Nauplius
The Journal of The Brazilian Crustacean Society
e-ISSN 2358-2936
www.scielo.br/nau
www.crustacea.org.br

Do the day/night periods and tidal cycles modulate the abundance and distribution of *Callinectes danae* Smith, 1869 (Brachyura, Portunidae) in an estuary-bay complex from southeastern Brazil?

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Abstract

We investigated the abundance and spatial distribution of *Callinectes danae* Smith, 1869 during the day/night periods and tidal cycles in a coastal area of Brazil. Sex ratio, size class distribution, and mean sizes of males and females were also analyzed. The sampling occurred between February and March 2011 in the estuary-bay complex of São Vicente. Collections occurred in six sampling stations during both daytime and nighttime. A total of 1997 specimens were collected in the bay and 963 specimens in the estuary. The abundance of males and females differed between the bay and estuary, with males more abundant in the estuary and adult females in the bay. Crabs in all demographic categories were more abundant at night. The species distribution was intrinsically related to the interaction between environmental factors. In addition to the higher capture during nocturnal collections, a positive correlation was found between the abundance of reproductive females and salinity, while juveniles were more abundant in shallower stations and at lower salinities. Our results contribute to a better understanding of the influence of day/night periods and tidal cycles on the abundance and distribution of the swimming crab *C. danae*.

Keywords

Coastal waters, Crustacea, fisheries resource, population features, swimming crab

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SUBMITTED 11 February 2020
ACCEPTED 08 July 2020
PUBLISHED 28 October 2020

DOI 10.1590/2358-2936e2020038

Introduction

Coastal ecosystems in southeastern Brazil have suffered continuous degradation by anthropogenic pressures that have consequently affected the environment and local fauna, including crustacean species (Suciu *et al.*, 2017). These ecosystems are subject to degradation, which is accentuated by predatory fishing, leading to a reduction in biological diversity, especially for benthic species present in bycatch of commercial shrimp fisheries (Keunecke *et al.*, 2009).

Portunid crabs inhabit mostly tropical and subtropical areas, with a significant decrease in abundance in temperate and cold regions (Boschi, 2000). This crab family is one of the most well known, both due to its ecological importance and since it is a plentiful and promising food source in coastal waters (Mantelatto and Fransozo, 1999). The predominance of these animals within estuarine systems contributed to the popularization of fishing and exploitation of swimming crabs *Callinectes* Stimpson, 1860. Crab fishing is one of the oldest activities along the Brazilian coast, which persists today in several local communities that survive almost exclusively on trading these fishery resources (Pereira *et al.*, 2009).

This swimming crab *Callinectes danae* Smith, 1869 is widely distributed, occurring from Florida (USA) to Uruguay (Spivak *et al.*, 2019), and is commonly found in coastal regions, including areas impacted by human activities (Bordon *et al.*, 2018). This species is the second most abundant along the São Paulo coast (Mantelatto and Fransozo, 2000), inhabiting mangroves and muddy estuaries up to 75 meters deep and exhibiting high tolerance to salinity variation (Williams, 1966). The life cycle of *C. danae* is characterized by sex-specific segregation, causing habitat partitioning in which males and juveniles of both sexes are present in upper estuaries, while adult females and mainly ovigerous females inhabit areas with marine influence and migrate to deeper and more saline places to hatch their larvae (Chacur *et al.*, 2000). The species is intensely caught in shallow waters off the coast of Brazil by artisanal fisheries and is one of the main species caught as bycatch in the commercial Penaeidae shrimp fishery (Keunecke *et al.*, 2009; Bochini *et al.*, 2019).

The presence of benthic species can be determined by biotic factors such as predators or prey, as well as abiotic factors such as the physiochemical gradient, temperature, salinity and the tidal cycle (Almeida and Coelho, 2008; Levinton *et al.*, 2015). Studies indicate that the highest crustacean catch rates occur at night, which is likely due to most species remaining buried during the day to avoid predators and emerging at nightfall (Penn, 1984; Simões *et al.*, 2010; Lopes *et al.*, 2014).

The tidal cycle (high and low) also affects many marine organisms (Libini and Khan, 2012). Changes may occur in the behavior, distribution, and abundance of these animals as well as in the catching of specimens by coastal communities (Barletta and Costa, 2009). Studies concerning the influence of tidal cycles on *C. danae* are fundamental for providing clearer and more reliable information about the behavior and distribution of species, including all demographic categories from larvae to adults (Ramos *et al.*, 2011).

Considering the ecological and economic importance of the swimming crab *C. danae* to coastal ecosystems, in addition to the importance of knowledge about distributional and behavioral patterns under different environmental factors, we investigated the abundance and spatial distribution of this species during the day/night periods and tidal cycle (high/low) in an estuary-bay complex influenced by human impacts on the southeastern coast of Brazil. Population features such as sex ratio, size class distribution and the mean size of males and females were also analyzed.

