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Original Article

Dynamics of a subtropical population of the purse crab *Persephona punctata* (Decapoda: Brachyura: Leucosiidae) in Southeastern Brazil

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Abstract

This study investigated the population dynamics of *Persephona punctata* with emphasis on population structure, sex-ratio, spatial distribution, maturity and reproductive period. Crabs and environmental factors (*i.e.*, water temperature and salinity, and sediment texture and organic matter content) were collected monthly, from July 2012 to June 2014 in four sites within the Federal Environmental Protection Area of Cananéia-Iguape-Peruíbe: located in the oceanic area adjacent to the Cananéia region. The population had a female-biased sex-ratio. *Persephona punctata* had a seasonal reproduction and the higher percentage of ovigerous females (OF) occurred in spring and summer. There was a positive correlation ("lag 0") between temperature and number of OF (cross-correlation, $p < 0.05$) and a negative correlation between salinity and OF ("lag-2"), suggesting that periods of higher salinity may be favorable to larval hatching. The estimated size (carapace width — CW_{50}) at the onset of gonadal maturity of males (35.0 mm) was larger than that of females (30.1 mm), which is a common feature of Brachyura. Our results extend the knowledge on the life history of *P. punctata* and may be useful for the development of future mitigation measures aimed at its conservation.

Keywords

Reproductive period, sexual maturity, sex-ratio, population dynamics, Western Atlantic

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Introduction

Leucosiid crabs have been little studied worldwide, mostly due to the small size and rareness of most species, and the lack of economic importance (Almeida *et al.*, 2013; Kobayashi and Archdale, 2017). Crabs of the genus *Persephona* Leach, 1817 play an essential ecological role in the trophic web of benthic environments. In Brazil they are commonly caught as bycatch in marine shrimp fisheries off the southeastern coast (Mantelatto *et al.*, 2016).

Fishing is the main economic activity in Cananéia, in the southern coast of the State of São Paulo, Brazil (Mendonça, 2015). This activity employs a variety of techniques to capture fishes, mollusks, and crustaceans, and especially shrimps, which are the main marine resource of the region (Mendonça, 2015). Given that trawling uses non-selective gear, shrimp and prawn fisheries have a high bycatch rate, which represents 35% of the global commercial fishery discards (Lopes *et al.*, 2017; Varisco *et al.*, 2017). Due to the ineffective implementation of fishery management regulations in tropical and subtropical countries, the bycatch of tropical shrimp fisheries is 3–15 times higher than the captured target species (FAO, 2015). Despite that, in the State of São Paulo the evaluation of the discarded bycatch is still incipient and most studies have focused on the bycatch composition.

The purse crab *Persephona punctata* (Linnaeus, 1758) is one of the most common leucosiid species of the Brazilian coast (Bertini *et al.*, 2001). This species occurs throughout the Western Atlantic, in the Caribbean Sea, the Antilles, Colombia, Venezuela, Guianas, Suriname, and in Brazil (from Amapá to Rio Grande do Sul) (Melo, 1996; Magalhães *et al.*, 2016). Since populations of *P. punctata* have been negatively affected by shrimp trawling, it is imperative to understand the main ecological features of these populations to enable the protection and management of this local marine resource (Branco and Fracasso, 2004; Mantelatto *et al.*, 2016).

In Brazil, studies about *P. punctata* are mostly restricted to the tropical region, such as, Bertini *et al.* (2001) and Pereira *et al.* (2014) that described the spatial-temporal distribution of this specie in Ubatuba, State of São Paulo. Also, Almeida *et al.* (2013) estimated the relative growth, gonadal maturity, and reproductive period of *P. punctata* in Ubatuba, and Carvalho *et al.* (2010) estimated the sexual maturity in Ilhéus, in the state of Bahia. The exception is the study of Perroca *et al.* (2019), which estimated the abundance and distribution of a *P. punctata* population in Cananéia, in the subtropical region.

Compared with other coastal areas of São Paulo, Cananéia stands out due to the presence of an estuarine-lagoon complex constantly influenced by tidal waves and abundant rainfall. The estuary receives water from hundreds of small rivers, which create a mixture of continental and marine waters with salinities that fluctuate seasonally throughout the year (Mishima *et al.*, 1985). Cananéia is located within a United Nations Educational, Scientific and Cultural Organization (UNESCO) Biosphere Reserve (Mahiques *et al.*, 2009), and its biodiversity is well preserved (Diegues, 1987). Aiming to protect this biodiversity and to ensure the sustainable use of its natural resources, the Federal Environmental Protection Area of Cananéia, Iguape and Peruíbe (APA-CIP) was established in 1984 (Mendonça, 2007).

