

Research Article

Cite this article: Pinheiro MAA, Dias-Silva I, Kriegler N, Santana W, João MCA (2024). Beneath the surface: co-habitation of recruits of the land crab *Johngarthia lagostoma* and its relevance for conservation on oceanic islands. *Journal of the Marine Biological Association of the United Kingdom* **104**, e102, 1–9. <https://doi.org/10.1017/S0025315424000869>

Received: 5 June 2024

Revised: 26 August 2024

Accepted: 12 September 2024

Keywords:

endangered species; Gecarcinidae; insular crabs; recruitment; reproduction

Corresponding author:

Marcelo Antonio Amaro Pinheiro;
Email: marcelo.pinheiro@unesp.br

Beneath the surface: co-habitation of recruits of the land crab *Johngarthia lagostoma* and its relevance for conservation on oceanic islands

Marcelo Antonio Amaro Pinheiro^{1,2,3} , Isabella Dias-Silva¹ ,

Nicholas Kriegler^{1,3} , William Santana⁴  and

Marcio Camargo Araujo João^{1,3} 

¹Departamento de Ciências Biológicas e Ambientais, Universidade Estadual Paulista (UNESP), Instituto de Biociências – Campus do Litoral Paulista (IB/CLP), Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), São Vicente, SP, Brazil; ²Programa de Pós-Graduação em Biodiversidade de Ambientes Costeiros (PPG-BAC), UNESP IB/CLP, São Vicente, SP, Brazil; ³Programa de Pós-Graduação em Ecologia, Evolução e Biodiversidade (PPG-EEB), UNESP Campus de Rio Claro (IB/RC), Rio Claro, SP, Brazil and ⁴Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri (URCA), Crato, CE, Brazil

Abstract

Gecarcinid crabs have their life cycles in antagonistic scenarios, with their larvae developing in the sea and the juvenile/adult phases occurring on land. Adults migrate from land to sea to release their larvae, which return to land upon reaching the megalopa stage. Recruitment and early instar traits in gecarcinid crabs remain unknown, leading to some species lacking age-specific information. Despite massive recruitment observed in some insular gecarcinid species (e.g. *Gecarcoidea natalis*), recruits are generally expected to be few and exhibit cryptic behaviour, potentially occupying the burrows of conspecifics. We evaluated whether recruits of *Johngarthia lagostoma* on Trindade Island, Brazil, co-inhabit larger conspecific burrows, analysing this occurrence and examining their growth patterns, density, and body size across different lunar phases. *Johngarthia lagostoma* recruits inhabit conspecific burrows, either abandoned or occupied by adult crabs, but always with leaves stored in the inner chamber. Recruits in co-inhabiting behaviour reach a maximum carapace width of 7.3 mm, and after that, they are likely detected by the adults and possibly cannibalized or leave burrows naturally. During the full moon, the higher density and smaller size of recruits were recorded, indicating a recruitment lunar phase. It is crucial to ascertain the prevalence of co-inhabitation behaviours in other land crab species to expand the knowledge about recruitment patterns in these key community species.

Introduction

Currently, around 4900 crustacean species have been recognized for their terrestrial conquest, among which crabs from the Brachyura infraorder are included. These crabs are part of the Order Decapoda, one of six crustacean lineages known to have successfully colonized terrestrial ecosystems (Marin and Tiunov, 2023). According to Wolfe *et al.* (2022), crabs transitioned from marine to non-marine habitats between 5 and 15 times, while making the reverse journey 3–4 times. This diversification primarily occurred in the Triassic period, with family-level divergences happening in the late Cretaceous and early Paleogene periods. The most derived crabs, commonly referred to as ‘true crabs’ (Eubrachyura), diverged from their ancestral brachyurans during the Cretaceous period (Tsang *et al.*, 2014; Luque *et al.*, 2021; Watson-Zink, 2021), and present some of the highest levels of terrestrial adaptations among the six grades proposed by Watson-Zink (2021), which were possible due to morphological, reproductive (e.g. aerial respiration, moulting, and development) and physiological changes (e.g. osmoregulation, nitrogen excretion, desiccation resistance, and thermoregulation).

Terrestrial and semi-terrestrial crabs comprise approximately 300 species. A high adaptation to a terrestrial lifestyle can be observed in the family Gecarcinidae (Marin and Tiunov, 2023), where the species colonize land through marine environments (including intertidal mudflats, sandflats, mangrove forests, etc.) (Watson-Zink, 2021). These crabs have a life history characterized by juvenile and adults occurring in terrestrial habitats, while their larvae undergo a planktotrophic development that spans approximately 15–30 days in the marine environment (five to six zoeal stages and one megalopa) (Colavite *et al.*, 2021). The success of these species depends equally on the capacity of migration between the land-sea gradient in both phases and on their adaptations to survive in both environments (Bliss and Mantel, 1968; Burggren and McMahon, 1988; Hartnoll, 2010; Watson-Zink, 2021; Marin and Tiunov, 2023). Some gecarcinid species are endemic to oceanic islands, which poses an additional challenge for their migratory behaviour since the residence sites are even further from the sea (Doi *et al.*, 2019; João *et al.*, 2021), and sometimes reach more than 1000 metres of altitude (e.g. *Gecarcinus ruricola* in Caribbean Islands - Hartnoll *et al.*, 2006). Indeed, studying



insular gecarcinid species can be challenging due to their isolated habitats; however, there is existing well-documented research focused on understanding the biology and behaviours of crabs within this family (Bliss *et al.*, 1978; Hicks, 1985; Foale, 1999; Adamczewska and Morris, 2001; Green, 2004; Hartnoll *et al.*, 2006, 2007, 2009, 2017; Liu and Jeng, 2007; López-Victoria and Werding, 2008; Turner *et al.*, 2011; Perger, 2014; Sanvicente-Añorve *et al.*, 2016; Tavares and Mendonça, 2022; João *et al.*, 2023a). However, there is a knowledge gap concerning how these species transition from the larval phase to land. The process of recruitment in these species has received limited attention, with only a few documented events and scarce information available (Hartnoll and Clark, 2006; Hartnoll *et al.*, 2014).

There are two well-documented recruitment processes for insular gecarcinids in the literature, the Christmas Island red crab *Gecarcoidea natalis* (Hicks, 1985; Hicks *et al.*, 1990) and the Caribbean black crab *Gecarcinus ruricola* (Hartnoll and Clark, 2006). In both cases, a notable similarity is the mass return of megalopae, which creates a visually striking phenomenon where the tideline is painted with a red colour. This mass return event greatly facilitates the understanding of the overall recruitment process in both species. Furthermore, it appears that the behaviours of egg release and subsequent return of recruits in gecarcinid crabs are connected to the phases of the full or new moon (Hicks, 1985; Liu and Jeng, 2005, 2007; Hartnoll and Clark, 2006). Among all other gecarcinid species where there is some recorded information about recruitment in the literature, the only common characteristic is the presence of megalopae on land (*Johngarthia lagostoma* (H. Milne Edwards 1837) and *J. weileri* – Hartnoll *et al.*, 2014; *J. planata* – Erhardt and Niassaut, 1970; *Gecarcoidea lalandii*, erroneously named as *G. natalis* in the study – Webb, 1922; and *Tuerkayana celeste* – Hicks *et al.*, 1990). Although these works provide only basic records, they do suggest that gecarcinid megalopae could live on land, even venturing more than 100 metres away from the shoreline. Unfortunately, the recruitment events can be infrequent and sporadic, as observed for *Gecarcinus ruricola* presenting an interval between each recruitment every 5 or 6 years (Hartnoll and Clark, 2006), which makes documenting and studying these events difficult.

Population studies on insular gecarcinids have highlighted the absence of records on first crab instars and juvenile individuals. As a result, these studies have indicated a concerning pattern of population aging (Hartnoll *et al.*, 2009; Turner *et al.*, 2011); however, this could partially be attributed to methodological limitations. The habitat preferences and distribution of juvenile crabs remain unclear, which can lead to sampling biases that primarily capture adult individuals (Turner *et al.*, 2011). In addition, there is evidence that juveniles of certain crab species occupy specific habitats such as crevices and areas under rocks (as *Tuerkayana hirtipes* – Hicks *et al.*, 1990) or could be associated with adult burrows (as described for *T. hirtipes* – Hicks *et al.*, 1990; and for *Cardisoma carnifex* – Vannini *et al.*, 2003). Clearly, associating with adult burrows can be considered an adaptive strategy because burrows remain for at least five years in some cases (Green, 2004), providing a humid and thermally stable habitat (Greenaway, 1989; Berti *et al.*, 2008), with chambers where leaves are stored by the owner crab (O'Dowd and Lake, 1989; Vannini *et al.*, 2003).