Materials and Methods

Study area and sampling

The estuary-bay complex is composed of the estuaries of São Vicente, São Vicente Bay, and Santos Bay, on the southern coast of São Paulo (23°55'S – 24°00'S 46°20'W – 46°25'W), with extensive mangroves present in the estuary. The mangroves exhibit high food availability and several marine species use this habitat for spawning (Santos *et al.*, 2008). The region exhibits intense commercial, tourist and fishing activities, as it is a major industrial center and holds the largest harbor in Latin America.

Therefore, this estuarine complex is constantly being degraded, mainly by the constant deposition of domestic and industrial effluents (Virga *et al.*, 2007).

Four collections were performed between February and March 2011 in six sampling stations: 1, 2 and 3 in the estuarine region and 4, 5 and 6 in the São Vicente Bay region, near the entrance of the estuary (Fig. 1). The sampling stations and periods were selected after verifying the high abundance of *C. danae* during collections of Penaeoidea shrimp between May 2008 and April 2010 (Simões *et al.*, 2017). The swimming crab was also abundant during collections of *Farfantepenaeus* spp. Burukovsky, 1997 and *Litopenaeus schmitti* (Burkenroad, 1936) juveniles from the same six sampling stations used herein (R.C. Costa, pers. obs.).

Specimens were collected using a 5 m longboat with a 15 HP outboard motor and equipped with an otter trawl net with doors weighing 7 kg each. Trawl nets were 4 m long, 2 m wide at the mouth and had a mesh size of 13 mm. This mesh size was used because it efficiently captures juveniles and prevents mud from accumulating during trawling in the estuary (R.C. Costa, pers. obs.). The sampling effort was 10 minutes/trawl at each sampling site. In each collection, two samples were collected during the day (low tide and high tide) and two at night (low tide and high tide) from the six sampling stations. Considering the six sampling stations, a total of 96 samples were collected during the study period (48 during the day and 48 during the night).

Additionally, during each trawl, bottom water samples were collected with a Van Dorn bottle to measure the temperature (mercury thermometer 0.1 °C) and salinity (specific optical refractometer).

The captured crabs were stored on ice and subsequently transported to the Laboratory of Biology of Marine and Freshwater Shrimp (LABCAM, São Paulo State University).

Data analysis

Species were identified according to Melo (1996). In each sample, crabs were sexed according to abdomen morphology; males were distinguished from females by the inverted "T" shape of the abdomen, while females were identified by a semicircular shaped abdomen. Crabs with the abdomen sealed to the thoracic sternites were classified as juveniles. The maturation stages of ovaries and testes were identified by macroscopic observation, according to the color and volume in relation to the hepatopancreas and the thoracic cavity (see Costa and Negreiros-Fransozo, 1998). Males with developed testes and females with developed ovaries and/or eggs attached to pleopods were classified as reproductive individuals.

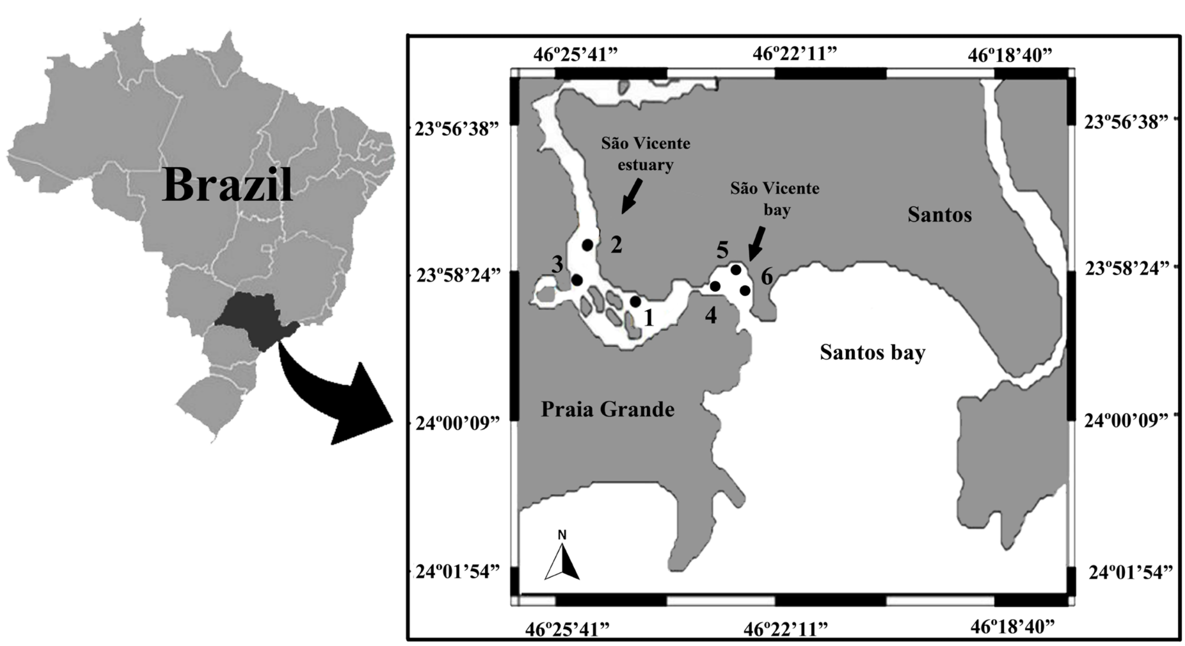

Figure 1. Map of the estuary-bay complex of São Vicente, SP, highlighting the six sampling stations (estuary = 1, 2, 3; bay = 4, 5, 6).

