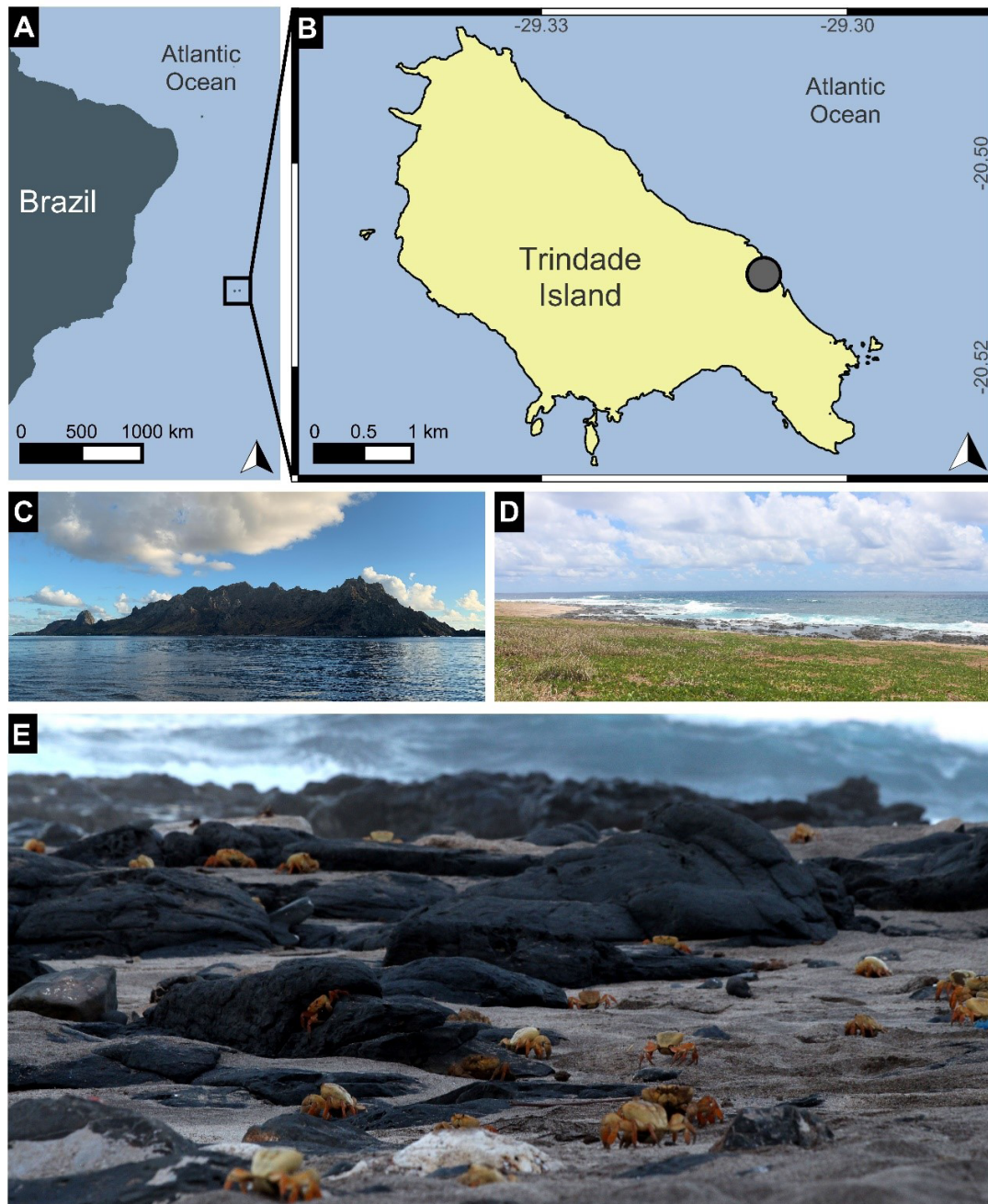


Figure 1. Geographic location of the study area showing Trindade Island and Andradas Beach. **A**, Southeast Brazilian coast showing the distance between the islands from the Brazil coast; **B**, general view of Trindade Island; Andradas Beach (grey dot); **C**, general view of Trindade Island; **D**, study area view showing vegetation on Andradas Beach; **E**, *Johngarthia lagostoma* ovigerous females waiting on Andradas Beach for larval release.