Johngarthia lagostoma, commonly known as the yellow land crab, is an endemic species of insular land crab found in four islands around the world, in the South Atlantic Ocean (Rocas Atoll, Fernando de Noronha, Ascension Island, and Trindade Island, according to Melo, 1996). Few studies were conducted about their biology, mostly on Ascension and Trindade islands (Ascension: Hartnoll *et al.*, 2009, 2010; Trindade: João *et al.*, 2021, 2022, 2023a, 2023b; Tavares and Mendonça, 2022;

Entringer and Srbek-Araujo, 2023), where *J. lagostoma* population structure was considered skewed for adult individuals (Hartnoll *et al.*, 2009; João *et al.*, 2023a). In addition, the lack of clear information about the recruitment of *J. lagostoma* is of particular concern for Brazilian islands (Rocas Atoll, Fernando de Noronha, and Trindade Island) where this species is categorized as Endangered – EN (Santana and Coelho, 2018; MMA, 2022), following the IUCN criteria (IUCN, 2012). A pressing concern that requires immediate investigation is the recruitment of *J. lagostoma* to each island, as this information is crucial for assessing the species' demographics and informing conservation strategies (Pinheiro *et al.*, 2016). The only note about the species recruitment in Trindade Island was made in 1987, where initial crab stages were observed in galleries constructed by adults (Tavares and Mendonça, 2022). So, in this study, we evaluate the association between the first instars of *J. lagostoma* and adult crab burrows in Trindade Island (Brazil) to co-inhabiting behaviour, analysing recruits' relative growth, population density, and size in function of the lunar phases (full, waning, new, and waxing moons).

Materials and methods

Study area and recruits sampling

All the samples were carried out on Trindade Island (20° 29' S- 29° 20.7' W), a volcanic island located in the South Atlantic, approximately 1200 km off the Brazilian coast (Figure 1A, B). A portion of Trindade Island has been designated as a large marine protected area since 2018 (ICMBio, 2018). The island is permanently inhabited by the Brazilian Navy, with a human population of around 40 people, including military and researchers. The sampling took place on the eastern face of Trindade Island, specifically at Andradas Beach (Figure 1C), which is known to be an important reproductive site for *J. lagostoma* (João *et al.*, 2023a). To evaluate the co-habitation of recruits on galleries of adult conspecific, we conduct samples in January 2020, during the reproductive season of *J. lagostoma*, which typically occurs between December and May for Rocas Atoll and Ascension Island (Teixeira, 1996; Hartnoll *et al.*, 2010), and between October to April for Trindade Island (Tavares and Mendonça, 2022; João *et al.*, 2023a).

At Andradas Beach (Figure 1D), *J. lagostoma* is the exclusive species known to construct galleries in the supralittoral zone, primarily associated with sand hill vegetation. These burrows are called 'transit burrows' by Hartnoll *et al.* (2010) due to be constructed during migration or larval release but subsequently abandoned. For each lunar phase (full, waning, new, and waxing), we systematically examined a minimum of 25 random and visibly active burrows, characterized by the absence of debris accumulation and the presence of other biogenic signals (e.g. tracks and faeces) close to the opening. During the day period, when crabs typically remain within their burrows, each gallery was carefully and manually excavated until reaching its end or until to attain an adult of *J. lagostoma* (Figure 1E). In this process, all excavated sediment was collected and placed in a plastic tray and then sieved. All adult crabs collected during the excavation were identified based on their respective gallery numbers, sexed, and reserved in plastic boxes to be released back onto the beach at the end of these procedures. The sex was verified by inspection of abdominal dimorphism (males, subtriangular; and females, semi-rounded) and the number of pleopod pairs (males, two uniramous pairs; and females, four biramous pairs). Following the sieving of the sediment, the recruits (Figure 1F) of each burrow were carefully placed in labelled individual plastic tubes with their corresponding gallery number. These tubes were transported

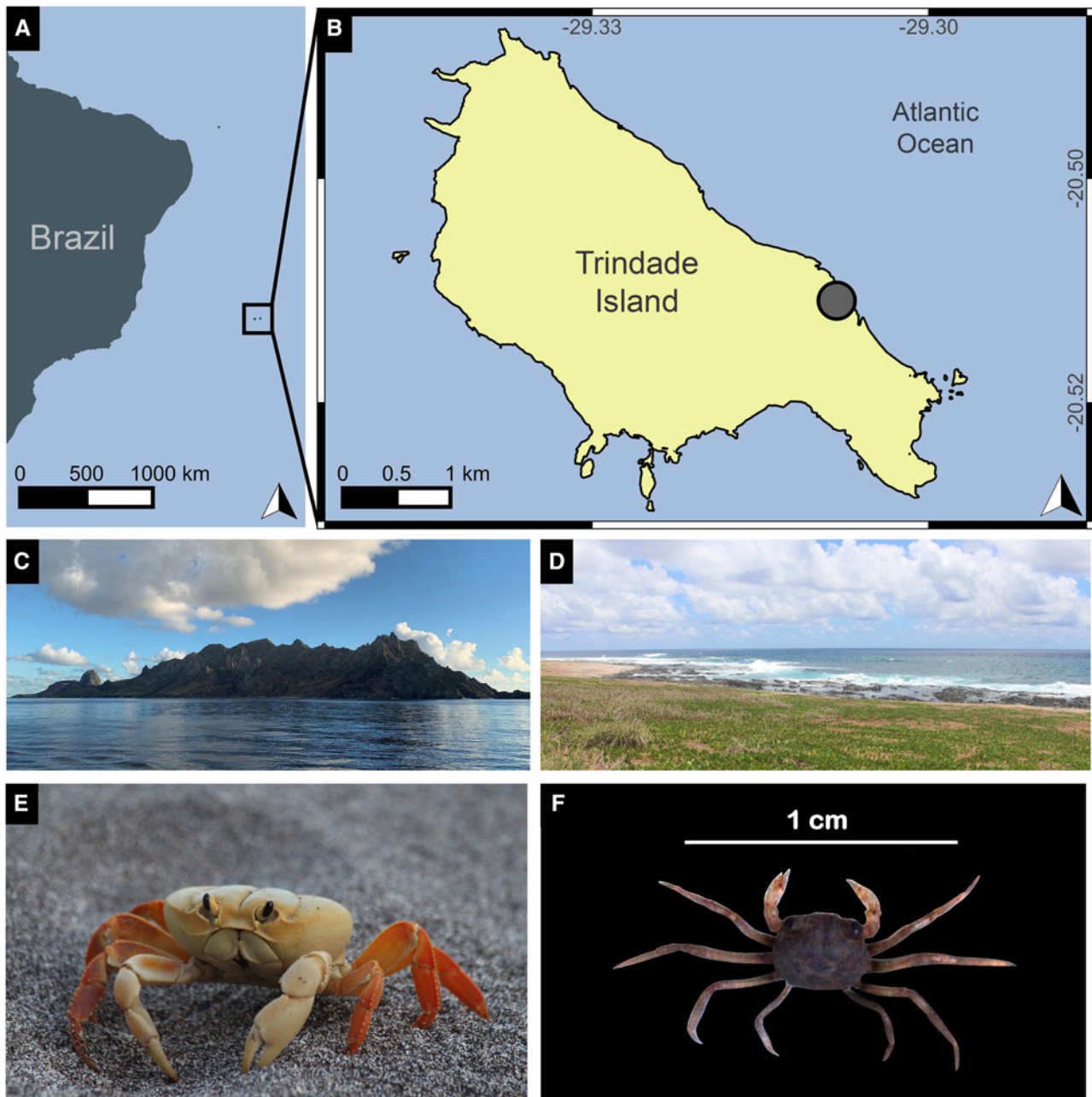


Figure 1. Geographic location of Trindade Island (Brazil). Where: (A) Southeast Brazilian coast showing the position of the Trindade Island; (B) general view of the Trindade Island indicating the study area location (gray circle); (C) general view of Trindade Island; (D) general view of the study area (Andradas Beach); (E) frontal view of a *Johngarthia lagostoma* adult in the Andradas Beach; and (F) dorsal view of a *J. lagostoma* recruit (scale: 1 cm).

to the laboratory, where the recruits were crioanesthetized and subsequently preserved in 70% alcohol. Finally, after excavation, the sediment surrounding the burrows collapsed, mitigating the risk of sampling the same burrow other times. Moreover, during each lunar phase, samples were taken from different locations within the sand dune vegetation to prevent potential bias due to previous sampling.

