SEXUAL MATURITY, HANDEDNESS AND SEXUAL DIMORPHISM OF THE FRESHWATER CRAB Dilocarcinus pagei IN SOUTHEASTERN BRAZIL

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ABSTRACT

This study estimated the sexual maturity of *Dilocarcinus pagei* Stimpson, 1861 based on relative growth and gonadal development. In addition, a possible sexual dimorphism was reported. The specimens were monthly captured from October 2005 to September 2007 in the Marimbondo/Furnas Hydroelectric Plant Reservoir, municipality of Icem in northwestern São Paulo State. Handedness was recorded for males, with the right cheliped propodus invariably longer and wider than the left. The estimated carapace width for morphological sexual maturity in males was 28.7 mm, based on the biometric relationship of the cheliped propodus length *vs.* carapace width; for females, this value was 24.2 mm, using the relationship of the abdominal width *vs.* carapace width. The size at gonadal maturity was estimated at 39.2 mm and 39.9 mm, for males and females respectively (CW₅₀). There was not sexual dimorphism in relation to carapace width. For a crab to be able to procreate, it must reach morphological maturity and have developed gonads. Thus a minimum capture size based on the size, at which 50% of the population is considered reproductive, can ensure the continued preservation of this species.

Keywords: allometry; gonadal maturity; morphological maturity; reproduction

MATURIDADE SEXUAL, LATERALIDADE E DIMORFISMO SEXUAL DO CARANGUEJO DULCÍCOLA Dilocarcinus pagei NO SUDESTE DO BRASIL

RESUMO

O objetivo do presente estudo foi estimar a maturidade sexual de *Dilocarcinus pagei* Stimpson, 1861, por meio do estudo do crescimento relativo e desenvolvimento gonadal. Adicionalmente, um possível dimorfismo sexual foi avaliado. As coletas foram realizadas mensalmente de outubro de 2005 a setembro de 2007, no reservatório da Usina Hidrelétrica de Furnas/Marimbondo, município de Icém, Estado de São Paulo. Lateralidade foi registrada para o sexo masculino, com o própodo do quelípodo direito invariavelmente mais longo e mais largo que o esquerdo. O valor estimado da largura da carapaça para a maturidade sexual morfológica nos machos foi de 28,7mm a partir da relação comprimento do própodo do quelípodo *vs.* largura da carapaça, enquanto que para as fêmeas, esse valor foi de 24,2mm a partir da relação largura do abdome *vs.* largura da carapaça. A maturidade gonadal foi estimada em 39,2mm e 39,9mm para machos e fêmeas respectivamente (LC₅₀). Não foi observado um dimorfismo sexual em relação à largura da carapaça. Para que um caranguejo esteja apto à reprodução, é necessário atingir a maturidade morfológica e ter desenvolvido as gônadas. Com isso, um possível tamanho mínimo de captura baseado no tamanho em que 50% da população é considerada reprodutiva, pode assegurar uma consequente preservação dessa espécie.

Palavras-chave: alometria; maturidade gonadal; maturidade morfológica; reprodução

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INTRODUCTION

The trichodactylid crab Dilocarcinus pagei Stimpson, 1861 is distributed in Brazil from the states of Amapá to São Paulo (MAGALHÃES, 2003). According to MAGALHÃES et al., (2005), this species is not considered to be native to the Alto Paraná Basin. The authors suggested that *D*. pagei may have been introduced in some locations of São Paulo State through activities related to fish culture and/or sport fishing. Some fish species captured from the natural environment of Pantanal were often marketed for these uses. Thus, juveniles of D. pagei may have been transported among the roots of aquatic macrophytes used as fish shelters in transport containers. According to MAGALHÃES (2001), these crabs are abundant in habitats formed by large patches of floating aquatic vegetation, a common characteristic in the vast Pantanal floodplains.

In addition to the importance of these crabs for nutrient recycling through their maceration of detritus, *D. pagei* is used in sport fishing as bait for several fish species (TADDEI and HERRERA, 2010). According to MANSUR *et al.* (2005), this continual harvesting, combined with a lack of studies on the basic biology of *D. pagei*, has contributed to reduce the population of these crabs in the Pantanal Matogrossense region. Population reductions have also been observed in the northwestern part of São Paulo, as attested by the crab catchers themselves.

