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Original Article

Notes on the fecundity of the caridean shrimp *Cuapetes americanus* (Kingsley, 1878) in two preserved areas in São Paulo State: Laje de Santos and Vitória Island

Isabela Ribeiro Rocha de Moraes[1] orcid.org/0000-0003-2889-9356
Marcia Rafaela Ramos Trevisan[1] orcid.org/0000-0002-7442-7619
Gabriel Fellipe Barros Rodrigues[1] orcid.org/0000-0002-1679-9270
Alexandre Ribeiro da Silva[2] orcid.org/0000-0001-8921-8767
Antonio Leão Castilho[1] orcid.org/0000-0003-0001-9054

1 Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), Instituto de Biociências de Botucatu, LABIAQUA- Laboratório de Biologia de Invertebrados Aquáticos, Programa de Pós-Graduação em Ciências Biológicas (Zoologia). Rua Prof. Dr. Antônio Celso Wagner Zanin, 250 - Distrito de Rubião Júnior. 18618- 689, Botucatu, São Paulo, Brasil.
IRRM E-mail: isabela.moraes@unesp.br
MRRT E-mail: ramos.trevisan@unesp.br
GFBR E-mail: gabriel.fb.rodrigues@unesp.br
ALC E-mail: antonio.castilho@unesp.br

2 Universidade de São Paulo, Museu de Zoologia. São Paulo, São Paulo, Brazil
ARS E-mail: alers.dino@gmail.com

ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub:537E4E67-3F12-48B6-9F0E-0544088EC52C

Corresponding Author
Isabela Ribeiro Rocha de Moraes
isabela.moraes@unesp.br

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Abstract

In the Atlantic Ocean, the shrimp *Cuapetes americanus* (Kingsley, 1878) is well distributed. This species has been studied regarding its taxonomic status, distribution records, and some biological and reproductive traits. However, its fecundity and reproductive aspects have never been evaluated in Brazilian waters before. SCUBA (Self Contained Underwater Breathing Apparatus) diving and Artificial Refuge Substrate were used to sample *C. americanus* specimens quarterly in a sheltered location in the Marine State Parks of Laje de Santos and Vitória Island for a year (2015–2016). A total of 45 animals (carapace length 1.35–4.54 mm) were sampled: 6 females; 18 ovigerous females; 3 juveniles; and 17 males. The major axis references were employed to analyze the relationship between the second pleura (SPL) and the carapace length (CL). The fecundity was 87.05 ± 80.50 eggs and it was similar to other populations connected to it, and it was exclusively associated favorably with CL. Despite being a small and inconspicuous species, *C. americanus* is a caridean shrimp species that has evolved to thrive and breed on continental islands. The importance of the creation and revision of management plans for no-take marine areas on the Brazilian coast is supported when many kinds of information about the ecology and biology of the species are available, such as caridean shrimps, which can be present as a link between trophic levels of the aquatic food web.

Keywords
Crustacean, embryo, no-take areas, Palaemonidae, reproduction

Introduction

Cuapetes americanus (Kingsley, 1878), a caridean shrimp, was first described as *Anchistia americana* by Kingsley (1878) and has since undergone numerous taxonomic revisions, with at least four synonymic names. The last one, *Kemponia americanus* (Bruce, 2004) was recently changed to the genus *Cuapetes* (Okuno, 2009). It is a marine shrimp from the family Palaemonidae that is distributed in the Western Atlantic Ocean, from North Carolina (USA) to São Paulo (Brazil) (Williams, 1984; Ramos-Porto and Coelho, 1998; Almeida et al., 2012, Moraes et al., 2021).

It is considered a tiny and translucent shrimp that is found in association with many invertebrate species, in seagrass beds, or even free-living in consolidated substrates (Román-Contreras and Martínez-Mayén, 2010; Giraldes et al., 2015; Negri et al., 2017). This species has been studied regarding its taxonomic status, distribution records, and biological and reproductive traits (Martínez-Mayén and Román-Contreras, 2014; Negri et al., 2017). Despite being ubiquitous in Brazilian waters, the fecundity and reproductive aspects of this species have never been evaluated before.