Recruits: recognition, measurements, and biometric relationships

In the laboratory, all recruits were evaluated to be identified as megalopae or juveniles of *J. lagostoma* species, using diagnostic characters informed for Gecarcinids by Cuesta *et al.* (2007), respectively. Following, each exemplar was measured using an image analysis system (KS-300[®]-Zeiss[®]) integrated to a stereomicroscope (Axiolab[®]-Zeiss[®], 0.01 mm). The carapace width

(*CW*, mm) was determined as the maximum cephalothorax distance between the lateral margins and used as the reference for body size in crabs. Frequency histograms were constructed using 1 mm *CW* size classes, from which the Fisher asymmetry coefficient (*SK*, skewness) was calculated according to Sokal and Rohlf (2012), as recommended by Pinheiro *et al.* (2022), and categorizing the size distribution as symmetric ($-0.5 \leq SK \leq 0.5$), positive asymmetric ($SK > 0.5$) or negative asymmetric ($SK < -0.5$).

Biometry of juveniles was registered in some morphological structures (also in millimetres), represented by: carapace length (*CL*, distance between the frontal to posterior margin of carapace); major cheliped propodus length (*PL*, distance between end of the fixed finger and the tooth at the propodus-carpus joint); and abdominal width (*AW*, greatest width in the fifth somite). Additionally, the weight of each recruit (*WT*, in grams) was recorded using a digital analytical scale (Ohaus, 0.0001 g). Individuals with carapace damage or missing appendages were

excluded from the biometric analysis. Since sexual dimorphism recognized was not present in the recruits, they were not sexed.

To test the fit between all biometric measures, morphological relationships were examined by using carapace width (*CW*) as the independent variable and the other measures (*CL*, *PL*, *AW*, and *WT*) as the dependent variables. Regression analysis was employed to determine the fit, employing the power function ($Y = aX^b$) in each biometric relationship. To accomplish this, all variables were log-transformed to calculate the linear models for allometric growth rates. The slope value (constant 'b') was used to determine relative growth to each relationship (*CL* × *CW*, *PL* × *CW*, and *AW* × *CW*), where growth patterns could be categorized as isometric ($b = 1$), positive allometric ($b > 1$), or negative allometric ($b < 1$). The same was conducted with the *WT* × *CW* relationship, in this case with b-values characterizing these weight's growth patterns in relation to 3 (Pinheiro and Fiscarelli, 2009). Student's *t*-tests were conducted to assess departures from isometry in all relationships ($\alpha = 0.05$), using b-values of 1 or 3 in each case.

Relationship between juvenile recruits' traits with lunar phases and adult body size

To assess the influence of lunar phases on *J. lagostoma* recruitment, the density of juvenile recruits (*DE*, individuals per burrow) and corporal measures (*CW* and *WT*) values were used as dependent variables, while the lunar phases (full, waning, new, and waxing) were treated as factors. The normality assumption and homogeneity of variances for all dependent variables were assessed using Shapiro–Wilk (*W*) and Levene (*L*) tests, respectively. Since the data did not meet the assumptions of parametric distribution, a Kruskal–Wallis test (Sokal and Rohlf, 2012) was conducted. In cases where statistically significant differences were observed, post-hoc Dunn tests were performed to compare the median values across different lunar phases. All these statistical analyses were performed using R version 4.2.1 (R Core Team, 2022) with the 'dunnTest' function available in the 'FSA' package (Ogle *et al.*, 2023).

Evaluation of a possible association between juvenile recruits' density/burrow (*DE*) and mean juvenile recruits' body size (*CW_J*), both in relation to adults' body size (*CW_A*), was submitted to regression analysis by linear regression analysis, represented by *DE* vs *CW_J* and *CW_J* vs *CW_A*, respectively. This association was also evaluated by Pearson's linear correlation coefficient (*r*), considering 'n-2' degrees of freedom.

Results

Recruits' occurrence and biometric relationships

A total of 128 burrows were examined, of which 54.7% ($n = 70$) were empty without any recruits or owners. In 23.4% of the burrows ($n = 30$), both *J. lagostoma* owner and recruits were present, while in 21.9% ($n = 28$) only the recruits were found inhabiting the galleries. Among the burrows with both owners and recruits, 53.3% had ovigerous females ($n = 16$), 43.3% had males ($n = 13$), and only 3.3% had non-ovigerous females ($n = 1$). A total of 113 *J. lagostoma* recruits were sampled, with a density (*DE*) ranging from 1 to 10 ind./burrow (mean ± standard deviation: 1.7 ± 0.9 ind./gallery; and variation coefficient: 52.9%), and their carapace width (*CW*) ranged from 2.9 to 7.5 mm (4.9 ± 0.7 mm; and 14.3%, respectively) (Table 1). The size frequency histogram indicated a symmetric distribution for all sampled recruits (*SK* = 0.3, Figure 2).

Inside the burrows, the presence of both owners and recruits was not random. Even in the absence of an owner, the burrows

appeared to have been recently abandoned, as indicated by the absence of debris and the well-structured entrance and tunnels. The owner was consistently found at the deepest part of the gallery, which varied in distance from approximately 20 to 100 cm from the ground surface. Regardless of the presence or absence of the owner, the recruits were never found in this deepest part of the gallery but were commonly associated with small crevices along the sides of the tunnels. These crevices seemed to be used by the owners for storing food, represented by the accumulation of leaves and bioturbated sediment.

All biometric relationships showed statistical significance ($P < 0.05$), displaying a positive correlation ($\rho \geq 0.85$; $P < 0.001$), and demonstrating good fits ($R^2 \geq 0.70$) in the regression analysis (Table 1). The slopes calculated for *CL* × *CW* ($b = 0.93$) and *AW* × *CW* ($b = 0.93$) indicated isometry, meaning there was proportional growth between the dependent variables and *CW*. On the other hand, the *PL* × *CW* relationship exhibited a lower slope ($b = 0.77$) and confirmed negative allometry, indicating that there was greater growth in *CW* compared to *PL*. Lastly, the *WT* × *CW* relationship confirmed isometry ($b = 3.11$), showing that the weight (*WT*) and *CW* grew proportionally in the recruited individuals.

Relationship between juvenile recruits' traits with lunar phases and adult body size

Firstly, all dependent variables (*DE*, *CW*, and *WT*) were significantly influenced by the lunar phases (*DE*: *KW* = 28.3, $P = 0.003$; *CW*: *KW* = 21.4, $P = 0.0001$; *WT*: *KW* = 22.3, $P = 0.0001$ – Figure 3). For density of juveniles the highest values were recorded during the full moon phase (*DE*: 1 to 10 ind./gallery = 2.0 ± 2.5 ind./gallery), which decreased significantly during subsequent moon phases (Figure 3A). In the case of *CW* and *WT* values (Figure 3B, C), an opposite pattern was observed, with the lowest values registered during the full moon phase (*CW*: 3.2 to 5.7 mm, 4.7 ± 0.5 mm; *WT*: 0.003 to 0.06 g, 0.03 ± 0.01 g), followed by an increase, with the highest values observed during the waxing moon phase (*CW*: 5.4 to 7.5 mm = 6.4 ± 0.9 mm; *WT*: 0.06 to 0.1 g = 0.1 ± 0.04 g).

Overall, recruits increased an average size of 1.4 times between full and waxing moons (=39.4% per month), corresponding to an average increase in weight of 3.23 times (323% per month) for the same period. Furthermore, a higher frequency of occurrence of recruits in the galleries (65.9%) was recorded during the full moon, being reduced by 50.5% after one month (lunar cycle), in relation to the lowest percentage recorded on the waxing moon (15.4%). Finally, only one megalopa was registered during the studied period, found inside the galleries inspected in 7.1% ($n = 1$) in the full moon.

The linear regression analysis for *DE* vs *CW_A* relationship was not significant ($DE = 0.039 CW_A - 0.394$; $R^2 = 0.028$; $n = 25$) with a positive but not significant association between them ($r = 0.168$; $P > 0.001$). The same was verified for *CW_J* vs *CW_A* relationship, which was not significant for the regression ($CW_J = 0.0033 CW_A - 4.73$; $R^2 = 0.002$; $n = 25$) and association among these variables ($r = 0.045$; $P > 0.001$).