Usually, a minimum size of capture is proposed for commercially exploited species, and is stipulated based on their size at sexual maturity. This management strategy is very important, since it allows the organisms to reach sexual maturity, a necessary condition for reproductive success (CONAN *et al.*, 2001; BARÓN *et al.*, 2009). The size at which a crab becomes able to reproduce is a key component in the understanding of the species' life history, and involves a period of changes in the ecological and/or biological functions that these individuals will play in the population, leading to new habits and behaviors (MOURA and COELHO, 2004; GOES *et al.*, 2010).

In Brachyura, the adult stage begins with the puberty molt, characterized by alterations in the growth pattern of some appendages (FERNÁNDEZ-VERGAZ *et al.*, 2000). These

alterations can be analyzed by studying the relative growth, with an estimate of the size at which an individual reaches morphological sexual maturity. Usually, this differential growth occurs in different body structures in males and females, differentiating two ontogenetic post-larval stages (juvenile and adult). This was observed in some studies of relative growth of the cheliped and abdomen for males and females, respectively (CASTIGLIONI and NEGREIROS-FRANSOZO, 2006; COBO and ALVES, 2009; HIROSE et al., 2012; LIMA et al., 2012). Heterochely is common in Pleocyemata (GÓES and FRANSOZO, 1998) and may involve only one cheliped, or be independent, i.e., either the right or left cheliped can grow larger than the other. As a result, handedness should be evaluated as a prerequisite for a growth analysis involving cheliped dimensions when evaluating a species with heterochely.

Another method used to estimate the size at which decapods reach their reproductive stage is by calculating the size at which 50% of the individuals of a population have developed gonads (CW₅₀) (CORGOS and FREIRE, 2006). A crab can be considered able to reproduce when it shows both gonadal and morphological signs of maturity.

The present study estimated the size at which the freshwater crab *D. pagei* reaches sexual maturity, and also evaluated handedness in the males. Additionally, the possibility of sexual dimorphism was evaluated.

MATERIAL AND METHODS

Samples were collected at night, using flashlights in order to see the crabs. Specimens were monthly captured from October 2005 to September 2007 in Marimbondo/Furnas Hydroelectric Plant Reservoir (20°19'40.0"S and 49°10'18.1"W), Icem city, northwestern region of the São Paulo State, Brazil. This reservoir is located on the border between the states of São Paulo and Minas Gerais, in Rio Grande basin, a sub-basin of Paraná River (Bauru Aquifer System), and has a flooded area of 438 km² (DAVANSO *et al.*, 2013).

Crabs were captured manually and with sieves passed through the shoreline vegetation (grass). Four people, with a capture effort of 3 hours/person, covered a sampling area, approximately 2.5 km long.

Captured individuals were stored in plastic bags. Ovigerous females and females carrying early juveniles in the incubation chamber were identified and also stored in plastic bags. Afterwards, the crabs were transported to the laboratory and kept frozen until analysis. Animals were sexed based on the abdomen morphology and number of pleopods (PINHEIRO and TADDEI, 2005).

Crabs were measured with a precision caliper (0.01 mm) for the carapace width (CW), carapace length (CL), right cheliped propodus length (RCPL), and abdomen width (3rd somite for males and 4th for females) (AW) (Figure 1). For the analysis of handedness, a random sub-sample (108 individuals) of male individuals was measured for length (CPL) and height (CPH) of the propodus cheliped (right and left).

Morphological Sexual Maturity

Handedness

Whereas existing heterochely for males of *D. pagei* (MANSUR *et al.*, 2005), prior to the study of the relative growth, the possibility of handedness was tested by Student's t-test (significance level 5%), using the propodus length of the right and left chelipeds. Additionally, a scatter graph was plotted using as data the difference between length and height of the cheliped propodus (right and left).

Relative Growth

Morphological sexual maturity was estimated based on the analysis of relative growth, corresponding to the CW of the smallest individual after the 'break point' of the equations for juvenile and adult. The body structures used to analyze the relative growth were chosen based on their relationship to reproduction in Brachyura (MANSUR *et al.*, 2005; GREGATI and NEGREIROS-FRANSOZO, 2007; HIROSE *et al.*, 2010; LIMA *et al.*, 2012).