Ovigerous females of *J. lagostoma* were manually captured at night while walking in the sandhill vegetation or sheltering in burrows on Andradas beach (Fig. 1D, E). Sampling occurred in December 2019, during the reproductive season, confirming records by Hartnoll et al. (2010) for Ascension Island (December to May). To ensure representativeness across ontogeny, a minimum of three ovigerous females were collected per body size class (10 mm carapace width, CW), with sizes ranging from 50 to 110 mm CW. The minimum size class corresponded to the smallest ovigerous female of *J. lagostoma* recorded on Trindade Island (50.3 mm CW, according to João et al., 2022). The captured ovigerous females were carefully cleaned, individually placed in plastic bags to prevent egg loss, and subject to cryo-anesthesia for further laboratory processing.

Ovigerous female processing

In the laboratory, each ovigerous specimen underwent biometric analysis, with measurements of body size (CW, carapace width) using a mechanical caliper (0.05 mm), and weight (FW, wet female with eggs) using a digital scale (0.01 g). Additionally, ten eggs from each ovigerous mass were evaluated for embryonic stage under a microscope, following characteristics based on yolk-embryo proportion, color, and internal structures, as described by Pinheiro and Hattori (2003). Thus, the eggs were categorized into three embryonic stages (initial, intermediate, or final) based on their lateral view as follows: 1) Initial (stages 1–4), where the egg is fully divided with yolk droplets of similar size, and the embryo occupies less than 1/3 of the egg volume. The ocular region may be delimited but is not yet pigmented; 2) Intermediate (stages 5, 6), with yolk occupying approximately half of the egg volume. The ocular region is oval, with black pigmentation in the central area; and 3) Final (stages 7, 8), where the embryo occupies more than 3/4 of the egg volume, with six abdominal somites and a differentiated telson.

The egg mass from each female was removed by cutting the pleopods with scissors at the insertion with the abdominal somite. For the analyzes of

fecundity and reproductive effort, only eggs in the final stage were used, to avoid possible error related to different embryonic stages. Therefore, these final stage eggs were removed from the pleopods using fine-tip tweezers and distilled water. Finally, the wet weight without eggs was recorded for each ovigerous female. Individuals with perceptible damage to the egg mass or malformations in the abdomen or pleopods were excluded from subsequent analytical steps.

Reproductive potential analysis

The difference between the wet weight of females with eggs (FW) and without eggs was recorded as the wet egg weight (EW), to estimate reproductive effort (RE), defined as the percentage of EW relative to FW.

With all variables obtained, the reproductive effort (expressed as a percentage) was calculated for each ovigerous female using the equation $RE = (EW / FW) \times 100$, as described by Clarke et al. (1991). To determine the fecundity of each female, the number of eggs (NE) was quantified using the volumetric method (see João and Pinheiro, 2019), which is an alternative procedure for estimating fecundity through the gravimetric method (Tuck et al., 2000).

Separately, the egg mass of each female was placed in a plastic container with water (5 L) under constant aeration to homogenize the eggs in the liquid. We obtained five subsamples (2 mL) of eggs for each female using a Stempel pipette and calculated the mean between these subsamples. NE was then calculated by extrapolating the number of eggs counted in the subsamples (2 mL) to the total volume of the container (5 L) using a simple rule of proportion. The coefficient of variation (CV%) was calculated using the mean and standard deviation of the number of eggs counted for each female. Values greater than 15% were recounted or excluded from the analysis, thereby minimizing possible errors resulting from dehydration and counting (see Pinheiro and Terceiro, 2000).

The dependent variables (NE, EW, and RE) were correlated with size (CW) using the Spearman correlation coefficient (ρ) for each biometric

relationship due to the curvilinear tendency of these reproductive parameters (Hines, 1982; Pinheiro and Terceiro, 2000). The empirical points of each of these relationships (NE×CW, EW×CW, and RE×CW) were subjected to regression analysis using the power function ($Y = aX^b$), with a good fit defined by a determination coefficient (R^2 , expressed as a percentage) of $\geq 70\%$ (João and Pinheiro, 2019). All statistical analyses were performed using R version 4.2.1 (R Core Team, 2022).

