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Sexual maturity of *Callinectes danae* and *C. ornatus* from Paraguaçu river estuary, Bahia state, Brazil

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ABSTRACT

Callinectes danae and *C. ornatus* are economically important species in several countries, including Brazil. Therefore, this study aimed to estimate the L_{50} of these species using morphological, morphometric, and physiological data. The estimated values were statically compared and results from previous studies were analyzed to verify latitudinal variations among the sizes of sexual maturity at different latitudes of the Brazilian coast. Individuals were monthly collected in the Paraguaçu River estuary from August 2013 to July 2014, using cage traps. L_{50} estimates for *C. danae* were morphological=55.80 mm, morphometric=59.04, mm, and physiological=60.41 mm for males and morphological=54.63 mm, morphometric=55.33 mm, and physiological=57.29 mm for females. Considering *C. ornatus*, estimates were morphological=42.63 mm, morphometric=50.81 mm, and physiological=43.95 mm for males and morphological=42.33 mm, morphometric=42.75 mm, and physiological=40.43 mm for females. Our results indicated that the minimum catch sizes should be equal to 61.00 mm for *C. danae* and 51.00 for *C. ornatus* and that the mesh of traps used by fishermen must be adjusted to prevent the capture of immature animals.

Keywords: artisanal fishing; sustainable; relative growth; gonad.

Maturidade sexual de *Callinectes danae* e *C. ornatus* no estuário do rio Paraguaçu, Bahia, Brasil

RESUMO

Callinectes danae e *C. ornatus* são siris economicamente importantes em vários países, incluindo o Brasil. O presente estudo objetivou determinar o L_{50} dessas espécies com base em dados morfológicos, morfométricos e fisiológicos. Os valores estimados foram comparados estatisticamente e os resultados de estudos anteriores no Brasil foram analisados para verificar variações latitudinais nos tamanhos de maturidade sexual em diferentes regiões da costa brasileira. Os exemplares foram coletados mensalmente, de agosto de 2013 a julho de 2014, por meio de armadilhas do tipo gaiola. As estimativas de L_{50} em *C. danae* foram morfológica=55,80 mm, morfométrica=59,04 mm e fisiológica=60,41 mm para machos e morfológica=54,63 mm, morfométrica=55,33 mm e fisiológica=57,29 mm para fêmeas. Considerando *C. ornatus*, as estimativas foram: morfológica=42,63 mm, morfométrica=50,81 mm e fisiológica=43,95 mm para machos e morfológica=42,33 mm, morfométrica=42,75 mm e fisiológica=40,43 mm para fêmeas. Nossos resultados indicaram que os tamanhos mínimos de captura deveriam ser iguais a 61,00 mm para *C. danae* e 51,00 mm para *C. ornatus* e a malha das armadilhas usadas pelos pescadores ajustada para impedir a captura de animais imaturos.

Palavras-chave: pesca artesanal; sustentável; crescimento relativo; gônada.

INTRODUCTION

In decapod crustaceans, sexual maturity can be understood as a set of morphological, physiological, and behavioral transformations, from which juvenile or immature individuals reach the ability to reproduce (Hartnoll, 1978, 1985). In general, sexual maturity in decapods can be estimated using morphological, physiological, and functional criteria (Somerton, 1980). These different types of maturity are defined according to the following criteria:

1. morphological (or morphometric) maturity is expressed by changes in the shape of different organs or tagmas as an adaptation for mating or egg incubation;
2. physiological maturity is characterized by the capacity to produce gametes and can be estimated by macroscopic or microscopic observation of the gonadal development stage; and

3. functional maturity is defined as the existence of all necessary functionalities for successful reproduction (for review, see González-Pisani et al., 2017; Waiho et al., 2017).

The sequence of events that characterize sexual maturity varies among different species and among individuals of the same species (Gerhart and Bert, 2008; González-Pisani et al., 2017). The morphological, physiological, and functional changes mentioned above may or may not occur in synchrony with each other (Hartnoll, 1982; Sastry, 1983; Conan and Comeau, 1986; Choy, 1988; Haefner Jr, 1990; Mantelatto and Fransozo, 1996; Barreto et al., 2006; Gerhart and Bert, 2008; Carvalho et al., 2011; Araujo et al., 2012). Thus, several authors have already emphasized the need to use more than one method to determine the size at the onset of maturity (Haefner Jr, 1990; Overton and Macintosh, 2002; Barreto et al., 2006).

The infraorder Brachyura has enormous diversity and includes species of great economic importance, such as crabs of the family Portunidae. These crustaceans typically have the abdomen adhered to the thoracic sternites until puberty molt occurs, when they become adults and copulatory organs can be exposed for copulation (Hartnoll, 1969; Haefner Jr, 1990). In addition, there are also evident changes in the abdomen morphology of female and male chelipeds, but without marked changes in the shape of the cephalothorax in both sexes (Hartnoll, 1969, 1978, 1982; Choy, 1988; Pinheiro and Fransozo, 1993, 1998). Such modifications are related to secondary sexual characters that develop at different rates in immature and mature life phases (Haefner Jr, 1990; Barreto et al., 2006). In this context, it is well established that, in portunids, the most used variables to estimate the size at the onset of maturity are the morphology of chelipeds (in males) and abdomen (in females), as well as the macroscopic observation of the maturation stage of gonads (Hatnoll, 1974, 1982; Mantelatto and Fransozo, 1996; Pinheiro and Fransozo, 1993, 1998; Barreto, et al., 2006; Johnston and Yeoh, 2021).

From the economic point of view, swimming crabs of the genus *Callinectes* are of relevant importance in several countries, including several regions of Brazil (Severino-Rodrigues, 2012; Andrade et al., 2013; Haimovici and Cardoso, 2017; Santos et al., 2021; Braga et al., 2021). The fishing of swimming crabs in the Northeastern region of Brazil occurs in an artisanal way and is a fishing resource of wide acceptance in the regional market (Barreto et al., 2006; Furia et al., 2008; Magalhães et al., 2011). Specifically, in the Todos os Santos Bay, swimming crabs are caught regardless of the species (mainly *Callinectes danae* Smith, 1869, *Callinectes ornatus* Ordway, 1863, and *Callinectes bocourti* A. Milne-Edwards, 1879) and processed in the form of "catado," which is a type of pre-cooked shredded meat obtained after the separation of the swimming crab meat from the exoskeleton (Walter et al., 2012).