This species is reported from continental islands on the Brazilian coast and has been specially recorded from marine protected areas in São Paulo State (Giraldes et al., 2015; Moraes et al., 2021), an important fact since preserved areas aim to maintain biodiversity and manage natural resources at all ecological levels (Balmford et al., 2002; Gamarra et al., 2019). Furthermore, caridean shrimps are an important component of the trophic structure and aquatic food webs (Bauer, 1985; Amaral and Nallin, 2011). *Cuapetes americanus* populations that are well-structured can suggest a well-preserved location and be used as a reference for biological elements of the faunal composition of no-take marine environments.

The Marine State Park of Laje de Santos (MSPLS) was the first region in São Paulo State considered a "No-Take" marine area, and it is a very representative location, due to the presence of local and migratory species. Evaluations regarding MSPLS biodiversity, such as checklist records and ecological features from its species have been recently made (Luiz et al., 2008; Moraes et al., 2021; 2022; da Silva et al., 2019). The Vitória Island (VI) belongs to the Ilhabela Archipelago, which is also a marine protected region, but with particular characteristics because it is used for subsistence by a small local fishing community (OCA, 2015). The checklist and ecological evaluation of other crustacean animals has been published in Vitória Island literature (Alves et al., 2011, 2012; Moraes et al., 2021).

In both regions, most of the effort made in studying the crustacean fauna is focused on checklists and ecological features. There are 13 species of caridean shrimps registered for Vitória Island and 12 in Laje de Santos. *Alpheus formosus* Gibbes, 1850 and *C. americanus* are the most represented species with at least 30% of all specimens recorded. Only one of these species, *A. formosus*, was previously studied for population and reproductive features, and it is the only study, other than species composition, providing information on how the population of one of the most significant species is regulated (Moraes et al., 2020).

The aim of the present study is to evaluate the fecundity of *C. americanus* in two preserved areas in São Paulo State, Brazil, by linking morphological features with the number of embryos attached to female pleopods. Crucial biological information on the reproductive capacity and stock size of decapod crustaceans at important locations, such as no-take marine regions, is also provided.

Material and Methods

Sample methods

All specimens were sampled quarterly for one year (2015–2016) in sheltered areas of MSPLS (24° 15′S 46°10’W) and Vitória Island (23°44′S 45°01′W), using SCUBA. Capture methods, included both passive (Artificial Refuge Substrate) and active (visual search and manually capture). At each site, five Artificial Refuge Substrates (ARS) were placed and attached to natural substrates at the maximum depth of each rocky shore (20 m and 12 m at MSPLS and VI respectively). The ARS were placed in sites where cryptic animals (such as *C. americanus*) are commonly found, such as crevices, fissures, and cavities in the rocky bottom. The ARS were left in the field for three months. After this period, all ARS were retrieved, placed in sealed bags, and replaced with new ones until sampling was completed after one year. Concurrent with the ARS installation and retrieval, two SCUBA divers actively searched for specimens on the rocky bottom where the ARS were installed, totaling 4 hours of catching effort per expedition (Fig. 1). Details of the sample methods are provided in Moraes et al. (2020; 2021; 2022).