Discussion

The knowledge of gecarcinid crabs recruitment is generally limited (Vannini *et al.*, 2003; Hartnoll and Clark, 2006; Hartnoll *et al.*, 2014), with few reports available for some species, such as *J. lagostoma* (von Fimpel, 1975; Hartnoll *et al.*, 2014). Specifically, research on *J. lagostoma* recruitment has mainly focused on Ascension Island, where megalopae and first instar crabs (4.2 mm *CW*) were found over 100 metres from the sea (Hartnoll *et al.*, 2014).

Table 1. Regression analysis using all biometric relationships of *Johngarthia lagostoma* recruits from Trindade Island, Brazil

Biometric relationships	Function ($Y = a \cdot X^b$)	R^2 (%)	t	Allometry
$CL \times CW$	$CL = 0.82 \cdot CW^{0.93}$	78.9	-1.27 ^{ns}	Isometry
$PL \times CW$	$PL = 0.72 \cdot CW^{0.77}$	72.5	-4.01*	Negative
$AW \times CW$	$AW = 0.33 \cdot CW^{0.93}$	80.0	-1.23 ^{ns}	Isometry
$WT \times CW$	$WT = 0.0003 \cdot CW^{3.11}$	83.1	-0.67 ^{ns}	Isometry

Where: *AW*, abdominal width; *CL*, carapace length; *CW*, carapace width; *PL*, cheliped propodus length; R^2 , coefficient of determination; t , calculated t -value evaluating departure from isometry ($b = 1$), expressed by * $P \leq 0.05$ or ^{ns} $P > 0.05$; and *WT*, weight.

In Brazilian islands (Fernando de Noronha, Rocas Atoll, and Trindade), information is limited and sometimes unclear. A report mentions a 7 mm dark brown crab leaving the sea on Trindade Island (von Fimpel, 1975), raising doubts since other gecarcinid crab recruitment records have found megalopae on land (see Lafaix, 1969; Klaassen, 1975; Hicks, 1985; Hartnoll and Clark, 2006; Hartnoll *et al.*, 2014), including the anomuran *Birgus latro* (Drew *et al.*, 2010). Thus, we support the pattern suggested by previous studies, where gecarcinid megalopae enter land and then metamorphose into the first instar stage (Hartnoll *et al.*, 2014).

Chemical cues influence the metamorphosis from megalopa to the first juvenile instar in both aquatic and semi-terrestrial brachyurans (see Christy, 1989; Wolcott and de Vries, 1994; Andrews *et al.*, 2001; Diele and Simith, 2007; Simith *et al.*, 2010; Christy, 2011). These studies suggest that metamorphosis is faster and more targeted when megalopae encounter conspecific cues in sediment. However, its relevance to gecarcinid crabs, especially as their megalopae transition to land, remains unclear. In terrestrial environments, detecting and interpreting chemical cues presents unique challenges (Krång *et al.*, 2012; Waldrop *et al.*, 2016). Although it has been hypothesized that the odour within a species' burrow is more concentrated (Schmidt and Diele, 2009), this aspect was not studied for *J. lagostoma*.

The lack of records on the early instars of land crab species can be attributed to three main factors, as suggested by Vannini *et al.* (2003): (1) irregular recruitment patterns, which complicate the timing of first instar detection; (2) previous sampling efforts focused primarily on adults, potentially overlooking juvenile

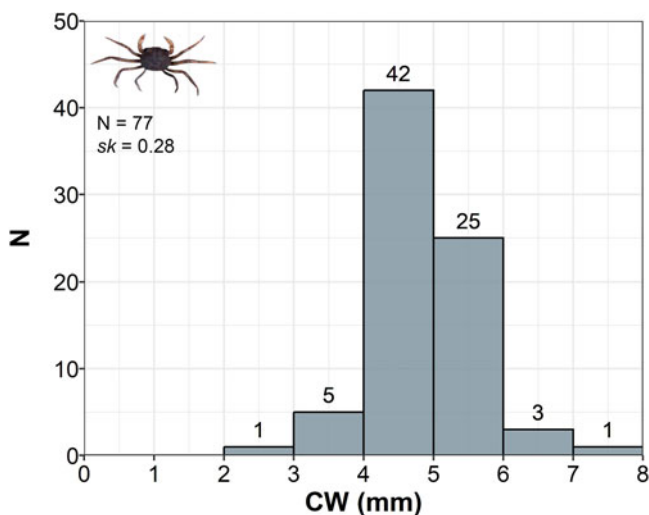


Figure 2. Abundance of *Johngarthia lagostoma* recruits in a size-frequency histogram showing a symmetric distribution ($SK = 0.28$). Where: *CW*, carapace width; and numbers above the bars, N of each size-class.

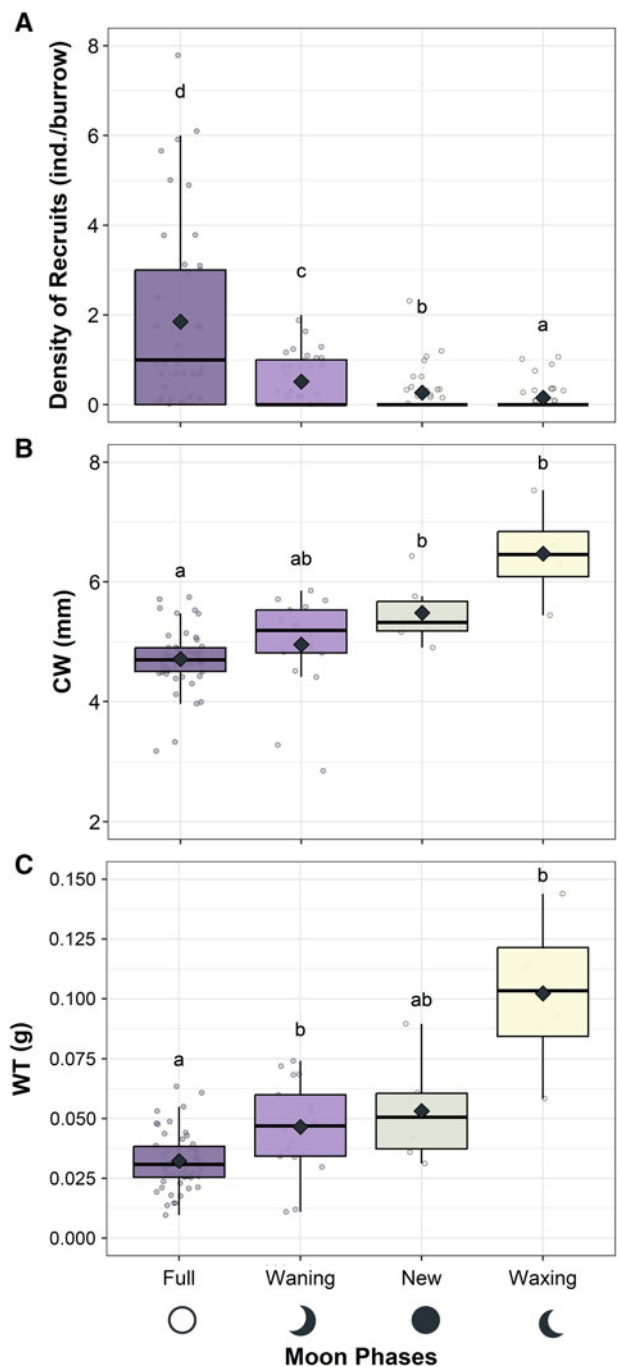


Figure 3. Variation of the density (ind./burrow: A) and size (*CW*, carapace width: B) and weight (*WT*, wet weight: C) of the *Johngarthia lagostoma* recruits co-inhabiting burrows with conspecific crabs along the lunar phases. Where: line inside the box, median values; rhombus dot, mean values; box, interquartile range (IQRs); whiskers, lowest and highest values within 1.5×IQRs; circle dot, original data on which a random noise was added to avoid overlap. Distinct letters indicate significant differences in the dependent variables between the lunar phases ($P \leq 0.05$).

habitats; and (3) juvenile recruits, although present, often remain concealed within refuges. Our findings suggest that the latter two factors are particularly relevant to the recruitment of *J. lagostoma*. The co-habitation observed in our study indicates that *J. lagostoma* recruits occupy the same habitat as adults but with varying levels of concealment. However, no recruits were found in higher elevation environments (e.g. non-flooded supralittoral or mountainous areas), with or without vegetation.