Data were plotted on dispersion graphs with carapace width (CW) as the independent variable, and fitted to the allometric equation $y = ax^b$ (HARTNOLL, 1974, 1978, 1982), in which: y = dependent variable; x = independent variable; a =

source index; b = constant of allometric growth. The equations obtained from this analysis were linearized ($\log y = \log a + b \log x$) (HUXLEY, 1950) and the log-transformed data were analyzed by simple linear regression. The fit of the mathematical model was determined from the coefficient of determination (R^2) for each relationship (PINHEIRO and FRANSOZO, 1993). Student's *t*-test (significance level 5%) was utilized to test the null hypothesis (H₀: b = 1) (ZAR, 1996).

A non-hierarchical K-means cluster analysis was performed to separate individuals into the groups of interest (juveniles and adults). Data were distributed into a previously determined number of groups by an interactive process that minimizes the variance within groups and maximizes the variance between them. Applying a discriminant analysis a more refined result could be obtained to K-means classification. This statistical methodology was based on the work of SAMPEDRO *et al.* (1999), who used a similar statistical procedure.

After the size categories have been correctly determined, the log-transformed data for each category were submitted to a covariance analysis (ANCOVA) to test the angular and linear coefficients between groups (juveniles and adults). This procedure was used to determine whether the data for each relationship were better adjusted to a single straight line, or if the size categories should be represented by different linear equations.



Figure 1: Dimensions of *Dilocarcinus pagei* utilized in the morphometric analysis of each structure (not in a same scale). (CW) carapace width, (CL) carapace length, (AW) abdomen width, (PL) cheliped propodus length. a = male and b = female.

Gonadal Maturity

The following stages of gonadal development were identified macroscopically: immature (IM), defined by the absence of visible gonads, both males and females; maturing (Mt), characterized by the beginning of folding in both sexes, with a white color in males and orange in females; mature (M), defined by greater folding of the gonads, enlargement, and a milky-white color in males and red in females. Individuals without visible gonads but with a body size equal to (or greater than) that estimated for morphological sexual maturity were classified as adults during gonadal maturity analysis.

To identify the size at gonadal maturity, the CW₅₀ method was used, comprising the size at a half of the population which has morphologically mature gonads. This procedure analyzes the distribution of individuals according to size classes based on carapace width (CW) as an independent variable, and on the relative frequencies of reproductive individuals (Mt + M). Subsequently, the equation of the logistic curve $(y=1/(1+e^{r(CW-CW_{50})}))$ was fitted to the data by the least-squares method (VAZZOLER, 1996), and the size at gonad maturity was defined by the interpolation point (50%).

Sexual Dimorphism

A discriminant analysis (DA) was performed in order to check for possible sexual dimorphism, searching for evidence of morphometric differences between sexes, and determining which variables (body structures) were more important in this dimorphism. The discriminatory power of each variable was observed by means of Wilks' lambda, combined with statistical values of *F* and *p* (*F* values < 1 were included in the DA) (ANASTASIADOU and LEONARDOS, 2008).

RESULTS

Handedness

Right-handedness was recorded for males, with the right cheliped propodus invariably longer and wider than the left (p < 0.05). Values of length and width of the cheliped propodus were observed deviating only to the right, which indicates the right cheliped larger than the left one in all individuals (Figure 2). Individuals with smaller CW showed less deviation, whereas the deviation increased for larger crabs (Figure 2).



Figure 2: Handedness of *Dilocarcinus pagei* observed from the difference in length (CPL) and height (CPH) of the right and left cheliped propodus.

Morphological Sexual Maturity

Relative Growth

In total, 568 males and 434 females were used in the analyses. The carapace width of the males ranged from 5.2 to 58.3 mm (mean $31.40 \pm$ 12.89);.85). in the females, the CW ranged from 5.8 to 59.3 mm (mean 31.45 ± 12

The covariance analysis (ANCOVA) showed that the growth pattern differed between juveniles and adults in both sexes (p < 0.05). The straight lines obtained at different stages (juvenile and adult) were best fitted to the data separately, with the exception of the AW *vs.* CW relationship for males and CL *vs.* CW for females (Table 1).

The RCPL *vs.* CW relationship was significant for males, indicating negative allometric growth for juveniles (b = 0.908) and positive allometric growth for adults (b = 1.68). This relationship was isometric for the juvenile stage in females (b = 0.973) and with a low degree of positive allometry for the adult stage (b = 1.098), compared to males. The AW *vs*. CW was significant in females, and showed negative allometry in the juvenile stage (b = 0.919) and positive allometry in the adult stage (b = 1.246) (Table 2).

