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Population structure, recruitment, and mortality of the freshwater crab *Dilocarcinus pagei* Stimpson, 1861 (Brachyura, Trichodactylidae) in Southeastern Brazil

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Freshwater crabs of the family Trichodactylidae are widely distributed in major river basins of the South American continent. The population structure of one species, *Dilocarcinus pagei*, was analyzed in an artificial reservoir in Southeastern Brazil, recording data on the sex ratio, recruitment, and mortality. A total of 1339 crabs were collected and included 804 males and 535 females (3 ovigerous and 4 with hatchlings); the sex ratio was 1:0.61 (males: females). Two modes of male and female carapace width (CW) were recorded, with means of 14.4 mm ($n = 407$) and 38.9 mm ($n = 394$) for males and 17.9 mm CW ($n = 269$) and 39.2 mm ($n = 267$) for females. The mean size of males (CW = 26.6 ± 13.8 mm) was significantly larger than that of females (CW = 28.5 ± 12.8 mm). The data indicated that recruitment occurs in summer (January–March), with the reproductive period in spring (October–December), periods with the highest rainfall and temperature values in the region. Reproduction leads to the death of the parents, influencing the sex ratio, which oscillates mainly during the reproductive period.

Keywords: crustacea; reproduction; juvenile recruitment; ecology

Introduction

For crustaceans, knowledge of population characteristics is important to develop conservation methods, mainly in species of economic interest such as *D. pagei*. Freshwater crabs show several morphological, physiological, behavioral, and reproductive modifications, related to the invasion of this environment (Cumberlidge & NG 2009) including low fertility rates with oversized eggs; epimorphic development; limited geographic distributions with a high rate of endemism; and seasonal recruitment (Sternberg & Cumberlidge 2003). These features make species more vulnerable to extinction. The rapid degradation of water bodies and intense overexploitation have alerted researchers and government agencies to the need of monitoring brachyuran species inhabiting these environments (Teodósio & Masunari 2009). In Brazil, 45 species of freshwater crabs are listed in the IUCN Red List of Threatened Species (IUCN 2001), but there are relatively few studies on this group of crustaceans, and this number may be underestimated (Amaral & Leite 2008).

Several biological and ecological aspects of freshwater decapod crustaceans are still scarce in the literature, such as trophic ecology, behavioral ecology, functional

diversity, population dynamics studies, sex ratio, reproductive period, size at maturity, population delimitation, and the relation of the species with different environments (Davanso et al. 2013; Herrera et al. 2013; Sharma & Gupta 2013; Williner et al. 2014). Approximately, 20% of brachyurans inhabit fresh waters (Yeo et al. 2008), and they can be found on every continent (Cumberlidge et al. 2009). In the Neotropical region, they are represented by two families: Pseudothelphusidae, with about 250 species distributed in South American mountain systems up to 3000 m altitude (Rodríguez & Magalhães 2005), and Trichodactylidae, with fewer than 50 species distributed in Central and South America, inhabiting coastal plains (Rodríguez 1992) and the Amazon, Orinoco, and Paraná-Paraguay river basins (Magalhães 2003). The family Trichodactylidae is divided into 10 genera, of which *Dilocarcinus* H. Milne-Edwards, 1853, is represented by two species: *D. septemdentatus* (Herbst, 1783), found in northern South American drainages, and *D. pagei*, with a wide distribution in South America and found in the major river basins in Brazil, mainly in the Amazon and Paraná-Paraguay (Magalhães 2003).

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D. pagei has a cryptic, nocturnal life (Williner & Collins 2002), and may even leave the water at night. During the day, these crabs are usually associated with macrophytes (Taddei & Herrera 2010). They are important components of the trophic web, acting as organic matter processors (Melo GAS 2003) and mainly as saprophages. They are omnivorous, feeding on macrophyte debris, algae (filamentous algae, diatoms, and other unicellular groups), fungi, amoebae, ciliates, rotifers, earthworms, and microcrustaceans (Williner & Collins 2002). These crabs are usually preyed by bony fishes such as *Piaractus mesopotamicus* (Homborg, 1818) (Peixer & Petreli 2007), cartilaginous fishes of the family Potamotrygonidae (Almeida et al. 2010), terrestrial vertebrates, including birds of the families Accipitridae and Falconidae (Magalhães 1990; Olmos et al. 2006), didelphid marsupials (Aragona & Martins-Filho 2009), and artiodactyls such as the wild boar *Sus scrofa* (see Herrera et al. 1994). The species is an important element in the transfer of resources between aquatic and terrestrial environments (Collins et al. 2007).

D. pagei is exotic in several locations in Southeastern Brazil (Magalhães et al. 2005), where it has been introduced for use as bait for sport fishing (Taddei & Herrera 2010). The species is present in the majority of Brazilian southeastern hydroelectric reservoirs and, owing to its recent introduction, it is under intense selective pressure (Taddei & Herrera 2010).

Studies on freshwater crabs are still relatively sparse compared to marine species. Studies of *D. pagei* have mainly examined population characteristics, such as growth (Mansur et al. 2005; Pinheiro & Taddei 2005b; Taddei & Herrera 2010; Davanso et al. 2013), sexual maturity (Herrera et al. 2013), fecundity (Mansur & Hebling 2002), locomotor activity (Renzulli & Collins 2001), the circadian cycle and feeding habits (Williner & Collins 2002), and the relationship between weight and size (Pinheiro & Taddei 2005a) and juvenile development (Vieira et al. 2013). Physiological studies have examined gill physiology (Furriel et al. 2010; Granado et al. 2010; Firmino et al. 2011) and biochemical characteristics (Zanotto & Baptista 2011).

Studies concerning the population biology of freshwater species are urgent in view of the rapid environmental degradation due to pollution of water bodies and also the introduction of exotic species, which can cause major changes in the biodiversity of inland waters (Strayer 2010; Affonso & Signorelli 2011) and environmental impact (Silva & Taddei 2014). In this study, we characterized the population structure of *D. pagei* by investigating the reproductive period, recruitment, mortality, and sex ratio, in total, by month and by size classes, in the Barra Mansa Reservoir, Municipality of Mendonça, São Paulo State, Southeastern Brazil. We aimed to set parameters that could be used in

management projects, studies on delimitation and population growth, individual growth, and reproductive aspects, providing essential information for a better understanding of the relationships of this introduced species with the environment.