Although our field research predominantly identified conspecific burrows as habitats for recruits, this does not imply they are the exclusive refuges. Due to the scope of our investigation on Trindade Island, other potential habitats such as crevices and spaces beneath rocks in the supralittoral zone were not explored, leaving open the possibility of additional juvenile habitats. Nevertheless, the information from our study, along with previous records for *J. lagostoma* (Tavares and Mendonça, 2022) and similar findings for *C. carnifex* and *Gecarcinus lateralis* (see Vannini *et al.*, 2003 and Klaassen, 1975, respectively), offers valuable insights into where recruits might undergo moulting stages before constructing their own burrows.

The transition to terrestrial environments poses significant challenges for crabs, with desiccation being a major concern, especially on oceanic islands near the equator and tropics. Trindade Island is characterized by intense east winds and frequent heavy rains, often escalating into tropical storms that flood its valleys (Pires *et al.*, 2013). These rain events, known as ‘Pirajás,’ occur almost daily during the summer, triggered by the humid oceanic air rising over the island’s highest peak, ‘Desejado’ (~600 m), resulting in storm clouds that precipitate around the island (SECIRM, 2017). This study was conducted in January, one of the island’s driest months, with an average rainfall of 65 mm (SECIRM, 2017). Although Trindade is the only Brazilian oceanic island with perennial watercourses and springs (Marques *et al.*, 2019), beaches like Calhetas and Andradas have type IV drainage (direct to the ocean or with limited flow). This highlights the importance of ‘Pirajás’ in maintaining sediment and undergrowth moisture during the key reproductive period of this species, a factor that must be considered.

Gecarcinidae crabs dig burrows in sediment to cool off and may inhabit areas influenced by tides or vegetation (Watson-Zink, 2021). Bliss (1963) observed that terrestrial crabs often occupy elevated areas, creating shallow burrows that avoid groundwater and help maintain low internal moisture. Gecarcinid species within the genera *Johngarthia*, *Gecarcinus*, and *Gecarcoidea* possess a ventral tuft of hydrophilic setae that aids in water retention (Bliss, 1963, 2014; Guinot *et al.*, 2018). In *J. lagostoma*, these setae are located between the 5th pereopod and the margins of the 1st–2nd pleonal somites (Oliveira, 2014). More terrestrial species, such as *Cardisoma guanhumi* and *J. lagostoma*, also utilize arthroal membranes for water absorption and have adaptations to minimize water loss, including a strong seal of the branchial chambers (Wolcott, 1984).

After these rainy events, the water can be retained in the interstices of the sediment, particularly at greater depths, as well as in the larger biomass of undergrowth vegetation (e.g. the grass *Cyperus atlanticus*). Even during the drier summer months, this vegetation can provide a humid, shaded environment as its dried tussocks droop over the sediment, forming so-called ‘vegetation crowns’. These areas frequently harbour adult *J. lagostoma*, but notably not their juvenile counterparts. This suggests that factors such as moisture levels and potential chemical signals from adults may not be as influential in recruit behaviour as initially hypothesized, given that recruits are not found in association with adults in these ‘vegetation crowns’.

Further investigation is necessary to fully understand these dynamics.

Adults of *J. lagostoma* are more active at night, likely due to lower temperatures and higher humidity (Hartnoll *et al.*, 2006). Daytime activity varies, with individuals seen at dawn and dusk, but rarely during intense sunlight and low humidity, particularly in the absence of ‘Pirajás’. This susceptibility to desiccation likely affects megalopae and juveniles, suggesting a reliance on summer rains. Additionally, their activity may be synchronized with moon phases that generate higher tidal flooding amplitudes, a pattern common among semi-terrestrial crabs. The association of juvenile recruits with adult burrows could be due to chemical attraction to plant material stored within the burrows, a behaviour also noted in other gecarcinid crabs [e.g. *C. carnifex* and *C. guanhumi* as reported by Micheli *et al.* (1991) and Novais *et al.* (2021), respectively], as well as in some semi-terrestrial crabs [e.g. *Ucides occidentalis* and *Ucides cordatus* as noted by Twilley *et al.* (1997) and Schories *et al.* (2003), respectively]. The plant material, rich in nitrogen and carbon, undergoes decomposition, which increases nitrogen content through microbial activity (Nordhaus *et al.*, 2017; Tongununi *et al.*, 2021; Gao and Lee, 2022). The decomposition process is further enhanced by *J. lagostoma* during ingestion, breaking down complex molecules into more absorbable forms (Johnston *et al.*, 2005). Microbial volatile organic compounds (M-VOCs – e.g. alcohols, phenols, etc.) are produced during decomposition (Gray *et al.*, 2010; Tongununi *et al.*, 2021), with their composition depending on the vegetable matrix, microorganisms involved, and fermentation conditions (Rajendran *et al.*, 2023). The odours emitted during this process can provide information about food quality and potential benefits or dangers to consumers (Price *et al.*, 2011; Davis *et al.*, 2013). Gecarcinid crabs are particularly sensitive to these odours, as evidenced by their frequent capture using traps baited with aromatic or strong-smelling fruits (e.g. lemon, pineapple, banana, jackfruit) (Krång *et al.*, 2012). Despite this common attraction in adults, no studies have yet confirmed olfactory attraction in juvenile Gecarcinidae species, highlighting an area for future research.

A question that remains unanswered pertains to the mechanisms through which recruits enter the burrows of larger crabs. Possible factors could include the attractiveness of a moist or shaded environment, the release of pheromonal signals by adults, or the availability of pre-processed food within the burrows, among other factors not addressed by us. While these aspects remain speculative, answers to them could significantly contribute to our understanding of the species’ ecology.

The symmetric size distribution of recruits suggests the range at which co-inhabiting behaviour begins and ends, likely around 7 mm CW (Figure 2), when recruits either leave the burrow or are detected and consumed by adults. A similar pattern is observed in *U. cordatus*, where recruits co-inhabit conspecific burrows until reaching a size that risks detection and cannibalism (Vannini *et al.*, 2003; Schmidt and Diele, 2009). Cannibalism is common among gecarcinid species (Erhardt and Niassaut, 1970; Bliss *et al.*, 1978; Hicks, 1985; Wolcott, 1988). This risk increases when food is scarce or during stressful periods, such as when females await larval release (Wolcott and Wolcott, 1984, 1987; Hartnoll *et al.*, 2010). Consequently, crabs larger than 7 mm CW likely leave the burrow to find alternative refuges.

Biometric analysis of recruits reveals trends typical of terrestrial crabs but distinct from adult gecarcinids. For the $CL \times CW$ relationship, recruits have a more square-shaped carapace, reflecting a transitional morphology. While megalopae generally have a longer carapace (Cuesta and Anger, 2005; Hartnoll and Clark, 2006; Cuesta *et al.*, 2007; Hartnoll *et al.*, 2014), adults show a wider carapace due to negative allometry (Hartnoll *et al.*, 2006). This shift likely aids in adapting to terrestrial habitats, where a

broader carapace improves gill chamber space for respiration (Bliss and Mantel, 1968; Vannini *et al.*, 2003). In contrast to typical positive allometry seen in juvenile gecarcinids (Hartnoll *et al.*, 2006; Molina-Ortega and Vázquez-López, 2018; Doi *et al.*, 2019; João *et al.*, 2022), our study found negative allometry for chelipeds and isometry for the abdomen in recruits. This suggests that growth during this phase prioritizes overall body size rather than specific structures linked to sexual maturity (Hartnoll, 1982). The $WT \times CW$ relationship in recruits also displayed isometry, unlike the negative allometry seen in adults (Hartnoll *et al.*, 2006; Molina-Ortega and Vázquez-López, 2018), reinforcing the focus on balanced body growth during recruitment.

Our findings regarding the density of recruits and their body measurements (CW and WT) reveal a distinct pattern associated with lunar phases, at least during our sampling period (January 2020). We observed an inverse relationship, whereby higher recruit densities were observed during the full moon, which subsequently decreased in the following phases. Furthermore, we found that the smallest recruits were sampled during the full moon, while their mean size and weight increased in subsequent moon phases. These observations suggest that there was a peak in recruitment activity during the full moon, followed by growth of the recruits within the owner burrows during the subsequent phases. Worth noting, that only one megalopa was captured in this study during the full moon, confirming the starting point of the recruitment process of this species. The reproductive process of many gecarcinids is known to be influenced by lunar phases, particularly during periods of larger tidal amplitudes, such as the full and new moon (Klaassen, 1975; Liu and Jeng, 2005, 2007). However, the specific timing of recruitment for *J. lagostoma* remains largely unknown, with only two instances associated with the new moon reported for individuals from Ascension Island (Hartnoll *et al.*, 2010). In the case of other gecarcinid species, such as *G. lalandii* and *Epigrapsus notatus*, a significant release of larvae by females has been observed during the new moon (Liu and Jeng, 2007) and full moon (Liu and Jeng, 2005), respectively.