According to Vasconcellos et al. (2011), the lack of policies and ineffectiveness of government strategies hinder the sustainable production of artisanal fisheries along the Brazilian coast, leading to over-exploitation or depletion of resources. Regarding the sustainability of swimming crabs, in addition to the fishing activity itself, many authors reported threats to these crustaceans, such as their presence as bycatch in shrimp fishing (Branco and Fracasso, 2004; Keunecke et al., 2012; Tudesco et al., 2012; Santos et al., 2016), the possible competition with the non-indigenous crab *Charybdis hellerii* (A. Milne-Edwards, 1867) for resources, and the presence of metals (e.g., Cu, Pb, Zn, Cd, and Hg) in males, females, and eggs (Lavradas et al., 2014; Rodrigues et al., 2021). Finally, Peres et al. (2020) highlighted that economically important crabs along the Brazilian coast (e.g., *C. danae* and *Callinectes sapidus* Rathbun, 1896) lack genetic structure among Brazilian populations and can be considered a single genetic stock. This condition could result in harmful consequences, such as inbreeding depression and loss of evolutionary potential (Frankham, 2005; Peres et al., 2020). Thus, information on the size at the onset of maturity is of great importance from the biological and economic point of view, contributing to the elaboration of normative laws for regulation of catches and sustainable use of population stocks (Smith et al., 2004; Carvalho et al., 2011).

Among portunids, *C. danae* and *C. ornatus* are two species that are morphologically similar and generally occur in sympatry, both on the continental shelf and in bays and estuarine areas (Furia et al., 2008; Golodne et al., 2010; Keunecke et al., 2012; Carvalho, 2011; Andrade et al., 2013). *Callinectes ornatus* has been recorded from North Carolina (USA) to Rio Grande do Sul (Brazil), and *C. danae* is distributed from Florida (USA) to Rio Grande do Sul (Brazil) (Melo, 1996).

Although *C. ornatus* occurs throughout the coast of Northeastern Brazil, there are still few scientific articles that have addressed its maturation size (when compared to *C. danae*). In this context, a study by Carvalho et al. (2011) is the only available research article held in the state of Bahia. In addition, other studies were conducted in the Southern (Branco and Lunardon-Branco, 1993; Baptista et al., 2003; Branco and Fracasso, 2004) and Southeastern (Mantelatto and Fransozo, 1996) regions of Brazil. In contrast, the sexual maturity of *C. danae* was estimated in Northeastern Brazil by Pereira-Barros (1980), Barreto et al. (2006) (only for females), Araújo et al. (2012), and Shinozaki-Mendes et al. (2013); in the Southern by Branco and Thives (1991), Branco and Masunari (2000), Baptista-Metri et al. (2005), Pereira et al. (2009), and Marochi et al. (2013); and in the Southeastern by Keunecke et al. (2012), Severino-Rodrigues et al. (2012), and Andrade et al. (2015).

SUDEPE Ordinance No. 24 from July 26, 1983, regulated fishing for blue crab (*C. danae* and *C. sapidus*) in Brazilian territorial waters, establishing, among other criteria, minimum catch size of 120 mm of carapace width (CW) and prohibition of capture, industrialization, and commercialization of ovigerous females (Ibama, 1983). More recently, ICMBio Ordinance No. 313, from April 12, 2018, regulated fishing for *C. danae* and *Callinectes exasperatus* (Gerstaecker, 1856) at RESEX-mar Canavieiras, in the southern region of the state of Bahia, establishing minimum catch size at 70 and 80 mm of CW for *C. danae* and *C. exasperatus*, respectively. Furthermore, this Ordinance also established minimum mesh size and number of traps per fishermen and prohibition of capture of ovigerous females. Therefore, both Ordinances do not include *C. ornatus*, which is also commercially exploited by artisanal fishermen from the Todos os Santos Bay.

Considering the economic importance of *C. danae* and *C. ornatus* for artisanal fishermen in the Todos os Santos Bay, this study aimed to determine the size at the onset of maturity of these two species, using morphological, morphometric, and physiological data. Additionally, the estimated values were compared to verify whether or not there is synchrony between the different maturities and results from previous studies were analyzed in order to verify latitudinal variations. Finally, we checked if the estimated size at the onset of maturity is in accordance with the Brazilian legislation, if adjustments are necessary to SUDEPE Ordinance, or even the elaboration of a specific Ordinance for the study region. Thus, this study has contributed to the definition of management strategies and sustainable use of this important fishing resource.

MATERIAL AND METHODS

Study area and sampling

Callinestes danae and *C. ornatus* individuals were monthly collected from August 2013 to July 2014, in the fishing community of São Francisco do Paraguaçu (S 12°44'30.56"; W 038°52'23.35"), at Resex-mar of the Iguape Bay, Paraguaçu River estuary (Figure 1), which is within the Todos os Santos Bay (BTS), state of Bahia. The BTS is the largest coastal bay in Brazil (total area of 1,223 km² and average depth of 9.8 m). The water circulation within the bay is predominantly tidal and does not vary significantly throughout the year. However, the rainy and dry seasons generate a significant change in the properties of the water inside the BTS. During the dry season, the water has