Collected specimens of *C. americanus* (Fig. 2) were immediately bagged individually, in situ, and frozen to preserve morphological and color integrity. They were then transferred to the laboratory of the São Paulo State University, Campus Botucatu, where all

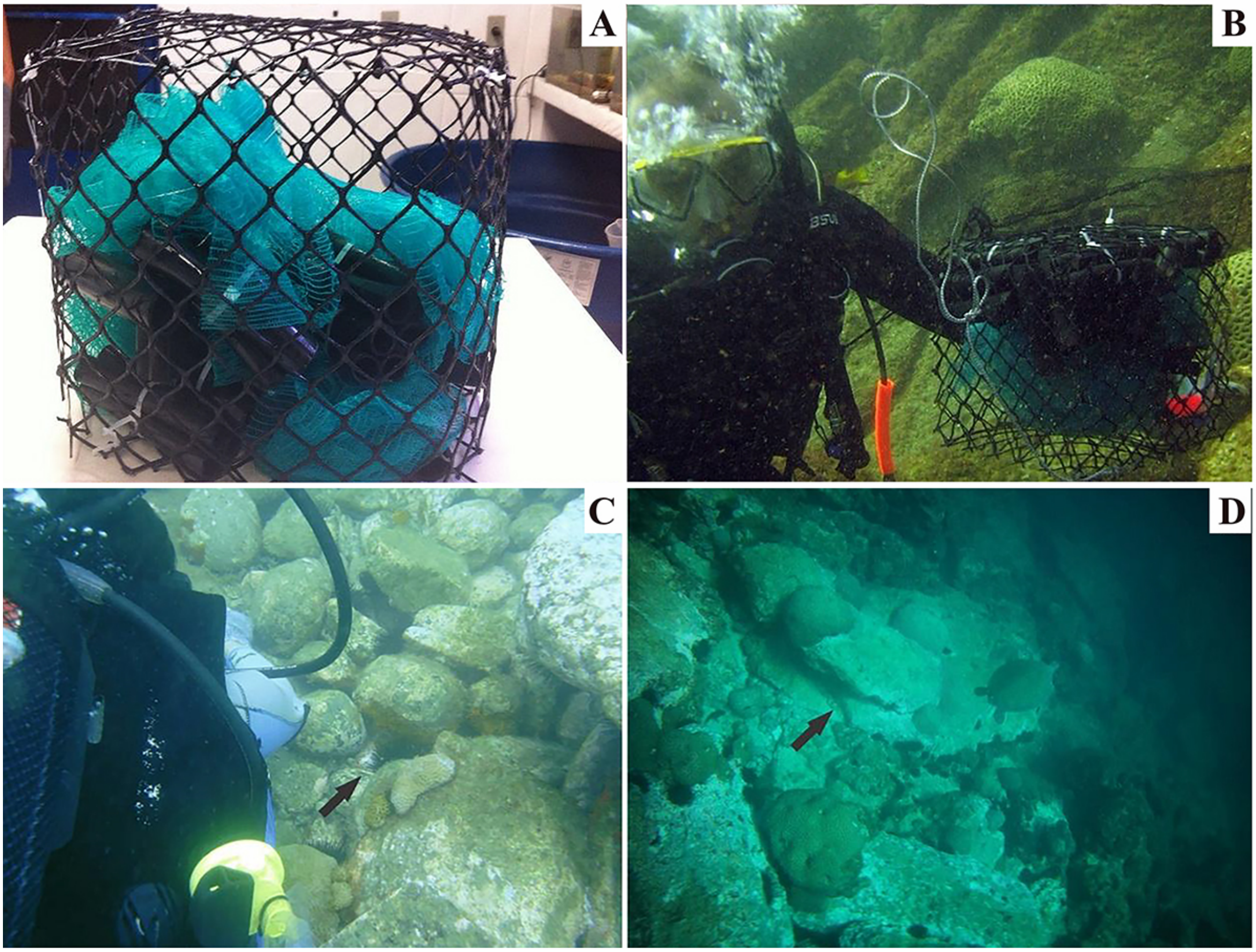

Figure 1. Sampling methods of the present study. A) Artificial Refuge Substrates (ARS) ready for installation; B) ARS being installed between rocks by the SCUBA diver; C) Rocky subtidal zone of Vitória Island. Arrow points to the exact location where the ARS were installed; D) Rocky subtidal zone of Laje de Santos. Arrow points to the exact location where the ARS were installed.