Recruitment in gecarcinid species is generally sparse, raising concerns for their conservation (Hicks, 1985; Hartnoll and Clark, 2006). Demographic studies of the Gecarcinidae family show low juvenile proportions, ranging from 8.5% for *T. hirtipes* (Turner *et al.*, 2011) to 26% for *Gecarcinus ruricola* (Hartnoll *et al.*, 2006) and 36.4% for *E. notatus* (Doi *et al.*, 2019). Recruitment of individuals under 10 mm CW is rare, typically seen only in species with massive recruitment events (Hicks, 1985; Hartnoll and Clark, 2006). Juvenile *J. lagostoma* populations vary across islands: 0.7% on Ascension Island, 4.0% at Rocas Atoll (Teixeira, 1996; Hartnoll *et al.*, 2009), and 16.4% on Trindade Island (João *et al.*, 2023a). This percentage for Trindade could increase if individuals from this study are included, showing a relatively better recruitment scenario. Replicating this study's methodology on other islands could confirm co-inhabiting behaviour and reveal changes in population structure, contributing significantly to the management and conservation of *J. lagostoma* in Brazilian islands.

Our findings offer valuable insights into the recruitment of *J. lagostoma*, focusing on three key aspects: the behaviour of recruits in conspecific burrows, growth patterns in morphometric traits, and the influence of lunar phases on recruitment. While some findings align with existing literature, others reveal new aspects, such as co-inhabiting behaviour. These insights enhance our understanding of the species' biology and have important implications for conservation efforts.

Data. The original data of this manuscript are available in https://github.com/marcio-joao/j.lagostoma_recruitment.

Acknowledgements. We thank the Brazilian Navy (First District), Inter-ministerial Secretariat for Marine Resources (SECIRM) and 'Programa de Pesquisas Científicas da Ilha da Trindade' (PROTRINDADE), under the commander C. C. Vitória-Régia, who guaranteed our presence in Trindade Island and helped with the project logistic. We thank members of the 'Projeto Caranguejos de Ilhas Oceânicas' for help during the field sampling. We thank Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) by the sample permission supported by Sistema de Autorização e Informação da Biodiversidade (SISBIO # 65446). MAAP thanks 'Conselho Nacional de Desenvolvimento Científico e Tecnológico' (CNPq) for the financial support provided by Universal Project (CNPq # 404224-2016) and for the Research Productivity Fellowship (CNPq # 305957/2019-8 and # 307482/2022-7). IDS thanks 'Programa Institucional de Bolsas de Iniciação Científica' (PIBIC) for the scientific-initiation fellowship (#143295/2020-9). MJ thanks 'Fundação de Amparo à Pesquisa do Estado de São Paulo' (FAPESP) for the master fellowship (# 2019/16581-9). WS thanks CNPq (PQ2 # 315185/2020-1 e PQ1D 312823/2023-1) and the 'Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico' (FUNCAP) for the fellowships (# 6647309/2017 and # PV1-0187-00033.01.00/21).

Authors' contributions. M.A.A.P. and M.C.A.J. conceived and designed the study. M.C.A.J. and N.K. conducted the field samples. M.A.A.P., I.D.S., and M.C.A.J. analysed the data and made the figures. M.A.A.P., I.D.S., and M.C.A.J. made the first draft of the manuscript. All authors read and approved the final version of the manuscript.

Financial support. This work was supported by 'Conselho Nacional de Desenvolvimento Científico e Tecnológico' (CNPq) by Universal Project (CNPq # 404224-2016).

Competing interests. None.

Ethical standards. All permits for sampling were obtained with the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) that was given to the first author the sample permission supported by Sistema de Autorização e Informação da Biodiversidade (SISBIO # 65446).

References

- Adamczewska AM and Morris S (2001) Ecology and behavior of *Gecarcoidea natalis*, the Christmas Island red crab, during the annual breeding migration. *Biological Bulletin* **200**, 305–320.
- Andrews WR, Targett NM and Epifanio CE (2001) Isolation and characterization of the metamorphic inducers of the common mud crab, *Panopeus herbstii*. *Journal of Experimental Marine Biology and Ecology* **261**, 121–134.
- Berti R, Cannicci S, Fabbroni S and Innocenti G (2008) Notes on the structure and the use of *Neosarmatium meinerti* and *Cardisoma carnifex* burrows in a Kenyan mangrove swamp (Decapoda Brachyura). *Ethology, Ecology and Evolution* **20**, 101–113.
- Bliss DE (1963) The pericardial sacs of terrestrial Brachyura, 59–78. In HB Whittington and WDI Rolfe (eds), *Phylogeny and Evolution of Crustacea*. Museum of Comparative Zoology, Special Publication. Cambridge: Harvard University.
- Bliss DE and Mantel LH (1968) Adaptations of crustaceans to land: a summary and analysis of new findings. *American Zoologist* **8**, 673–685.
- Bliss DE, Van Montfrans J, Van Montfrans M and Boyer JR (1978) Behavior and growth of the land crab *Gecarcinus lateralis* (Fréminville) in southern Florida. *Bulletin of the American Museum of Natural History* **160**, 112–152.
- Burggren WW and McMahon BR (1988) *Biology of the Land Crabs*. New York: Cambridge University Press.
- Christy JH (1989) Rapid development of megalopae of the fiddler crab *Uca pugilator* reared over sediment: implications for models of larval recruitment. *Marine Ecology Progress Series* **57**, 259–265.
- Christy JH (2011) Timing of hatching and release of larvae by brachyuran crabs: patterns, adaptive significance and control. *Integrative and Comparative Biology* **51**, 62–72.
- Colavite J, Tavares M, Mendonça JB Jr and Santana W (2021) The first zoeal stage of *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Crustacea: Brachyura: Gecarcinidae), with comments on the validity of the genus. *Thalassas* **37**, 767–773.
- Cuesta JA and Anger K (2005) Larval morphology and salinity tolerance of a land crab from West Africa, *Cardisoma armatum* (Brachyura: Grapsoidea: Gecarcinidae). *Journal of Crustacean Biology* **25**, 640–654.