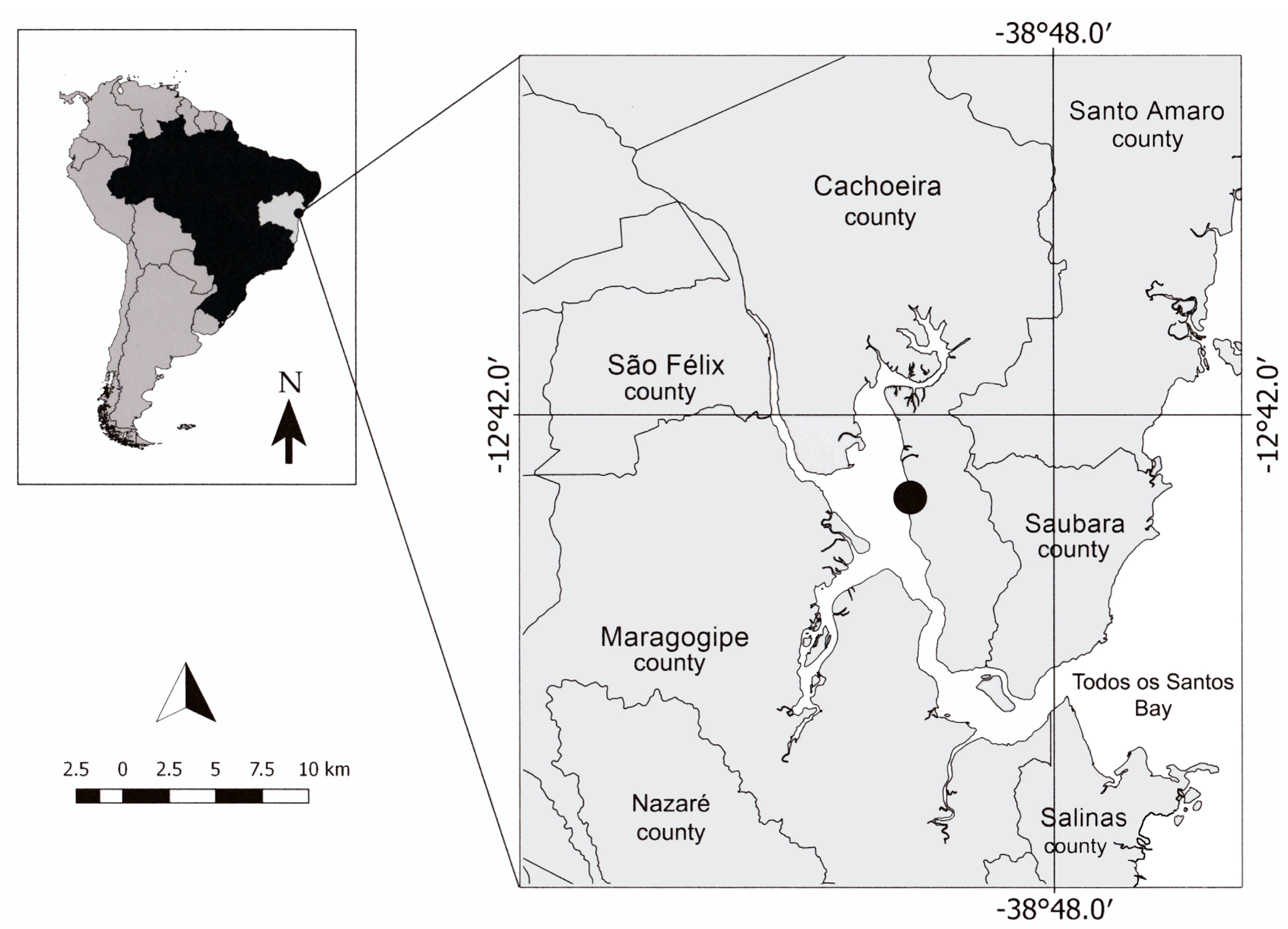

Figure 1. Map of Baía do Iguape (Estuary of Paraguaçu River). Black circle marks the location of São Francisco do Paraguaçu district, municipality of Cachoeira, State of Bahia.

oceanic characteristics, with Tropical Water (TW) penetrating the entire area, with the exception of the mouth of the Paraguaçu River. In contrast, during the rainy season, with the increase in freshwater input, salinity variations of about 4 ppm occur between the innermost parts of the bay. Salinity values within the BTS can reach up to 32.3 and water temperature is higher than that of the adjacent coastal region, reaching a maximum of 30°C (Cirano and Lessa, 2007). The Iguape Bay, which is part of the BTS, is formed by the meeting of the waters of the Guaí and Paraguaçu Rivers, is surrounded by extensive mangroves and is widely used by numerous extractive communities. The Resex-mar of the Iguape Bay was created in August 2000, covering an area of approximately 8,117.53 ha, in the municipalities of Maragogipe, Cachoeira, and São Félix, in order to guarantee the self-sustainable exploitation and conservation of natural resources traditionally used by those communities (Casal and Souto, 2018; Aguiar and Cançado, 2020).

Sampling was carried out by a local fisherman, always on the same fishing grounds and tidal range, using 12 cage traps, which were installed at late afternoon of 1 day and recovered in the early morning of the following day. Therefore, traps remained submerged for about 15 h. The fishing boat, fishing gear, and capture technique were the same as used by local fishermen (Figure 2). The traps are handcrafted by the fishermen themselves and have a PVC pipe structure, covered with polyethylene mesh (10-mm mesh size), with an opening of 50 cm in diameter. Inside the trap, there is a hook for placing the bait (Figure 2B).

In the laboratory, captured specimens were identified based on Melo (1996), sexed, and had their CW measured from base to base of lateral spines. Other measurements and characters were taken and observed to evaluate the morphological, morphometric, and physiological maturities (as described below). All biometric procedures were performed with the aid of digital caliper (precision: 0.01 mm).

Morphological maturity criteria

Morphological maturity was determined according to criteria established by Taissoun (1969) and Millikin and Williams (1984), which consist of the analysis of shape and adherence of abdominal somites to thoracic sternites. Males were considered adults when they had inverted T-shaped abdomen, not adhered to thoracic sternites. Females were considered adults when they had round abdomen, not adhered to thoracic sternites. Individuals with triangular-shaped abdomen and adhered to thoracic sternites were considered juveniles.

Morphometric maturity criteria

To determine the morphometric maturity, in addition to standard body size (CW) measurement, the propodus length of the major cheliped (MPL) in males and width of the fifth abdominal somite (AW) in females were measured. These variables were chosen due to their significance during the passage from juvenile to adult stage and in the reproductive processes (Hartnoll, 1974; Araújo et al., 2012; Marochi et al., 2013; Waiho et al., 2017). Damaged crabs or individuals with regenerating or anomalous limbs were discarded (Somerton, 1980; Pinheiro and Fransozo, 1998). The size at morphometric maturity was determined by detecting discontinuity in the MPL versus CW (males) and AW versus CW (females) biometric relationships between juvenile and adult phases.

Physiological maturity criteria

Physiological maturity was determined from the macroscopic analysis of gonads, according to criteria established by Johnson (1980), Choy (1988), and Abelló (1989). Gonadal development stages were classified as immature (IM), rudimentary (RU),

Figure 2. (A) Fishing boat used by local fishermen during the artisanal fishing of swimming crabs in São Francisco do Paraguaçu, state of Bahia. (B) Cage traps ('gaiolas') used by local fishermen to capture swimming crabs.

developing (ID), developed (DE), and spent (SP). Females were considered adults (mature) when they had gonads in ID, DE, and SP stages, while males were considered mature only when gonads were observed in the DE stage. Specifically in the case of *C. danae*, ovigerous females were also considered adults, with no need for observation of the gonadal stage condition. No ovigerous females of *C. ornatus* were captured during the study.