For the CL *vs.* CW relationship, negative allometry was observed for males in the two stages (juvenile and adult), while for females, negative allometric growth was observed in the juvenile stage and isometry in the adult stage.

The estimated value of CW for morphological sexual maturity in males was 28.7 mm from the RCPL *vs.* CW relationship, while for females this value was 24.2 mm from the AW *vs.* CW relationship (Figure 3).



Figure 3: Determination of *Dilocarcinus pagei* morphological sexual maturity for both sexes. Morphological sexual maturity was estimated as the size of the smallest adult after the break-point of the lines.

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Table 1: Results of Dilocarcinus pagei the Covariance Analysis (ANCOVA) of the morphometric data.						
Relationship	Factor (Group)	Parameters (log)	F	р		
RCPL vs. CW	Male (J x A)	А				
		В	133.829	0.000*		
	Female (J x A)	Α				
		В	4.125	0.043*		
AW vs. CW	Male (J x A)	А	1.535	0.216		
		В	2.875	0.090		
	Female (J x A)	Α				
		В	46.887	0.000*		

Notes: CW= carapace width; RCPL= right cheliped propodus length; AW= abdomen width; J= juvenile; A= adult; a= linear coefficient; b= angular coefficient; *= p < 0.05.

Table 2: Regression analysis of *Dilocarcinus pagei* morphometric data using carapace width (CW) as independent variable.

Relationship	Category	Ν	Intercept	Slope	R ²	Т	р	Allometry
			(log)			(b=1)		
RCPL vs. CW	JM	194	-0.115	0.908	0.906	4.676	< 0.001	-
	AM	299	-1.173	1.68	0.657	8.463	< 0.001	+
	JF	157	-0.197	0.973	0.869	0.867	>0.001	0
	AF	231	-0.381	1.098	0.654	1.869	< 0.001	+
AW vs. CW	JM/AM	554	-0.169	0.925	0.957	8.957	< 0.001	-
	JF	160	-0.161	0.919	0.898	3.276	< 0.001	-
	AF	257	-0.604	1.246	0.780	5.233	< 0.001	+

JM= juvenile male; AM= adult male; JF= juvenile female; AF= adult female; 0= isometry; - = negative allometry; + = positive allometry; CW= carapace width; RCPL= right cheliped propodus length; AW= abdomen width.

Gonadal Maturity

Considering the total number of crabs captured in this study, 387 were reproductive (Mt + M), including 296 males (14.8 to 58.3 mm CW) and 91 females (19.8 to 59.3 mm CW). Two of these were classified as ovigerous females (OF), and eight carried early juveniles in the incubation chamber (EJF).

The crabs were distributed into 15 size classes defined by intervals of 4 mm. For males the size at

gonadal maturity was estimated as 39.2 mm, and for females as 39.9 mm (Figure 4).

Sexual Dimorphism

Regarding body size (CW and CL), the individuals measured showed no difference between the sexes (DA, p > 0.05) (Table 3). However, sexual dimorphism was observed in the cheliped propodus length and abdomen width (DA, p < 0.05) (Table 3).

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Body structures	Factor (Group)	Wilks' lambda	F	p	
CW	Male vs. Female	0.6222	0.324	0.570	
CL	Male vs. Female	0.6222	0.279	0.597	
RCPL	Male vs. Female	0.8032	261.103	0.000000*	
AW	Male vs. Female	0.7015	114.500	0.000000*	

Notes: CW= carapace width; CL= carapace length; RCPL= right cheliped propodus length; AW= abdomen width; *= p < 0.05.



Figure 4: Adjustment of Dilocarcinus pagei the empirical data based on the logistic curve indicating the carapace width at which 50% of the individuals (males and females) are considered reproductive.

DISCUSSION

During their life cycle, decapod crustaceans show differences in body growth between the juvenile and adult stages of the same sex (HARTNOLL, 1974). This has influenced the trade of species of economic interest, since larger individuals are more valuable than smaller ones. According to HARTNOLL (1982), individuals in the pre-pubertal stage have developed their primary sexual characteristics, which allow sexual differentiation, and the secondary sexual characteristics appear with the puberty molt, occurring changes in the growth rate of some body structures (e.g., male cheliped and female abdomen). The results from this study corroborate this sequence for *D. pagei*.