Methods

Specimens of *D. pagei* were identified by observing the carapace which is strongly convex in the antero-posterior region, with six spines in the antero-lateral margins, and by the presence of a transverse carina along the anterior margin of the third abdominal somite, both for males and females (Magalhães et al. 2005). Individuals were collected monthly from July 2005 to June 2007, during the day, in Barra Mansa Reservoir (21°14' 27"S and 49°56'28"W) (Figure 1), located in the Paraná Basin. Four collectors sampled for 3 h, covering an area of 2 km². Specimens were collected with sieves (3-mm internodes) and were found associated with the underwater vegetation, mainly *Eichhornia azurea* (Sw.) Kunth, *E. crassipes* (Mart.), *Salvinia molesta* Mitchell, and *Cabomba* sp. and *Egeria densa* Planch. The crabs were placed in plastic bags; females with eggs or hatchlings in the incubation chamber were stored in separate bags. The crabs were transported to the laboratory, which is approximately in a two-hour distance from the sampling site, and crabs were kept frozen until analysis. Individuals were thawed at room temperature and sexed according to abdominal morphology and number of pleopods (Mansur et al. 2005). The carapace width (CW) was measured at the widest point, between the bases of the last marginal spines, with a precision caliper (0.01 mm).

Specimens were separated into demographic groups to characterize the population structure: males (M), females without eggs or hatchlings (F), ovigerous females (FO), and females with hatchlings in the incubation chamber (FH). The population structure was described by dividing individuals into size classes. The demographic groups were distributed in 4-mm classes (CW), which were plotted in histograms for each month. The overall data for each sex were used to construct a total histogram, and decomposition of the modes was performed following Bhattacharya (1967), confirmed by the NORMSEP routine (separation of the normally distributed components) (Pauly & Caddy 1985) and subroutines in the FISAT II program (FAO-ICLARM; Stock Assessment Tools). Modes were accepted when the separation index (SI) was equal to or greater than 2.

The data of Taddei and Herrera (2010) were used to analyze recruitment patterns and to estimate mortality. These authors worked with the same population and found for males a maximum size of 52.6 mm CW and a

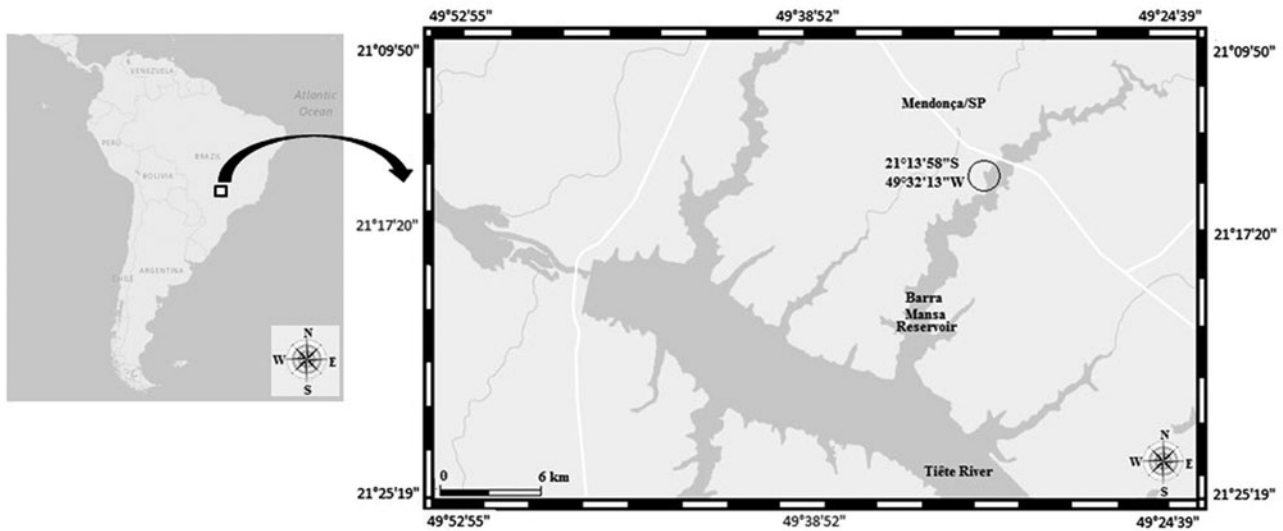


Figure 1. Sampling locations of specimens of *D. pagei* collected in Southeastern Brazil during the study period (July 2005 to June 2007).

growth rate (K) of 0.68 and for females, a maximum size of 63.65 mm CW and a growth rate (K) of 0.73. Males measuring 21.5 mm CW or larger, and females 19.7 mm CW or larger were considered adults; individuals smaller than these measurements were considered juveniles (Herrera et al. 2013).

The number of individuals in each size class was entered in the FISAT II program, which estimated the recruitment pattern for the percentage of males and females. The empirical natural mortality (M) (Pauly 1984) and total mortality (Z) were calculated by the Beverton and Holt method in the FISAT II program (Beverton & Holt 1959). Mortality owing to fishing (F) was calculated as the difference between Z and M ($M = Z - M$), and overexploitation (E) was calculated by the ratio between F and Z ($E = F/Z$) (Dutta et al. 2012). The mean air temperature of the region in the period of the study was used for the recruitment analysis by FISAT II program and was 28.7 °C.

The reproductive period was defined by the presence of ovigerous females (FO) and females with hatchlings in the incubation chamber (FH) (Davanso et al. 2013), contrasting with the recruitment period. The sex ratio was calculated using the chi-square test (χ^2) with a significance level of 5% (Sokal & Rohlf 1995), which evaluated the deviation from a 1:1 ratio between sexes in the size classes, in the sampling months, and for the total of individuals.

Temperature and rainfall data were obtained from the Agrometeorology Information Center (CIIAGRO). The relationships among these abiotic factors, recruitment, and the reproductive period were tested by the Spearman correlation.

Results

The mean rainfall in the region during the sampling period was 87.7 ± 82.9 mm, with the highest mean recorded during spring (October–December) (157.1 ± 79.7 mm) and the lowest in autumn (April–June) (51.03 ± 49.0 mm). The highest mean monthly temperatures were observed in October 2005 (36.7 °C), September 2006 (36.5 °C), and April 2007 (36.1 °C). The lowest mean temperatures were recorded in July 2005 (31.4 °C) and June 2006 (29.8 °C) (Table 1).

A total of 1339 crabs were collected, including 804 males and 535 females (3 were FO and 4 were FH). The size of males ranged from 3.3 to 53.2 mm CW (26.6 ± 13.8 mm) and females from 4.1 to 58.3 mm CW (28.5 ± 2.8 mm). The sexes differed significantly in size, where females were significantly larger than males (Mann Whitney, $p < 0.05$). The FO ranged from 43.6 to 46.7 mm CW and FH ranged from 39.5 to 45.9 mm CW.

The distribution of individuals in 4-mm (CW) size classes in monthly histograms in both years is shown in Figures 2 and 3. Monthly abundance showed no relationship to temperature and rainfall ($p < 0.05$). Smaller individuals, size classes 0–4; 4–8, were collected from November 2005 to January 2006, May to June 2006, December 2006 to March 2007, and May to June 2007. The FO or FH were collected in November 2005 and 2006 and in April 2007. The size distributions were bimodal for males, except those in January, February, and December 2006 and January and May 2007 were unimodal. For females, only size distributions obtained for January and February 2006 were unimodal. No adult males or females were found in January, in both years.