Data analysis

Morphometric maturity was estimated from linear regressions of MPL versus CW in males and AW versus CW in females (Pinheiro and Fransozo, 1998). Data from all measurements were converted into the linear form by means of natural logarithm transformation. Log-transformed values of carapace width (lnCW) were used as independent variable, and LnMPL and lnAW were considered dependent variables. Data were submitted to successive linear regression analysis, and data with corresponding absolute values of standardized residuals higher than 2.57 ($p<0.01$) were considered outliers and excluded from the analysis. Then, each data group from the regression analysis was submitted to non-hierarchical k-means clustering, to separate the data set into juveniles and adults. Discriminant analysis was used a posteriori to re-allocate any misclassified data. Finally, slope and intercept of equations obtained from each linear regression ($\ln y=\ln a+bx$) of juveniles and adults were statistically tested using Student's t-test.

The resulting patterns of relative growth were plotted in graphics and checked for overlapping band of juveniles and adult-sized swimming crabs. Whenever an overlap was detected, the statistical method Mature I developed by Somerton (1980) was performed. If there were no overlapping and juveniles and adults showed intercepting growth phase lines or if the increment gained in the Y dimension is sufficiently large, the statistical method Mature II was performed (Somerton, 1980).

Therefore, using morphological, morphometric, and physiological criteria independently, swimming crabs were separated into four demographic groups: juvenile males (JM), adult males (AM), juvenile females (JF), and adult females (AF). Average size at the onset of maturity (L_{50}) was determined as the CW at which 50% of males and females were considered sexually mature adults according to criteria presented above. Average size at the onset of maturity was determined by interpolation of the equation obtained by logistic regression (Pagano and Gauvreau, 2006) on maturation condition of specimen (immature=0; mature=1) versus CW data points.

All statistical procedures were based on Sokal and Rohlf (1995) and Zar (1996), considering significance level of 0.05. Statistical analysis were performed with PAST – Paleontological Statistics Software (version 4.08) (Hammer et al., 2001), Microsoft Office® EXCEL 2013, and *R Language* (R Core Team, 2021) provided by *RStudio version 1.4.1106© 189 2009-2021*, packages readr and mfx (Torres-Reyna, 2014).

RESULTS

In total, 2,417 *C. danae* specimens (916 males and 1,501 females) and 1,471 *C. ornatus* specimens (943 males and 528 females) were collected. CW of males varied from 23.14 to 98.56 mm in *C. danae* and from 32.18 to 75.36 mm in *C. ornatus*. In females, CW varied from 27.03 to 83.34 mm in *C. danae* and from 30.21 to 59.87 mm in *C. ornatus*.

All linear regression parameters obtained for each data set of both species are shown in Figure 3. The MPL versus CW scatterplots of males from both species showed overlapping lines of juveniles and adult phases, prompting the use of the statistical method Mature I in the analysis of the two size groups (Figure 3A, C). Comparison between juveniles and adults indicated significant differences in all linear equations obtained from regression analyses (Table 1). Therefore, different relative growth patterns (Figure 3) were found between the two life phases that mark the transition from immature to adult life.

Considering *C. danae,* the morphological, morphometric, and physiological maturities (L_{50}) estimated were, respectively, 55.80, 59.04, and 60.41 mm for males (Figure 4A-C) and 54.63, 55.33, and 57.29 mm for females (Figure 4D-F).

Considering *C. ornatus*, the morphological, morphometric, and physiological maturities estimated were, respectively, 42.63, 50.81, and 43.95 mm for males (Figure 5A-C) and 42.33, 42.75, and 40.43 mm for females (Figure 5D-F).

Considering the size at the onset of maturity estimated by each criteria, *C. danae* males had mean L_{50} value equal to 58.42±2.37 mm, while for *C. ornatus*, this value was 45.80±4.39 mm. For females, the mean L_{50} values of *C. danae* and *C. ornatus* were 55.75±1.38 and 41.84±1.24 mm, respectively. The maximum L_{50} value found in the study area was 60.41 mm for *C. danae* and 50.81 mm for *C. ornatus*.

Comparisons between the estimated L_{50} performed by the *R Language* showed that, in the case of males of *C. danae*, the morphometric (OR 4.144; CI 2.846–6.895), morphological (OR 1.381; CI 1.324–1.447), and physiological (OR 1.254; CI 1.219–1.293) estimated maturities differed statistically. In the case of females, only physiological maturity (OR 1.182; CI 1.161–1.205) differed from morphometric (OR 1.341; CI 1.302–1.385) and morphological (OR 1.308; CI 1.274–1.346) maturities. In the case of *C. ornatus* males, only morphometric maturity (OR 4.70; CI 3.316–7.341) differed from morphological (OR 1.432; CI 1.361–1.515) and physiological (OR 1.487; CI 1.398–1.592). In females, only the morphometric (OR 1.919; CI 1.701–2.211) and physiological (OR 1.43; CI 1.337–1.541) maturities were statistically different.

DISCUSSION

Our results revealed difference in the size at the onset of maturity between species and between sexes. We also compared them with studies previously carried out with *C. danae* and *C.*