The specimens were analyzed in classes of carapace width (CW) (not including the lateral spines) distributed in intervals of 5 mm. Homoscedasticity (Levene) and normality (Shapiro-Wilk) tests were first performed as prerequisites for later statistical tests. The Mann-Whitney test (0.05) was used to verify the difference between the sizes of each body structure of males and females.

A chi-square test (X^2) with a significance level of 5% was used to determine whether the sex ratio followed a 1:1 ratio by size class (Sokal and Rohlf, 1995). Size classes with fewer than 20 specimens were excluded from this analysis. A generalized linear model (GLM) with a Poisson distribution was used to analyze the effect of collection locations (estuary/bay), sampling stations (1–6), period (day/night) and tide (low/high) on juvenile and adult abundance, as well as the interactions between the variables.

The redundancy analysis (RDA) was used to evaluate the variation in abundance of *C. danae* considering a set of environmental variables (salinity and bottom water temperature).

Results

Abiotic factors and population features

The bottom water temperature did not differ significantly between the estuary and bay (T-test, $P > 0.05$), ranging from 26.0 to 31.0 °C (28.8 ± 1.5 °C) in the estuary and from 26.0 to 30.5 °C (28.6 ± 1.3 °C) in the bay. Salinity differed statistically between environments (T-test, $P < 0.05$) with lower salinity values observed in the estuary, ranging from 20.5 to 33.5 (27.2 ± 3.5), while in the bay they ranged from 25.0 to 34.5 (30.2 ± 3.1) (Fig. 2).

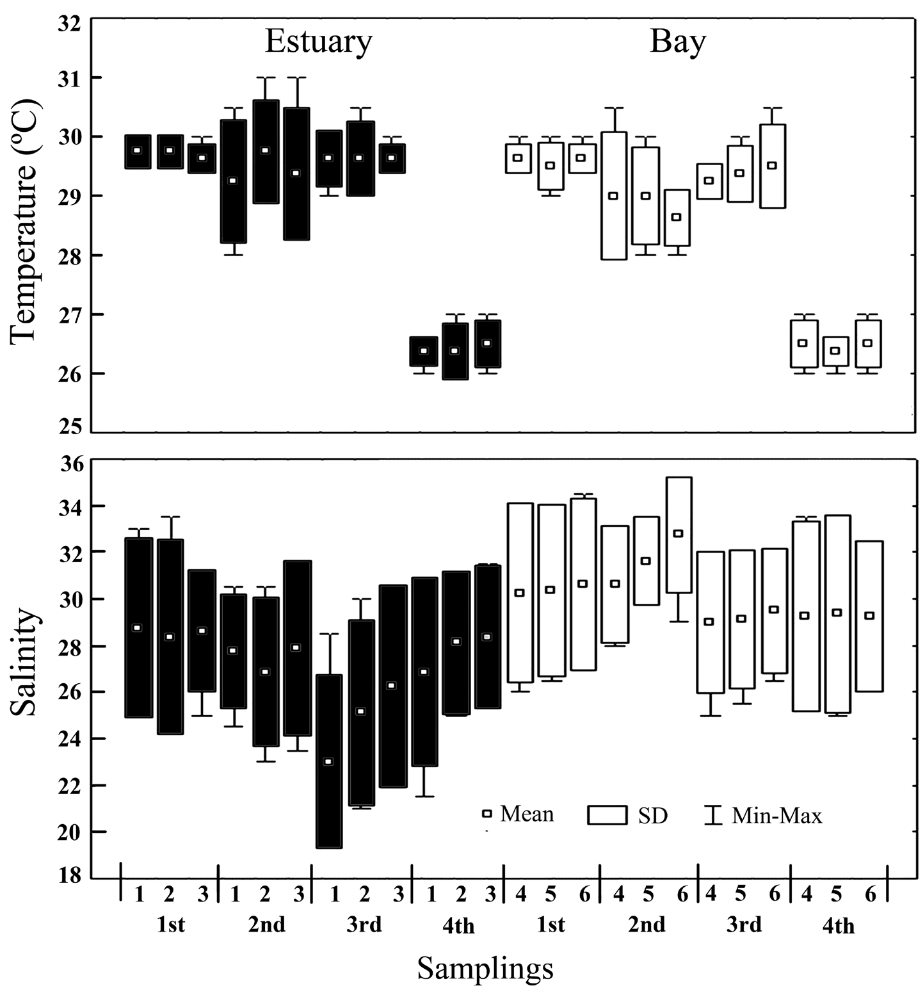

Figure 2. Mean, maximum (Max), minimum (Min) and standard deviation (SD) of the temperature (ºC) and salinity at the sampling stations of the estuary-bay complex of São Vicente between February and March 2011.