Table 1. Maximum and minimum mean temperatures and rainfall in the sampling period.

Month	Temperature (average) \pm SD		Rainfall (mm) \pm SD
	Maximum ($^{\circ}$ C)	Minimum ($^{\circ}$ C)	
July/2005	31.4 \pm 3.1	16.3 \pm 4.6	48.7 \pm 13.4
August/2005	32.7 \pm 4.1	18.4 \pm 3.5	107.5 \pm 64.5
September/2005	34.2 \pm 4.3	18.0 \pm 3.3	222.1 \pm 79.8
October/2005	36.7 \pm 3.4	17.3 \pm 4.1	167.5 \pm 101.4
November/2005	34.3 \pm 5.8	17.6 \pm 4.7	239.9 \pm 174
December/2005	32.1 \pm 6.4	15.7 \pm 5.4	180.2 \pm 87.5
January/2006	34.2 \pm 6.7	24.3 \pm 4.4	7.6 \pm 1.2
February/2006	33.1 \pm 6.3	20.5 \pm 5.3	13.6 \pm 9.6
March/2006	32.7 \pm 5.6	22.6 \pm 4.8	2.6 \pm 0.8
April/2006	33.2 \pm 3.4	19.5 \pm 3.9	29.8 \pm 13.1
May/2006	35.3 \pm 3.8	14.3 \pm 4.1	63.4 \pm 45.5
June/2006	29.8 \pm 4.2	12.5 \pm 6.3	145.2 \pm 90.8
July/2006	32.1 \pm 3.5	16.8 \pm 4.3	0 \pm 0
August/2006	32.9 \pm 3.6	17.5 \pm 3.8	9.7 \pm 6.8
September/2006	36.5 \pm 2.8	18.6 \pm 3.9	224.5 \pm 125.6
October/2006	35.9 \pm 2.5	17.6 \pm 3.1	119 \pm 87.7
November/2006	31.3 \pm 4.3	18.8 \pm 2.8	216.7 \pm 193.4
December/2006	34.7 \pm 2.5	20.8 \pm 4.1	114.5 \pm 79.8
January/2007	34.6 \pm 3.7	21.3 \pm 2.5	31.2 \pm 17.6
February/2007	34.9 \pm 4.1	22.8 \pm 3.8	88.4 \pm 66.9
March/2007	35.3 \pm 3.2	20.7 \pm 2.6	16.8 \pm 9.8
April/2007	36.1 \pm 2.8	19.2 \pm 3.5	11.6 \pm 7.4
May/2007	33.3 \pm 4.6	19.8 \pm 6.8	8.7 \pm 3.6
June/2007	30.2 \pm 4.3	16.3 \pm 3.6	35.9 \pm 23.7

The highest estimated recruitment levels were recorded in November–December 2005 and December 2006, with a modal pattern from November to February in the first year of sampling, and from November to January in the second year. The normality tendency was not homogeneous, owing to the values obtained in April 2006 and 2007, and did not confirm a separate mode ($SI < 2$) (Figure 4).

The sex ratio favored males (males: females = 1:0.61; $p < 0.05$). Males were more abundant than females in August 2005 and January, July, and December 2006 ($p < 0.05$). Females were present in a higher proportion only in November 2006 ($p < 0.05$) (Figure 5(A)). Only size classes 4–8; 8–12 showed statistically significant differences for the higher proportion of males in the population ($p < 0.05$) (Figure 5(B)).

The size-class distributions of each sex were polymodal. One mode for males was identified, with a mean of 14.4 mm CW (SD = 6.360/SI > 2; $N = 407$) and another mode had a mean of 38.9 mm CW (SD = 6.470/SI > 2; $N = 397$) (Figure 6(A)). Females also had two modes: the smaller one with 17.95 mm CW (SD = 7.210/SI > 2; $N = 269$) and the larger one with 39.2 mm CW (SD = 7.350/SI > 2; $N = 267$) (Figure 6(B)).

Empirical natural mortality (M) was estimated as 1242 for males and 1233 for females. Total mortality (Z)

was 0.734/yr for males and 0.968/yr for females. Mortality owing to fishing (F) was calculated as 0.508 for males and 0.265 for females. The overexploitation rate (E) was estimated as 0.408 for males and 0.214 for females.

Discussion

Our results of monthly distribution of individuals by demographic and size classes, as well as the recruitment analysis, indicated that *D. pagei* in Southeastern Brazil has a single annual reproductive period in the spring (October–December), with recruitment occurring in spring and summer (January–March). These observations corroborate other studies on this species in Brazil: Mansur and Hebling (2002) in the mid-west, Pinheiro and Taddei (2005a) and Davanzo et al. (2013) in the southeast. In these regions of the country, abiotic factors, such as rainfall and temperature, determine the reproductive period of freshwater brachyurans (Hartnoll & Gould 1988), where the values are highest in spring and summer. Higher temperatures stimulate development and maturation of gonadal tissues of decapods (Wear 1974). The higher luminosity in summer also increases the amount of plant protein, and consequently the supply of plant-derived food, which optimizes individual growth and survival of juveniles (Hartnoll & Gould 1988).