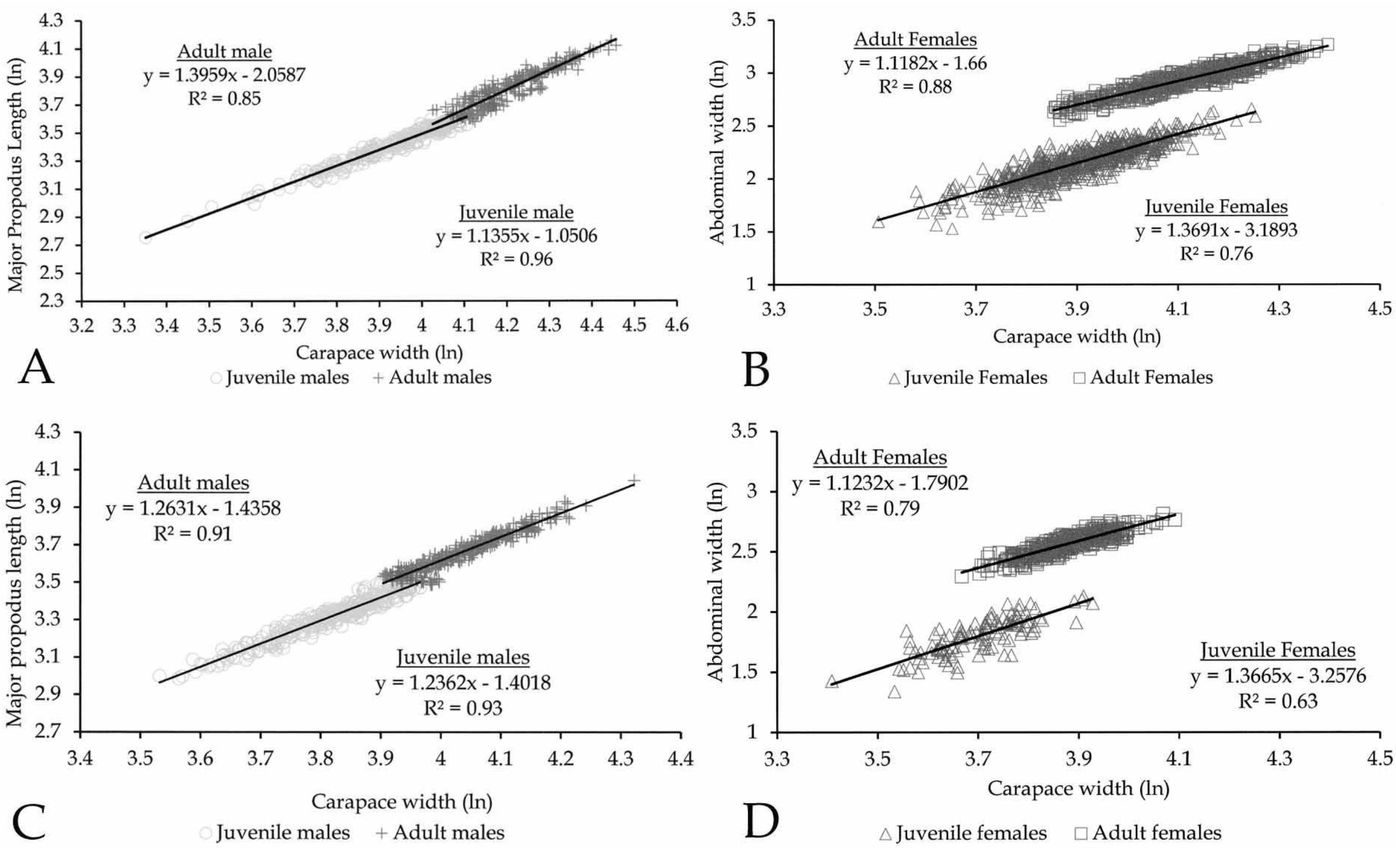

Figure 3. Biometric relationships (log-transformed data) of juveniles and adults. (A) and (B) *Callinectes danae;* (C) and (D) *Callinectes ornatus*.

Table 1. Student's t-test comparisons of linear regression parameters between juvenile and adult life stages, (v) degrees of freedom.

Life stages	Species	Relationship	Comparison of slopes	Comparison of intercepts
Juvenile males vs. Adult males	*Callinectes danae*	MPL vs. CW	t=8.91; v=512; p<0.05	—
	Callinectes ornatus	MPL vs. CW	t=0.89; v=590; p>0.05	t=16.8; v=590; p<0.05
Juvenile females vs. Adult females	*C. danae*	AW vs. CW	t=15,5; v=1354; p<0.05	—
	C. ornatus	AW vs. CW	t=3,24; v=477; p<0.05	—

MPL: propodus length of the major cheliped; CW: carapace width; AW: width of the fifth abdominal somite.

ornatus in other regions. Additionally, differences in L_{50} were observed depending on criteria used. In this context, public policies aimed at stock management must take into account such variations, in order to consider the population characteristics of each region and the uncertainties inherent to each method used to estimate size at maturity.

Although *C. danae* generally shows larger sizes at maturity when compared to *C. ornatus* (see Table 2 for review), previous studies have not statistically compared these estimates. In the Paraguaçu River estuary, females of *C. danae* showed larger sizes of morphometric, morphological, and physiological maturities, while in males only the latter was higher. Larger sizes at maturity in *C. dana* could indicate greater investment in growth, leading to larger sizes compared to *C. ornatus* or it could be reflecting a natural body size difference between the species.

In the present study, the values of the estimated maturity of females of both species were lower than those calculated for males. However, statistical comparisons showed that females of *C. danae* reached physiological and morphometric maturities with smaller size than males, while in *C. ornatus,* only the latter was smaller. The early sexual maturity of females is a constant in both species, since similar studies have also observed this pattern in both sexes (see Table 2 for review). This sexual dimorphism (particularly related to morphometric maturity) is part of the reproductive strategy of portunids, in which pre- and post-copulatory guards are typical and larger adult males take