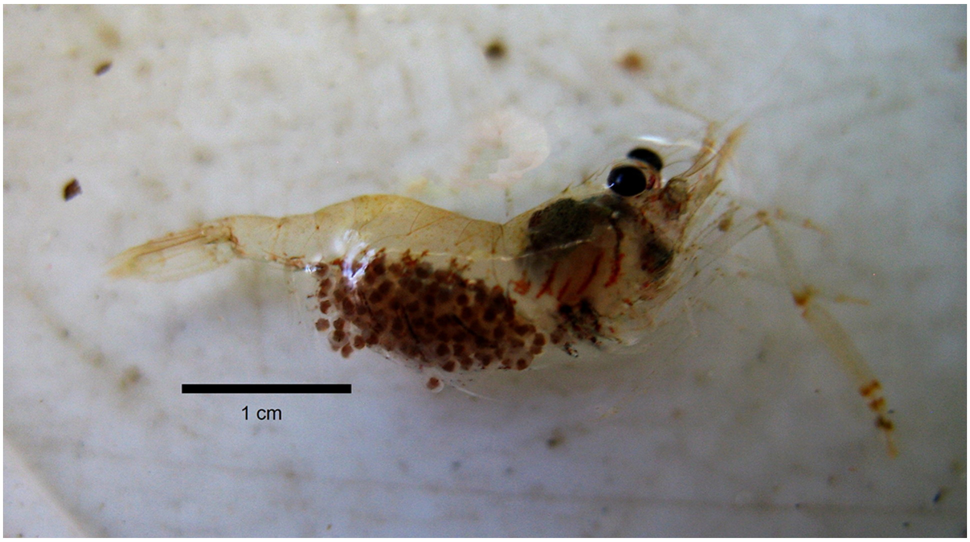

Figure 2. Lateral view of the studied species *Cuapetes americanus* (Kingsley, 1878). Ovigerous female sampled in the Marine State Park of Laje de Santos (MSPLS).

specimens are now deposited. All specimens were identified in the laboratory using the taxonomic key proposed by Chace (1972).

Animals were sexed according to the morphology of secondary sexual characteristics, such as the presence of the male appendix associated with the endopod of the second male pleopod (M) or the presence of the internal appendix in the same region for females (F). Individuals without well-defined gonopore regions were defined as juveniles (J) and ovigerous females (OF) were identified by the presence of embryos adhered to the pleopods of the abdominal region (Bauer, 2004).

The carapace length (CL) of shrimps was measured from the orbital angle to the posterior margin of the carapace. The second pleura length (SPL) was also measured from each lateral of the abdominal segment. To evaluate fecundity, only females with non-damaged embryos were used, and the embryos were manually counted using a manual counter. The developmental stage of the eggs was classified into either initial (with no eyes visible) or final (with visible eyes) stages.

Statistical analysis

The relationship between the second pleura and the carapace length was evaluated employing the major axis routine (known as Type II linear regression) through the SMATR package (Warton et al., 2012) in R (R Core Team, 2021). This routine is recommended for allometric evaluations because it decreases the effect of residuals, providing a better fitting line for this type of relationship (Warton et al., 2006). The following demographic groups were tested: males, females, ovigerous females, and juveniles.

The data were log-transformed before analysis, and the elevation (a) and slope (b) were tested for differences between groups. The allometric relationships were examined by pooling data from both locations (MSPLS and VI) due to the small number of individuals. Additionally, linear mixed models (LMM) were created to test whether fecundity (explanatory variable) and both SPL and CL (response variables) were related, in which the location was treated as a random effect to control the geographic singularities of population features. The package "lme4" (Bates et al., 2015) was installed in the statistical program R (R Core Team, 2021) and used to create LMM models.