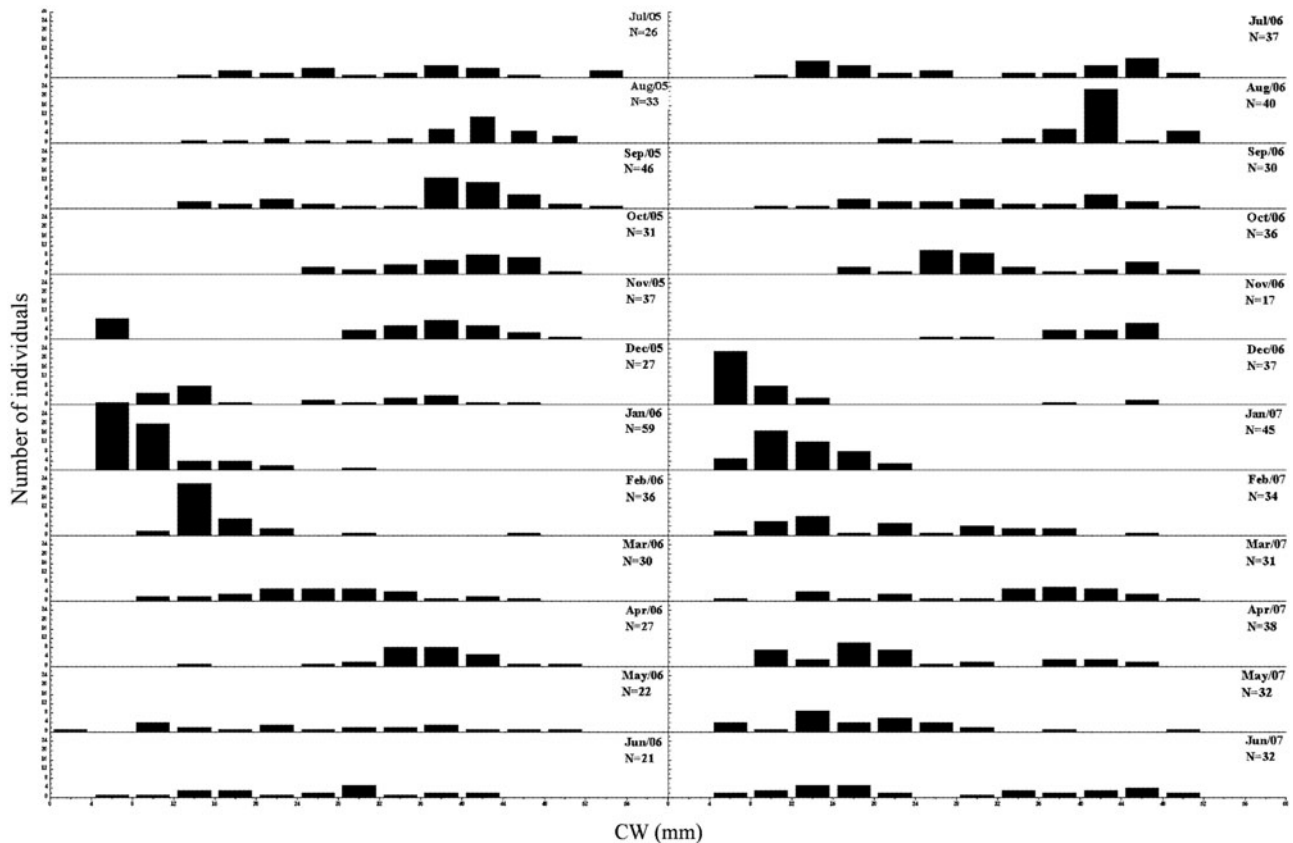


Figure 2. *D. pagei*: Histograms of male monthly size-class distribution (carapace width).

The bimodality obtained for male and female size combined supports the hypothesis of seasonal reproduction, which is common in tropical species (Mansur & Hebling 2002; Pinheiro & Taddei 2005b; Taddei & Herrera 2010; Venâncio & Leme 2010; Davanso et al. 2013). The monthly distribution of individuals (males and females) in size classes consisted mostly of two modes, one of juveniles and one of adults, stages defined by Herrera et al. (2013). This pattern is probably related to the seasonality of reproduction and recruitment (Tsuchida & Watanabe 1997). Bimodality has been previously recorded for this species: Mansur and Hebling (2002); in the mid-west of Brazil; Pinheiro and Taddei (2005b) and Davanso et al. (2013), in Southeastern Brazil; and also for other freshwater decapods, such as *Cherax quinquecarinatus* Gray, 1845 (see Beatty et al. 2005), *Parastacus defossus* Faxon, 1898 (see Noro & Buckup 2009), and *Macrobrachium potiuna* (Müller, 1880) (see Mattos & Oshiro 2009). This is probably related to the period of more abundant allochthonous material carried in by the rains (Fidalgo et al. 2001; Davanso et al. 2013). Dissolved particles of organic matter are filtered and accumulate in macrophyte roots, creating deposits that provide shelter and food for juveniles (Mansur & Hebling 2002).

The absence of adults in January of both years is probably related to egg and juvenile incubation. During this period, females stop feeding and spend most of their time out of water on aquatic plants (Senkman et al. 2015), mainly to increase the supply of oxygen for the hatchlings (Taddei & Herrera 2010). This behavior seems to favor predation of females and may account for the difference in the sex ratio. Field observations of the authors of the present study showed that hatchlings were released during rainy spring nights, when many females were located along the shore of the reservoir, moving their abdomens to release the hatchlings; copulating pairs were also observed. Even when not predated, females do not feed during the incubation period (Taddei & Herrera 2010), and probably die within a few days after releasing the hatchlings, which was evidenced by the presence of a large number of females found dead at the sampling area during the reproductive period. The absence of adults during the recruitment period supports this hypothesis. This behavior is not common in brachyurans, in which ovigerous females burrow during egg incubation (Macia et al. 2001; Sharma & Gupta 2013) and survive thereafter.

These considerations may explain the asynchronous reproduction of some females outside the reproductive