RESULTS

A total of 75 ovigerous females of *Johngarthia lagostoma* were collected in the field (Fig. 2), with sizes ranging from 50.4 to 100.1 mm CW (mean \pm standard deviation: 76.4 ± 12.0 mm), categorized into size classes between 50–110 mm CW, with the highest abundance of ovigerous females recorded at 70–80 mm CW ($n = 23$; 30.6%) (Fig. 2).

Forty-three ovigerous females in the final embryonic phase were analyzed to minimize errors related to different embryonic stages. However, for the fecundity analysis, 42 specimens were used,

with the exclusion of one spurious point, with sizes ranging from 55.3 to 100.1 mm CW (75.2 ± 13.1 mm). Females exhibited egg mass weights (EW) ranging from 6.0 to 30.3 g (15.8 ± 5.9 g), corresponding to 7.3 to 14.2% ($10.5 \pm 1.5\%$) of female's wet weight, considered the reproductive effort of this species. These dependent variables showed a significant Spearman correlation with size (CW), with a positive correlation to EW ($\rho = 0.92$; $P < 0.001$) and a negative correlation to RE ($\rho = -0.55$; $P < 0.001$). The relationship between EW and CW exhibited a good fit described by the equation $EW = 0.0011 \cdot CW^{2.21}$ ($R^2 = 85.6\%$; $n = 43$) (Fig. 3A), whereas for the RE \times CW relationship, the equation displayed a poor fit to empirical points ($RE = 70.65 \cdot CW^{-0.44}$; $R^2 = 26.4\%$; $n = 43$) (Fig. 3B).

The number of eggs per female ranged from 22,500 to 177,500 eggs ($82,938 \pm 43,673$ eggs). Finally, the empirical points of the NE \times CW relationship exhibited a strong positive correlation ($\rho = 0.86$; $P < 0.001$) between these variables, indicating an increase in fecundity as a function of size, described by the power function $NE = 0.45 \cdot CW^{2.78}$ ($R^2 = 73.9\%$; $n = 42$) (Fig. 4).

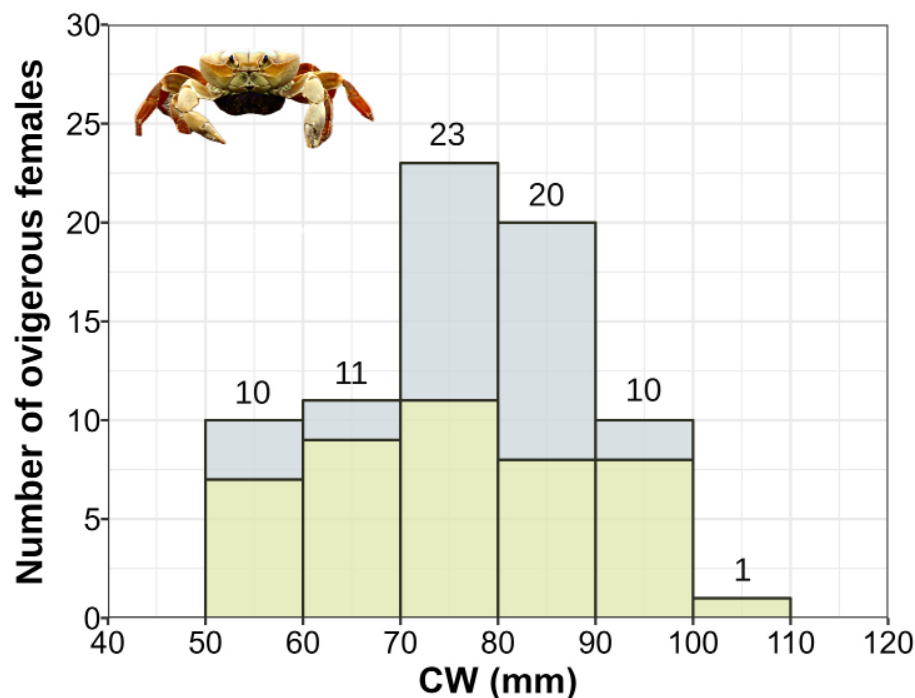


Figure 2. Size-frequency histogram of *Johngarthia lagostoma* ovigerous females by size class (CW, carapace width), with ovigerous females collected used (yellow bars) and not used (gray bars) in the reproductive potential analysis, respectively. Values at the top of each bar indicate the number of individuals in each size class.