The fisheries management plan for the APA-CIP states that the fisheries agreements (normative instruction IBAMA nº 29/2002) are the management strategies to regulate this activity in the area. In these fisheries agreements, fishing communities come together with representatives of the State Environmental Agency, Brazilian Institute of Environmental and Renewable Natural Resources (IBAMA) and NGOs to define specific rules, in order to regulate fishing in accordance with the interests of the local population and the preservation of fishing stocks. Still, no agreement was installed to regulate the shrimp fisheries. The APA-CIP is one of the largest shrimp producers in the state of São Paulo, with the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) being the most important economic resource. During the period of this study, according to the Fisheries Institute of São Paulo State, approximately 955 ton of this resource was captured by 232 productive entities in Cananéia.

In this study we investigated the population dynamics of *P. punctata* in Cananéia. We described the size frequency distribution, sex-ratio, spatial distribution, size at the onset of gonadal maturity, reproductive period, and estimated the influence of changes in environmental factors on the reproductive period.

Material and methods

Data collection

The samplings took place monthly from July 2012 to June 2014, in the Cananéia lagoon estuarine system, southern coast of the state of São Paulo, Brazil (25ºS, 48ºW). In March 2013 and February 2014 sampling could not be performed due to adverse environmental conditions. Crabs were captured by trawling in four sampling sites in the coastal area adjacent to the Cananéia region (sites S1, S2, and S3 at 10–15 m isobaths and site S4 at 5–10 m isobaths) (Fig. 1). The trawling was done with a shrimp fishing boat equipped with 10 m long double-rig nets (4 m mouth width, 20 mm mesh size, and 18 mm at the cod end). Each trawl was carried out for 30 min at a constant speed of 2.0 knots, covering a total area of approximately 16,000 m². The captured crabs were stored in labelled plastic bags and kept frozen until analysis. In the laboratory, they were identified according to Melo (1996) and separated by sex (Haefner, 1985).

During each trawl, bottom water samples were collected with a Van Dorn bottle (5 L) to record the temperature (mercury thermometer, ºC) and salinity (specific optical refractometer, ‰). Sediment samples were also collected at each site using a Van Veen Grab (area of 0.06 m²) to estimate the sediment grain size distribution, which was expressed in phi (φ) units according to Tucker (1988), and the organic matter content (OM).

The carapace width (CW) of males and females was measured using a caliper (0.1 mm). All crabs were dissected for the macroscopic examination of the gonads. Females (F) and males (M) were classified into four stages of gonadal development, according to the shape, color and volume of the gonads (Bertini *et al.*, 2010), according to the technique proposed by Johnson (1980). The stages were: immature (IM), rudimentary (RU), under development (ED), and developed (DE). Females carrying fertilized eggs were classified as ovigerous females (OF) (Bertini *et al.*, 2010), and immature individuals as juveniles.

Statistical analysis

Population structure and sex-ratio

The population structure was estimated based on the total number of crabs, including all sampling sites and months. The normality of the data was checked with the Shapiro–Wilk test (Zar, 1999). The crabs