Results

Of the 45 total animals collected and analyzed, 30 were from MSPLS, including 12 M, 3 F, 3 J, and 12 OF (10 with eggs at the initial stage and 2 with eggs at the final stage of development) and 5 M, 4 F, and 6 OF (all with eggs at the initial stage) were from VI (Fig. 3). Considering the pooled data from both regions, the carapace length varied from 1.35–4.54 mm, and males tended to reach slightly larger sizes than females, with a mean CL size of 3.32 ± 0.87 and 3.24 ± 0.91 mm, respectively. The fecundity varied from 8 to 291 embryos attached to pleopods with a mean of 87.05 ± 80.50. Analyzing data the independently, females from Laje de Santos reached a mean fecundity number of 100.58 ± 84.36 embryos (ranging from 21 to 291), and on Vitória Island with a lower number of females sampled, the mean fecundity was 52 ± 67.75 (ranging from 8 to 185).

The analysis showed a positive relationship between CL and SPL for all groups ($p < 0.05$), but we found differences in the elevation lines between groups ($p < 0.05$), i.e., OF were different from the others. However, there was no difference regarding the slopes ($p > 0.05$) (Fig. 4). Fecundity was positively associated with CL (Estimate = 1.58, *t-value* = 2.07, $p = 0.042$), while SPL was not associated with fecundity (Estimate = 2.02, *t-value* = 1.70, $p = 0.089$) (Fig. 5).

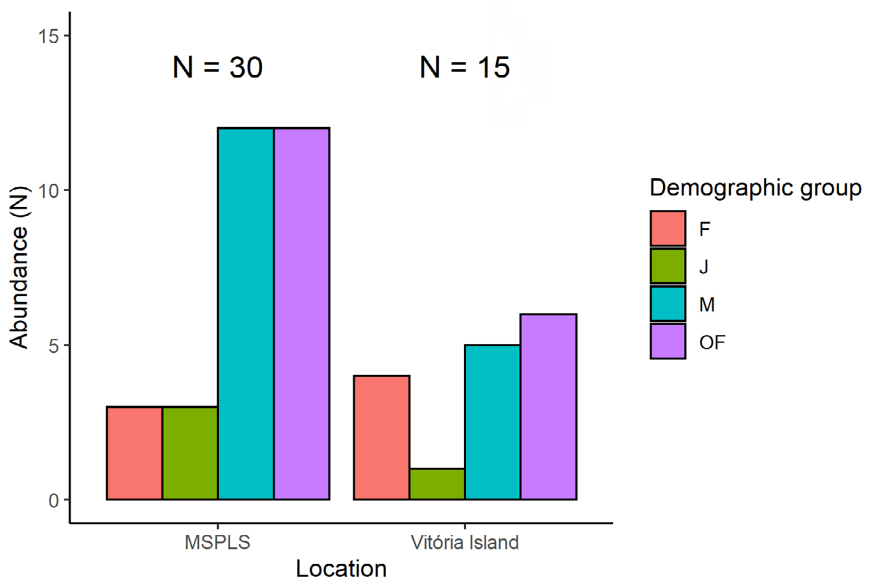

Figure 3. Bar plots of demographic groups of the studied species *Cuapetes americanus* (Kingsley, 1878) in both Laje de Santos and Vitória Islands region.