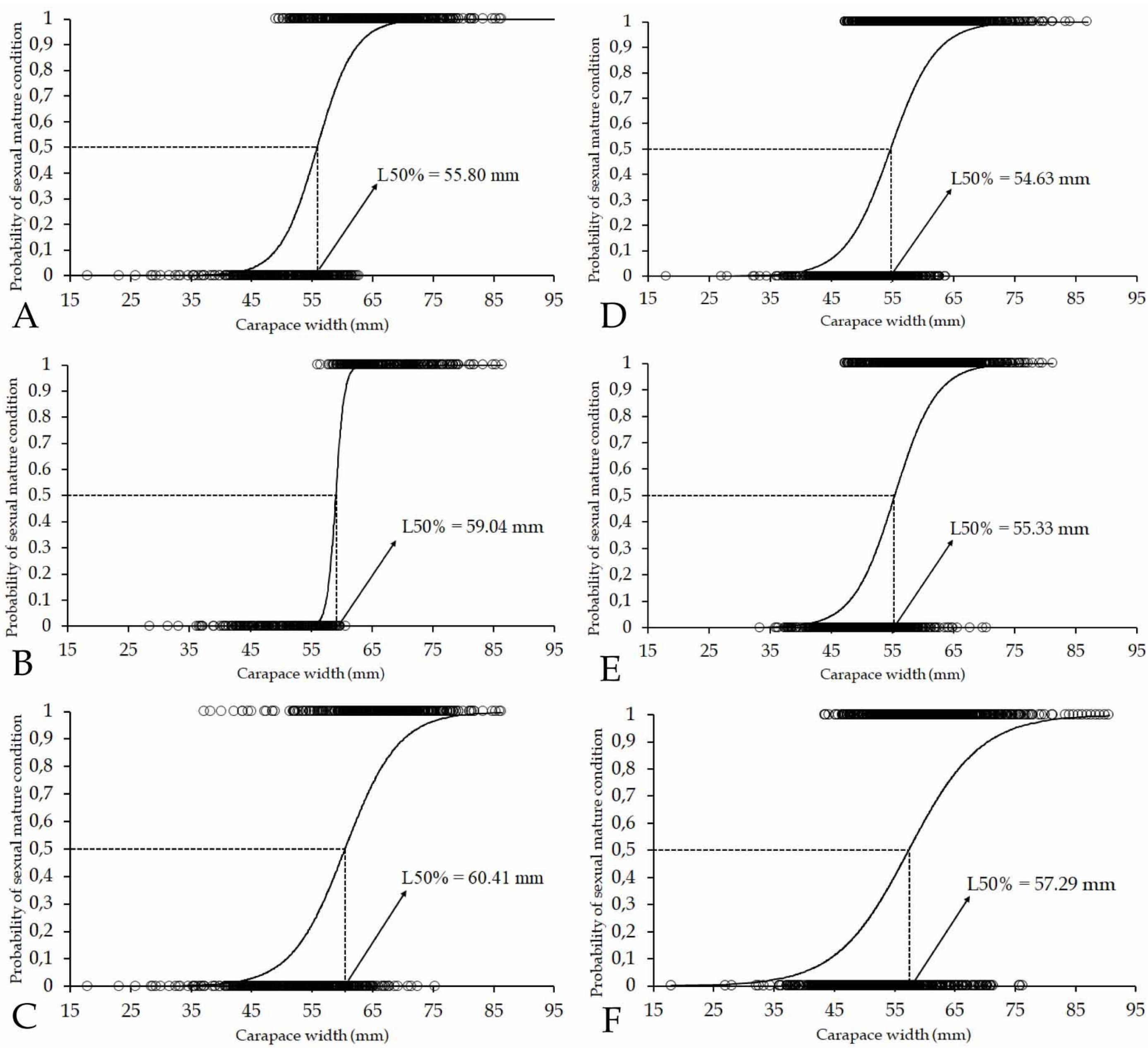

Figure 4. *Callinectes danae*. Size at the onset of functional maturity estimated by logistic regression based on the absence (0) or presence (1) of discrete reproductive traits plotted against carapace width. Males: (A) morphological maturity, (B) morphometric maturity, and (C) physiological maturity; Females: (D) morphological maturity, (E) morphometric maturity, and (F) physiological maturity.

more advantage in protecting females, guaranteeing the paternity of the offspring (Hartnoll, 1969; Sastry, 1983; Pinheiro and Fransozo, 1998; Mantelatto and Fransozo, 1999; Baptista et al., 2003; Andrade et al., 2015). Thus, after the puberty molt, males direct greater amount of metabolic energy to somatic growth, while females invest their energy in reproductive processes, leading to early sexual maturity and longer fertile life, increasing the reproductive output of the population (Hartnoll, 1985; Avila and Branco, 1996; Baptista-Metri et al., 2005; Fernandes et al., 2006; Keunecke et al., 2008).

The greater energetic investment of adult males in body size (CW) and development of chelipeds is an adaptation to their agonistic behavior of defending the territory, disputing, and guarding the female during the reproductive period, as the fertilization of Portunidae females only occurs after the puberty molt (Hartnoll, 1969, 1974; Mariappan et al., 2000). In contrast, females show greater abdomen development after the puberty molt, which is an adaptation for accommodation and adherence of the egg mass to the pleopods (Hartnoll, 1974; Mantelatto and Fransozo, 1997). In addition, the incubation of eggs in pleopods

