



# Reproductive traits, relative growth and maturity of blue crabs *Callinectes danae* and *Callinectes ornatus* in South Atlantic waters

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**Abstract** The reproductive strategies of species play a fundamental role in formulating effective management plans and maintaining local community structure and ecological balance. This study investigated the reproductive characteristics of two sympatric species, *Callinectes danae* and *Callinectes ornatus*, in Atlantic waters. Monthly sampling was conducted from July/12 to June/14 in the coastal (sites: S1, S2, S3 and S4) and estuarine-lagoon (sites: S5, S6 and S7) areas of Cananéia-Iguape, Brazil. Significant differences in allometric coefficients were observed, particularly in the relationships chelipod length vs. carapace width (CW) for males and abdominal width vs. carapace width (CW) for females. Morphological sexual maturity was estimated at 58.8 mm CW for *C. danae* males, 54.5 mm CW for females, 45.0 mm CW for *C. ornatus* males, and 41.2 mm CW for females. Gonadal sexual maturity sizes were identified at 69.4 mm CW for *C. danae* males, 61.4 mm CW for females, and 58.4 mm CW for *C. ornatus* males, 46.9 mm CW for females. Both species spawn predominantly during the austral summer, with higher

prevalence in site S5 for *C. danae* and S1 for *C. ornatus*. Recruitment occurred in austral spring and summer, with *C. danae* concentrated in estuarine-lagoon regions and *C. ornatus* along the coast. Reproductive patterns of *C. danae* were associated with temperature and salinity, while *C. ornatus* exhibited correlations with temperature and organic matter. This study highlights the influence of environmental factors on species' life cycles. Furthermore, it contributes to the evaluation of management and monitoring strategies, recognizing the economic and ecological significance of these species for sustaining these ecosystems.

**Keywords**  $L_{50}$  · Sexual maturity · Reproductive period · Juvenile recruitment

## Introduction

Blue crabs *Callinectes danae* Smith 1869 and *Callinectes ornatus* Ordway 1863 (Portunidae) are sympatric species distributed in the Western Atlantic, inhabiting areas around the southeast of the USA, Bermuda, Gulf of Mexico, Antilles, Colombia, Venezuela, Guianas, Brazil and Uruguay, being found at depths ranging from tides to 75 m (Melo 1996; Mantelatto et al. 2020). These species constitute an economically important group as food resource, either through the extraction of meat or through products used as bait in fishing (Rasheed and Mustaqim 2010; Herrera and Costa 2022).

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They are also ecologically important within the marine ecosystem, serving as opportunistic predators and playing a significant role in the balance and distribution of benthic fauna. Therefore, blue crabs are considered to be modulators of the benthic environment due to their omnivorous habits (Reigada and Negreiros-Fransozo 2001; Branco et al. 2002).

In Brazil, *C. danae* is distributed in Amapá, Pará, Ceará, Rio Grande do Norte, Pernambuco, Alagoas, Sergipe, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul; while *C. ornatus* is found in Amapá, Pará, Maranhão, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul (Mantelatto et al. 2020). Previous reproductive studies of blue crabs in Brazil using samples from different latitudes have determined that these species exhibit continuous reproduction (Mantelatto and Fransozo 1999; Baptista-Metri et al. 2005; Araújo et al. 2011; Andrade et al. 2015), a pattern expected for species that inhabit tropical and subtropical regions due to the stability of environmental conditions and low thermal oscillation throughout the year (Sastry 1983; Rasheed and Musraquim 2010). However, few studies such as Branco and Mansuani (2000), Watanabe et al. (2014), have included estuarine regions in their samplings, a location where juveniles of *C. danae* have been documented to be present.

The south coast of São Paulo state, Brazil, is one of the least studied regions in São Paulo and is distinguished by its significant inflow of continental waters, nourished by numerous rivers. It is also considered one of the most biodiverse wetlands on the Brazilian coast (Mendonça et al. 2010). The coastal area of Cananéia and its associated estuarine-lagoon system serve as habitats for various commercially important fish and crustacean species. The oceanographic conditions and dynamics in the lagoon-estuarine system are complex due to the convergence of oceanic waters masses with freshwater runoff from fluvial sources (Garcia et al. 2018). This leads to spatial variations in primary productivity (Cuevas et al. 2019) and, as a result, can influence physiological conditions and impact vital rates in individuals inhabiting these areas (Flores et al. 2020).

Reproductive results documented for *C. danae* and *C. ornatus* indicated that the size of sexual maturity

varies across latitudes, with individuals maturing at larger sizes in regions at lower latitudes. Indeed, some reproductive traits of these species appear to vary across the latitudinal gradient, deviating from the expected latitudinal pattern (Hartnoll 1982; Carvalho et al. 2011; Cardim et al. 2022). In addition to latitudinal differences, variations in size of sexual maturity can also be attributed to genotypic variation, capture pressure, daylight duration, substrate changes and food availability, often quantified by chlorophyll-*a* levels in the marine ecosystem (Hines 1989; Fisher 1999; Orensanz et al. 2007; Pérez-Arvizu et al. 2013; Andrade et al. 2015). These factors regulate the size of sexual maturity and provide variations that modulate different growth patterns, with their influence often surpassing that of latitudinal parameters (Hines 1989).

Size at sexual maturity in Portunidae is determined by morphological factors, specifically related to allometric growth patterns in certain body parts (González-Gurriarán and Freire 1994; Mantelatto and Fransozo 1996; Rasheed and Mustaqim 2010; Zairion et al. 2015; Cardim et al. 2022), as well as gonadal maturity, assessed by the development of the gonads ( $L_{50}$ ) (Castiglioni and Negreiros-Fransozo 2006; Cardim et al. 2022). In some cases, both morphological and gonadal maturity values can occur asynchronously (Pinheiro and Fransozo 1998).

Understanding the size at which organisms reach sexual maturity is of paramount importance in fisheries management, as it forms the base for establishing minimum catch sizes. This strategy is centered on the protection of the reproductive period and breeding habitats, ensuring that females have the opportunity to reproduce at least once before being subject to capture (Rodríguez-Domínguez et al. 2015). Therefore, insights into the diverse reproductive strategies exhibited by species not only is crucial for the development of effective management plans but also play a central role in sustaining the ecosystem of local community structure and the ecological balance.

In this context, one of the goals of studies on reproductive ecology is to develop and test generalizations concerning latitudinal variation in reproductive and recruitment patterns and use them to generate hypotheses about specific environmental stimuli (proximal factors) and selective pressures (final factors). These factors are responsible for the observed reproductive and recruitment patterns and enable predictions about

their possible alterations due to natural or anthropogenic fluctuations (Bauer and Rivera Vega 1992).

The aim of this research was to explore the reproductive traits of the sympatric species *Callinectes danae* and *Callinectes ornatus* in Atlantic waters. Specifically, we addressed (1) relative growth and gonadal analysis to estimate sexual maturity, (2) determination of the reproductive period, and evaluation of the importance of the lagoon-estuarine and coastal bay areas for the development of the crab species, (3) investigation of the presence of recruits in the area throughout the sampling period, and (4) assessment of the effect of environmental factors on reproductive periodicity of both species.

## Materials and methods

### Study area

The Cananéia-Iguape region located on the southern coast of São Paulo state, Brazil (25°S, 48°W) is distinguished by its vast estuarine-lagoon system (Besnard 1950; Miranda et al. 1995). This complex system is connected to the ocean by bars located between three major islands: Cardoso, Cananéia and Comprida (Miranda et al. 1995). The lagoon is linked to the Atlantic Ocean through the Icapara Strait in the north and the Cananéia Strait in the south. Estuarine conditions prevail due to the presence of these straits, which gradually introduce marine water into the area, either through major rivers like the Ribeira de Iguape or via the convergence of numerous smaller rivers that flow into this region (Mendonça and Katsuragawa 2001; Herrera and Costa 2022).

The Cananéia-Iguape estuarine-lagoon system is considered the third most important in terms of marine productivity in the South Atlantic, due to its well-preserved environmental characteristics and the prevalent mangroves that act as natural breeding grounds for numerous marine species. These areas represent the most significant wetlands along the Brazilian coast in terms of biodiversity and natural productivity (UNESCO 2005; Herrera and Costa 2022).