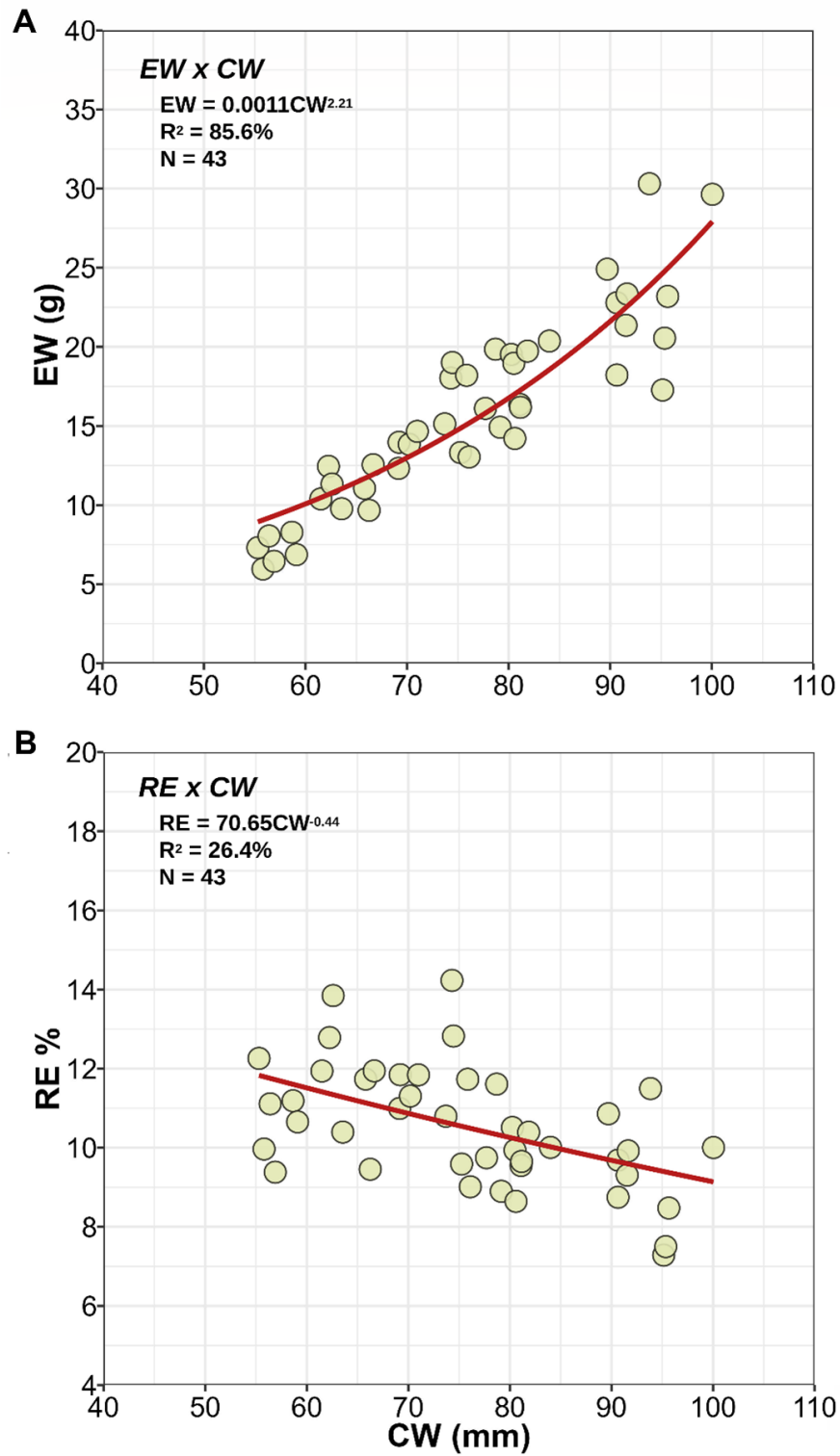


Figure 3. Relationships between egg mass weight (EW, **A**) and reproductive effort (RE %, **B**) as a function of carapace width (CW, mm) of *Johngarthia lagostoma* ovigerous females, from Trindade Island (Brazil).