During the study, 2960 specimens were collected and analyzed, 2288 females and 672 males. A total of 328 juveniles and 1960 adult females (1595 ovigerous), and 284 juveniles and 388 adult males were collected. Data was not normally distributed (Shapiro-Wilk). Carapace width ranged from 5.7 to 91.3 mm (61.3 ± 10.5 mm) in males and from 5.6 to 99.6 mm (59.9 ± 10.5 mm) in females, and no statistically significant differences were detected between the mean sizes (Mann-Whitney test $P > 0.05$). However, the females in the estuary were smaller than those in the bay (Mann-Whitney test $P < 0.05$).

The overall sex ratio differed significantly from 1:1 in the population of *C. danae*, with a sex ratio skewed towards females 1:0.29 ♀:♂ ($X^2 = 882$, $P < 0.05$). Sex ratio also varied in the size classes, with a predominance of females in almost all size classes for juveniles and adults (Fig. 3).

Period (day/night), tides (low/high) and spatial distribution

The set of environmental factors (Period*tide*stations) showed a significant impact on the abundance and distribution of *C. danae* in the generalized linear model with a Poisson distribution (Fig. 4). The greatest abundances were observed at night and during high tide as detailed below.

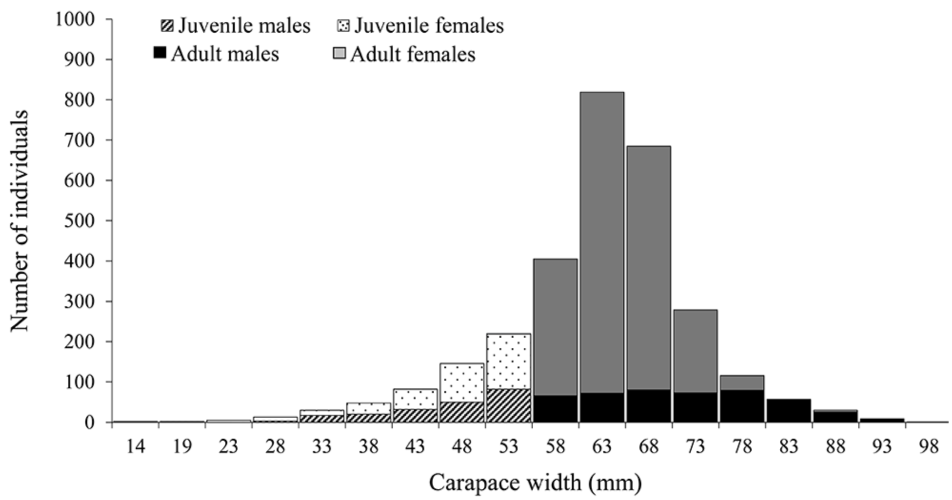

Figure 3. *Callinectes danae* Smith, 1869. Size-frequency distribution of demographic classes.

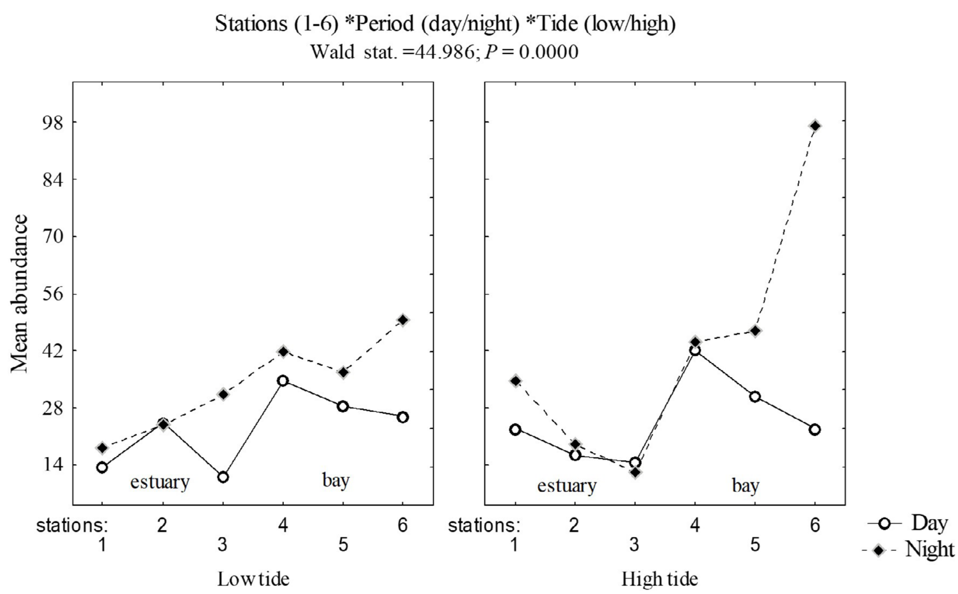

Figure 4. Generalized linear models (GLM) with a Poisson distribution showing the relationship between the mean abundance of *Callinectes danae* Smith, 1869 in relation to the set of environmental factors (Stations*Period*Tide).