Studies on crabs of the superfamily Majoidea that the morphometric relationship showed cheliped width between vs.carapace distinguished immature and mature stages of males before the puberty molt (HARTNOLL, 1978; COMEAU and CONAN, 1992; BARÓN et al., 2009). These characteristics were also observed in males of the D. pagei, showing an expressive change of allometric growth rate between juveniles (negative allometry) to adults (positive allometry). Juvenile crabs probably use their energy resources for somatic growth, while in adults this energy is also used to reproduction. This difference could be observed in this study, i.e., a more rapid increase in cheliped growth in larger males. Similar results were revealed with marine brachyuran species, such as those of PINHEIRO and FRANSOZO (1993) for *Arenaeus cribrarius* (Lamarck, 1818) and ALVES *et al.* (2005) for *Austinixa patagoniensis* (Rathbun, 1918).

The pattern of differential growth tending to one of the chelipeds is characteristic of many species of Brachyura (SCALICI and GHERARDI, 2008). This pattern is known as handedness; this study found that males of D. pagei were righthanded. The increase in the cheliped propodus growth of *D. pagei* may be related to reproduction. For example, it might be related to visual displays as occurs with ocypodid crabs of the genus Uca Leach, 1814, studied by CRANE (1957); to protect females after mating, as shown for Callinectes danae Smith, 1869 by COSTA and NEGREIROS-FRANSOZO (1998); or to force copulation, as observed in both the field and the laboratory by LIU and LI (2000) for the freshwater crab Candidiopotamon rathbunae (De man, 1914). Sexual dimorphism related to the growth of the male cheliped can also be linked to inter- and/or intraspecific combats, such as competition with other males for females, territory competition, and

according to WARNER (1970), to determine the hierarchy in a population.

For adult females there was also a positive allometry for the RCPL *vs.* CW relationship (p = 0.04), but this development of the female cheliped in freshwater crabs is related to protection of the eggs and early juveniles stored in the incubation chamber against predators (DANIELS, 2001), increasing the chances of survival of the offspring. For this reason, there is no reproductive importance associated with the differentiated growth of the female cheliped in Brachyura when compared to males, as previously observed by other investigators (MANSUR *et al.*, 2005; GREGATI and NEGREIROS-FRANSOZO, 2007).

In brachyurans, the female abdomen and its pleopods have an important reproductive function, mainly for freshwater crabs, since they form an incubation chamber, retaining eggs and early juveniles. BECK and COWELL (1976) and PINHEIRO and TADDEI (2005) argued that the presence of macrolecithal eggs in freshwater crabs is a vital survival characteristic in species with epimorphic development. Newly hatched early juveniles are stored in the female incubation chamber with no access to food, using the yolk for nutrition in the first stages of development (DAVANSO et al., 2007). A larger abdomen (compared to males) helps to protect the eggs and early juveniles against physical abrasion, for example (BAEZA and FERNÁNDEZ, 2002). These features explain the differentiated growth of the female abdomen in D. pagei, considering the importance of this structure with its incubation chamber.

Adult brachyuran females often direct more energy to reproductive processes such as development and maturation of oocytes; also, ovigerous females may undergo food restriction (HARTNOLL, 2006). According to the same author during these processes, females can slow or interrupt somatic growth, which would result in a smaller size than males. We did not observe this sexual dimorphism for *D. pagei* in relation to size (CW). Additionally, DAVANSO et al. (2013) found very similar longevities between the sexes of this species (2.6 and 2.8 years for males and females, respectively). However, although gonadal maturity has been estimated at similar for both sizes sexes, females reached morphological sexual maturity at a smaller size than males. These characteristics may be associated with the seasonal spawning observed for the population (DAVANSO et al., 2013), and for the earlier morphological sexual maturity of females compared to males. This could be an adjustment to increase the success of copulation, allowing their participation in at least two reproductive events in their life cycle. ADIYODI (1985) reported that the spermatozoids of some crab species can survive stored in seminal receptacles (or spermathecas) for a year or more. This fact, in addition to continuous copulation year-round), not during (i.e., only the reproductive season was observed for C. rathbunae (LIU and LI, 2000).

For a crab to be able to reproduce, it must have both morphological maturity and developed gonads (HARTNOLL, 1982). The present results suggest that with gonadal maturity, the crab *D. pagei* also has reached its morphological maturity. In view of the commercial importance of this species, the estimated size for sexual maturity should be used to develop a closed-season regulation.