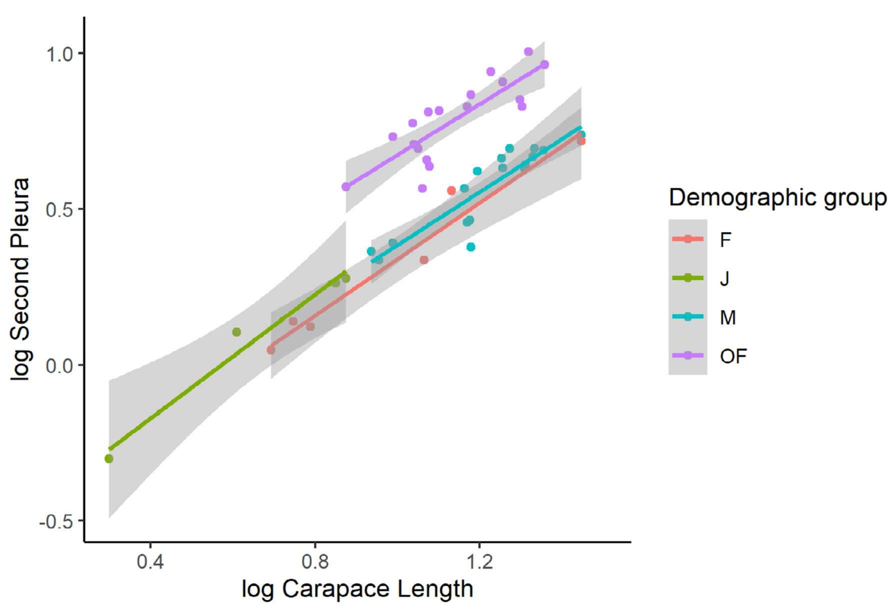

Figure 4. Scatter plot by demographic groups representing the linear relationship between second pleura and carapace length. F: females, OF: ovigerous females, J: juveniles, M: Males.

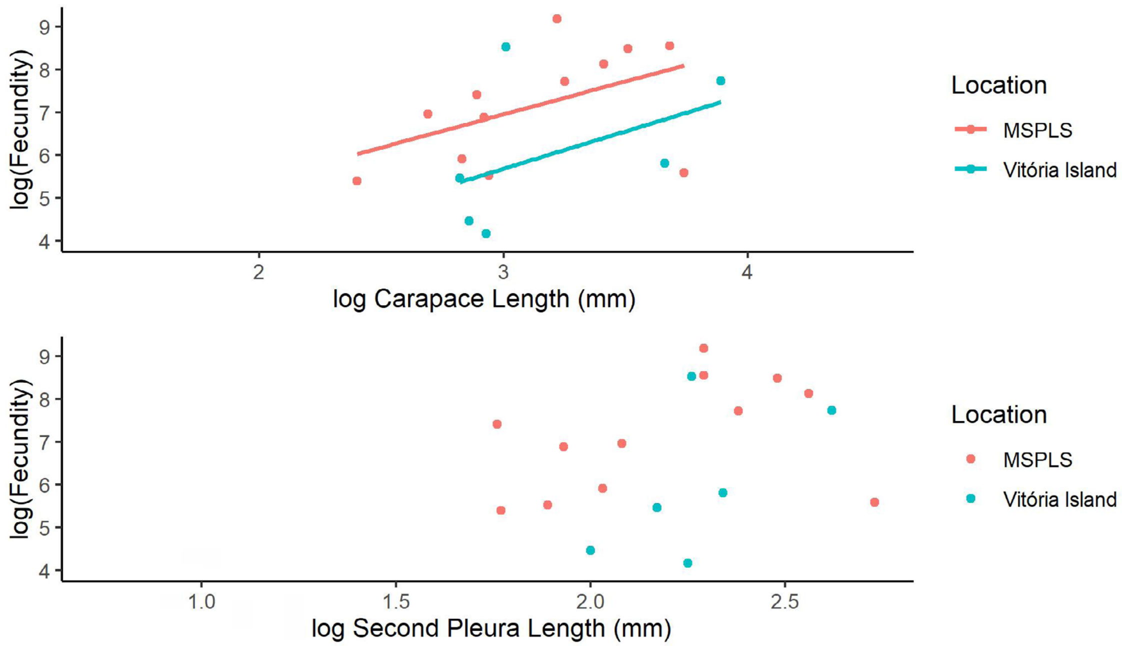

Figure 5. Fitted linear mixed models (LMM) for the relationship between both carapace length (CL) and second pleura length (SPL), and fecundity. Sample locations were treated as random variables. Fitted line indicates a significant relationship.