A total of 1140 (38.5%) specimens were collected in the day and 1820 (61.5%) at night (Fig. 5A). The generalized linear model showed an interaction between the mean abundance of both juveniles and adults and the period at the sampling stations and estuary and bay (Tab. 1). At low tide, 1351 (46%) specimens were collected, while 1609 (54%) specimens were collected at high tide (Fig. 5B). The tide influenced the abundance less than the period, but it was significant when analyzing the interaction between all GLM factors (Tab. 1).

There was a predominance of reproductive females in the bay, especially at stations 4 (526 specimens) and 6 (656 specimens). Temperature did not correlate with abundance, but there was a positive correlation between mean salinity and reproductive females (Fig. 6A).

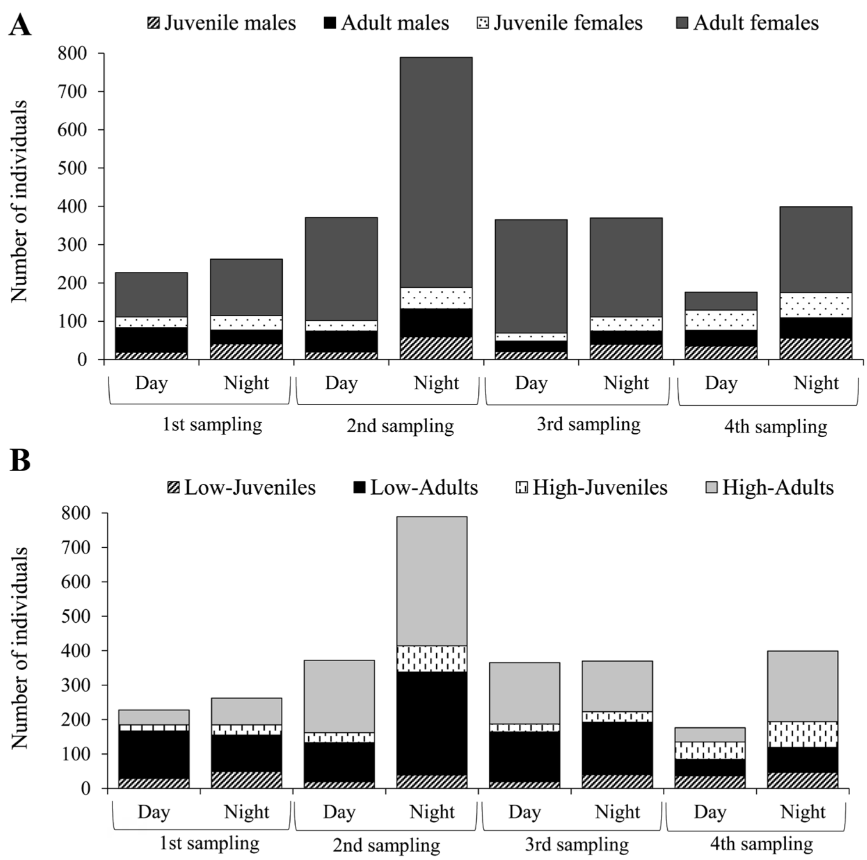

Figure 5. *Callinectes danae* Smith, 1869. **A.** Number of males and females collected during the day and night in four samplings. **B.** Number of individuals collected during the low and high tide in four samplings between February and March of 2011 in the estuary-bay complex of São Vicente, Brazil.

Table 1. Results of a generalized linear model with a Poisson distribution, showing the effects of environmental factors on the abundance of *Callinectes danae* Smith, 1869.

Factors	df	Juveniles + adults		Juveniles		Adults	
		Wald Stat.	*P*	Wald Stat.	*P*	Wald Stat.	*P*
Bay*Estuary	1	302.91	0.000	192.64	0.000	523.05	0.000
Station (1-6)	5	310.15	0.000	162.64	0.000	607.56	0.000
Period (day/night)	1	90.44	0.000	33.66	0.000	15.53	0.000
Tide (low/high)	1	4.3	0.038	4.7	0.031	1.01	0.314
Station*Period	5	82.17	0.000	19.2	0.001	98.79	0.000
Station*Tide	5	48.34	0.000	29.72	0.000	34.37	0.000
Period*Tide	1	0.05	0.828	0.17	0.671	5.56	0.018
Station*Period*Tide	5	44.99	0.000	4.83	0.030	57.57	0.000