For commercial species, caution is needed in estimating a minimum size of capture. In a study of a fish population, CONOVER and MUNCH (2002) reported that a reduction in body size and a consequent decrease in female fecundity may be due to an erroneous estimate of the minimum capture size. Determining the size at which 50% of the population is reproductive can ensure continued conservation of the species.

Normative Instruction No. 25 of September 1, 2009, promulgated by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), established periods for protection of the natural reproduction of the fishes in this region, including closed seasons for bait species such as *D. pagei*. This normative does not define a minimum capture size for this crab, which would be essential to ensure reproductive success, considering that *D. pagei* has a seasonal reproductive period (DAVANSO *et al.*, 2013).

CONCLUSIONS

Dilocarcinus pagei reaches the morphological sexual maturity prior to the gonadal maturity, allowing females copulate before the gonad development. This fact is considered a reproductive strategy, since the reproductive period is seasonal. The sexual dimorphism observed concerning body structures, with the right cheliped propodus length (RCPL) larger for males and abdomen width (AW) larger for females, highlights the importance of these structures to the reproduction of the species. From this study, a minimum capture size using as reference the size of sexual maturity can be proposed for a species conservation project.

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REFERENCES

- ADIYODI, R.G. 1985 Reproduction and its control, pp. 147-215. In: BLISS, D. E. and MANTEL, L. H. *The Biology of Crustacea.* Academic Press, New York.
- ALVES, E.S.; RODRIGUES, A.S.; PEZZUTO, P.R.
 2005 Estudo do crescimento relativo de Austinixa patagoniensis (rathbun) (Decapoda, Pinnnotheridae) simbionte de Callichirus major (say) (Decapoda, Callianassidae) no mesolitoral da praia de Balneário Camboriú, Santa Catarina, Brasil. Revista Brasileira de Zoologia, 22: 784-792.
- ANASTASIADOU, C.A. and LEONARDOS, I.D.
 2008 Morphological variation among populations of *Atyaephyra desmarestii* (Millet, 1831) (Decapoda: Caridea: Atyidae) from freshwater habitats of northwester Greece. *Journal of Crustacean Biology*, 28: 240-247.
- BAEZA, J.A. and FERNÁNDEZ, M. 2002 Active brood care in *Cancer setosus* (Crustacea: Decapoda): the relationship between female behavior, embryo oxygen consumption and the cost of brooding. *Functional Ecology*, 16: 241-251.
- BARÓN, P.J.; QUIROGA, A.P.; LEAL, G.A.; GONZÁLEZ-PISANI, X. 2009 Morphological

maturity of the knobbed spider crab, *Leurocyclus tuberculosus* (H. Milne Ewards & Lucas, 1842) (Brachyura: Majidae) in the Northen patagonian gulfs. *Crustaceana*, 82: 267-273.

- BECK, J.T. and COWELL, B.C. 1976 Life history and ecology of the freshwater caridean shrimp, *Palaemonetes paludosus* (gibbes). *American Midland Naturalist*, 96: 52-65.
- CASTIGLIONI, D.S. and NEGREIROS-FRANSOZO, M.L. 2006 Physiologic sexual maturity of the fiddler crab *Uca rapax* (Smith, 1870) (Crustacea, Ocypodidae) from two mangroves in Ubatuba, Brazil. *Brazilian Archives of Biology and Technology*, 49: 239-248.
- COBO, V.J. and ALVES, D.F.R. 2009 Relative growth and sexual maturity of the spider crab, *Mithrax tortugae* Rathbun, 1920 (Brachyura, Mithracidae) on a continental island off the southeastern brazilian coast. *Crustaceana*, 82: 1265-1273.
- COMEAU, M. and CONAN, G.Y. 1992 Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio. Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2460-2468.
- CONAN, G.Y.; COMEAU, M.; MORIYASU, M. 2001 Are morphometrical approaches appropriate to establish size at maturity for male American lobster, *Homarus americanus*? *Journal of Crustacean Biology*, 21: 937-947.
- CONOVER, D.O. and MUNCH, S.B. 2002 Sustaining fisheries yields over evolutionary time scales. *Science*, 297: 94-96.
- CORGOS, A. and FREIRE, J. 2006 Morphometric and gonad maturity in the spider crab *Maja brachydactyla*: a comparison of methods for estimating size at maturity in species with determinate growth. *Journal of Marine Science*, 63: 851-859.
- COSTA, T.M. and NEGREIROS-FRANSOZO, M.L. 1998 Reproductive cycle of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) in the Ubatuba region, Brazil. *Crustaceana*, 71: 615-627.
- CRANE, J. 1957 Basic patterns of displays in fiddler crabs (Ocypodidae, genus Uca). *Zoologica*, 43: 113-130.
- DANIELS, S.R. 2001 Allometric growth, handedness, and morphological variation in *Potamonautes warren* (Calman, 1918) (Decapoda, Brachyura, Potamonautidae) with a redescription of the species. *Crustaceana*, 74: 237-253.
- DAVANSO, T.M.; DARIM FILHO, M.; DAVID, F.S.; TADDEI, F.G. 2007 Número de filhotes em