Discussion

Our results help to elucidate information on the fecundity of an cryptic shrimp living in, and dependent on, protected regions. Despite being considered "cryptic," as hard to find translucent animals that live under rocks, *C. americanus* form small, but well-established, populations at both Laje de Santos and Vitória Island regions (Moraes et al., 2021).

Specimens analyzed in the present study reach bigger sizes (considering carapace length) than populations studied from the Caribbean Sea, with most OF being around 3 mm CL, but their fecundity is very close to other populations of the same species, and other closely related shrimps (Tab. 1) (Zimmermann et al., 2015).

Looking at the present results and past literature records (Tab. 1), we can propose that fecundity can be related in part to female size (CL), but also to physiological features and energy production that depend mostly on the environment to which the animals are exposed. In the same way, as described by Wenner and Dugan (1991), we believe that decapods of the same size can present different patterns of fecundity in some cases. Despite the fact that associated structures (such as CL and pleura diameters) can be analyzed separately, those factors can also be correlated with food availability, or intrinsic aspects of the environment, since these will impact energy supply and proteins to make and maintain viable embryos (Bauer, 2004).

The low fecundity of *C. americanus* matches with other Palaemonidae shrimps such as the genus *Periclimenes* (Tab. 1). This trait is not uncommon in nature, especially in neotropical species that are normally capable of reproducing continuously throughout the year, and it is likely that *C. americanus* specimens from the localities studied here exhibit the same reproductive pattern. This low fecundity could be compensated for by simultaneous spawning (Martínez-Mayén and Román-Contreras, 2009).

The embryos of *Periclimenes* and *Cuapetes* species are generally lower in number and size than other Palaemonidae. Corey and Reid (1991), evaluating fecundity in more than 20 caridean shrimp species, pointed out that despite their low number, the embryos of these species tend to be bigger in size during ontogeny, and the CL size tends to strongly correlate with embryo volume. We were not able to test embryo volume for *C. americanus* in the present

Table 1. Comparative fecundity between Palaemonidae marine species. All data gathered were from animals in stage I of embryo development (modified from Moraes et al., 2017). CL: Carapace Length, SD: standard deviation.

Species	Number of Individuals	CL mm (Average ± SD)	Fecundity (Average ± SD)	Locality	Reference
Cuapetes americanus (Kingsley, 1878)	18	2.90 ± 0.91	87.05±80.50	Marine State Park of Laje de Santos and Vitória Island, São Paulo, Brazil	Present study
	345	2.20 ± 0.23	47 ± 21	Bahía de la Ascensión, Quintana Roo, Mexico	Martínez-Mayén and Román-Contreras (2014)
	46	2.07 ± 0.36	75.84 ± 40.16	Cólon Island, Bocas del Toro, Panama	Negri et al. (2017)
	99	2.1 ± 0.2	56 ± 27	Dorado, north coast of Puerto Rico.	Bauer (1991)
	9	2-28 – 3.88 (range)	76 – 519 (range)	Seahorse Key - Florida	Corey and Reid (1991): as *Periclimenes americanus*
Phycomenes siankaanensis (Martinez-Mayén and Román- Contreras, 2006)	100	1.91 – 3.2	23 – 141	Bahia de la Ascensión, Quintana Roo, Mexico	Martínez-Mayén and Román-Contreras (2009) as *Periclimenes siankaanensis*
Periclimenes paivai (Chace, 1969)	65	4.54 ± 0.48	229 ± 120.04	Santos Bay, and Santos and São Vicente Estuaries, São Paulo, Brazil	Moraes et al. (2017)
Periclimenes rathbunae (Schmitt, 1924)	70	4.2 ± 0.6	289 ± 120	Puerto Viejo-Punta Mona, Caribbean coast of Costa Rica	Azofeifa-Solano et al. (2014)

study. In this regard, Martínez-Mayén and Romero-Rodríguez (2018), looking into the population of a closely related *Urocaris* species, registered one example of a small CL species presenting greater fecundity and pointed out the same pattern discussed here that the embryo number and volume can be the result not only of morphological features but also of some ecological and genetic reproductive output.