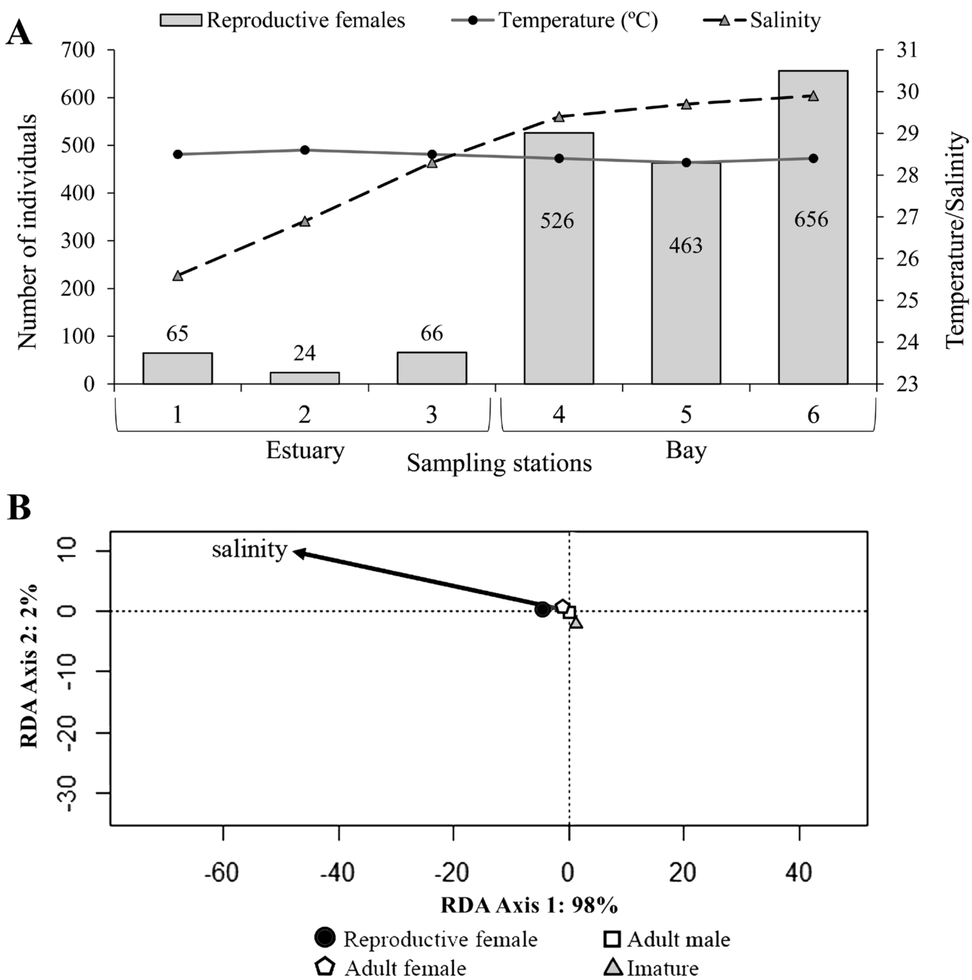

Figure 6. *Callinectes danae* Smith, 1869. **A.** Relationship between mean temperature and salinity and the number of reproductive females at the sampling stations. **B.** Redundancy Analysis (RDA), relationship between environmental factors and demographic classes.

As indicated by the redundancy analysis (RDA), the relationships between the species and their habitat conditions were mainly represented by the first and second axes. The first chart axis explained 98% of the total variance, while the second explained 2%. The Monte-Carlo test indicated that only one canonical axis was significant ($P < 0.05$). The bottom salinity was positively correlated with the abundance pattern of ovigerous and adult females and negatively correlated with immature and adult males ($P < 0.05$) (Tab. 2, Fig. 6B).

A total of 1997 specimens were sampled in the bay (stations 4, 5 and 6) and 963 in the estuary (stations 1, 2 and 3). The generalized linear model also showed an interaction between mean abundance and spatial distribution, both between estuary and bay and between sampling stations GLM (Tab. 1). The abundance was higher in the bay, with an emphasis on sampling stations 4 and 6. Ovigerous females were significantly more abundant in the bay (n = 1466), comprising 92% of the total collected crabs in this region. The abundance of males and females also differed significantly between the bay and estuary, with males more abundant in the estuary and females more abundant in the bay. Females were most abundant at stations 4 and 6 in the bay and station 1 in the estuary (Fig. 7).

The mean size of females was statistically different between estuary and bay, with larger females in the bay (Mann-Whitney test $P < 0.05$). Males did not differ in mean size between estuary and bay (Mann-Whitney test $P > 0.05$) (Fig. 8).

Table 2. Results of the redundancy analysis (RDA) of the abundance of *Callinectes danae* Smith, 1869 in the demographic classes in relation to temperature and salinity.

Explained proportion		Environmental factors	RDA1	RDA2	r^2	Pr(>r)
RDA1	0.9771	Temperature	-0.34444	0.93881	0.0448	0.130
RDA2	0.0229	Salinity	-0.97888	0.20443	0.1100	0.004 **

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
P values based on 999 permutations.