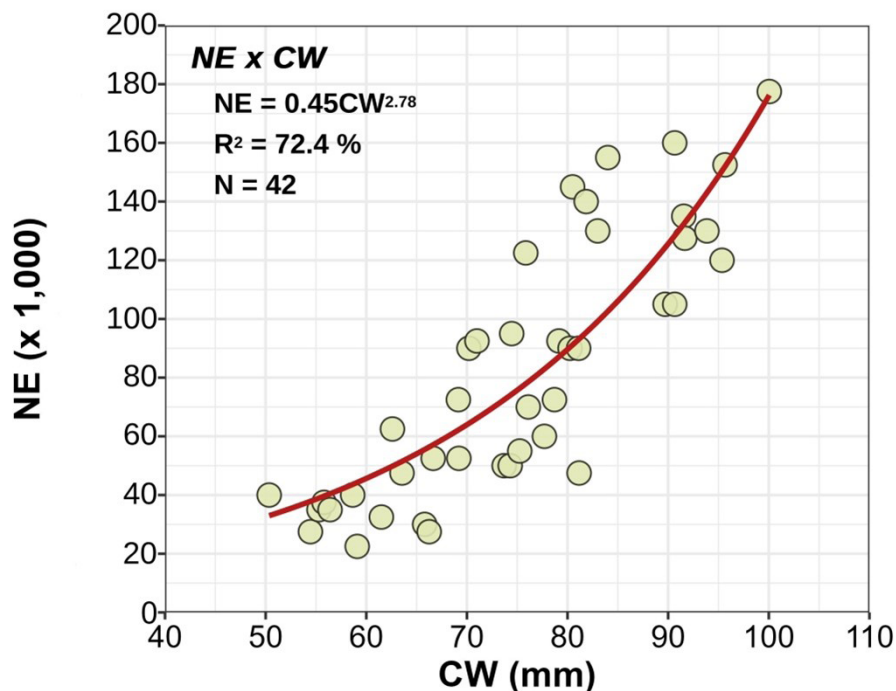


Figure 4. Relationship between number of eggs (NE) and carapace width (CW) of *Johngarthia lagostoma* from Trindade Island (Brazil).

DISCUSSION

The estimate of reproductive potential is a parameter that allows the inspection and monitoring of island crab populations, based on the observation of their reproductive health, which becomes relevant especially for endangered species. In our study of *J. lagostoma*, we confirmed an increase in fecundity in correlation with body size of females from Trindade Island. However, we noted an inverse pattern in reproductive effort, which decreased in larger ovigerous females, in addition to a poor adjustment of the empirical points. A notable aspect of the Trindade Island population of this species is the robustness of our findings, supported by substantial sample sizes of ovigerous females ($n = 43$) covering a wide range of sizes (55.3 to 100.1 mm CW). Consequently, the models we developed for fecundity and reproductive effort in *J. lagostoma* are fundamental as foundational data for estimating population size, aiding in contrasting with populations on other islands where the species is distributed.

Most studies on reproductive potential in pleocyemate crustaceans rely on ovigerous females in the early stages (Hines, 1982) of egg development,

before demarcation and pigmentation of ocular areas (see Pinheiro and Hattori, 2002; 2003), to minimize potential errors in estimating reproductive metrics caused by egg loss during embryonic development due to abrasion, mortality, or related processes (Pinheiro and Terceiro, 2000; González-Pisani and López-Greco, 2014; Shields, 2022). However, both our study and one conducted at Ascension Island by Hartnoll et al. (2010) encountered a scarcity of *J. lagostoma* ovigerous females in the early stages of embryonic development. Similar occurrences were noted in other gecarcinid species (Tab. 1), where ovigerous females in early embryonic stages were rarely found in the field [e.g., *Gecarcinus ruricola* (Linnaeus, 1758), according to Hartnoll et al., 2007; and *Epigrapsus notatus* (Heller, 1865), studied by Liu and Jeng, 2005]. Moreover, some gecarcinid species (e.g., *E. notatus* and *Gecarcoidea lalandii* H. Milne Edwards, 1837) were exclusively observed within the beach surf zone, where they typically remain until their eggs hatch and disperse into the ocean (Liu and Jeng, 2005; Liu and Jeng, 2007).