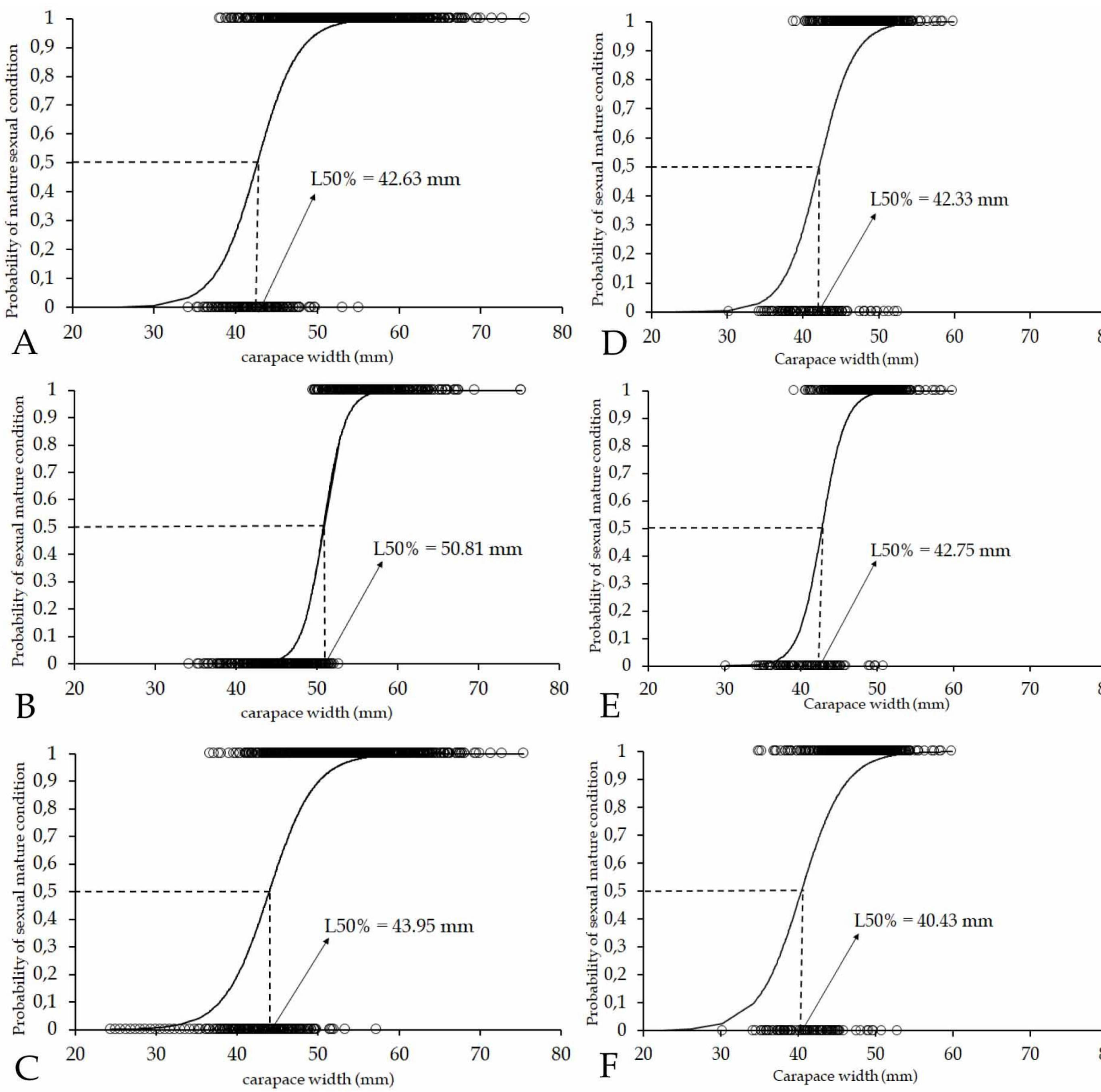

Figure 5. *Callinectes ornatus*. Size at the onset of functional maturity estimated by logistic regression based on the absence (0) or presence (1) of discrete reproductive traits plotted against carapace width. Males: (A) morphological maturity, (B) morphometric maturity, and (C) physiological maturity; Females: (D) morphological maturity, (E) morphometric maturity, and (F) physiological maturity.

prolongs intermolt periods, also contributing to the smaller body size of females compared to males (Hartnoll, 2006).

In the present study, estimates of morphological and morphometric maturity of females of both species did not show statistical difference, indicating synchrony between them. In brachyurans, the puberty molt of females is quite evident and may involve changes in the abdomen, pleopods, and sternum characteristics (Hartnoll, 1969). Therefore, after the puberty molt, the abdomen detaches from the thoracic sternum (morphological maturity) and changes its shape (morphometric maturity).

We observed that the physiological maturity of *C. ornatus* females occurred at smaller size compared to morphometric maturity and in synchrony with morphological maturity. In contrast, in *C. danae*, the pattern was different, with physiological

Table 2. Size at the onset of maturity (L_{50}) recorded for *Callinectes danae* and *Callinectes ornatus* in different locations in Brazil.

Species	Locality (coordinates)	L_{50} (mm)		References
		Males	Females	
Callinectes danae	Santa Cruz Chanel, Pernambuco State (07°34'S, 34°04'W)	70.50^{Mf}	59.50^{Mf}	Araújo et al. (2012)
	Santa Cruz Chanel, Pernambuco State (07°34'S, 34°04'W)	74.50^{P}	62.50^{P}	Araújo et al. (2012)
	Carrapicho River, Itamaracá, Pernambuco State (07°39'S, 34°51'W)	n/a	56.46^{Mo}	Barreto et al. (2006)
	Botafogo River, Itamaracá, Pernambuco State (07°43'S, 34°53'W)	n/a n/a n/a	61.59^{P} 57.13^{Mo} 63.58^{P}	Barreto et al. (2006)
	Santa Cruz Chanel, Pernambuco State (08°43'00"S; 034°51'00"W)	94.50^{*Mo}	83.80^{*Mo}	Shinozaki-Mendes et al. (2013)
	Paraguaçu River estuary, Bahia State (12°44'30.56S"; 038°52'23.35"W)	55.80^{Mo} 59.04^{Mf} 60.41^{P}	54.63^{Mo} 55.33^{Mf} 57.29^{P}	Present study
	Guanabara Bay, Rio de Janeiro State (22°S; 48°W)	n/a	79.90^{*P}	Keunecke et al. (2012)
	Ubatumirim Bay, São Paulo State (23°20'09.46"S; 44°53'55.63"W)	$60,20^{P}$	55.10^{P}	Andrade et al. (2015)
	Ubatuba Bay, São Paulo State (23°26'22.87"S; 45°03'39.02"W)	58.00^{P}	55.40^{P}	Andrade et al. (2015)
	Mar Virado Bay, São Paulo State (23°31'57.41"S; 45°12'44.30"W)	58.40^{P}	54.60^{P}	Andrade et al. (2015)
	Cananéia, São Paulo State (25°06'S, 47°50'W)	n/a	57.10^{Mo}	Severino-Rodrigues et al. (2012)
	Pontal do Paraná, PR (25°37'30"S, 48°25'08"W)	60.50^{P}	52.70^{P}	Baptista-Metri et al. (2005)
	Guaratuba Bay, Paraná State (25°51'S, 48°33'W)	86.50^{*P} 88.47^{*Mf}	67.00^{*P} 67.87^{*Mf}	Marochi et al. (2013)
	Babitonga Bay, Santa Catarina State (26°02'S; 48°28')	86.00^{*Mo}	71.00^{*Mo}	Pereira et al. (2009)
	Conceição Lagoon, Santa Catarina State (27°30'30"S, 48°00'00"W)	94.00^{P}	84.00^{P}	Branco and Masunari (2000)
	Itacorubi Mangrove, Santa Catarina State (27°34' 14" S; 048°30'07" W)	98.50^{*Mo}	88.80^{*Mo}	Branco and Thives (1991)
Callinectes ornatus	Paraguaçu River estuary, BA (12°44'30.56" S; 038°52'23.35" W)	42.63^{Mo} 50.81^{Mf} 43.95^{P}	42.33^{Mo} 42.75^{Mf} 40.43^{P}	Present study
	Ilhéus, Bahia State (14°43'S, 39°01'W)	43.50^{P} 44.20^{Mo}	40.70^{P} 41.40^{Mo}	Carvalho et al. (2011)
	Northern Rio de Janeiro State (21°30' S; 41°05' W)	79.00^{*Mo}	65.00^{*Mo}	Tudesco et al. (2012)
	Guanabara Bay, Rio de Janeiro State (22°S; 48°W)	n/a	67.40^{*P}	Keunecke et al. (2012)
	Ubatuba Bay, São Paulo State (23°26'S, 45°02'W)	50.00^{P}	43.00^{P}	Mantelatto and Fransozo (1996)
	Paraná Pontal, Paraná State (25°37'30" S; 048°25'08" W)	55.00^{P}	48.00^{P}	Baptista et al. (2003)
	Matinhos, Paraná State (25°40' S; 048°30' W)	67.00^{*P}	61.00^{*P}	Branco and Lunardon-Branco (1993)
	Penha, Santa Catarina State (26°40' S; 48°36'W)	58.00*	52.00*	Branco and Fracasso (2004)

*Carapace width including lateral spines. Mo: morphological maturity; Mf: morphometric maturity; P: physiological maturity.

maturity occurring after morphological and morphometric maturities. Therefore, the reproductive strategy observed for *C. danae* could be similar to that reported for *C. sapidus*. In the latter species, mating occurs after the puberty molt, when adult males inseminate females with developing gonads, and the sperm mass remains in the seminal receptacle until gonadal development is complete (Hard, 1942; Millikin and Williams, 1984).