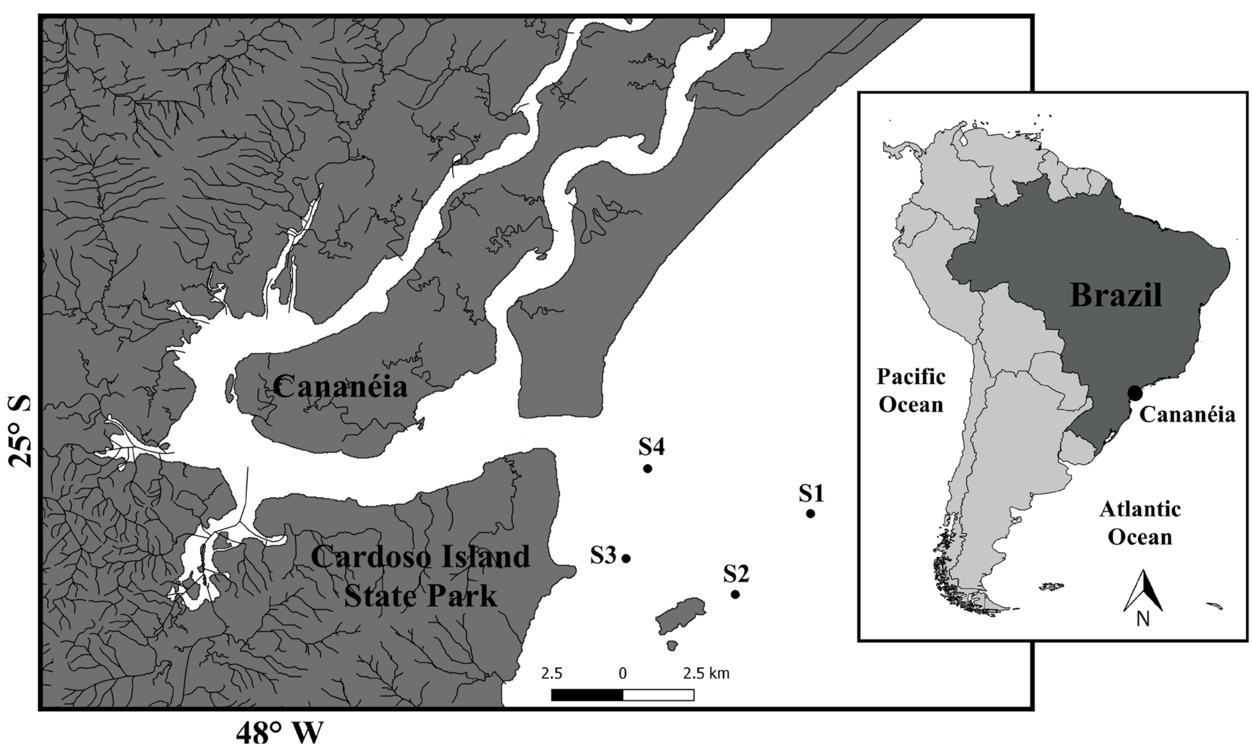

Figure 1. Location of the sampling sites in the coastal marine adjacent areas (S1, S2, S3, S4) in Cananéia, São Paulo, Brazil.

were distributed into 10 size classes, which were established according to Sturges (1926). The mean CW of males and females of the different demographic classes was compared with the Mann-Whitney test ($\alpha < 0.05$) (Zar, 2010). The sex-ratio was estimated as the quotient between the number of males and the total number of crabs captured per month. A sex-ratio higher or lower than 0.5 indicates that the population is skewed towards males or females, respectively (Miazaki *et al.*, 2019). Deviations from the 1:1 sex-ratio were tested using a binomial test ($\alpha = 0.05$) (Wilson and Hardy, 2002; Baeza *et al.*, 2013).

Spatial distribution was evaluated with a one-way ANOVA (Poisson distribution) followed by *a posteriori* Tukey test ($\alpha = 5\%$) in order to verify differences in the total abundance of juveniles, OF and reproductive males between sites. ANOVA was performed separately on each demographic category.

Gonadal sexual maturity

The L_{50} method was used to estimate the size at the onset of gonadal maturity, using the CW as the independent variable and the relative frequencies (%) as the dependent variable. Crabs were distributed into size classes, and the data were fitted to a sigmoid curve following the result of the logistic equation ($y = 1(1+ e^{r(CW-CW_{50})})$), where CW_{50} is the carapace width at which 50% of the crabs reach gonadal maturity, and r is the angular coefficient. The equation was adjusted using the least squares method (Vazzoler, 1996) to estimate the maturity size (CW_{50}) by the interpolation point (50%).

Reproductive aspects

The reproductive period was estimated by the number of ovigerous females relative to the total number of adult females. To investigate a possible relationship between the environmental factors (water temperature and salinity, and sediment grain size distribution and organic matter content) and the reproductive period, a time-series analysis (cross-correlation, Statistica 7.0, StatSoft, Inc) was applied (5% significance level) to estimate a premature or late relationship ("lag") between variables (Zar, 1999; StatSoft, 2004).

Results

Environmental factors

The bottom water temperature ranged from 17.28°C ± 0.04 in July 2013 to 28.67°C ± 0.41 in January 2014 (Fig. 2A). Bottom water salinity ranged from 27.22‰ ± 0.94 in November 2013 to 37.38‰ ± 0.63 in October 2012 (Fig. 2A). Phi ranged from 2.99 ± 0.72 in winter 2012 to 4.59 ±1.01 in the spring of the same year (Fig. 2C). Organic matter content ranged from 2.57% ± 1.13 in winter 2012 to 7.56% ± 6.13 in spring 2012 (Fig. 2C).

Spatially, the mean bottom temperature ranged from 22.50 ºC ± 2.91 in site 1 to 22.74ºC ± 1.99 in site 4 (Fig. 2B). The mean bottom salinity ranged from 33.79 ‰ ± 2.21 in site 2 to 34.32 ‰ ± 1.99 in site 4 (Fig. 2B). Phi varied from 3.52 ± 1.18 in site 2 to 4.77 ± 0.95 in site 4 (Fig. 2D). Organic matter content varied from 3.13% ± 2.37 in site 3 to 3.93% ± 2.71 in site 2 (Fig. 2D).

Population structure

A total of 395 individuals were collected during the two-year sampling period: 299 females (with 249 of them ovigerous, 28 non-ovigerous and 22 juveniles), and 96 males (89 adults and seven juveniles). The CW ranged from 13.4 to 32.13 mm (20.15 mm ± 4.81) in juvenile females, from 26.2 to 35.7 (29.13 mm ± 2.48) in non-ovigerous females, from 21.0 to 37.4 (28.83 mm ± 2.67) in ovigerous females, 15.3 to 26.1 (20.76 mm ± 3.97) in juvenile males and 21.6 to 40.8 (33.20 mm ± 4.60) in adult males. The carapace width differed between males and females ($U = 7680$; $p = 3.32e^{-12}$), with males reaching larger sizes.