### Sampling and laboratory procedure

Sampling was conducted monthly from July 2012 to June 2014 in two study areas: the coastal area and

estuarine-lagoon system of Cananéia-Iguape. In the coastal area of the Cananéia region, we established four sampling sites: S1, S2, S3 and S4, located at isobaths of 10–15 m and 5–10 m. In addition, three sampling sites, S5, S6, and S7, all at isobaths of 5–10 m, were situated within the estuarine-lagoon system known as Mar Pequeno (Fig. 1).

Crab sampling was conducted using a commercial fishing boat equipped with double-rig nets featuring mesh sizes of 20 and 18 mm and a mouth width of 4 m. The nets were dragged for 30 min, covering an approximate area of 16,000 m<sup>2</sup>. Due to adverse environmental conditions, sampling was not possible in the marine areas in March 2013. In February 2014, sampling was not conducted in both marine and estuarine areas.

Water temperature (°C) (T) and salinity (S) measurements were obtained using a Van Dorn bottle (5 L) at all sampling sites. To assess chlorophyll-*a* concentrations (µg/L) (Chl-*a*), water samples were collected from July 2012 through January 2014. The Chl-*a* concentrations were determined using a Eureka multiparameter probe. Sediment samples were collected using a Van Veen grab with a 0.06 m<sup>2</sup> area to determine the mean sediment grain size (Phi) and organic matter (OM) content, as the methodology detailed in the study by Herrera and Costa (2022).

After sample collection, all individuals of *C. danae* and *C. ornatus* were immediately placed on ice and transported to the laboratory. The specimens were sexed, and measurements were taken using a digital caliper (0.01 mm). The measurements included carapace width (CW); carapace length (CL); width, length and height for the chelipod (ChW, ChL, ChH, respectively); and width of the fifth abdominal somite (AW). In males, the length of the gonopodium (GL) was also recorded.

The blue crabs were dissected in the laboratory after each sample collection to provide a window for gonadal observations. Careful removal of the carapace and connective tissue exposed the ovaries and hepatopancreas beneath. Both females (F) and males (M) were categorized into four stages of gonadal development using three classification criteria based on the shape, color, and volume of the gonads. This classification followed the technique adapted from Costa and Negreiros-Fransozo (1998) and Mantelatto and Fransozo (1999). The four stages were immature (IM), rudimentary (RU), developing (DE), and



**Fig. 1** Map of the study area in Cananéia, São Paulo state, Brazil. Sampling sites are marked in the coastal area (S1, S2, S3, and S4) and the estuarine-lagoon system (S5, S6, and S7)

mature (MA). Females carrying fertilized eggs were classified as ovigerous females (OF), while immature individuals were categorized as juveniles (J).

#### Data analysis

To assess morphological sexual maturity, the relative growth analysis based on the allometric technique (Huxley 1950) was applied from the morphometric data. Prior to the relative growth analysis, the possibility of heterochely (differences between right and left chelipods) was examined using Mann–Whitney test ( $\alpha=0.05$ ) with measurements of ChW, ChL, and ChH. As no significant differences were found between the chelipods, we standardized the data using

measurements from the right chelipod as the variable for analysis.

The relationships among the measured structures were established, with CW as the independent variable and CL, ChW, ChL, ChH, AW and GL as dependent variables. Data were plotted on scatter plots and fitted to the allometric equation  $y=ax^b$  (Hartnoll 1982), where  $y$  represents the dependent variable,  $x$  the independent variable;  $a$  the intercept of the curve on the ordinate axis and  $b$  the allometric coefficient. The data were transformed into neperian logarithm ( $\ln$ ) and subjected to simple linear regression analysis, resulting in linearized equations ( $\ln y = \ln a + b \ln x$ ) (Huxley 1950). The value of the allometric constant  $b$  was calculated for each biometric relationship,

and the null hypothesis ( $H_0: b=1$ ) was tested using Student's t-test ( $\alpha=0.05$ ), considering isometric growth ( $b=1$ ), positive allometry ( $b>1$ ) and negative allometry ( $b<1$ ) (Zar 2009).

A non-hierarchical K-means clustering analysis was performed to identify the morphometric relationships that displayed significant differences in growth patterns. The results of the K-means classification were further refined by applying discriminant analysis (DA) (Sampedro et al. 1999). Following the categorization of data into demographic groups (juvenile and adult) after logarithmic transformation, analysis of covariance (ANCOVA) was applied to test for differences between the groups in angular ( $b$ ) and linear ( $a$ ) coefficients. This analysis enabled the determination of whether each relationship should be represented by a single straight line or by different linear equations for the groups (Herrera et al. 2013).

The cutoff point between groups, as identified in the significant ( $p<0.05$ ) biometric relationships, was considered as the onset of morphological sexual maturity. In cases where there was overlap in growth lines between juveniles and adults, the  $L_{50}$  method was employed to identify the size at morphological sexual maturity. This method analyzed the distribution of individuals into size classes based on CW. Subsequently, the logistic curve equation  $y=1/(1+e^{-r(CW-CW_{50})})$  was fitted to the data using the least-squares method (Vazzoler 1996). The size at morphological maturity was defined as the interpolation point (50%).

We calculated the  $L_{50}$  values for males and females, representing the carapace width (CW) at which 50% of the *C. danae* and *C. ornatus* populations were expected to be sexually mature, based on the presence of mature gonads (DE and MA). The data were fitted to a logistic sigmoid curve following the equation  $y=1/(1+er(CW-L_{50}))$ , where  $y$  represents the proportion of adult blue crab,  $r$  is the slope coefficient of the curve, CW is the carapace width and  $L_{50}$  is the size at gonadal sexual maturity.

We calculated  $L_{50}$  values along with a 95% confidence interval by combining data from all available stations. An ordinary least squares linear regression was applied to the overall  $L_{50}$  estimates to examine trends across the entire population over time (Vazzoler 1996).

To facilitate the comparison of the sizes of gonadal maturity in *C. ornatus* obtained in this study (CW)

with those data available in the literature measured using the carapace width between the ends of the lateral spines (LS), the following formulas were used, as suggested by Carvalho et al. (2011):  $CW=0.79LS-0.56$  (females) and  $CW=0.77LS-0.59$  (males), where CW corresponds to the carapace width between the bases of the lateral spines and LS represents the carapace width between the ends of the lateral spines.

The reproductive period of *C. danae* and *C. ornatus* was determined by assessing ovigerous female (OF) and reproductive individuals relative to the total number of adults in each sampled sites and month. Reproductive individuals were identified based on the presence of developing (DE) and mature (MA) gonadal development in both males and females. The presence of recruits was evaluated considering entry of juvenile specimens (males and females) relative to the total number of individuals. This assessment was conducted using monthly and sites data for each species throughout the study.

The environmental variables (bottom temperature and salinity, sediment Phi and organic matter content) were related to the abundance of reproductive and non-reproductive males and females of *C. danae* and *C. ornatus*, across various stages of gonad development, as follows: (F1) females with RU gonads, (F2) reproductive females, (F3) ovigerous females, (M1) males with RU gonads, (M2) reproductive males. These relationships were analyzed using the Canonical Correspondence Analysis (CCA). This analysis calculates combinations of scores for a set of data with maximum linear correlations, which explain the highest levels of data variance. The canonical coefficients were used to interpret this ordering technique, allowing us to relate variations in the abundance of different species to variations in environmental factors. A significance level of 5% ( $\alpha=0.05$ ) was used to assess the statistical significance of the tests. The statistical analysis was conducted using the R software package vegan (R Core Team 2021).

To test possible relationship between temperature, salinity, Chl-*a* concentration, and the percentage of ovigerous females, a time series analysis was performed using Statistical Cross Correlation 7.0 (Statsoft, Inc), with a significance level of 5%. This analysis allowed us to determine potentially delayed or early relationships ("lags") between variables (Zar 2009; Statsoft 2004).

## Results

A total of 13,262 *C. danae* individuals were captured, 1,648 juveniles, 5179 adult females (RU = 715, DE = 1945, MA = 2519), 5202 ovigerous females, and 1233 adult males (RU = 367, DE = 497, MA = 369). Size of females ranged from 13.1 to 91.9 mm (CW) ( $63.3 \pm 7.1$  mm CW), while size of males ranged from 12.1 to 99.6 mm (CW) ( $61.7 \pm 14.7$  mm CW). Size of ovigerous females ranged from 45.0 to 91.9 mm (CW) ( $64.6 \pm 5.5$  mm CW).