Considering the life history of several species, a more significant energetic investment in the reproductive process post-sexual maturity onset in terrestrial female crabs is expected compared to the growth

Table 1. Summary of body size (CW, carapace width), fecundity (NE, number of eggs) and reproductive effort (RE) in Gecarcinidae species with a focus on the female ovigerous stage (I, initial; IN, intermediate; and F, final), number of individuals used in the studies (N) and summary of carapace width (mm), reproductive effort (%) and fecundity (number of eggs per female). Where: ~, estimated approximate values; *, fertility-based studies, using number of larvae as fecundity; Min-Max, interval between minimum and maximum values; na, not available information; sd, standard deviation; and superscript number, cited works included in table footnote.

Species	EmbryoPhase	N	CW (mm)		NE (x 1.000)		RE (%)	
			Min – Max	Mean ± SD	Min – Max	Mean ± sd	Min – Max	Mean ± sd
<i>Cardisoma crassum</i> ¹	na	34	52.3 – 84.7	81.2 ± 1.7	174 – 867	501 ± 269	6.1 – 17.3	12.0 ± 4.7
<i>Cardisoma guanhumii</i> ²	F	7	na	na	na	na	na	11.9 ± 2.2
<i>Epigrapsus notatus</i> ³	F	36	16.9 – 34.8	27.0 ± 3.9	12 – 58	~ 35 ± na *	na	na
<i>Gecarcinus ruricola</i> ⁴	F	55	51.3 – 90.0	70.0 ± na	18 – 213	115 ± na	1.7 ± 9.8	5.0 ± na
<i>Gecarcoidea lalandii</i> ⁵	F	23	~ 47.0 – 70.0	~ 58.5 ± na	70 – 210	~ 140 ± na	na	na
<i>Johngarthia lagostoma</i> ⁶	I+IN+F	8	81.0 – 104.0	94.3 ± 7.1	35 – 109	72 ± 25	4.2 – 15.1	9.0 ± 3.6
<i>Johngarthia lagostoma</i> ⁷	F	44	50.4 – 100.1	75.2 ± 13.1	22 – 178	83 ± 44	7.3 – 19.6	10.7 ± 2.0

Citations: 1 Vázquez-López and Ramírez-Pérez (2015); 2 Gifford (1962); 3 Liu and Jeng (2005); 4 Hartnoll et al. (2007); 5 Liu and Jeng (2007); 6 Hartnoll et al. (2010); 7 Present study.

phase. Furthermore, larger females are anticipated to exhibit higher energetic investments than smaller ones (Willians, 1966; Calow, 1979; Hines, 1982; Sastry, 1983; Hartnoll et al., 2007; João and Pinheiro, 2019). Additionally, models adjusted based on measures of reproductive potential (e.g., number of eggs/larvae, reproductive effort, and others) are anticipated to positively correlate with size (Hines, 1982; Sainte-Marie, 1993; López-Greco et al., 2000), with better fits using curvilinear models (see Pinheiro and Terceiro, 2000; Hamasaki et al., 2006; Rameshbabu et al., 2006; Rasheed and Mustaquim, 2010).

Generally, the average percentage of reproductive effort (RE%) in females of marine pleocyemate crustaceans is approximately 10% (Hines, 1982; González-Pisani and López-Greco, 2014), a figure akin to land crabs, averaging 9.7% for species studied thus far (Tab. 1) (Gifford, 1962; Hartnoll et al., 2007; Hartnoll et al., 2010; Vázquez-López and Ramírez-Pérez, 2015). However, *G. ruricola* appears to deviate from this norm, with an estimated reproductive effort corresponding to half of this percentage (5%). This reduced RE may be attributed to the dry egg weight relative to the wet body weight of females (see Hartnoll et al., 2007). Similar observations were made by Hartnoll et al. (2010) regarding *J. lagostoma* on Ascension Island, with estimates based on dry and wet eggs resulting in values of 5.4% and 8.9%, respectively. These data underscore the importance of using wet measurements as

the standard for estimating reproductive effort, avoiding problems associated with dehydration, and preferably employing females with eggs at the same embryonic stage to standardize the analytical method and avoid future comparative issues.