The highest absolute frequency of adult males was found in size class 35.5 mm followed by 38.5 mm (Fig. 3). Non-ovigerous females were more abundant in the size class 29.5 mm followed by 26.5 mm, while ovigerous females were more abundant in the size classes 26.5 and 29.5 mm (Fig. 3). Juveniles occupied the size classes 14.5–32.5 mm, but were more abundant up to the class 23.5 mm (Fig. 3).

The seasonal sex-ratio was skewed towards females in all seasons, but the difference was significant only in summer (Binomial test, $p < 0.05$) (Fig. 4A). The sex-ratio of the size classes 20.5, 38.5, and 41.5 mm was biased towards males, whereas in the classes 14.5, 17.5, 26.5, 29.5, and 32.5 it was biased towards females (Binomial test, $p < 0.05$) (Fig. 4B).

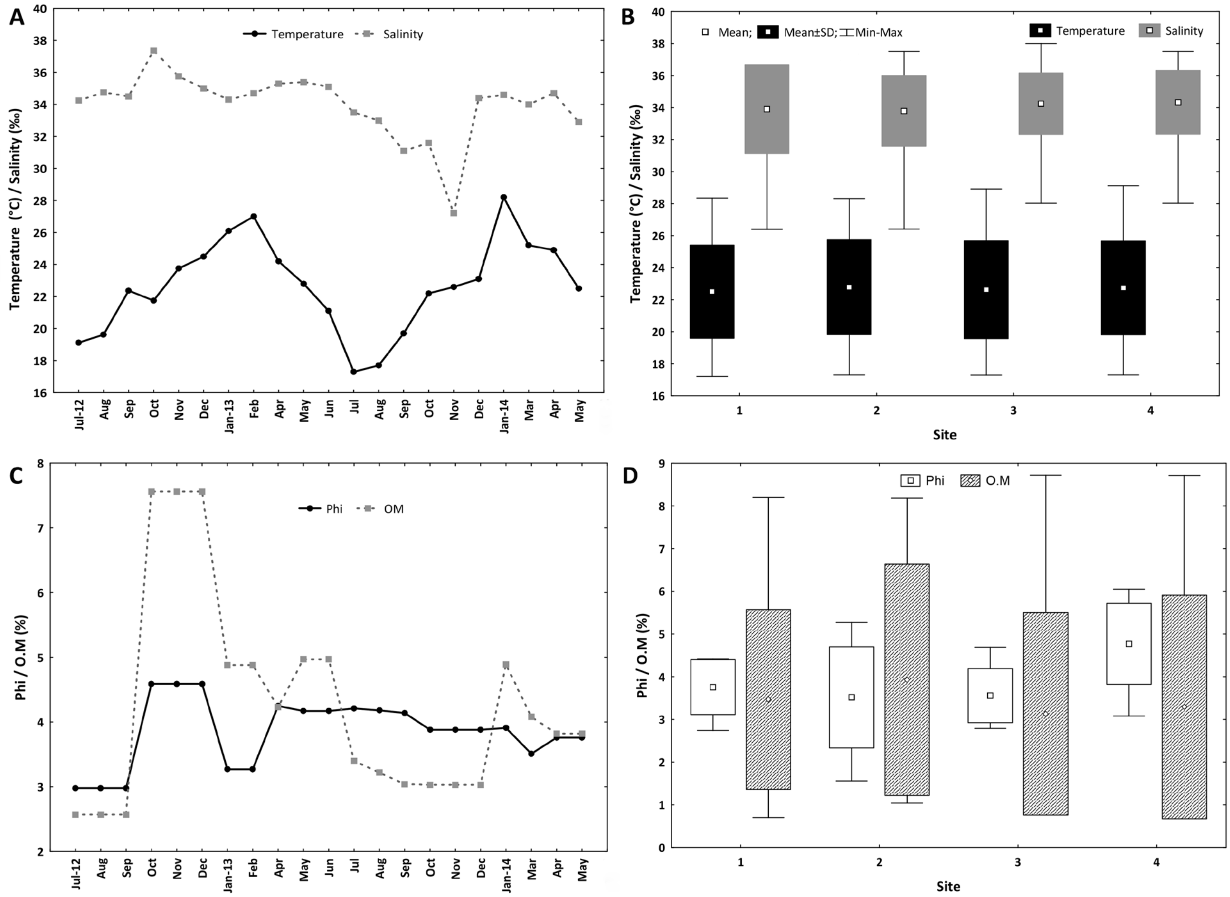

Figure 2. A, Monthly variation of mean values of bottom salinity and temperature; B, Mean values and minimum and maximum amplitudes of bottom salinity and temperature per site; C, Seasonal Phi and organic matter content (OM); D, Mean values and minimum and maximum amplitudes of Phi and OM per site. Abiotic factors were recorded from July 2012 to May 2014 in Cananéia, São Paulo, Brazil. (Mean; SD = standard deviation; Min = minimum; Max = maximum).