Dilocarcinus pagei Stimpson, 1861 (Decapoda: Brachyura: Trichodactylidae) da Represa de Furnas/Marimbondo, Icém, SP. In: CONGRESSO DE ECOLOGIA DO BRASIL, 8., Caxambú, 23-28/set/2007. Anais do VIII Congresso de Ecologia do Brasil, 237p.

- DAVANSO, T.M.; TADDEI, F.G.; SIMÕES, S.M.; FRANSOZO, A.; COSTA, R.C. 2013 Population dynamics of the freshwater crab *Dilocarcinus pagei* in tropicalwaters in southeastern Brazil. *Journal of Crustacean Biology*, 33: 235-243.
- FERNÁNDEZ-VERGAZ, V.; LÓPEZ-ABELLÁN, L.J.; BALGUERÍAS, E. 2000 Morphometric, functional and sexual maturity of the deep-sea red crab *Chaceon affinis* inhabiting canary island waters: chronology of maturation. *Marine Ecology Progress Series*, 204: 169-178.
- GÓES, J.M. and FRANSOZO, A. 1998 Heterochely in *Eriphia gonagra* (Fabricius, 1781) (Crustacea, Decapoda, Xanthidae) of the rocky coast from Praia Grande, Ubatuba (SP), Brazil. *Biotemas*, 11: 71-80.
- GOES, P.; BRANCO, J. O.; PINHEIRO, M. A. A.; BARBIERI, E.; COSTA, D.; FERNANDES, L. L. 2010 Bioecology of the uçá-crab, Ucides cordatus (Linnaeus, 1763), in Vitória Bay, Espírito Santo State, Brazil. Brazilian Journal of Oceanography, 58(1) 153-163.
- GREGATI, R.A.G. and NEGREIROS-FRANSOZO, M.L. 2007 Relative growth and sexual morphological sexual maturity of *Chasmagnathus granulatus* (Crustacea, Varunidae) from a mangrove area in southeastern brazilian coast. *Ilheringia*, 97: 268-272.
- HARTNOLL, R.G. 1974 Variation in growth pattern between some secondary sexual characters in crabs (Decapoda, Brachyura). *Crustaceana*, 27: 131-136.
- HARTNOLL, R.G. 1978 The determination of relative growth in Crustacea. *Crustaceana*, 34: 282-292.
- HARTNOLL, R.G. 1982 Growth, pp. 111-185. In, L. G. Abele and D. E. Bliss (eds.), *The Biology of Crustacea*, Vol. 2: Embryology, Morphology and Genetics. Academic Press, New York.
- HARTNOLL, R.G. 2006 Reproductive investment in brachyura. *Hydrobiologia*, 557: 31-40.
- HIROSE, G.L.; BOLLA-JÚNIOR, E.A.; NEGREIROS-FRANSOZO, M.L. 2010 Post-larval morphology, growth, and development of *Uca cumulanta* Crane, 1943 (Crustacea, Decapoda, Ocypodidae)

under laboratory conditions. *Invertebrate Reproduction and Development*, 54: 95-109.