Considering males of both species, different patterns emerged. In *C. danae*, morphological maturity occurred earlier, followed by morphometric and then physiological maturities. The few previous studies that addressed more than one criteria to estimate the sexual maturity of *C. danae* showed different patterns, although without comparative statistical analyses, as performed in the present study. Similar to our results, Araújo et al. (2012) also estimated that morphometric maturity occurs before physiological maturity in males collected in Santa Cruz Channel, State of Pernambuco. In contrast, Marochi et al. (2013) observed opposite pattern in males collected in Guaratuba Bay, State of Paraná. For *C. ornatus* males, we estimated that the morphometric maturity occurs at larger size and there was synchrony between morphological and physiological maturities. Therefore, the pattern observed in our study is similar to that reported by Carvalho et al. (2011) for males collected in Ilhéus, State of Bahia. According to Hartnoll (1978), the appearance of secondary sexual characters (i.e., morphological changes) occurs with the passage from juvenile to the adult phase (i.e., puberty molt), with or without synchronization with physiological maturity. In the absence of synchrony, there is no pattern for brachyurans, since the external characteristics of adults can develop before or after the maturation of gonads (Sastry, 1983; Conan and Comeau, 1986; Choy, 1988; Marochi et al., 2013; Waiho et al., 2017).

In general, there is a tendency for *C. danae* and *C. ornatus* to reach sexual maturity with smaller size at lower latitudes. This suggests that latitudinal variation in maturation size occurs especially when comparing the estimated values for populations in the Northeastern and Southeastern regions with those in the Southern region of Brazil (see Table 2 for review). There is consensus in the scientific community that the size at maturity of decapods is inversely related to water temperature and photoperiod, which in turn are correlated with latitude (Jones and Simons 1983, Dugan et al. 1991; Waiho et al., 2017). Thus, decapod populations that inhabit areas of lower latitude (where water temperatures are higher) would achieve sexual maturity at smaller size when compared to those living in higher latitudes, where water temperatures are lower (Hartnoll, 1982; Jones and Simons, 1983; Castilho et al., 2007; Carvalho et al., 2011). However, variations in this pattern can occur, because other factors such as precipitation, food availability, genotypic variation, capture pressure, predation, and population density can influence the growth, maturation, and reproductive behavior of decapod crustaceans (Hartnoll, 1982; Hines, 1989; Hines et al., 2010; Carvalho et al., 2011; Rodríguez-Félix et al., 2015; Waiho et al., 2017; Bakke et al., 2018).

Estimating the size at the onset of maturity is essential for the management of fishing stocks, since the current legislation is based on minimum catch size derived from the maturity size (Keunecke et al., 2012; Andrade et al., 2013). SUDEPE Ordinance n. 24 (Ibama, 1983), which regulates the exploitation of swimming crabs on the Brazilian coast, allows the capture of specimens from 120 mm in total CW (including lateral spines), for *C. danae* and *C. sapidus*. In addition, ICMBio Ordinance No. 313 allows the capture of *C. danae* and *C. exasperatus* in the southern region of the state of Bahia with, respectively, 70 and 80 mm of CW. In this context, our results show that no specimen could be captured in the Iguape Bay, since even adult individuals do not reach the size stipulated in the above-mentioned legislations. Therefore, it is necessary to update this Ordinance, with the definition of the minimum catch size based on recent scientific studies and preferably with different values for each species in each region of the Brazilian coast. Finally, considering that *C. ornatus* is also included in the "catado," it is necessary to include this species in the Ordinance for regulation of swimming crab fishing on the Brazilian coast, as this species is not covered by current legislation.

Despite the occurrence or not of synchrony between size estimates at the onset of maturity obtained from the three criteria, the definition of minimum catch size larger than the largest L_{50} for fishing management purposes is recommend. Thus, it is also recommended that only individuals with CW larger than 61.00 mm (*C. danae*) and 51.00 mm (*C. ornatus*) would be captured, since reproduction only occurs after the animal develop all conditions (morphological and physiological) to engage in the reproductive process (González-Pisani *et al*., 2017; Waiho *et al*., 2017). Based on these values, high percentage of individuals (67.9% for *C. danae* and 59.3% for *C. ornatus*) captured below the first maturation size recommended for fishing management purposes was found. These percentages indicate that the fishing gear used by artisanal fishermen in São Francisco do Paraguaçu may be affecting population balance.

Keunecke et al. (2012) also found percentages of immature *C. danae* (16.2%) and *C. ornatus* (85.6%) females captured by trawling pink shrimp. Populations of overfished portunids can have their asymptotic size reduced and, consequently, the size of maturity can also decrease, reducing the fertility and reproductive output of the population (Keunecke et al., 2012; Andrade et al., 2015). Based on this assumption, the mesh of traps used in the swimming crab fishing at São Francisco do Paraguaçu and other fishing areas of the Todos os Santos Bay should be adjusted to prevent immature animals from being captured. Moreover, fishermen must also check the size of captured specimens, releasing those that are below the minimum catch size.

CONCLUSIONS

Callinectes danae and *C. ornatus* populations under study followed the expected pattern for portunids, in which females are smaller than males and reach sexual maturity at smaller sizes.

There is latitudinal variation in maturation size of *C. danae* and *C. ornatus,* especially when comparing populations from the Northeastern and Southeastern regions with those in the Southern region of Brazil.

The minimum catch sizes (CW excluding lateral spines) must be stipulated at 61.00 mm for *C. danae* and 51.00 mm for *C. ornatus* for a better management of the swimming crab fishing activity at São Francisco do Paraguaçu and other fishing areas of the Todos os Santos Bay.

The high percentages of individuals captured below the maturity size show the need to adapt the fishing gear used to capture swimming crabs in the region.

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CONFLICT OF INTERESTS

Nothing to declare.

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AUTHOR'S CONTRIBUTIONS

Cardim, R.W.S.: Investigation, Methodology, Formal Analysis, Writing – original draft, Writing – review & editing. Souza, E.R.: Investigation, Methodology, Formal Analysis, Resources, Writing – original draft. Serafim Junior, M.: Conceptualization, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. Carvalho, F.L.: Formal Analysis, Methodology, Validation, Writing – original draft, Writing – review & editing. Rocha, S. S.: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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