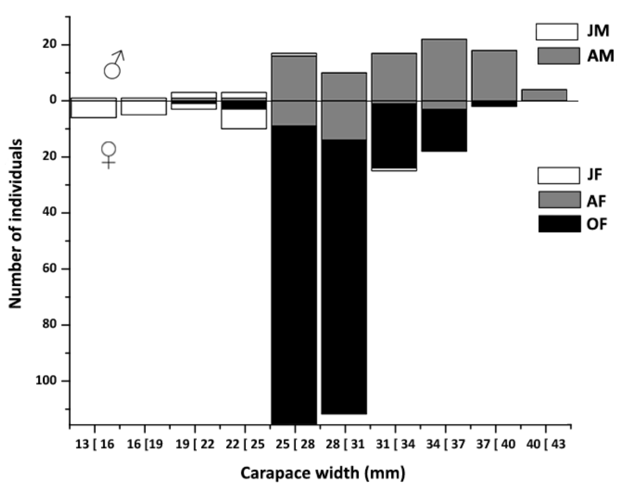

Figure 3. *Persephona punctata* (Linnaeus, 1758). Size-frequency distribution of juvenile males (JM), juvenile females (JF), adult males (AM), non-ovigerous adult females (AF) and ovigerous females (OF), captured monthly from July 2012 to June 2014, in Cananéia, São Paulo, Brazil.

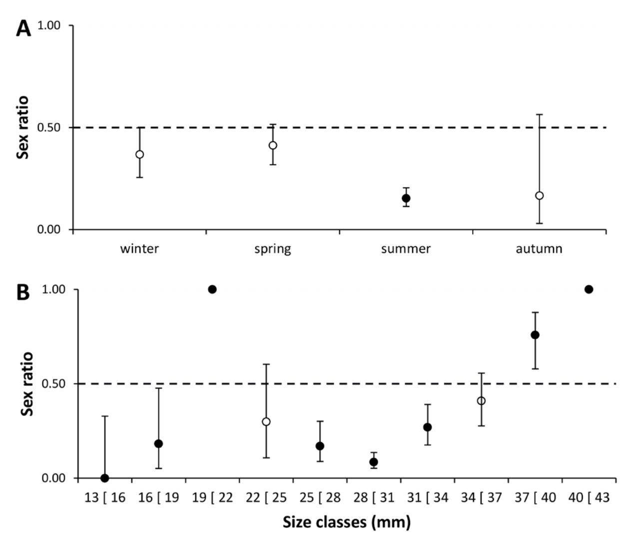

Figure 4. *Persephona punctata* (Linnaeus, 1758). A, Seasonal variation of the proportion of males and females (estimate ± standard error) and B, sex-ratio by size classes from July 2012 to June 2014, in Cananéia, São Paulo, Brazil. Black circles indicate a significant statistical difference from the 1:1 ratio (Binomial test, $p < 0.05$).

Regarding the spatial distribution, OF were more abundant at site 1 than in sites 2, 3 and 4 (one-way ANOVA, 3 df, $p < 0.001$; Tukey Test $p < 0.05$) (Fig. 5). Juveniles were more abundant at site 2, although there was no statistical difference between sites (one-way ANOVA, 3 df, $p = 0.2058$) (Fig. 5). Reproductive males were also more abundant at site 1 than in sites 2, 3 and 4 (one-way ANOVA, 3 df, $p < 0.001$; Tukey Test $p < 0.05$) (Fig. 5).

Gonadal sexual maturity

According to the analysis of gonadal sexual maturity, 82 females were RU, 106 were ED and 88 were DE. Regarding the males, 34 were RU, 28 were ED and 27 were DE. The fit of the logistic equation indicated that 50% of males were mature at 35.0 mm (CW), and females at 30.1 mm (Fig. 6).

Reproductive aspects

The reproductive period was seasonal: ovigerous females occurred in August, October and December 2012, January, February and August–November 2013, and January and March 2014 (Fig. 7). The highest abundance of ovigerous females occurred in January 2014. Ovigerous females at different stages of gonadal maturity were observed throughout the reproductive period (Fig. 7). Overall, few juveniles were captured, and the highest abundance occurred in August 2013, followed by June of the same year (Fig. 7).