- Cuesta JA, García-Guerrero MU and Hendrickx ME (2007) The complete larval development of *Johnngarthia planatus* (Brachyura: Grapsoidea: Gecarcinidae) described from laboratory reared material, with notes on the affinity of *Gecarcinus* and *Johnngarthia*. *Journal of Crustacean Biology* 27, 263–277.
- Davis TS, Crippen TL, Hofstetter RW and Tomberlin JK (2013) Microbial volatile emissions as insect semiochemicals. *Journal of Chemical Ecology* 39, 840–859.
- Diele K and Smith DJB (2007) Effects of substrata and conspecific odour on the metamorphosis of mangrove crab megalopae, *Ucides cordatus* (Ocypodidae). *Journal of Experimental Marine Biology and Ecology* 348, 174–182.
- Doi W, Kato S, Itoh D, Mizutani A and Kohno H (2019) Distribution, size structure, and relative growth of *Epigrapsus politus* (Brachyura: Gecarcinidae) in a subtropical bay in Japan. *Crustacean Research* 48, 145–157.
- Drew MM, Harzsch S, Stensmyr M, Erland S and Hansson BS (2010) A review of the biology and ecology of the robber crab, *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae). *Zoologischer Anzeiger – Journal of Comparative Zoology* 249, 45–67.
- Entringer H Jr & Srbek-Araujo AC (2023) Habitat use, non-breeding groupings and chromatic pattern in *Johnngarthia lagostoma* (H. Milne Edwards, 1837) (Decapoda, Gecarcinidae) in Trindade Island, South Atlantic Ocean. *Neotropical Biology and Conservation* 18, 83–95.
- Erhardt JP and Niassaut P (1970) Ecologie et physiologie du brachyoure terrestre *Gecarcinus planatus* Stimpson (d'après les individus de l'atoll de Clipperton). *Bulletin de la Société Zoologique de France* 95, 41–54.
- Foale S (1999) Local ecological knowledge and biology of the land crab *Cardisoma hirtipes* (Decapoda: Gecarcinidae) at West Nggela, Solomon Islands. *Pacific Science* 53, 37–49.
- Gao X and Lee SY (2022) Feeding strategies of mangrove leaf-eating crabs for meeting their nitrogen needs on a low-nutrient diet. *Frontiers in Marine Science* 9, 872272.
- Gray CM, Monson RK and Fierer N (2010) Emissions of volatile organic compounds during the decomposition of plant litter. *Journal of Geophysical Research and Biogeosciences* 115, G03015.
- Green PT (2004) Burrow dynamics of the red land crab *Gecarcoidea natalis* (Brachyura, Gecarcinidae) in the rain forest on Christmas Island (Indian Ocean). *Journal of Crustacean Biology* 24, 340–349.
- Greenaway P (1989) Sodium balance and adaptation to fresh water in the amphibious crab *Cardisoma hirtipes*. *Physiological Zoology* 62, 639–653.
- Guinot D, Ng NK and Moreno PAR (2018) Review of grapsoid families for the establishment of a new family for *Leptograpsodes* Montgomery, 1931, and a new genus of Gecarcinidae H. Milne Edwards, 1837 (Crustacea, Decapoda, Brachyura, Grapsoidea MacLeay, 1838). *Zoosystema* 40, 547–604.
- Hartnoll RG (1982) Growth. In Abele LG (ed.), *The Biology of Crustacea* 2. New York: Academic, pp. 111–196.
- Hartnoll RG (2010) Chastity belts and planktotrophic larvae: constraints on gecarcinid reproductive behaviour. In Castro P, Davie PJJ, Ng PKL and Richer de Forges B (eds), *Studies on Brachyura: A Homage to Danièle Guinot*, 11th Edn. Leiden: Brill, pp. 153–171.
- Hartnoll RG, Baine MSP, Britton A, Grandas Y, James J, Velasco A and Richmond MG (2007) Reproduction of the Black Land Crab, *Gecarcinus ruricola*, in the San Andres Archipelago, Western Caribbean. *Journal of Crustacean Biology* 27, 425–436.
- Hartnoll RG, Baine MSP, Grandas Y, James J and Atkin H (2006) Population Biology of the Black Land Crab, *Gecarcinus ruricola*, in the San Andres Archipelago, Western Caribbean. *Journal of Crustacean Biology* 26, 316–325.
- Hartnoll RG, Broderick AC, Godley BJ and Saunders KE (2009) Population structure of the land crab *Johnngarthia lagostoma* on Ascension Island. *Journal of Crustacean Biology* 29, 57–61.
- Hartnoll RG, Broderick AC, Musick S, Pearson M, Stroud SA and Saunders KE (2010) Reproduction in the land crab *Johnngarthia lagostoma* on Ascension Island. *Journal of Crustacean Biology* 30, 83–92.
- Hartnoll RG and Clark PF (2006) A mass recruitment event in the land crab *Gecarcinus ruricola* (Linnaeus, 1758) (Brachyura: Grapsoidea: Gecarcinidae), and a description of the megalop. *Zoological Journal of the Linnean Society* 146, 149–164.
- Hartnoll RG, Régnier-McKellar C, Weber N and Weber SB (2014) Return to the land: the stages of terrestrial recruitment in land crabs. *Crustaceana* 87, 531–539.
- Hartnoll RG, Weber N, Weber SB and Liu H-C (2017) Polymorphism in the chelae of mature males of the land crabs *Johnngarthia lagostoma* and *Epigrapsus* spp. *Crustaceana* 90(7–10), 931–951. <https://doi.org/10.1163/15685403-00003596>
- Hicks JW (1985) The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). *Australian Journal of Zoology* 33, 101–110.
- Hicks JW, Rumpff H and Yorkston H (1990) *Christmas Crabs*. Christmas Island: Christmas Island Natural History Association.
- ICMBio - Instituto Chico Mendes para Conservação da Biodiversidade (2018) ICMBio. Decreto no. 9.312 de 19 de março de 2018. [Online]. Cria a Área de Proteção do Arquipélago de Trindade e Martim Vaz e o Monumento Natural das Ilhas de Trindade e Martim Vaz e do Monte Columbia. Diário Oficial.
- ICMBio - Instituto Chico Mendes para Conservação da Biodiversidade – International Union for Conservation of Nature (2012) IUCN Red List categories and criteria (version 3.1). [Online]. Available at <https://www.iucnredlist.org/resources/categories-and-criteria> [2023, June 16].
- João MCA, Duarte RC, Bispo da Silva IS, Freire AS and Pinheiro MAA (2022) Sexual maturity of an endemic insular land crab: priority information toward the conservation of *Johnngarthia lagostoma*. *The Biological Bulletin* 243, 14–27.
- João MCA, Duarte RC, Freire AS and Pinheiro MAA (2023b) Intraspecific color diversity and camouflage associated with ontogeny in an insular land crab. *Behavioral Ecology and Sociobiology* 77, 120.
- João MCA, Duarte RC, Krieglner N, Freire AS and Pinheiro MAA (2023a) Population biology of the endangered land crab *Johnngarthia lagostoma* (H. Milne Edwards, 1837) in the Trindade Island, Brazil: identifying crucial areas for future conservation strategies. *Marine Ecology* 45, e12778.
- João MCA, Krieglner N, Freire AS and Pinheiro MAA (2021) Mating strategies of the endangered insular land crab *Johnngarthia lagostoma* (H. Milne Edwards, 1837). *Invertebrate Reproduction and Development* 65, 256–267.
- Johnston MD, Johnston DJ and Richardson AMM (2005) Digestive capabilities reflect the major food sources in three species of talitrid amphipods. *Comparative Biochemistry and Physiology* 140, 251–257.
- Klaassen F (1975) Ökologische und ethologische Untersuchungen zur Fortpflanzungsbiologie von *Gecarcinus lateralis* (Decapoda, Brachyura). *Forma et Functio* 8, 101–174.
- Krång AS, Knaden M, Steck K and Hansson BS (2012) Transition from sea to land: olfactory function and constraints in the terrestrial hermit crab *Coenobita clypeatus*. *Proceedings of the Royal Society B: Biological Sciences* 279, 3510–3519.
- Lafaix JM (1969) Contribution à l'étude de l'écologie et de la reproduction de *Gecarcinus planatus* Stimpson. *Rapport Particulier* 53, 1–13.
- Liu HC and Jeng MS (2005) Reproduction of *Epigrapsus notatus* (Brachyura: Gecarcinidae) in Taiwan. *Journal of Crustacean Biology* 25, 135–140.
- Liu HC and Jeng MS (2007) Some reproductive aspects of *Gecarcoidea lalandii* (Brachyura: Gecarcinidae) in Taiwan. *Zoological Studies* 46, 347–354.
- López-Victoria M and Werdling B (2008) Ecology of the endemic land crab *Johnngarthia malpilensis* (Decapoda: Brachyura: Gecarcinidae), a poorly known species from the tropical Eastern Pacific. *Pacific Science* 62, 483–493.
- Luque J, Xing L, Briggs DEG, Clark EG, Duque A, Hui J, Mai H and McKellar RC (2021) Crab in amber reveals an early colonization of non-marine environments during the Cretaceous. *Science Advances* 7, eabj5689.
- Marin IN and Tiunov A (2023) Terrestrial crustaceans (Arthropoda, Crustacea): taxonomic diversity, terrestrial adaptations, and ecological functions. *ZooKeys* 1169, 95–162.
- Marques CPM, Magalhães-Júnior AP and Oliveira FS (2019) Hidrogeomorfologia da Ilha da Trindade: a única rede hidrográfica permanente nas ilhas oceânicas brasileiras. *Revista Brasileira de Geomorfologia* 20, 317–338.
- Melo GAS (1996) *Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro*. São Paulo: Plêiade/FAPESP.
- Micheli F, Gherardi F and Vannini M (1991) Feeding and burrowing ecology of two East African mangrove crabs. *Marine Biology* 111, 247–254.
- MMA - Ministério do Meio Ambiente (2022) Portaria do Ministério do Meio Ambiente (MMA) nº 148, de 07 de junho de 2022. Atualiza a lista oficial de espécies da fauna e flora ameaçadas de extinção. Diário Oficial da União, 108 (08/06/2022), Seção 1, p. 74.
- Molina-Ortega MG and Vázquez-López H (2018) Crecimiento relativo de *Cardisoma crassum* Smith, 1870 (Decapoda: Gecarcinidae) en el estero El