Regarding *C. ornatus*, a total of 4,892 individuals were captured, of which 3,205 juveniles, 351 adult females (RU = 197, DE = 105, MA = 49), 34 ovigerous females, and 1,302 adult males (RU = 316, DE = 512, MA = 474). Size of females ranged from

12.7 to 67.3 mm (CW) ( $35.8 \pm 9.6$  mm CW), while size of males ranged from 11.4 to 82.0 mm (CW) ( $45.6 \pm 15.4$  mm CW). Ovigerous females ranged from 41.0 to 62.8 mm (CW) ( $51.9 \pm 5.8$  mm CW).

### Sexual maturity

The morphometric relationships of *C. danae* and *C. ornatus* between juvenile and adult phases were statistically significant in both sexes (ANCOVA,  $p < 0.05$ ), with the exception for CL vs. CW in males and females and ChL vs. CW in females of *C. danae*. In *C. ornatus*, only CL vs. CW in males and ChW vs. CW in females did not show significant differences between juvenile and adult phases (ANCOVA,  $p > 0.05$ ) (Tables 1 and 2).

**Table 1** *Callinectes danae* Smith, 1869. Results of the analysis of covariance (ANCOVA) and analysis of morphometric relationships. Carapace width (CW) as independent variable (data transformed: log)

Covariance results					Regression (ln)			Test for isometry		
Dependent variable	F	P	Sex phase	n	Intercept	Slope (b)	r <sup>2</sup>	t	P	Level
CL	0.246	0.620	JM/AM	137	-0.161	0.958	0.990	6.274	<0.001	-
	0.031	0.860								
	0.224	0.637	JF/AF	123	-0.183	0.960	0.993	5.223	<0.001	-
	0.301	0.584								
ChL	-	-	JM	51	-0.209	0.976	0.877	0.453	<0.001	0
	11.548	0.000*	AM	87	-0.673	1.264	0.817	4.063	<0.001	+
	2.264	0.135	JF/AF	124	-0.448	1.105	0.944	4.322	<0.001	+
	1.248	0.266								
ChW	-	-	JM	50	-0.631	0.842	0.667	1.846	<0.001	+
	4.553	0.035*	AM	87	-1.061	1.127	0.598	1.264	<0.001	0
	15.424	0.000*	JF	56	-0.973	1.031	0.663	0.306	<0.001	0
	0.070	0.792	AF	68	-0.867	0.993	0.607	0.068	<0.001	0
ChH	35.179	0.000*	JM	53	-0.537	0.845	0.645	1.772	<0.001	-
	3.155	0.078	AM	85	-0.866	1.066	0.629	0.738	<0.001	0
	7.749	0.006*	JF	58	-1.016	1.124	0.599	1.945	<0.001	+
	0.375	0.541	AF	66	-0.804	1.022	0.559	0.190	<0.001	0
AW	-	-	JM	52	0.279	0.161	0.051	8.502	<0.001	-
	4.249	0.041*	AM	86	-0.002	0.397	0.302	9.150	<0.001	-
	-	-	JF	60	-1.408	1.393	0.775	4.991	<0.001	+
	13.584	0.000*	AF	62	-0.576	1.084	0.938	2.339	<0.001	+
GL	74.345	0.000*	JM	58	0.138	0.517	0.308	4.656	<0.001	-
	2.440	0.121	AM	79	-0.185	0.758	0.385	2.214	<0.001	-

CL carapace length, ChL chelipod length, ChW chelipod width, ChH chelipod height, AW abdominal width, GL gonopodium length, JM juvenile male, AM adult male, JF juvenile female, AF adult female, 0 isometric growth, + positive allometry, - negative allometry  
\* $p < 0.05$

**Table 2** *Callinectes ornatus* Ordway, 1863. Results of the analysis of covariance (ANCOVA) and analysis of morphometric relationships. Carapace width (CW) as independent variable (data transformed: log)

Covariance results					Regression (ln)			Test for isometry		
Dependent variable	F	P	Sex phase	n	Intercept	Slope (b)	r <sup>2</sup>	t	P	Level
CL	0.81	0.371	JM/AM	121	- 0.232	0.991	0.998	2.210	<0.001	-
	3.13	0.079								
	-	-	JF	30	- 0.157	0.940	0.992	3.859	<0.001	-
ChL	15.922	0.000*	AF	35	- 0.316	1.043	0.988	2.143	<0.001	+
	-	-	JM	53	- 0.299	1.026	0.959	0.888	<0.001	0
	32.807	0.000*	AM	69	- 0.847	1.375	0.908	7.032	<0.001	+
	-	-	JF	28	- 0.298	1.026	0.976	0.833	<0.001	0
ChW	6.776	0.011*	AF	37	- 0.544	1.179	0.941	3.579	<0.001	+
	-	-	JM	52	- 0.983	1.058	0.944	1.612	<0.001	0
	8.470	0.004*	AM	70	- 1.338	1.300	0.803	3.839	<0.001	+
	2.990	0.088	JF/	65	- 1.127	1.157	0.947	4.520	<0.001	0
ChH	3.996	0.050	AF							
	12.090	0.000*	JM	54	- 0.893	1.064	0.898	1.286	<0.001	0
	3.122	0.577	AM	69	- 0.943	1.120	0.713	1.382	<0.001	0
	-	-	JF	28	- 0.908	1.084	0.927	1.407	<0.001	0
AW	5.766	0.020	AF	37	- 1.444	1.411	0.781	3.255	<0.001	+
	-	-	JM	39	- 0.648	0.663	0.666	4.364	<0.001	-
	7.333	0.007*	AM	84	- 0.233	0.426	0.447	10.965	<0.001	-
	-	-	JF	32	- 1.204	1.290	0.634	1.620	<0.001	0
GL	11.494	0.001*	AF	33	- 2.923	2.445	0.702	5.050	<0.001	+
	-	-	JM	38	- 0.863	1.081	0.866	1.146	<0.001	0
	18.129	0.000*	AM	84	- 0.398	0.795	0.872	6.095	<0.001	-

CL carapace length, ChL chelipod length, ChW chelipod width, ChH chelipod height, AW abdominal width, GL gonopodium length, JM juvenile male, AM adult male, JF juvenile female, AF adult female, 0 isometric growth, + positive allometry, - negative allometry  
\*p < 0.05

The relationships that exhibited the most pronounced changes in allometric coefficients between demographic categories of *C. danae* and *C. ornatus* were ChL vs. CW for males and AW vs. CW for female. Specifically, the ChL relative growth in males of *C. danae* and *C. ornatus*, shifted from isometry in juveniles to positive allometry in the adult phase. The cutoff value of 58.5 mm CW was identified as valid for determining male morphological sexual maturity in *C. danae*. In the case of *C. ornatus*, while a value of 45.0 mm CW was deemed valid for morphological sexual maturity (Figs. 2 and 3).

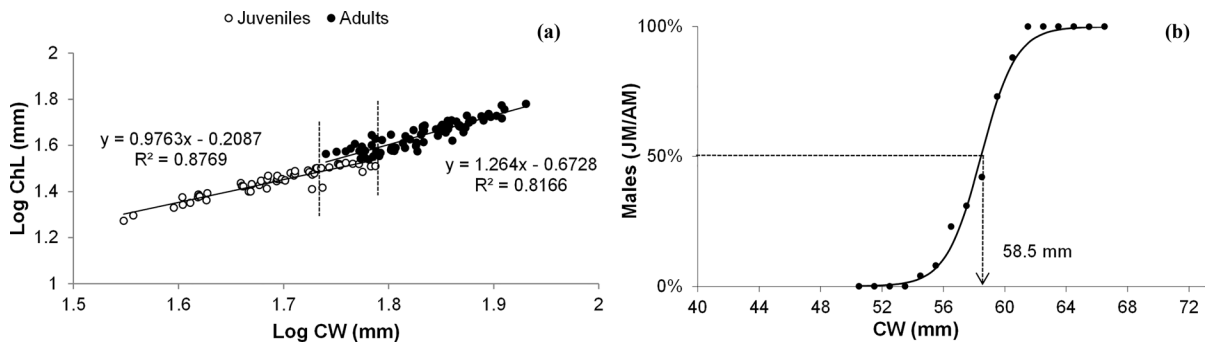
For females, the AW vs. CW relationship exhibited positive allometry in both juvenile and adult stages in *C. danae*. In *C. ornatus* females, this same relationship transitioned from isometry in the juvenile to

positive allometry in the adult phase. The valid value for female morphological sexual maturity in *C. danae* was determined as 54.5 mm CW, while for *C. ornatus*, it was 41.2 mm CW (Figs. 4 and 5).