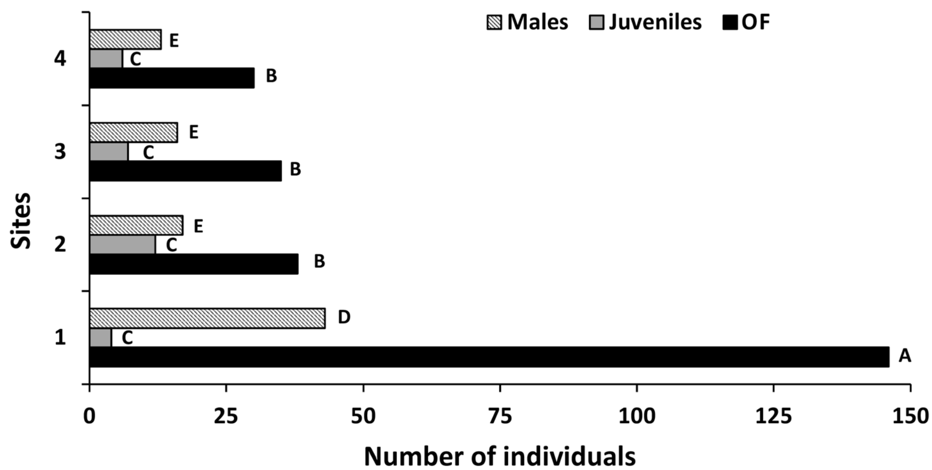

Figure 5. *Persephona punctata* (Linnaeus, 1758). Spatial distribution of ovigerous females (OF), juveniles and reproductive males captured from July 2012 to June 2014, in Cananéia, São Paulo, Brazil.

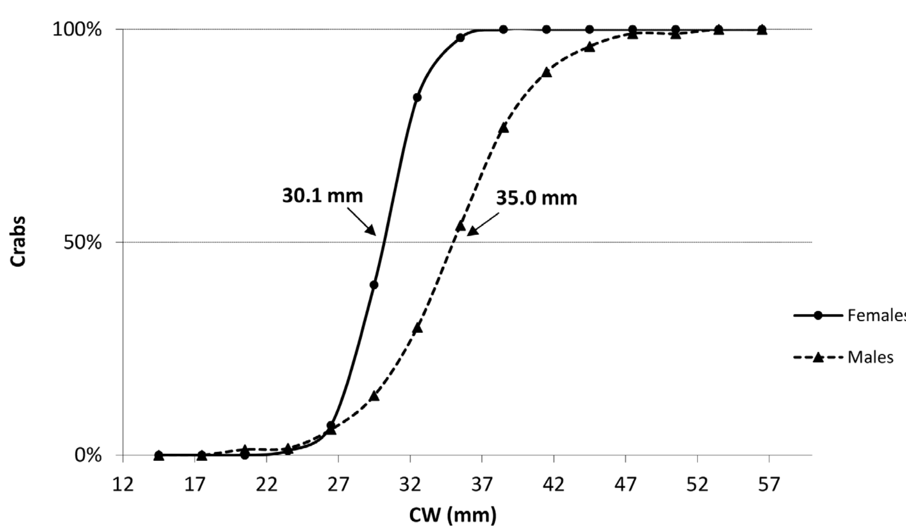

Figure 6. *Persephona punctata* (Linnaeus, 1758). Adjustment of the logistic equation indicating the carapace width (CW mm) at which 50% of males and females were mature, according to the analysis of gonadal development.

The abundance of ovigerous females was positively correlated with the bottom water temperature at time zero (Times Series, $p < 0.05$) (Fig. 8A). A negative correlation between ovigerous females and the bottom water salinity was also observed two months after time zero (Times Series, $p < 0.05$) (Fig. 8B). There was no correlation between the abundance of ovigerous females and organic matter content or grain size distribution.