Studies conducted with brachyuran crustaceans have consistently shown a lower percentage of reproductive investment in terrestrial species compared to marine species (Hartnoll et al., 2007; 2010). Hartnoll et al. (2010) proposed two hypotheses to explain this phenomenon in land crabs: (1) a preference for senescent plant material with poor nutritional quality, resulting in reduced energy available for gonadal development (Nordhaus et al., 2006; Christofolletti et al., 2013); and (2) higher oxygen demands in aquatic crabs (Baeza and Fernandez, 2002), which are minimized in land crabs and may impact the size of the ovigerous mass, even for large crabs, and may result in lower values for reproductive effort. However, none of these hypotheses have been tested, lacking empirical support and requiring future experiments to better understand reproductive effort in gecarcinid crabs.

The fecundity of *J. lagostoma* on Trindade Island follows the common trend of fecundity increases (number of eggs) with female size, a pattern observed in brachyuran crabs (Sastry, 1983; Hartnoll and Gould, 1988) and confirmed for Gecarcinidae species such as *G. lalandii* (see Liu and Jeng, 2007), *E. notatus* (see Liu and Jeng, 2005), and *Cardisoma crassum* Smith 1860 (Vázquez-López

and Ramírez-Pérez, 2015). Our study reinforces the observed increase in fecundity (NE) and egg mass weight (EW) with size, coupled with a gradual reduction in reproductive effort (RE), suggesting a decrease in reproductive investment with size. This may be attributed to lower hatching rates in larger females due to senescence, as observed in the semi-terrestrial crab *Ucides cordatus* (Linnaeus, 1763) (Hattori and Pinheiro, 2003), where females larger than 70 mm CW experienced up to an 80% reduction in hatching rate.

Comparing fecundity between crab species is complex and requires careful consideration of the dependence on the number of eggs relative to body size. Similar considerations apply when comparing different conditions (e.g., areas, months, climatic seasons) for the same species so that mathematical adjustments can be employed to account for size effects, as proposed by Pinheiro and Terceiro (2000). Additionally, fecundity may vary depending on somatic growth rates, longevity, niche occupation, dietary requirements, and mortality rates. Moreover, there is a clear correlation between the number and size of eggs produced (González-Pisani and López-Greco, 2014), an aspect still poorly understood for land crab species.

The average fecundity recorded for *J. lagostoma* females on Trindade Island (82,938 eggs/female) closely resembles that of females on Ascension Island (71,800 eggs/female) (Hartnoll et al., 2010). Although fecundity was similar, the authors mention some methodological problems, such as the small sample size ($n = 8$), with only large females carrying eggs at different embryonic stages. These factors collectively contributed to the poor fit observed in the mathematical models (reproductive effort: $R^2 = 2.6\%$; fecundity: $R^2 = 11.3\%$) obtained by Hartnoll et al. (2010). Such problems make it difficult to compare egg production between islands, considering environmental and temperature factors, making new studies necessary to re-evaluate the population of *J. lagostoma* on Ascension Island. Table 1 compares fecundity and reproductive effort among species of gecarcinids from oceanic islands, highlighting the challenges of comparing

these parameters based on the methodological limitations of studies in these environments. Thus, future studies should prioritize methodological improvements to minimize recurrent errors and yield more reliable and comparable data, advancing our understanding of land crab biology.

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ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

Conceptualization and Design: MCAJ and MAAP; Performed research: EEDM, MAM, MCAJ and MAAP; Acquisition of data: MCAJ and MAM; Analysis and interpretation of data: EEDM, MAM and MCAJ; Preparation of figures/tables/maps: EEDM, MAM and MCAJ; Writing – original draft: MAM; Writing – critical review and editing: EEDM, MAM, MCAJ and MAAP.

Consent for publication

All authors declare that they have reviewed the content of the manuscript and have given their consent to submit the document.

Competing interests

The authors declare no competing interest.

Data availability

The original data will be made publicly available on the GitHub page upon acceptance of the manuscript.

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Study association

This study was conducted by MAM to obtain her bachelor's degree in the Undergraduate Course in Biology with specialization in Marine Biology at UNESP IB/CLP, under the supervision of MAAP and co-supervision of MCAJ.

Study permits

This study was conducted with permission from ICMBio, based on the Authorization SISBIO # 65446 granted to MAAP.