For the gonadal sexual maturity in *C. danae*, females exhibited smaller estimated sizes (L<sub>50</sub>) compared to males, with a size of 61.4 mm CW for females and 69.4 mm CW for males (Fig. 6). The same pattern was observed for *C. ornatus*, with a size of 46.9 mm CW for females and 58.4 mm CW for males (Fig. 6).

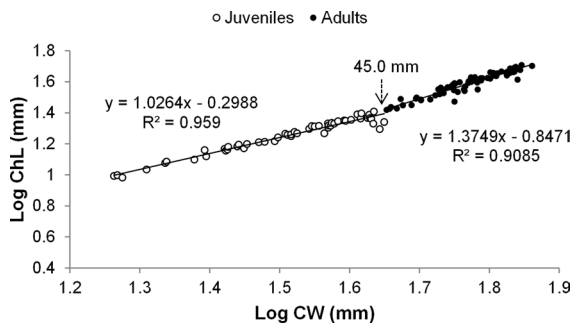
Reproductive period and presence of recruits

Reproductive females of *C. danae* were present in every sampled month with the higher percentages



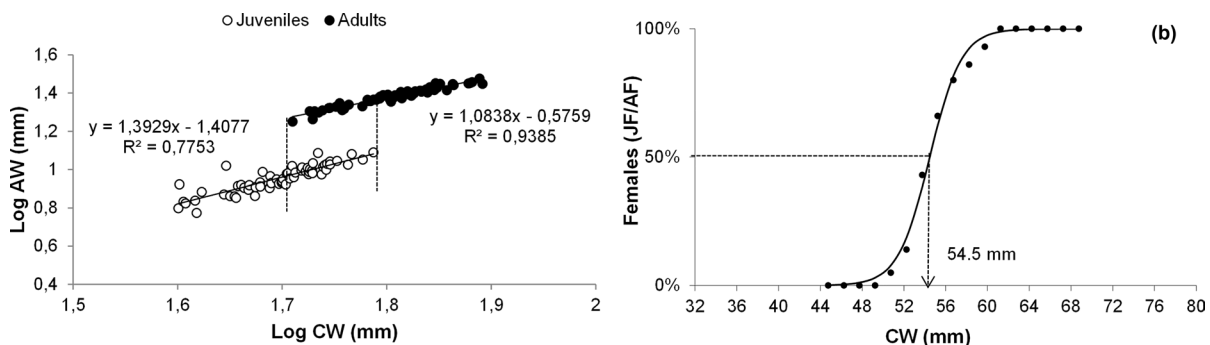
**Fig. 2** *Callinectes danae* Smith, 1869. **a** Estimated size at morphological sexual maturity for males. **b** In males, the estimated size corresponds to the carapace width (CW) of the adjusting regression of overlapping juveniles and adults, indi-

cating the size at which males are morphologically mature. Abbreviations: ChL=cheliped length, JM=juvenile males, AM=adult males



**Fig. 3** *Callinectes ornatus* Ordway, 1863. Estimated size at morphological sexual maturity for males. The estimated size refers to the smallest individual after the inflection point of the equations for juveniles and adults. ChL=cheliped length, CW=carapace width

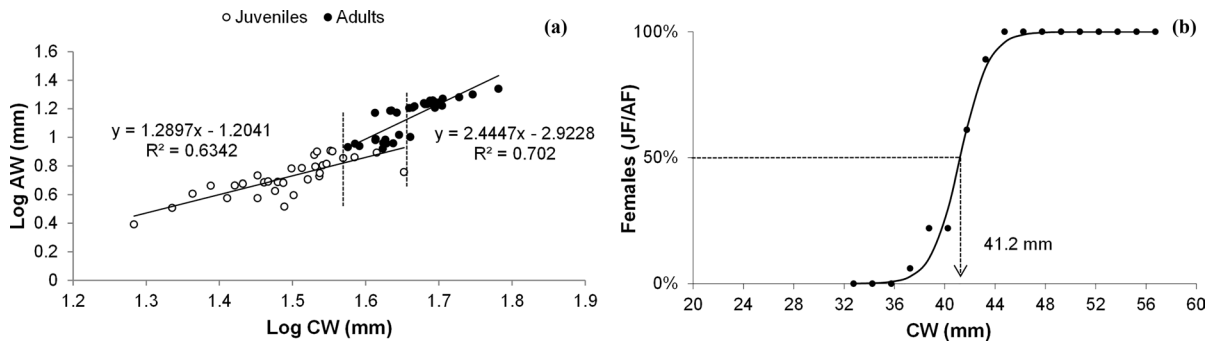
observed over austral spring (October and November/2013, at 67.9 and 63.5%, respectively). However, reproductive females were also observed in July/2012 (austral winter, at 65.1%), May/2013 (austral autumn, at 61.7%) and March/2014 (austral summer, at 66.0%) (Fig. 7a). Ovigerous females were also recorded throughout all months, with the highest peak occurring in January/2014 (austral summer, 85.5%) (Fig. 7a). Reproductive males were present almost year-round, except in September/2013, when only two rudimentary adults (RU) were captured (Fig. 7b). Males and females of *C. danae* with rudimentary gonads represent the smallest sampled percentages (Fig. 7).



**Fig. 4** *Callinectes danae* Smith, 1869. **a** Estimated size at morphological sexual maturity for females. **b** In females, the estimated size corresponds to the carapace width (CW) of the adjusting regression of overlapping juveniles and adults, indi-

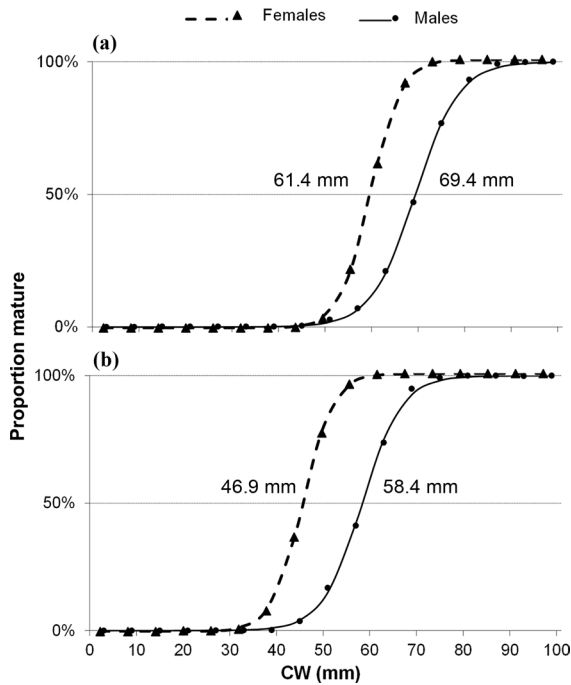
cating the size at which males are morphologically mature. Abbreviations: AW=abdominal width, JM=juvenile males, AM=adult males





**Fig. 5** *Callinectes ornatus* Ordway, 1863. **a** Estimated size at morphological sexual maturity for females. **b** In females, the estimated size corresponds to the carapace width (CW) of the adjusting regression of overlapping juveniles and adults, indi-

cating the size at which males are morphologically mature. Abbreviations: AW=abdominal width, JM=juvenile males, AM=adult males