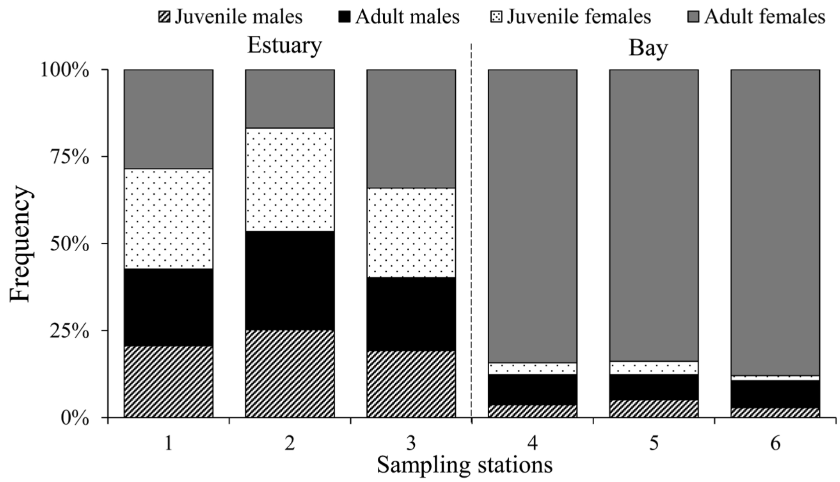

Figure 7. *Callinectes danae* Smith, 1869. Frequency of males and females at the sampling stations (estuary = 1, 2 and 3; bay = 4, 5 and 6).

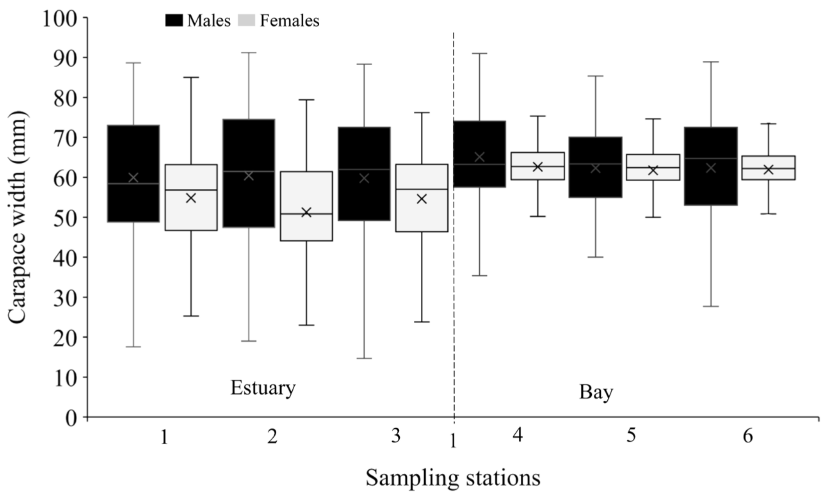

Figure 8. *Callinectes danae* Smith, 1869. Minimum, maximum (whiskers), median (horizontal lines) and mean (X) of males and females.

Discussion

This study showed the influence of a set of environmental factors, including the day/night period, sampling stations, tide, and salinity, with emphasis on nocturnal distribution and influence of water salinity, on the abundance and distribution of juvenile and adult swimming crabs *C. danae* in an estuary-bay complex from southeastern Brazil.

The nocturnal activity of juvenile and adult *C. danae* observed in the present study may be related to its feeding activity. Many species of portunid crabs are more active during the night, as they intensify their search for prey during this period (Bellwood, 2002). *Callinectes danae* is considered an opportunistic benthic predator, feeding on polychaete worms, other species of crustaceans, bivalves, gastropods and fishes (Branco and Verani, 1997). Considering that activity rhythms can be closely connected to feeding patterns (Reigada, 2002), the higher abundance of prey during day or night periods may influence the distribution and abundance of *C. danae*. According to Reigada and Negreiros-Fransozo (2001), feeding in *C. danae* and *Callinectes ornatus* Ordway, 1863 is mostly a nocturnal activity. This nocturnal feeding activity was observed by the authors analyzing the degree of stomach replenishment in the crabs from Ubatuba bay, São Paulo State, Brazil, in which a higher incidence of full stomachs was found during dusk and night. Reigada (2002) also observed higher nocturnal activity, analyzing the locomotory and feeding activity rhythms of *C. danae* and *C. ornatus* under laboratory conditions. The evident influence of light on the activity of species was verified by intense emergence from sediment during periods of low light intensity. During the day, crabs remain buried in the substrate, which reduces the risk of predation, as well as conserves energy for nocturnal activities (Bellwood, 2002).

The tidal cycle also significantly influenced the abundance and distribution of *C. danae*. Despite a higher number of crabs at high tide, there was no well-established pattern as observed between the periods (day/night). By analyzing the distribution between sampling stations, the highest abundance of females was found in stations 4 and 6 during the second sampling period. These stations are located near the entrance of estuaries and the highest abundance recorded coincides with the highest salinity values throughout the study period. According to our results, the abundance of reproductive females (females presenting developed gonads and ovigerous females) was positively correlated with salinity, and the highest abundance was collected in the bay.

Considering that the sex ratio skewed towards females with a predominance of ovigerous females, their highest abundance is reflected in the spatial distribution of species in the estuary-bay complex of São Vicente. Due to the life cycle of this species, there is a difference in the spatial distribution, not only between sexes, but also among demographic classes (Chacur *et al.*, 2000; Chacur and Negreiros-Fransozo, 2001; Pereira *et al.*, 2009). Similar results were found by Sforza *et al.* (2010) in Vitória bay (Espírito Santo), where males and immature individuals were observed in lower salinities, while reproductive females were associated with higher salinity values.