The species studied here kept the same morphological relationship between the carapace length and second pleura width as seen in the Infraorder Caridea. We observed a clear difference between the elevation lines (Fig. 4), with OF forming a particular pattern and being well separated from the other categories, such as M and non-OF. The second pleura becoming bigger at the time of egg spawning in OF is one of the strategies for the so-called "breeding dress," which involves changes in body morphology and size. The females have a "chamber" in their abdomen to protect and oxygenate their offspring (Bauer, 2004; Baeza, 2018). Despite being cryptic and small, we can observe *C. americanus* as a caridean shrimp that is well-adapted to different habitats and can use strategies, such as body morphology modulation and spawning, to survive and reproduce on neotropical continental islands.

The structural patterns mentioned above are not exclusive to the Palaemonidae. Alpheidae shrimps of the genus *Salmoneus,* studied by Oliveira et al. (2018), present a great correlation between fecundity and abdominal structures such as pleura and sternites, which are used to form the incubation chamber. Comparing the characteristics presented by a small species such as *Salmoneus*, which match with the size and ecological distribution of *Cuapetes*, we encourage future studies to look into more multidisciplinary approaches in order to evaluate the fecundity of female caridean shrimps: CL size, abdominal structures (in linear, morphometric, or volume perspectives), as well as the environmental characteristics that may directly influence the number of embryos that a female can carry on the abdomen and pleopods.

The Linear mixed models (LMM–Fig. 5) provide information about the growing pattern of structures on the female related to fecundity. The number of embryos attached to pleopods seems to be better related to CL size, for example. Despite the importance of the second pleura in the incubation process, the linear measure of the pleura width does not reflect this influence on fecundity numbers in OF as well as CL does. It can be influenced by the small sample size, and also by the linear measurement that is used in most studies, such as the present one. In future studies with this species, we suggest that researchers analyze other structures that compose the changes in the bodies of OF, as proposed for some Alpheidae shrimps, and not only use linear features, but evaluate the shape of these structures as well (Costa-Souza et al., 2019).

These reproductive features of *C. americanus* are also related to other factors, from genetic aspects, parental reproductive output, and latitudinal variation to local predation pressure (Bauer, 2004). As proposed by Moraes et al. (2017) for *Periclimenes* species associated with scyphozoan jellyfish, ecological linkages, such as symbiosis, have strong influences on fecundity and reproductive output. They can be considered as ecological parameters for some under-evaluated groups, such as shrimps of the genus *Periclimenes* and *Cuapetes*, that are under continuous systematic modification (Martínez-Mayén and Román-Contreras, 2009; Martínez-Mayén and Romero-Rodríguez, 2018).

It is essential to maintain no-take marine regions, such as the MSPLS and the State Park of Ilhabela, including Vitória Island, to guarantee the reproduction of these low fecundity species that greatly depend on a well-established area to complete their life cycle and maintain population structures and ecological balance (Lester et al., 2009; Rolim et al., 2019).

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Additional Information and Declarations

Author contributions

Conceptualization and Design: IRRM, MRRT. Performed research: IRRM, MRRT, GFBR, ALC, ARS. Acquisition of data: IRRM, MRRT, GFBR, ALC. Analysis and interpretation of data: IRRM, MRRT, GFBR, ALC, ARS. Preparation of figures/tables/maps: IRRM, MRRT, GFBR. Writing - original draft: IRRM, MRRT, GFBR. Writing - critical review & editing: IRRM, GFBR, ALC, ARS.

Consent for publication

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

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Conflicts of interest

The authors have no conflicts of interest to declare.

Data availability statement

All data generated and analyzed during this study are presented in this article.

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