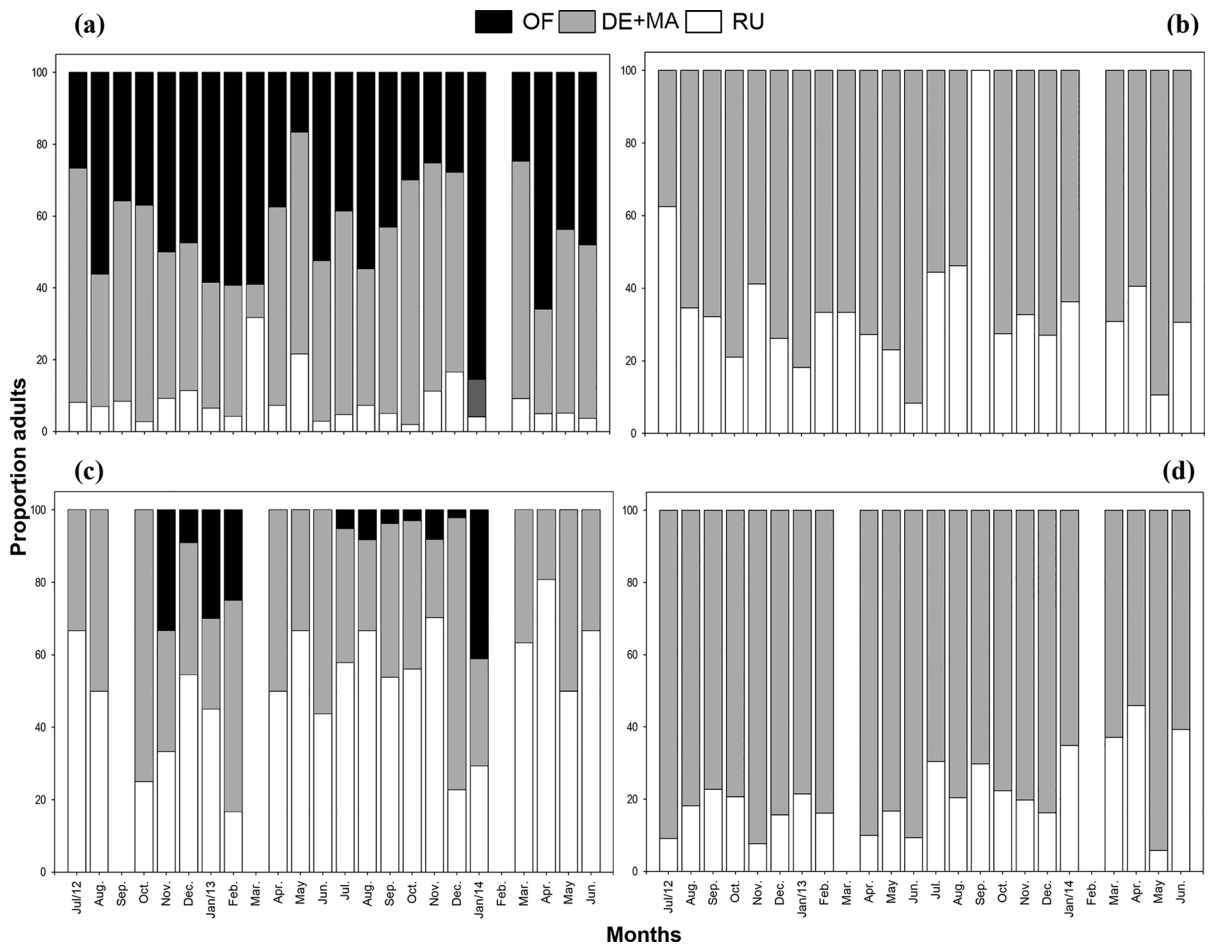
**Fig. 6** Calculations of estimated values of gonadal sexual maturity for **a** *Callinectes danae* and **b** *Callinectes ornatus* in Cananéia region. Points represent the proportion of mature male and female individuals (RU, DE or MA gonads) for each 6 mm size class of carapace width (CW), across all sites. The estimated size at which 50% of individuals are mature, based on the fitted curve, provides the estimate for  $L_{50}$

*Callinectes ornatus* exhibited reproductive females almost year-round, with the majority observed over austral spring (October/2012 and December/2013, both at 75.0%), followed

by February/2013 (austral summer, 58.3%) and June/2013 (austral autumn, 56.3%). Ovigerous females were observed in peaks from November/2012 to February/2013. There was a second peak from June/2013 to January/2014, with a higher percentage in January/2014 (austral summer, at 41.2%) (Fig. 7c). Reproductive males were present in every month and represent the highest percentages sampled, with the lowest percentage recorded from January to April/2014 (<65%) (Fig. 7d). Regarding rudimentary gonads (RU), females were sampled in higher percentages than males (Fig. 7).

Concerning the sites of reproductive females of *C. danae*, the values differed among the seven sites, with the highest percentage of ovigerous females in S3 and S5 (62.3 and 66.4%, respectively), and the lowest in S7 (30.7%). Reproductive females of *C. ornatus* also presented different values among the sites, with highest values of ovigerous females in S1 (14.8%) and S3 (13.9%), while the lowest values were observed in S6 and S7 (both 0.0%) (Fig. 8). Both species showed abundant reproductive males, with *C. danae* exhibiting sites in the estuarine area (Mar Pequeno) with more than 70.0% (S6=79.8%) and *C. ornatus* had their highest values at site S2 and S7 (77.3% in both) (Fig. 8).

Our dataset allowed the estimation of a seasonal recruitment index for the study area, revealing recruitment pulses of *C. danae* and *C. ornatus* during the austral spring and summer seasons. *Callinectes danae* exhibited higher peaks in November and December of 2012 (21.5 and 24.4%, respectively), while in 2013, they were recorded in March



**Fig. 7** Monthly variation in the proportion of adults of the *Callinectes danae* females (a) and males (b) and *Callinectes ornatus* females (c) and males (d). Abbreviations: OF: oviger-

ous females, DE: developing gonads, MA: mature gonads, RU: rudimentary gonads

(41.4%) and December (24.2%). In 2014, the highest peak was once again observed in March (26.3%).

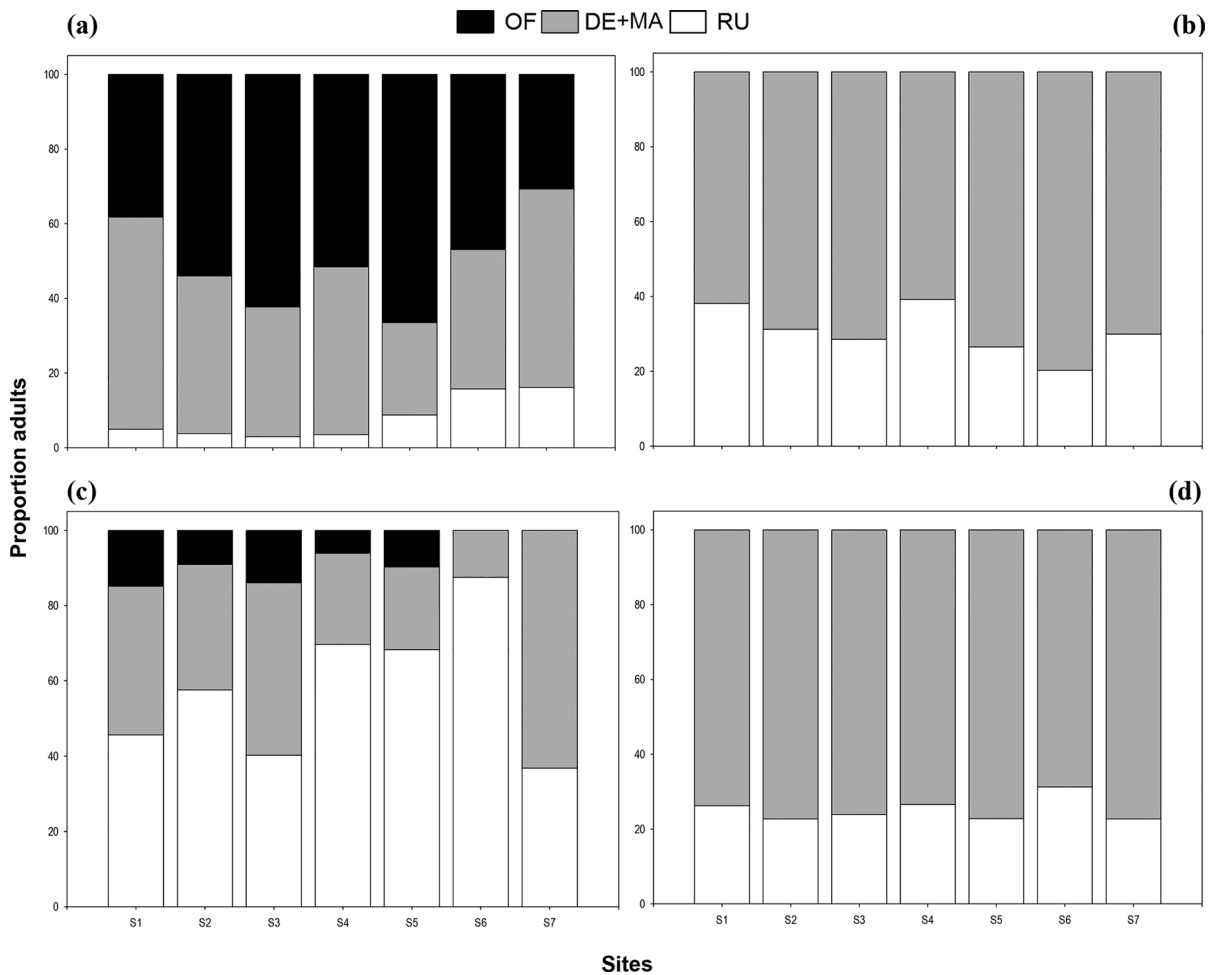
Comparing the monthly abundance of juveniles to the total number of individuals sampled, *C. ornatus* exhibited higher recruitment than *C. danae*. In 2012, the months of November (86.9%) and December (83.8%) were particularly marked by high recruitment. In 2013, peaks occurred in January (80.1%), March (100%) and August (80.4%) (Fig. 9).