The distribution pattern of swimming crabs mentioned above is the result of a complex combination of factors, involving habitat preferences and intra/interspecific interactions as feeding differences (Buchanan and Stoner, 1988). Females of many estuarine crab species settle in more saline areas of estuaries, where larvae grow — perhaps to improve dispersion chances and because early larval stages are less tolerant of low salinities (Hartnoll, 2015). This environmental condition is important during embryonic development (Pita *et al.*, 1985; Mantelatto, 2000; Fernandes *et al.*, 2006). Thus, salinity seems to be one of the most important limiting factors for the migration of these crabs (Chacur *et al.*, 2000). Adults and ovigerous females of *C. danae* migrate to deeper areas with favorable salinity and current conditions that provide the needed embryonic and larval development and dispersion, similarly observed in *C. ornatus* (see Mantelatto, 2000). Furthermore, the characteristics of each ecosystem determine how the species migrates between different habitats within its range (Keunecke *et al.*, 2009; Andrade *et al.*, 2015).

The feeding differences between the demographic categories of juveniles and adults could also be an important factor for the distribution of crabs. According to Mantelatto and Christofoletti (2001), the movement of *C. ornatus* ovigerous females to specific sites may be related to differences in feeding and the availability of food at these sites. Ovigerous females were found with high percentages of crustaceans and fishes in their stomachs, representing high-protein prey that is utilized for egg development in the ovaries (Mantelatto and Christofoletti, 2001).

After larval development, juveniles return to estuaries, which are brackish environments. The migration towards estuaries may be related to molting processes, possibly due to the osmotic advantage, since juveniles need to ingest larger amounts of water to expand their exoskeleton immediately after molting. As previously mentioned for ovigerous females, the feeding preferences of juveniles may be related to specific nutritional requirements during this growth phase. The study by Mantelatto and Christofoletti (2001) showed the highest consumption of calcareous prey by immature crabs as a function of the high molting frequency during this phase. Pre-molt and recently molted crabs consumed calcareous prey, which they may use for exoskeleton hardening (Mantelatto and Christofoletti, 2001).

Estuarine environments provide a larger food supply due to the higher concentrations of organic matter, lower predation rates due to greater turbidity, and higher variation of environmental factors, which limits the establishment of most species (Hines *et al.*, 1987). Despite the changing and potentially more stressful environmental conditions, small crabs survive better with fewer predators and greater protection (Buchanan and Stoner, 1988).

Studies performed on the southeastern coast of Brazil have shown the key role of estuarine environments in the maintenance and recruitment of species of economic interest (Albertoni *et al.*, 2003a; 2003b; Santos *et al.*, 2008; Simões *et al.*, 2010). Considering the high number of immature individuals found in these regions, protecting shallow areas close to estuaries is extremely important. The results showed that even though the estuary-bay complex of Santos and São Vicente is considered a highly anthropogenic impacted area, the swimming crab *C. danae* still maintains its life cycle; confirmed by the high abundance of ovigerous females in the bay. However, strategies to ensure the maintenance of population stocks, considering the life cycle of this species, are fundamental.

The highest number of economically attractive individuals (females and adult males) is located in the shallow areas of the bay, or near the estuary mouth, due to the life cycle of this species. However, in the bay areas, ovigerous females are predominant. Thus, spatial protection is necessary for areas with a higher concentration of juveniles, and temporal protection is necessary for periods of reproductive peaks and spawning for both environments (estuary and bay). Such protection measures could maintain the populations of *C. danae*, which is an economically important fishing resource.

Our study provides information about the abundance and spatial distribution of *C. danae* during the day/night periods and tidal cycle (low/high) in an estuary-bay complex on the southeastern coast of Brazil. Species distribution was intrinsically related to the interaction between these factors. In addition to the higher capture during nocturnal collections, a positive correlation between abundance of reproductive females and salinity was observed; while juveniles were more abundant in shallower stations with lower salinities. All the results show the influence of a set of abiotic factors that, added to biotic factors such as competition and predation, constitute the modulators of the distribution and abundance of *C. danae*.

Acknowledgments

The authors thank the National Council for Scientific and Technological Development (CNPq) for technical and financial support (119593/2013-0) to H.A.K; (155813/2018-8) to R.A.P. and to R.C.C. Thanks also to São Paulo Research Foundation – FAPESP (2008/54991-0) to M.L. and Thematic BIOTA – INTERCRUSTA (2018/13685-5). We thank LABCAM co-workers for their help during fieldwork. We are indebted to the anonymous reviewers and the Associate Editor Fernando L. Mantelatto for their suggestions that helped to improve the quality of this manuscript during the review process. The collection of specimens conducted in this study complied with current applicable state and federal laws of Brazil (Authorization of the Instituto Chico Mendes de Biodiversidade/ICMBio – SISBIO.

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