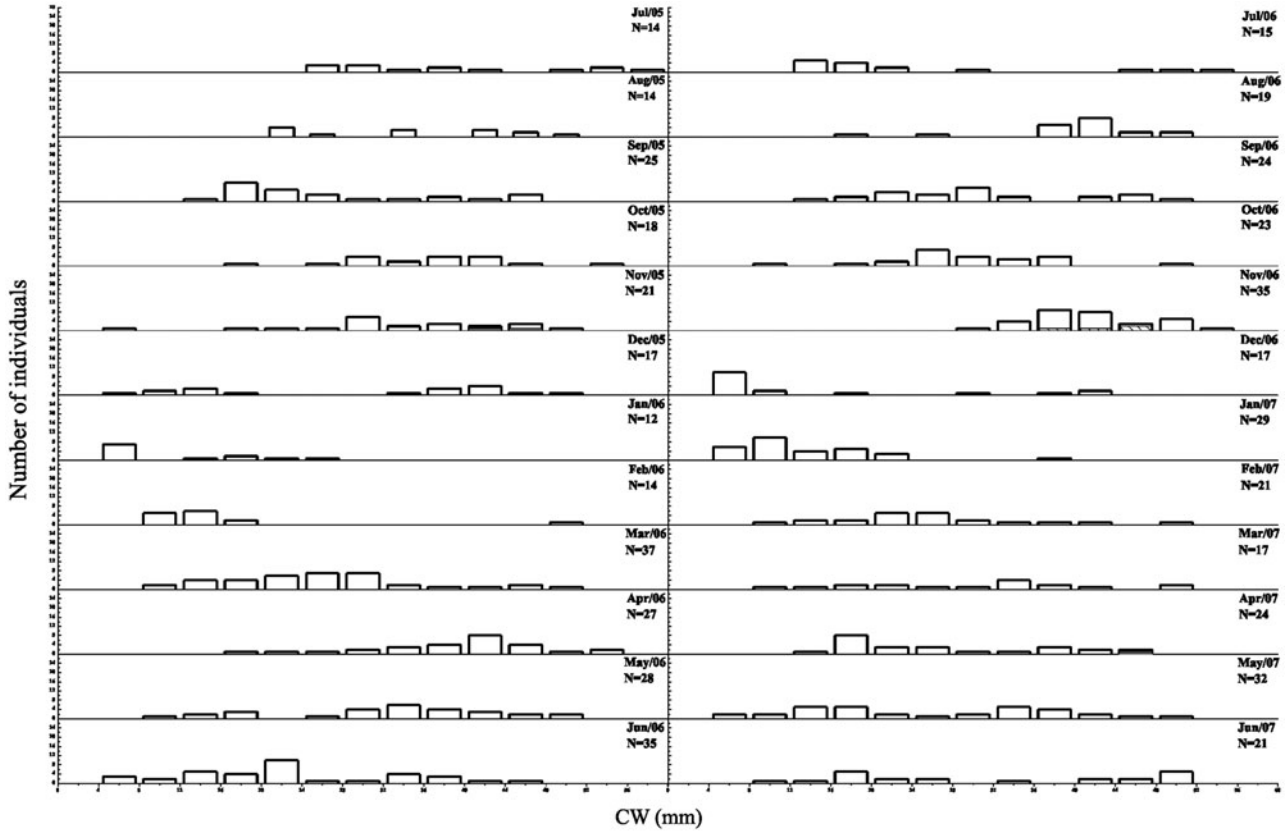


Figure 3. *D. pagiei*: Histograms of female monthly size-class distribution (carapace width).
 Notes: ▨ Females with hatchlings, ▒ Ovigerous females, and □ Females without eggs or hatchlings.

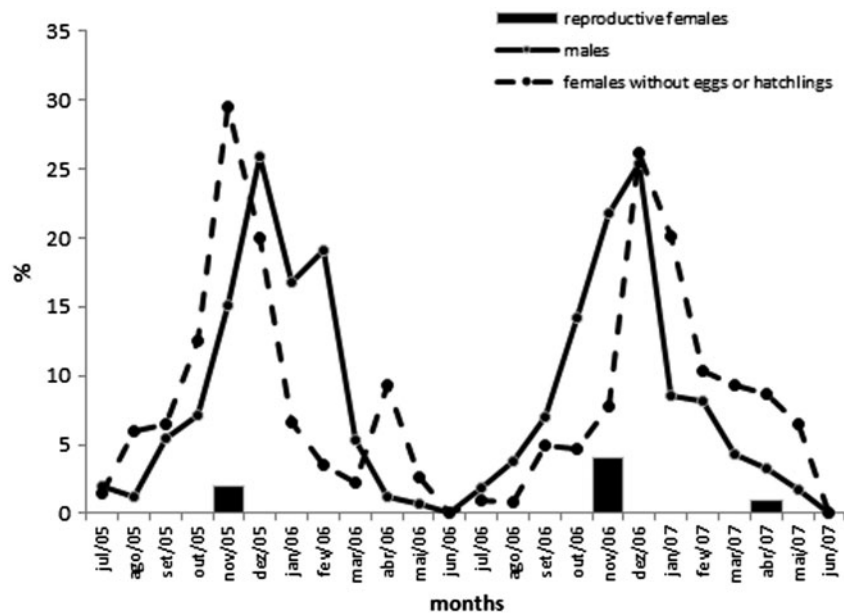


Figure 4. Recruitment patterns for both sexes of *D. pagiei* during the two-year sampling period.

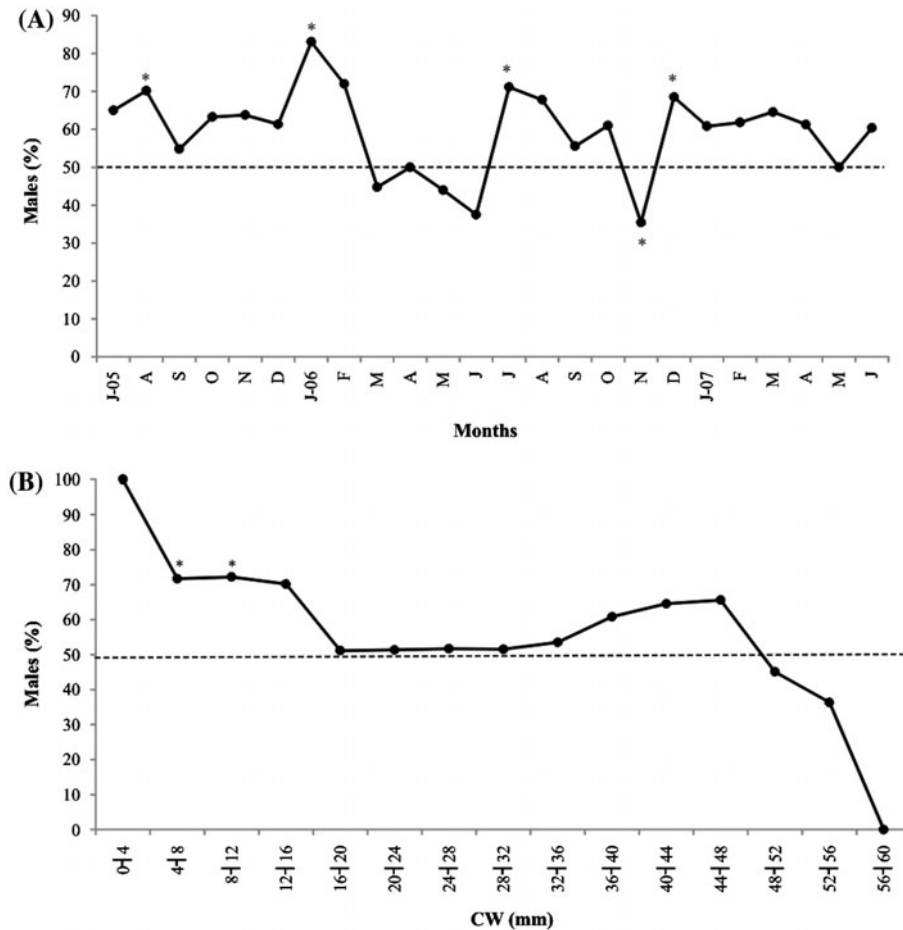


Figure 5. Sex ratio of *D. pagei* during the two-year sampling period (July 2005 to June 2007). (A) monthly; (B) size classes. *Statistically significant difference ($p < 0.05$).

period. The recruitment modes observed in April in both years are possibly related to the late reproduction of these females since individuals that failed in the reproductive period show a reproductive delay in relation to the others (Taddei & Herrera 2010). The distribution of males suggests that they also perish shortly after the reproductive period, which is corroborated by the greater longevity of males observed by Taddei and Herrera (2010).

Female decapods are often larger than males, and a larger abdomen allows a female to carry more eggs and hatchlings (Hines 1988; Taddei & Herrera 2010). In freshwater species, this specialization helps to optimize the reproductive potential (Herrera et al. 2013) since species with epimorphic development produce larger eggs than those with abbreviated development (Vogt 2013). The amount of available calf fosters the survival of hatchlings (Beck & Cowell 1976) during the period in the incubation chamber (Sternberg & Cumberland 2003; Senkman et al. 2015).