The spatial distribution of *C. danae* recruitment revealed a preference concentrated in sites S6 (21.6%) and S7 (22.2%) accounting for approximately 60% of the recruitment in the estuarine-lagoon area. For *C. ornatus*, sites S4 (77%) and S5 (77.3%), represented

over 65% of the total recruitment within the coastal area (Fig. 9).

The CCA revealed that *C. danae* correlates with temperature and salinity, with a total variance of the first two canonical axes of 98%. Analyzing axis 1 (66%), ovigerous females (F3) and reproductive males (M2) correlate positively with temperature and negatively with salinity (Table 3). For the *C. ornatus*, the CCA also showed two main axes, with a total of 88% of the variance of the data. Considering axis 1 (58%), F3 correlated positively with temperature and organic matter, and negatively with M1 (Table 3).

From all the correlation analyzes between environmental factors and percentage of ovigerous females of *C. danae* and *C. ornatus*, only FO of *C. ornatus* and



**Fig. 8** Spatial variation in the proportion of adults of the *Callinectes danae* females (**a**) and males (**b**) and *Callinectes ornatus* females (**c**) and males (**d**). Abbreviations: OF: ovigerous

females, DE: developing gonads, MA: mature gonads, RU: rudimentary gonads

temperature resulted in positive correlation. Thus, this analysis revealed the correlation in the increase in FO abundance one month before and at instant zero (lags) when there is an increase in temperature (Times Series,  $p < 0.05$ ) (Fig. 10).

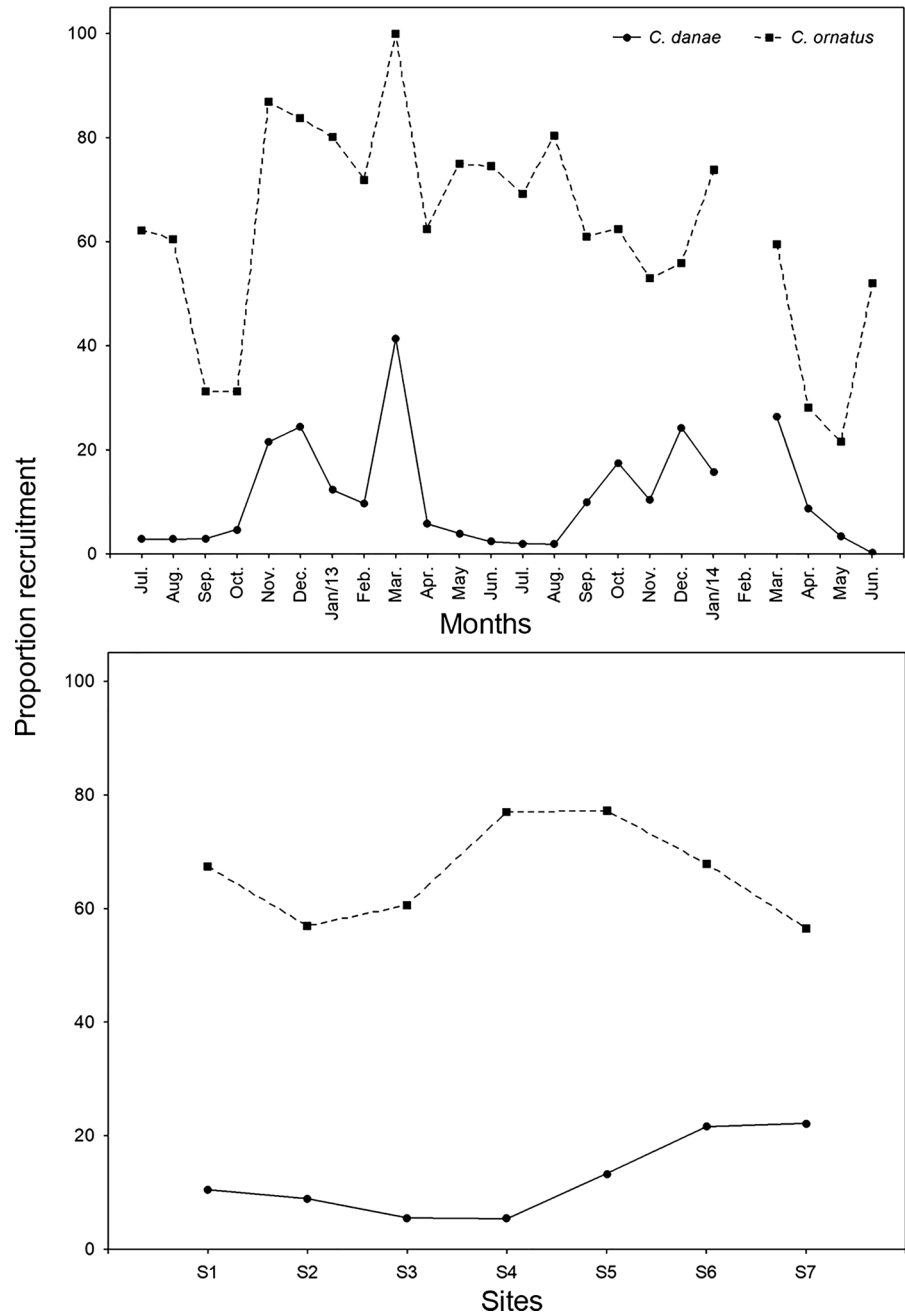
## Discussion

Our results indicate that both species inhabit the coastal area and the estuarine-lagoon system of Cananéia–Iguape and are present throughout the year, with *C. danae* being more abundant species. Analyses of sexual maturity and reproduction, in conjunction with the presence of recruits, reveal that both species

use this coastal and estuarine-lagoon system to complete their life cycle.

Reproductive aspects in crustaceans can be affected by several factors, including the physiological conditions of the species, seasonal reproductive patterns, latitude, population density, and local environmental conditions (Jensen 1958; Hines 1989; Marochi et al. 2013). Variations in carapace width recorded for *C. danae* and *C. ornatus* demonstrate that males reach larger sizes than females. Males invest metabolic energy in somatic growth, while females allocate their energy resources to reproduction, aligning with the expected pattern for the *Callinectes* spp. (Hartnoll 1985; Kevrekidis 2019; Cardim et al. 2022).

**Fig. 9** Proportion of juveniles (IM) of *Callinectes danae* and *Callinectes ornatus* show the monthly and spatial recruitment from Cananéia, São Paulo state, Brazil



Regarding the relative growth patterns of specific structures, we concluded that the chelipod length of males and abdomen width of females of both species serve as indicative structures for morphological sexual maturity. These results suggest that the differential growth of these structures is related to secondary sexual character, as seen in studies on brachyuran crabs (Pinheiro and Fransozo 1993; Costa and

Negreiros-Fransozo 1998; Mantelatto and Fransozo 1999; Fernández-Vergaz et al. 2000; Cardim et al. 2022).