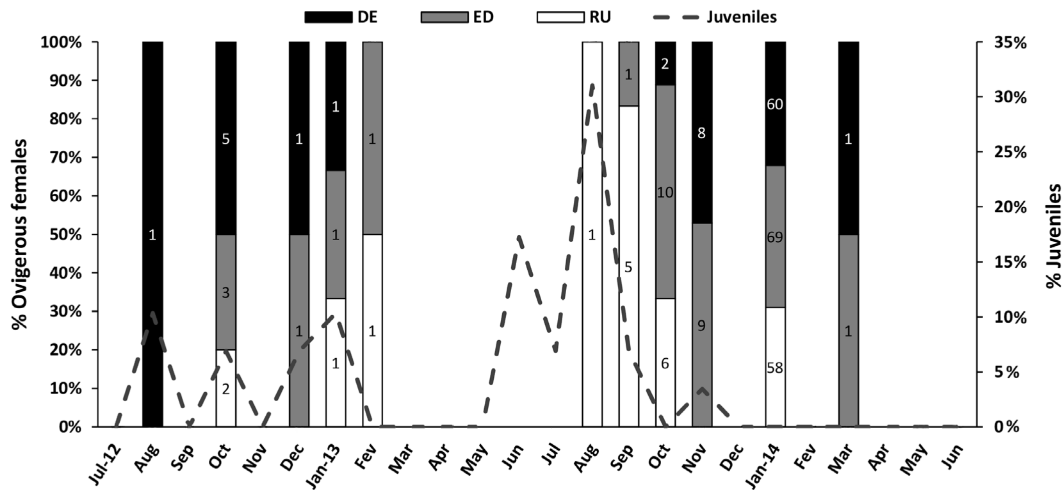

Figure 7. *Persephona punctata* (Linnaeus, 1758). Percentage of ovigerous females and their gonadal stages: rudimentary (RU); developing (ED) and developed (DE); and the number of juveniles captured monthly from July 2012 to June 2014, in Cananéia, São Paulo, Brazil.

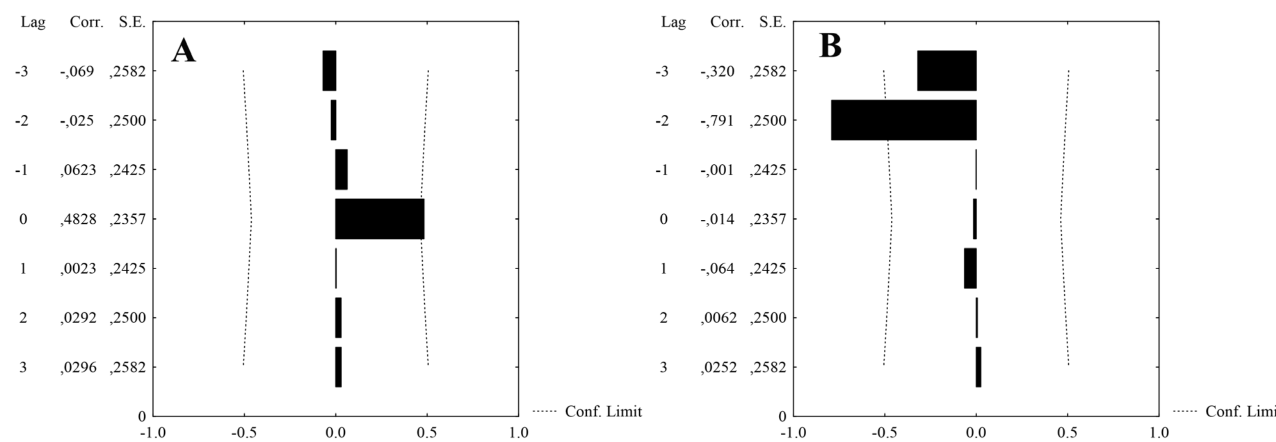

Figure 8. *Persephona punctata* (Linnaeus, 1758). Time series analysis of the abundance of ovigerous females and A, bottom water temperature, and B, bottom water salinity from July 2012 to June 2014, in Cananéia, São Paulo, Brazil. Lag: time; Corr: correlation value; S.E.: standard error; Conf. Limit: confidence limit.

Discussion

Although natural selection favors a sex-ratio of 1:1, an imbalance in this proportion is common in populations of marine crustaceans due to differences in migration, mortality, and growth rates between the sexes (Wenner, 1972). The sex-ratio of *P. punctata* differed from 1:1 and was skewed toward females only in summer, even though females were more abundant than males throughout the year. As most females were adults and ovigerous, we hypothesize that during reproduction and spawning they migrate to shallower areas, probably due to the greater food availability for the larvae. Pianka (1983) proposed that there is a tendency for female-biased sex-ratios in populations in which females copulate with more than one male. Indeed, McLay and Becker (2015) proposed that multiple matings and long-term sperm storage are possible in Leucosiidae because these crabs lack post-pubertal molts. This phenomenon was in fact observed in *Persephona mediterranea* (Herbst, 1794) by Hayer *et al.* (2017).

In contrast with the high abundance of adult females, the capture of adult males was low during the entire sampling period. Given that most males belonged to the size classes next to the class of the estimated size at the onset of gonadal sexual maturity (*i.e.*, 35 mm), we hypothesize that males live mostly outside our sampling area and migrate to shallower areas (within the scope of our sampling) to reproduce.

The sex-ratio of the largest size classes (38.5 and 41.5 mm) was skewed towards males, which corroborates our observation that males reach larger carapace sizes than females. This sexual dimorphism in size was also observed by Almeida *et al.* (2013) but was lacking in the study of Carvalho *et al.* (2010). Almeida *et al.* (2013) argued that such a result was due to the low number of individuals analyzed by Carvalho *et al.* (2010). Sexual dimorphism in size is common in Brachyura because a larger body size means a higher reproductive success during agonistic interactions, courtship, and protection of females during and after mating (Hartnoll, 1985; Teixeira *et al.*, 2009; Santos *et al.*, 2017).