Females larger than males are unusual for brachyurans (Hartnoll 1982). However, in freshwater crabs, this size difference has been observed in *D. pagei* (Davanso et al. 2013), *Trichodactylus petropolitanus* (Goeldi, 1886) (see Venâncio & Leme 2010), and *T. fluviatilis* (Latreille, 1828) (see Pescinelli et al. 2014; Silva et al. 2014). Usually, females use most of their energy for gonad production and maturation and for egg incubation (Castiglioni & Negreiros-Fransozo 2006; Hirose & Negreiros-Fransozo 2008). However, in freshwater crabs, both sexes copulate for several hours during the intermolt period (Gherardi & Micheli 1989; Taddei & Herrera 2010; Davanso et al. 2013; Senkman et al. 2015), which eliminates the need for male protection before, during, and after copulation (Pinheiro & Fransozo 1993). Another hypothesis for the large size of females in this species is the male energy input in the somatic growth of chelipeds, which are used in agonistic interactions and reduce growth rate (Costa & Soares-Gomes 2008). Males of *D. pagei* exhibit a marked heterochely (Davanso et al. 2013).

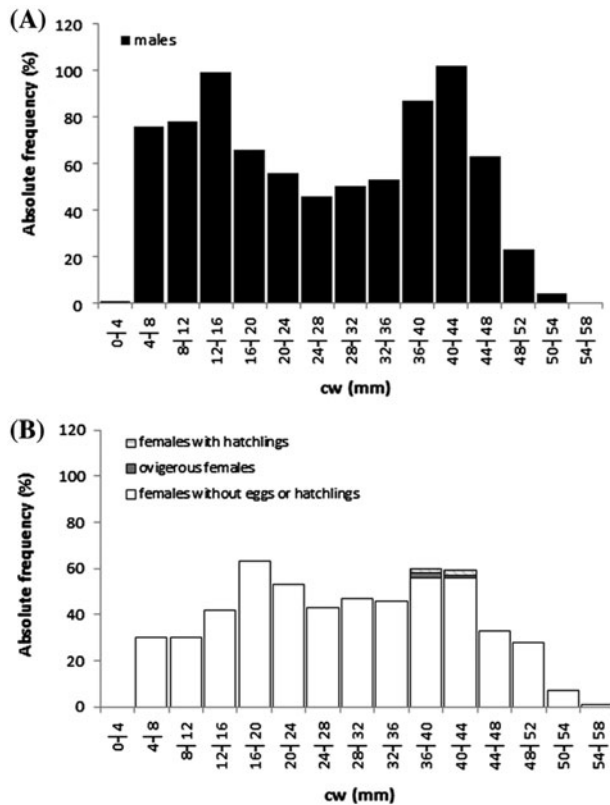


Figure 6. Size-class distribution of the total individuals of *D. pagei* captured during the sampling period (July 2005–June 2007). (A) males; (B) females.

Although females are often significantly larger than males, the largest individuals of each sex obtained in this study had sizes near 53.2 mm (CW) and 58.3 mm (CW) for males and females, respectively. According to Herrera et al. (2013), the species reaches maturity at similar sizes, probably owing to copulatory behavior, which in this species consists of forcing the partner to copulate (Liu & Li 2000). Courting does not occur (Senkman et al. 2015), as also observed in the freshwater crab *Candidiopotamon rathbunae* (De Man, 1914) (see Liu & Li 2000).

The male-biased sex ratio can be related to the higher total mortality (Z) estimated for females, which has also been observed for this species by Davanso et al. (2013). Differences in sex ratio are related to ethological aspects (Sharma & Gupta 2013), growth, food supply and migration (Mantelatto & Fransozo 1997), and selection processes (Mattos & Oshiro 2009). Comparing the monthly sex ratio in some months (August 2005, January, July, and December 2006), males occurred in a significantly higher proportion than females, which is in agreement with previous findings for the species (Davanso et al. 2013). However, some studies revealed a

predominance of females in the reproductive period (Pinheiro & Taddei 2005b; Davanso et al. 2013). Female migration for breeding was reported for the freshwater crab *Paratelphusa masoniana* (Henderson, 1893) by Sharma and Gupta (2013). Mattos and Oshiro (2009) related a predominance of females in the migration period to higher mortality of males, owing to their susceptibility to predation during the search for females.

In this study, the sex ratio did not vary significantly during the breeding period (Figure 5(A)). Females were significantly more abundant only in November 2006. Considering the size-class distribution, the predominance of males is not related to the size at maturity, which occurs close to 40 mm CW (Herrera et al. 2013), similar to the size observed for the species by Davanso et al. (2013) in another region of Southeastern Brazil. The predominance of males in classes 4–8:08–12 may be related to the presence of “jumpers” in the population (Taddei & Herrera 2010), i.e. individuals with a rapid growth rate. This phenomenon is observed mainly in female freshwater crabs in the first months of life, and allows larger females to be available in the next breeding season (Taddei & Herrera 2010).

The mortality data indicate that the sex ratio is closely related to biological factors. The mortality due to fishing (F) of males and females, lower than the natural mortality (M), indicates that the species is not being overexploited in the region ($F < 0.50$). This is corroborated by the low value of exploitation (E) obtained for both sexes. The higher natural mortality (M) obtained for females reinforces the hypothesis of reproductive behavior in which the females stop feeding (Taddei & Herrera 2010) and spend more time out of water (Senkman et al. 2015), favoring predation. In *D. pagei*, longevity is higher for females (Taddei & Herrera 2010). In brachyurans, variations in mortality rates are related to the energy cost during reproduction (Flores & Negreiros-Fransozo 1999), as well as predation and environmental conditions (Souza & Fontoura 1995). Generally, brachyuran females show higher mortality rates (Price & Payne 1984; Costa & Soares-Gomes 2008), but this was not observed in this study, possibly owing to the death of the parents after reproduction. This phenomenon is characteristic of the selective mortality proposed by Pauly (1980), which probably exerts greater influence on the mortality rate of *D. pagei*.

In view of the use of this species in sport fishing (Mansur & Hebling 2002; Mansur et al. 2005; Pinheiro & Taddei 2005a; Davanso et al. 2013), studies defining its reproductive period are important for the design of management measures and the development of specific conservation legislation. In Brazil, few states have regulations for off-season management of the species, and according to Davanso et al. (2013), the existing regulations do not concord with the biological data. The design of specific

regulations, e.g. prohibition of fishing during the breeding season and the taking of juveniles, is vital for the survival of the species (Dutta et al. 2012) and to allow them to replenish their stocks (Sharp & Csirke 1983). The indices obtained for recruitment as well as the presence of ovigerous females are in agreement with those reported by Davanso et al. (2013), which suggest that the closed season should extend from September to December.

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Disclosure statement

No potential conflict of interest was reported by the authors.