The positive allometry of the chelipod in adult males suggests a potentially greater energy investment in the development of this structure following the puberty molt. This indicates that chelipods are associated with reproductive processes (i.e., guarding

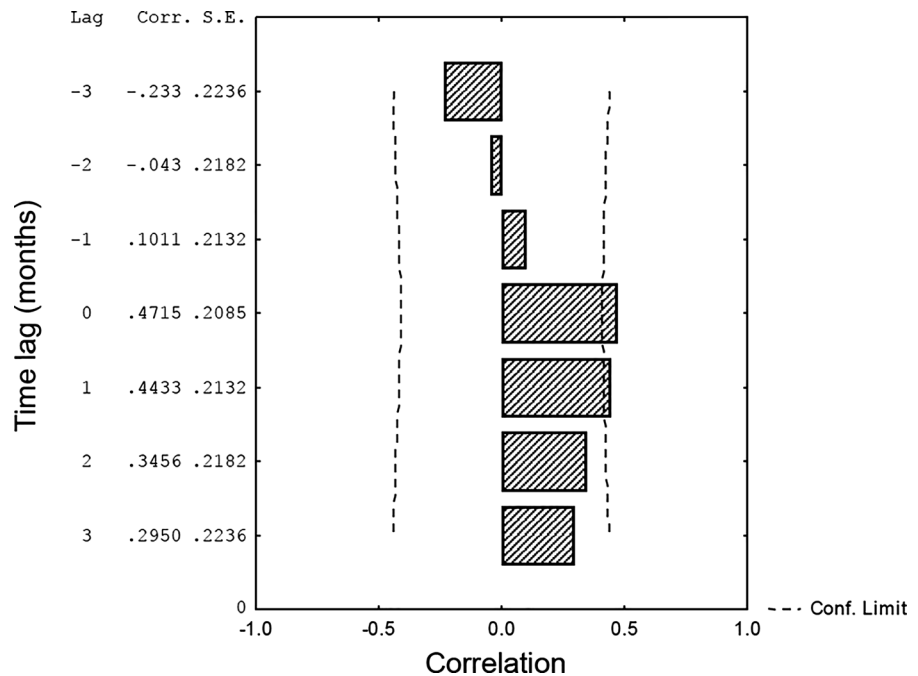
**Table 3** *Callinectes danae* Smith, 1869 and *Callinectes ornatus* Ordway, 1863. Results of Canonical Correspondence Analysis (CCA) for the abundance of reproductive and non-reproductive males and females and environment factors in Cananéia, São Paulo state, Brazil

Variables	<i>C. danae</i>				<i>C. ornatus</i>			
	Axis 1	Axis 2	r <sup>2</sup>	p	Axis 1	Axis 2	r <sup>2</sup>	p
F1	-0.75	-0.66	0.05	0.21	0.38	0.92	0.03	0.34
F2	0.98	0.22	0.14	0.06	0.75	0.66	0.08	0.05
F3	-0.96	0.27	0.46	0.00*	0.10	-0.01	0.37	0.00*
M1	-0.81	-0.59	0.10	0.08	-0.18	0.98	0.30	0.00*
M2	-0.85	-0.53	0.15	0.03*	0.99	0.12	0.02	0.39
<i>Environmental factors</i>								
T	-0.95	-0.30	0.32	0.00*	0.95	0.31	0.09	0.04*
S	0.28	0.96	0.24	0.01*	0.35	0.94	0.02	0.41
Phi	0.98	0.18	0.05	0.32	0.93	0.36	0.03	0.35
OM	0.85	-0.53	0.00	0.89	0.94	-0.34	0.09	0.03*

F1 females with RU gonads, F2 reproductive females, F3 ovigerous females, M1 males with RU gonadas, M2 reproductive males, T temperature, S salinity, Phi sediment grain size, OM organic matter

\*p < 0.05

**Fig. 10** *Callinectes ornatus* Ordway, 1863. Time Series analysis of ovigerous females and water temperature recorded in Cananéia, São Paulo state, Brazil. Lag: time; Corr: correlation value; S.E.: standard error; Config. Limit.: Confidence limit



the female before mating) and agonistic interactions with other males, regarding intra and interspecific competitions (Marochi et al. 2013; Mantelatto and Fransozo 1999). Consequently, larger males equipped with well-developed chelipods have an advantage in mate selection and related competitive events.

In females, the increase in abdominal width during the adult phase is expected in Portunidae, as they externalize and incubate eggs in the abdomen after fecundation (Mantelatto and Fransozo 1997; Pinheiro and Fransozo 1998). This feature can be explained by the fact that after the puberty molt, females of both

species exhibit an increase in abdominal size, resulting in positive allometry in abdominal growth relative to carapace growth, as observed in *C. danae* and *C. ornatus* in Cananéia. According to Mantelatto and Fransozo (1997), the increase in the abdomen in females represents an adaptation to maximize the number of eggs produced by the species, resulting in higher fecundity.

Based on these morphometric relationships, the estimation of morphological sexual maturity in males of *C. danae* and *C. ornatus* indicates that males attain maturity at larger sizes than females. This sexual dimorphism represents a reproductive adaptation, providing protection to post-molt females immediately after copulation (post-copulatory embrace). For females, reaching maturity at smaller sizes entails investing energy in reproductive processes early in life, which translates into a longer fertile life, thereby increasing the reproductive output of the population (Hartnoll 1985; Keunecke et al. 2008; Cardim et al. 2022). Regarding gonadal sexual maturity, a similar pattern was observed for both species, with males attaining larger sizes than females.

In Cananéia (25°S), the size at gonadal maturity in females (61.4 mm CW) closely approximated values estimated for populations of *C. danae* in Pernambuco (7°S) by Barreto et al. (2006) and Araújo et al. (2012) (61.6 and 62.5 mm CW, respectively), which represent the lowest latitude limit of the populations studied to date. Similarly, a comparable size of maturity for males had been recorded in Paraná (25°S) (60.5 mm CW) (Baptista-Metri et al. 2005). It is expected that marine crustaceans inhabiting lower latitude regions, characterized by higher temperatures, would exhibit sexual maturity at smaller sizes compared to those in higher latitude areas (Hartnoll 1982; Bauer 1992; Carvalho et al. 2011). However, at Pernambuco state (Araújo et al. 2012), males of *C. danae* reached maturity at larger sizes than those observed in Cananéia, São Paulo.

The larger sizes of maturity observed in the Pernambuco population may result from genetic differences influenced by geographical barriers, population density, and environmental factors such as precipitation, food availability, or fishing pressure (Schmiegelow 2004; Cardim et al. 2022), leading to higher maturity values. However, comparing our results with those from other regions presents challenges due to methodological differences. The variations in the

methods used to collect and analyze data can significantly influence the results obtained, making direct comparisons between studies difficult.

The estimated sizes at gonadal maturity in *C. ornatus* from Cananéia (58.4 mm CW for males and 46.9 mm for females) closely resembled those reported by Baptista et al. (2003) who recorded sizes of 55.0 mm CW in males and 48.0 mm CW in females, also in Paraná (25° S), which is geographically close to Cananéia. However, Mantelatto and Fransozo (1996) observed sizes of 50.0 mm CW in males and 43.0 mm CW in females in Ubatuba (23°S), while Branco and Lunardon-Branco (1993) found 51.0 and 47.6 mm CW in males and females, respectively, in Paraná (25°S). Conversely, Cardim et al (2022) documented smaller recorded sizes in Bahia (12°S), with males at 43.9 mm CW and females at 40.4 mm CW. This observation aligns with the latitudinal effect paradigm, which dictates that crustaceans in lower latitude regions tend to exhibit smaller sizes compared to their counterparts of higher latitude areas.

The morphological and gonadal sexual maturities of *C. danae* and *C. ornatus* are not synchronous. These species exhibit secondary sexual characters before the complete development of the gonads. Individuals become capable of reproduction only when they reach both maturities (Sastry 1983; Conan and Comeau 1986). For instance, females can copulate and store spermatophores in the vas deferens before their gonads are fully developed (Subramonian 1991). This phenomenon was observed in *C. danae* by Barreto et al. (2006), where females exhibited a developed seminal receptacle but immature gonads, suggesting copulation before reaching gonadal sexual maturity.