- Salado, Puerto Vallarta, Jalisco México. *Biología, Ciencia y Tecnología* **11**, 808–823.
- Nordhaus I, Salewski T and Jennerjahn TC** (2017) Interspecific variations in mangrove leaf litter decomposition are related to labile nitrogenous compounds. *Estuarine and Coastal Shelf Science* **192**, 137–148.
- Novais WRR, Carvalho FL and Couto ECG** (2021) Conservation of the endangered blue land crab *Cardisoma guanhumi* Latreille in Latreille, Le Peletier, Serville & Guérin, 1828 (Decapoda: Brachyura: Gecarcinidae) in Brazil: optimal habitats and environmental factors. *Journal of Crustacean Biology* **41**, 1–12.
- O'Dowd DJ and Lake PS** (1989) Red crabs in rain forest, Christmas Island: removal and relocation of leaf-fall. *Journal of Tropical Ecology* **5**, 337–348.
- Ogle DH, Doll JC, Wheeler AP and Dinno A** (2023) FSA: Simple Fisheries Stock Assessment Methods. R package version 0.9.4. Available at <https://cran.r-project.org/web/packages/FSA/index.html>
- Oliveira TSD** (2014) *Modificações esqueléticas e apendiculares torácicas para captação de água do solo em caranguejos semiterrestres (Crustacea: Brachyura: Grapsoidea: Ocypodoidea)*, Mestrado em Sistemática, Taxonomia Animal e Biodiversidade. Universidade de São Paulo, São Paulo.
- Perger R** (2014) The land crab *Johngarthia planata* (Stimpson, 1860) (Crustacea, Brachyura, Gecarcinidae) colonizes human-dominated ecosystems in the continental mainland coast of Mexico. *Biodiversity Data Journal* **2**, e1161. <https://doi.org/10.3897/BDJ.2.e1161>
- Pinheiro MAA and Fiscarelli AG** (2009) Length-weight relationship of the carapace and condition factor of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae). *Brazilian Archives of Biology and Technology* **52**, 397–406.
- Pinheiro MAA, Santana W, Rodrigues ES, Ivo CTC, Santos LCM, Torres RA, Boos H and Dias-Neto J** (2016) Avaliação dos caranguejos gecarcinídeos (Decapoda: Gecarcinidae). In Pinheiro MAA and Boos H (eds), *Livro Vermelho dos Crustáceos do Brasil: Avaliação 2010–2014*. Porto Alegre: Sociedade Brasileira de Carcinologia – SBC, pp. 167–181.
- Pinheiro MAA, Souza FVB, Boos H and Duarte LFA** (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.
- Pires GLC, Mansur KL and Bongioiolo EM** (2013) Geoconservação da Ilha da Trindade: Principais aspectos e potencial de uso. *Anuário do Instituto de Geociências UFRJ* **36**, 96–104.
- Price PW, Denno RF, Eubanks MD, Finke DL and Kaplan I** (2011) *Insect Ecology: Behavior, Populations, and Communities*. New York: Cambridge University Press.
- Rajendran S, Silcock P and Bremer P** (2023) Flavour volatiles of fermented vegetable and fruit substrates: a review. *Molecules* **28**, 3236.
- R Core Team** (2022) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at <https://www.r-project.org/>
- Santana W and Coelho P** (2018) *Johngarthia lagostoma* (H. Milne Edwards, 1837). In Instituto Chico Mendes de Conservação da Biodiversidade (Org) *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção*. Brasília: ICMBio, pp. 439–441.
- Sanvicente-Añorve L, Lemus-Santana E and Solís-Weiss V** (2016) Body growth pattern of an isolated land crab species (*Johngarthia planata*) (Decapoda, Gecarcinidae) from the eastern tropical Pacific: an ecological approach. *Crustaceana* **89**, 1525–1539.
- Schmidt AJ and Diele K** (2009) First field record of mangrove crab *Ucides cordatus* (Crustacea: Decapoda: Ucididae) recruits co-inhabiting burrows of conspecific crabs. *Zoologia* **26**, 792–798.
- Schories D, Bergan AB, Barletta M, Krumme U, Mehlig U and Rademaker V** (2003) The keystone role of leaf-removing crabs in mangrove forests of North Brazil. *Wetland Ecology and Management* **11**, 243–255.
- SECIRM - Secretaria Interministerial para os Recursos do Mar** (2017) *Protrindade: Programa de Pesquisas Científicas na Ilha da Trindade. 10 Anos de Pesquisas*. Brasília: SECIRM.
- Simith DJB, Diele K and Abrunhosa FA** (2010) Influence of natural settlement cues on the metamorphosis of fiddler crab megalopae, *Uca vocator* (Decapoda: Ocypodidae). *Academia Brasileira de Ciências* **82**, 313–321.
- Sokal RR and Rohlf FJ** (2012) *Biometry: The Principles and Practice of Statistics in Biological Research*, 4th Edn. New York: WH Freeman and Company.
- Tavares M and Mendonça JB** (2022) Brachyuran crabs (Crustacea, Decapoda) from the remote oceanic Archipelago Trindade and Martin Vaz, South Atlantic Ocean. *Zootaxa* **5146**, 1–129.
- Teixeira AL** (1996) Aspectos biológicos do caranguejo terrestre *Gecarcinus lagostoma* (H. M. Milne Edwards, 1837) no Atol das Rocas - Brasil (Master Dissertation). Universidade Federal de Pernambuco, Recife, Brazil.
- Tongununui P, Kuriya Y, Murata M, Sawada H, Araki M, Nomura M, Morioka K, Ichie T, Ikejima K and Adachi K** (2021) Mangrove crab intestine and habitat sediment microbiomes cooperatively work on carbon and nitrogen cycling. *PLoS ONE* **16**, e0261654.
- Tsang LM, Schubart CD, Ah Yong ST, Lai JCY, Au EYC, Chan TY, Ng PKL and Chu KH** (2014) Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution* **31**, 1173–1187.
- Turner LM, Hallas JP and Morris S** (2011) Population structure of the Christmas Island blue crab, *Discoplax hirtipes* (Decapoda: Brachyura: Gecarcinidae) on Christmas Island, Indian Ocean. *Journal of Crustacean Biology* **31**, 450–457.
- Twilley RR, Pozo M, Garcia VH, Rivera-Monroy VH, Zambrano R and Boderó A** (1997) Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. *Oecologia* **111**, 109–122.
- Vannini M, Berti R, Cannicci S and Innocenti G** (2003) *Cardisoma Carnifex* (Brachyura): where have all the babies gone? *Journal of Crustacean Biology* **23**, 55–59.
- von Fimpel E** (1975) Phänomene der Landadaptation bei terrestrischen und semi terrestrischen Brachyura der brasilianischen Küste (Malacostraca, Decapoda). *Zoologische Jahrbucher* **102**, 173–214.
- Waldrop LD, Miller LA and Khatri S** (2016) A tale of two antennules: the performance of crab odour-capture organs in air and water. *Journal of The Royal Society Interface* **13**, 20160615.
- Watson-Zink VM** (2021) Making the grade: physiological adaptations to terrestrial environments in decapod crabs. *Arthropod Structure & Development* **64**, 101089.
- Webb GE** (1922) Notes on some young stages of *Gecarcoidea lalandii*, Milne Edwards. *Annals and Magazine of Natural History* **9**, 530–534.
- Wolcott TG** (1984) Uptake of interstitial water from soil: mechanisms and ecological significance in the ghost crab *Ocypode quadrata* and two gecarcinid land crabs. *Physiological Zoology* **57**, 161–184.
- Wolcott TG** (1988) Ecology. In Burggreen WW and McMahon BR (eds), *Biology of the Land Crabs*. New York: Cambridge University Press, pp. 55–96.
- Wolcott DL and de Vries MC** (1994) Offshore megalopae of *Callinectes sapidus*: depth of collection, molt stage and response to estuarine cues. *Marine Ecology Progress Series* **126**, 655–661.
- Wolcott DL and Wolcott TG** (1984) Food quality and cannibalism in the red land crab, *Gecarcinus lateralis*. *Physiological Zoology* **57**, 318–324.
- Wolcott DL and Wolcott TG** (1987) Nitrogen limitation in the herbivorous land crab *Cardisoma guanhumi*. *Physiological Zoology* **60**, 262–268.
- Wolfe JM, Ballou L, Luque J, Watson-Zink VM, Ah Yong ST, Barido-Sottani J, Chan T, Chu KH, Crandall KA, Daniels SR, Felder DL, Mancke H, Martin JW, Ng PKL, Ortega-Hernández J, Theil EP, Pentcheff ND, Robles R, Thoma BP, Tsang LM, Wetzer R, Windsor AM and Bracken-Grissom HD** (2022) Convergent adaptation of true crabs (Decapoda: Brachyura) to a gradient of terrestrial environments. *Systematic Biology* **73**(2), 247–262. <https://doi.org/10.1093/sysbio/syad066>.