References

- Affonso IP, Signorelli L. 2011. Predation on frogs by the introduced crab *Dilocarcinus pagei* Stimpson, 1861 (Decapoda, Trichodactylidae) on a neotropical floodplain. *Crustaceana*. 84:1653–1657.
- Almeida OT, Lorenzen K, Mcgrath DG. 2010. Commercial fishing sector in the regional economy of the Brazilian Amazon. In: Welcomme R, Peter T, editors (Orgs). Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries FAO Regional Office for Asia and the Pacific/Publicación RAP, vol 2. Bangkok: Editora; p. 15–24.
- Amaral ACZ, Leite FPP. 2008. Invertebrados Aquáticos. In: Machado ABM, Drummond GM, Paglia AP, editors. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Belo Horizonte: MMA; p. 57–68.
- Aragona M, Martins-Filho J. 2009. História natural e biologia reprodutiva de espécies de Marsupiais no pantanal, Mato Grosso. *Revista Brasileira de Zoologia*. 26:220–230.
- Beatty DL, Morgan DL, Gill HS. 2005. Life history and reproductive biology of the gilgie, *Cherax quinquecarinatus*, a freshwater crayfish endemic to southwestern Australia. *Journal of Crustacean Biology*. 25:251–262.
- Beck JT, Cowell BC. 1976. Life history and ecology of the freshwater caridean shrimp, *Palaemonetes paludosus* (Gibbes). *American Midland Naturalist*. 96:52–65.
- Beverton RJH, Holt SJ. 1959. A review of the lifespans and mortality rates of fish in nature and the relation to growth and other physiological characteristics. *Ciba Foundation Symposia*. 5:142–177.
- Bhattacharya CG. 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics*. 23: 115–135.
- Castiglioni DS, Negreiros-Fransozo ML. 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.
- Collins P, Williner V, Giri F. 2007. Trophic relationships in crustacean decapods of river with a floodplain. In: Elewa AMT, editor. *Predation in organisms*. Heidelberg: Springer; p. 59–86.
- Costa T, Soares-Gomes A. 2008. Relative growth of the fiddler crab *Uca rapax* (Smith) (Crustacea: Decapoda: Ocypodidae) in a tropical lagoon (Itaipu), southeast Brazil. *Pan-American Journal of Aquatic Sciences*. 3:94–100.
- Cumberlidge N, Ng PKL. 2009. Systematics, evolution, and biogeography of freshwater crabs. In: Martin JW, Crandall KA, Felder D, editors. *Crustacean issues: decapod crustacean phylogenetics*. Boca Raton (FL): Taylor & Francis/CRC Press; p. 491–508.
- Cumberlidge N, Ng PKL, Yeo D, Magalhães C, Campos M, Alvarez F, Naruse T, Daniels S, Esser L, Attipoe F, et al. 2009. Freshwater crabs and the biodiversity crisis: importance, threats, status, and conservation challenges. *Biological Conservation*. 142:1665–1673.
- Davanso TM, Taddei FG, Simões SM, Fransozo A, Costa RC. 2013. Population dynamics of the freshwater crab *Dilocarcinus pagei* in tropical waters in southeastern Brazil. *Journal of Crustacean Biology*. 33:235–243.
- Dutta S, Maity S, Chanda A, Hazra S. 2012. Population structure, mortality rate and exploitation rate of Hilsa Shad (*Tenualosa ilisha*) in West Bengal Coast of Northern Bay of Bengal, India. *World Journal of Fish and Marine Sciences*. 4:54–59.
- Fidalgo ML, Carvalho AP, Santos P. 2001. Population dynamics of the red swamp crayfish, *Procambarus clarkii* (Girard, 1852) from the aveiro region, Portugal (Decapoda, Cambaridae). *Crustaceana*. 74:369–375.
- Firmino KCS, Faleiros R, Masui DC, McNamara JC, Furriel RPM. 2011. Short- and long-term, salinity-induced modulation of V-ATPase activity in the posterior gills of the true freshwater crab, *Dilocarcinus pagei* (Brachyura, Trichodactylidae). *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*. 160:24–31.
- Flores AAV, Negreiros-Fransozo ML. 1999. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. *Bulletin of Marine Science*. 65:59–73.
- Furriel RPM, Firmino KCS, Masui DC, Faleiros RO, Torres AH, McNamara JC. 2010. Structural and biochemical correlates of Na, K-ATPase driven ion uptake across the posterior gill epithelium of the true freshwater crab, *Dilocarcinus pagei* (Brachyura, Trichodactylidae). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*. 313A:508–523.
- Gherardi F, Micheli F. 1989. Relative growth and population structure of the freshwater crab, *Potamon potamios palestinesis*, in the Dead Sea area (Israel). *Israel Journal of Zoology*. 36:133–145.
- Granado M, Baptista BPS, Farah LS. 2010. Calcium transport and homeostasis in gill cells of a freshwater crab *Dilocarcinus pagei*. *Journal of Comparative Physiology B*. 180:313–321.
- Hartnoll RG. 1982. Growth. In: Bliss DE, editor. *The biology of crustacea embryology, morphology and genetics*. New York (NY): Academic Press; p. 383.
- Hartnoll RG, Gould P. 1988. Brachyuran life history strategies and the optimization of egg production. *Symposia of the Zoological Society of London*. 59:1–9.
- Herrera RP, Herrera-Junior HM, Mauro RA. 1994. Dieta de porco monteiro (*Sus acrofa*) no Pantanal da Nhecolândia. In: *Anais do Congresso de Ecologia do Brasil*. Londrina: Universidade Estadual de; p. 16–17.