The estimation and comparison of sexual maturity in brachyurans using different techniques are crucial. Data on sexual maturity size is important for monitoring and managing populations and can signal the negative impact of overfishing, especially of commercially important crab species. Waiho et al. (2017) recommends that monitoring and estimation of sexual maturity should be conducted over a longer time frame (e.g., over several consecutive spawning seasons) to reveal not only the health and growth of a population but also the effect of fishing pressure and/or other anthropogenic factors such as habitat destruction, pollution, and climate change. Fishing pressure

can influence the hereditary characteristics of a population, including the average size of individuals (Policansky 1993; Trippel 1995). Such changes can result in a reduction in size at maturity, incurring additional costs for the species. Smaller sizes are associated with lower fecundity and potentially higher predation risk, ultimately diminishing the reproductive potential of the population (Vazzoler 1996).

The presence of reproductive males and females of *C. danae* and *C. ornatus* throughout the study period confirms continuous reproduction. Both species exhibit asynchronous reproduction, indicating that although reproduction occurs year-round, not all adults are actively reproducing at all times (Bauer 1989). This is further supported by the varying peaks in ovigerous females observed in *C. ornatus* throughout the year, with notable peaks during the austral summer.

The summer season in the Cananéia region is characterized by increased rainfall, leading to a significant influx of continental nutrients into the environment. Elevated temperatures stimulate primary and secondary productivity (Ara 2004; Barrera-Alba et al. 2009), providing abundant food resources for larvae and enhancing the reproductive success of these species (Andrade et al. 2015).

*Callinectes* species employ reproductive optimization strategies, such as multiple spawning, where females can release more than one egg mass during a single reproductive period (Mantelatto and Fransozo 1999; Watanabe et al. 2014). This strategy was confirmed by Brown (2009) through an examination of ovarian morphology in *C. sapidus* and the observation of ovigerous females with varying stages of gonadal development. This observation aligns with an important finding from our study; ovigerous females of *C. danae* and *C. ornatus* exhibited a range of gonadal development stages, including individuals with fully matured gonads. This indicates the possibility of multiple spawning events within the genus.

According to Branco and Masunari (2000) and Sant'Anna et al. (2012), the life cycle of *C. danae* involves estuarine areas for growth, copulation, and egg exteriorization, while the marine environment serves as a spawning ground and larval dispersal zone. Larval development in *C. danae* benefits from high salinity, as larvae are less tolerant to salinity fluctuations than adults (Paul 1982). In contrast, *C. ornatus* exhibits lower tolerance to salinity

and temperature variations compared to *C. danae* (Negreiros-Fransozo and Fransozo 1995), prompting ovigerous females to occupy offshore areas (Lavrado et al. 2000). The low number of ovigerous females of *C. ornatus* observed in this study is likely due to their migratory behavior toward higher salinity areas, supported by absence of ovigerous females at lower salinity sites (S6 and S7). This reproductive strategy suggests avoidance of interspecific competition, particularly with larger species such as *C. danae* and *C. sapidus* (Buchanan and Stoner 1988; Watanabe et al. 2014). In contrast, *C. danae* exhibits a broader distribution of ovigerous females across the sampled sites, with a high abundance at S5, a site recognized as a migration route for ovigerous females, according to Severino-Rodrigues et al. (2009).

Juvenile recruitment, similarly to reproductive activity, was observed throughout the year for both *C. danae* and *C. ornatus*, with peak abundances during the austral spring and summer. Notably, *C. ornatus* exhibited higher juvenile abundance. Studies have suggested that juveniles of *Callinectes* spp. tend to favor calm, shallow waters with elevated organic matter content, which are conducive to their development (Negreiros-Fransozo and Fransozo 1995; Tudesco et al. 2012). These findings align with those from Watanabe et al. (2014), who reported similar patterns in the *C. ornatus* population within the São Vicente bay-estuary complex, indicating that shallow marine regions act as nurseries for this life stage. Conversely, as previously documented by Branco and Masunari (2000), juveniles of *C. danae* exhibit a migratory behaviour, returning to estuarine systems to complete their life cycle, a behaviour supported by the higher juvenile abundance observed in sites within the estuarine-lagoon complex (i.e., S6 and S7).

This migratory behavior can be influenced by environmental changes that impact reproductive activity. These changes are modulated by a combination of proximal factors (such as water temperature, salinity, sediment composition, and contaminants) and ultimate factors (selective pressure) that interact to synchronize these activities (Bauer and Lin 1994; Ortega et al. 2022). Temperature, in particular, has been identified as a key modulating factor in the reproductive activity of the studied populations. Abundant ovigerous females are typically observed during periods of elevated temperatures, which correlate with increase food availability and, subsequently, higher

growth rates (Severino-Rodrigues et al. 2009; Sforza et al. 2010).

The life cycle of *C. danae* was strongly influenced by salinity variation. Reproductive males exhibit higher abundance in areas with lower salinities due to their more efficient osmoregulation mechanism. This is attributed to the presence of an ammonia site responsible for osmotic balance and a more permeable gill epithelium, allowing them to tolerate significant salinity fluctuations (Masui et al. 2002). On the other hand, ovigerous females show a negative correlation with salinity. This is attributed to their preference for the reproductive migration route, an area influenced by oceanic waters, connecting the estuary and the sea (Severino-Rodrigues et al. 2009).

The positive correlation observed in ovigerous females of *C. ornatus* with high organic matter concentration is explained by the association between organic matter-rich sites and high primary productivity (Tyson 1995; Li et al. 2022). In Cananéia, the bay recorded the highest organic matter concentration, along with high salinity, creating favorable conditions for *C. ornatus*. Portunidae crabs can ingest sediment as a whole and extract its organic matter although these animals are primarily carnivorous, feeding on mollusks, bivalves, gastropods, and predated or decomposing animals (Warner 1977; Gencer and Vitorino 2023).

Animal behavior plays a crucial role in shaping ecological interactions within marine ecosystems. Competitors, predators, and prey engage in complex behavioral dynamics that can have cascading effects on trophic relationships (Grabowski and Kimbro 2005). For example, alterations in foraging behavior by predators can indirectly influence the abundance and distribution of prey species, thus affecting trophic cascades. Consequently, changes in the availability of organic matter, a fundamental resource in marine environments, can exert indirect effects on the behavior and distribution of bivalves and gastropods, two important groups of marine invertebrates.

For ovigerous females of *C. ornatus*, the observed positive correlation with a "lag" and at the moment of a temperature increase suggests an adaptation of the population to spawn during periods favorable for larval survival. Higher temperatures are correlated with an increase in primary productivity (Pérez-Arvizu et al. 2013). This biochemical parameter acts as an indicator of biological production zones and

food availability in aquatic ecosystems (Solanki et al. 2001). According to Sastry (1983), primary productivity is considered a key factor because food availability for larval stages significantly impacts the selection of the spawning period.

Pardieck et al. (1999) asserted that blue crabs can serve as models to illustrate how early developmental stages can be influenced by various physical and biological factors. Based on our results, it can be concluded that not only the development but also the reproductive strategies of these populations can be regulated by such factors. The distribution of *C. danae* and *C. ornatus* indicates reproductive plasticity, featuring distinct reproductive patterns and habitats preferences, which may be a strategy to enhance the reproductive success.

Understanding the biology and reproductive strategies of these species, particularly in marine and estuarine environments, is of paramount importance for ecosystem conservation. It offers crucial insights to maintain sustainable stocks, primarily determined by the minimum catch size regulations. Minimum catch size for *C. sapidus* and *C. danae* is legally defined at 12.0 cm CW, including consideration of lateral spines, and capture and commercialization of ovigerous females is prohibited (Brazil 1983). Nonetheless, such regulations are lacking for *C. ornatus* (Watanabe et al. 2014; Cardim et al. 2022).

Our study supports the proposed management plan for *C. danae*, prompting consideration for its extension to other species within the genus, such as *C. ornatus*. Consequently, a comprehensive evaluation of the management and monitoring of these species is imperative to ensure their sustainable coexistence within the ecosystems, given their economic and ecological significance.

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**Author contributions** DRH: Methodology, Data curation, Formal analysis, Writing-original draft, Writing-review and editing. RCC: Supervision, Writing-review and editing.



**Data availability** Data, associated metadata and calculation tools will be made available on request to the corresponding author (daphne\_herrera@hotmail.com).

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All work conducted in this study comply with current applicable state and federal laws (Authorization of the Instituto Chico Mendes de Biodiversidade/ICMBio – SIS-BIO number 23012-1).

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