- HIROSE, G.L.; FRANSOZO, V.; TROPEA, C.; LÓPEZ-GRECO, L.S.; NEGREIROS-FRANSOZO, M.L. 2013 Comparison of body size, relative growth and size at onset sexual maturity of *Uca uruguayensis* (Crustacea: Decapoda: Ocypodidae) from different latitudes in the South-Western Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 93 (3): 781-788.
- HUXLEY, J.S. 1950 Relative growth and form transformation. *Proceedings of the Royal Society of London*, 137: 465-469.
- LIMA, D.J.M.; COBO, V.J.; ALVES, D.F.R.; BARROS-ALVES, S.P.; FRANSOZO, V. 2013 Onset of sexual maturity and relative growth of the freshwater crab *Trichodactylus fluviatilis* (Trichodactyloidea) in South-Eastern Brazil. *Invertebrate Reproduction and Development*, 57 (2): 105-112.
- LIU, H.C. and LI, C.W. 2000 Reproduction in the fresh-water crab *Candidiopotamon rathbunae* (Brachyura: Potamidae) in Taiwan. *Journal of Crustacean Biology*, 20: 89-99.
- MAGALHÃES, C. 2001 Diversity, distribution, and habitats of the macro-invertebrate fauna of the Rio Paraguay and Rio Apa, Paraguay, with emphasis on decapod crustaceans, pp. 68-72. In: B. Chernoff, P.W. Willink and J.R. Montambault (eds.), A biological assessment of the aquatic ecosystems of the Rio Paraguay Basin, Alto Paraguay, Paraguay. RAP bulletin of biological assessment 19, Washington.
- MAGALHÃES, C. 2003 Famílias Pseudothelphusidae e Trichodactylidae, pp. 143-287. In: G. A. S. Melo (eds.), Manual de identificação dos Crustacea decapoda de água doce do Brasil. Edições Loyola, São Paulo.
- MAGALHÃES, C.; BUENO, S.L.; BOND-BUCKUP G.; VALENTI, W.C.; SILVA H.M.; KIYOHARA, F.; MOSSOLIN, E.C.; ROCHA, S. 2005 Exotic species of freshwater decapod crustaceans in the state of São Paulo, Brazil: records and possible causes of their introduction. *Biodiversity Conservation*, 14: 1929-1945.
- MANSUR, C.B.; HEBLING, N.J.; SOUZA, J.A. 2005 Crescimento relativo de *Dilocarcinus pagei* Stimpson, 1861 e *Sylviocarcinus australis* Magalhães & Turkay (Crustacea, Decapoda, Tricodactylidae) no pantanal do Rio Paraguai,

Porto Murtinho, Mato Grosso do Sul. *Boletim do Instituto de Pesca*, *31*: 103-107.

- MOURA, N.F.O. and COELHO, P.A. 2004 Maturidade sexual fisiológica em *Goniopsis cruentata* (latreille) (Crustacea, Brachyura, Grapsidae) no estuário do Paripe, Pernambuco, Brasil. *Revista Brasileira de Zoologia*, 21: 1011-1015.
- PINHEIRO, M.A.A. and FRANSOZO, A. 1993 Relative growth of speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Brachyura, Portunidae), near Ubatuba, State of São Paulo, Brasil. *Crustaceana*, 65: 377-389.
- PINHEIRO, M.A.A. and TADDEI, F.G. 2005 Crescimento do caranguejo de água doce *Dilocarcinus pagei* Stimpson (Crustacea, Brachyura, Trichodactylidae). *Revista Brasileira de Zoologia*, 22: 522-528.
- SAMPEDRO, M.P.; GONZÁLES-GURRIARÁN, E.; FREIRE, J.; MUIÑO, R. 1999 Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia, Spain. *Journal of Crustacean Biology*, 19: 578-592.

- SCALICI, M. and GHERARDI, F. 2008 Heterochely and handedness in the river crab, *Potamon potamios* (Oliver, 1804) (Decapoda, Brachyura). *Crustaceana*, 81: 507-511.
- TADDEI, F.G. and HERRERA, D.R. 2010
 Crescimento do caranguejo *Dilocarcinus pagei*Stimpson, 1861 (Crustacea, Brachyura, Trichodactylidae) na represa Barra Mansa, Mendonça, SP. *Boletim do Instituto de Pesca*, 36: 99-110.
- VAZZOLER, A.E.A.M. (1^aed.), 1996 Biologia da reprodução de peixes teleósteos: teorias e práticas. Eduem, Maringá, 169p.
- WARNER, G.F. 1970 Behavior of two species of grapsidae crab during intraspecific encountes. *Behavior*, *36*: 9-19.
- ZAR, J.H. (3^aed.), 1996 *Biostatistical Analysis*. Prentice Hall, New Jersey, 662p.