The size at the onset of gonadal sexual maturity of males was larger than that of females. Bertini *et al.* (2010) and Almeida *et al.* (2013) obtained similar results in Ubatuba (state of São Paulo; 23º26'S 45º01'W), and Carvalho *et al.* (2010) estimated the morphological sexual maturity in Ilhéus (state of Bahia; 14º79'S 39º03'W) and obtained the same result. Nevertheless, the sizes differed between these localities and were smaller in the northernmost localities (tropical). While in Cananéia males and females reached gonadal sexual maturity at 35.0 and 30.1 mm (CW), in Ubatuba males reached sexual maturity at 27.4 mm, and females at 24.9 mm (Almeida *et al.*, 2013). In Ilhéus, males were mature at 27.6, and females at 25.5 mm (Carvalho *et al.*, 2010).

The information about the occurrence of ovigerous females and individuals with developed gonads through the year has been used by several authors to infer about the reproductive cycle of brachyuran crabs (Mantelatto and Fransozo, 1999; Andrade *et al.*, 2017). Temperature, salinity, and food availability are some of the environmental factors that highly influence the reproduction and growth of crustaceans (O'Connor, 1993; Zang *et al.*, 1998). The population of *P. punctata* in this study had a seasonal reproductive period. The capture of males and reproductive females was not constant, and the highest percentage of ovigerous females occurred in spring and summer, due to the increase in temperature. In Ubatuba, however, Almeida *et al.* (2013) recorded a continuous reproductive period for *P. punctata*. Also, in Ubatuba, the highest reproductive peaks were registered in January and March (summer), alongside the arrival of SACW (South Atlantic Central Water) in the region. This cold-water mass brings nutrients that increase the primary productivity in the region and create favorable conditions for the survival of leucosiid crab larvae (Pires-Vanin and Matsuura, 1993; Almeida *et al.*, 2013). In this way, due to the food availability promoted by the SACW arrival, the reproduction of *P. punctata* in Ubatuba peaks in summer, when bottom temperatures are lower than in winter. In Cananéia, the reproductive period reaches the highest peak in spring and summer, when the highest bottom temperatures and rainfall were recorded. These settings also increase the organic matter content, and consequently, the food availability.

Besides temperature, another environmental factor that influenced the reproductive period of *P. punctata* was bottom water salinity: there was a decrease in the number of ovigerous females two months after salinity increased. This finding may indicate that periods of higher salinity are favorable to larval hatching, although it was not tested in this study. Salinity is known to affect the growth, survival, and larval development of decapod crustaceans (Costlow *et al.*, 1960; Anger, 2003), as well as feeding (Anger, 2001) carbon accumulation rates (Anger *et al.*, 1998), and larval biochemical composition of some species (Torres *et al.*, 2002). The ovigerous females caught in this study were in different gonadal/egg development stages, which indicates the occurrence of multiple spawning during the reproductive cycle. The same pattern was observed by Bertini *et al.* (2010) regarding *P. mediterranea* in Ubatuba, and by Kobayashi and Archdale (2017) with *Pyrhila pisum* (De Haan, 1841), another leucosiid crab.

The recruitment took place mainly in winter, in both years. Nonetheless, the low number of juveniles in our samples indicates that recruitment occurs in offshore areas, and not in the coastal marine adjacent areas (*i.e.*, sites S1–S4), where our trawling was held.

In Cananéia, individuals of *P. punctata* reach gonadal sexual maturity at larger carapace sizes, compared with tropical populations, which means that their growth rate is slower. Also, the reproductive period in Cananéia is seasonal, unlike in the more tropical regions where reproduction is known to be continuous. These results corroborate the latitudinal effect paradigm, which states that reproduction may be continuous in tropical regions (lower latitudes) due to constant favorable environmental conditions for gonadal development, feeding, and spawning, while in temperate regions, with the increase in latitude, reproduction is usually restricted to fewer months due to limiting resources and temperature variation (Bauer, 1992).

Knowledge about the dynamics of populations of marine species must be considered fundamental information to understand their life cycle (Emmerson, 1994). This study, held in Cananéia, characterized the population dynamics of *P. punctata* in a region where it has not been studied yet. Our results extend the knowledge on its life cycle and provide baseline information for future strategies aiming at the conservation of this species. This is particularly important since, despite being an area for environmental protection, the only management plan that regulates the shrimp fisheries at the APA-CIP is the closed season (normative instruction IBAMA nº 189/2008), forbidding the fishing in the recruitment period of pink shrimp (*Farfantepenaeus* spp. Burukovsky, 1997) juveniles from March 1 to May 31. No plan or agreement was created to manage the shrimp fisheries and its bycatch (mainly other crustaceans and fishes), which leads to the conclusion that this population of *P. punctata* is hardly being protected more than populations in unprotected areas.

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