- Herrera DR, Davanso TM, Costa RC, Taddei FG. 2013. The relative growth and sexual maturity of the freshwater crab *Dilocarcinus pagei* (Brachyura, Trichodactylidae) in the northwestern region of the state of São Paulo. *Iheringia Série Zoologia*. 103:232–239.
- Hines AH. 1988. Fecundity and reproductive output in two species of deep-sea crabs, *Geryon feneri* and *G. quinqueedens* (Decapoda: Brachyura). *Journal of Crustacean Biology*. 8:557–562.
- Hirose GL, Negreiros-Franzoso ML. 2008. Population biology of *Uca maracoani* Latreille 1802–1803 (Crustacea, Brachyura, Ocypodidae) on the south-eastern coast of Brazil. *Pan-American Journal of Aquatic Sciences*. 3:373–383.
- IUCN. 2001. IUCN red list categories and criteria. Version 3.1 [cited 2015 Jan 19]. Available from <http://iucnredlist.org>
- Liu HC, Li CW. 2000. Reproduction in the fresh-water crab *Candiodipotamon rathbunae* (Brachyura: Potamidae) in Taiwan. *Journal of Crustacean Biology*. 20:89–99.
- Macia A, Quincardete I, Paula J. 2001. A comparison of alternative methods for estimating population density of the fiddler crab *Uca annulipes* at Saco mangrove, Inhaca Island (Mozambique). *Hydrobiologia*. 449:213–219.
- Magalhães CA. 1990. Hábitos alimentares e estratégia de forrageamento de *Rosthramus sociabilis* no Pantanal do Mato Grosso, Brasil. *Ararajuba*. 1:95–98.
- Magalhães C. 2003. Famílias Pseudothelphusidae e Trichodactylidae. In: Melo GAS, editor. Manual de identificação dos Crustacea Decapoda de água doce do Brasil. São Paulo: Editora Loyola; p. 143–287.
- Magalhães C, Bueno SL, Bond-Buckup G, Valenti WC, Silva HM, Kiyohara F, Mossolin EC, Rocha S. 2005. Exotic species of freshwater decapod crustaceans in the state of São Paulo, Brazil: records and possible causes of their introduction. *Biodiversity and Conservation*. 14:1929–1945.
- Mansur CB, Hebling NJ. 2002. Análise comparativa entre a fecundidade de *Dilocarcinus pagei* Stimpson e *Sylviocarcinus australis* Magalhães & Turkay (Crustacea, Decapoda, Trichodactylidae) no Pantanal do Rio Paraguai, Porto Murtinho, Mato Grosso do Sul. *Revista Brasileira de Zoologia*. 19:797–805.
- Mansur CB, Hebling NJ, Souza JA. 2005. Crescimento relativo de *Dilocarcinus pagei* Stimpson, 1861 e *Sylviocarcinus australis* Magalhães e Turkay, 1996 (Decapoda: Trichodactylidae) no Pantanal do Rio Paraguai, Porto Murtinho – Mato Grosso do Sul. *Boletim do Instituto de Pesca*. 31:103–107.
- Mantelatto FLM, Franzoso A. 1997. Fecundity of the crab *Calinectes ornatus* Ordway, 1863 (Decapoda, Brachyura, Portunidae) from the Ubatuba region, São Paulo, Brazil. *Crustaceana*. 70:214–226.
- Mattos LA, Oshiro MY. 2009. Estrutura populacional de *Macrobrachium potiuna* (Crustacea, Palaemonidae) no Rio do Moinho, Mangaratiba, Rio de Janeiro, Brasil. *Biota Neotropica*. 9:15–23.
- Melo GAS, editor. 2003. Manual de Identificação dos Crustacea Decapoda de Água Doce do Brasil. São Paulo: Edições Loyola.
- Noro CK, Buckup L. 2009. O crescimento de *Parastacus defossus* (Crustacea: Decapoda: Parastacidae). *Revista Brasileira de Zoologia*. 26:1063–1074.
- Olmos F, Pacheco JF, Silveira LF. 2006. Notas sobre aves de rapina (Cathartidae, Acciptridae e Falconidae) brasileiras. *Revista Brasileira de Ornitologia*. 14:401–404.
- Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*. 39:175–192.
- Pauly D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. Makati: WorldFish.
- Pauly D, Caddy JF. 1985. A modification of Bhattacharya's method for the analysis of mixtures of normal distribution. Makati: FAO Fisheries Circular.
- Peixer J, Petreli Jr. M. 2007. Hook selectivity of the pacu *Piaractus mesopotamicus* (Holmberg, 1887) in the Pantanal, the State of Mato Grosso do Sul, Brazil. *Brazilian Journal of Biology*. 67:339–345.
- Pescinelli RA, Pantaleão JAF, Davanso TM, Costa RC. 2014. Relative growth and morphological sexual maturity of the freshwater crab *Trichodactylus fluviatilis* Latreille 1828 (Decapoda, Trichodactylidae) from west central São Paulo State, Brazil. *Invertebrate Reproduction & Development*. 58:108–114.
- Pinheiro MAA, Franzoso A. 1993. relative growth of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Brachyura, Portunidae), near Ubatuba, State of São Paulo, Brazil. *Crustaceana*. 65:377–389.
- Pinheiro MAA, Taddei FG. 2005a. Relação peso/largura da carapaça e fator de condição em *Dilocarcinus pagei* Stimpson, 1861 (Crustacea: Trichodactylidae) em São José do Rio Preto, SP, Brasil. *Revista Brasileira de Zoologia*. 22: 825–829.
- Pinheiro MAA, Taddei FG. 2005b. Crescimento do caranguejo de água doce, *Dilocarcinus pagei* Stimpson (Crustacea, Brachyura, Trichodactylidae). *Revista Brasileira de Zoologia*. 22:522–528.
- Price JO, Payne JF. 1984. Size, age, and population dynamics in an R-selected population of *Orconectes neglectus chaenodactylus* Williams (Decapoda, Cambaridae). *Crustaceana*. 46:29–38.
- Renzulli PY, Collins P. 2001. Ritmo nictimeral de la actividad locomotora dos cangrejos dulcuacuícolas *Dilocarcinus pagei pagei* Stimpson, 1861 y *Trichodactylus borellianus* Nobili 1896. *Revista FABICIB*. 5:145–153.
- Rodríguez G. 1992. The freshwater crabs of America: family Trichodactylidae and supplement to the family Pseudothelphusidae. Caracas: Faune Tropical XXXI.
- Rodríguez G, Magalhães C. 2005. Recent advances in the biology of the neotropical freshwater crab family Pseudothelphusidae (Crustacea, Decapoda, Brachyura). *Revista Brasileira de Zoologia*. 22:354–365.
- Senkman LE, Negro CL, Lopretto EC, Collins PA. 2015. Reproductive behaviour of three species of freshwater crabs of the family Trichodactylidae (Crustacea: Decapoda) including forced copulation by males. *Marine and Freshwater Behaviour and Physiology*. 48:77–88.
- Sharma KK, Gupta RK. 2013. Population structure of freshwater crab *P. masoniana* (Henderson) in the lower reaches of Chenab river, J&K State, India. *International Journal of Fish Aquaculture Science*. 3:1–6.
- Sharp GD, Csirke YJ. 1983. Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. FAO Fisheries Circular. 2:1–553.
- Silva TE, Taddei FG. 2014. Predação de ovócitos de *Piaractus mesopotamicus* (Pacu-caranha) por *Macrobrachium amazonicum* em condições laboratoriais. *Boletim do Instituto de Pesca*. 40:207–214.
- Silva TR, Neto EMC, Rocha SS. 2014. Etnobiologia do caranguejo de água doce *Trichodactylus fluviatilis* Latreille,

- 1828 no povoado de Pedra Branca, Santa Teresinha. Bahia Gaia Scientia. 8:51–64.
- Sokal RR, Rohlf FJ. 1995. Biometry the principles of practices of statistics in biological research. New York (NY): W.H. Freeman and Company.
- Souza GD, Fontoura NF. 1995. Crescimento de *Macrobrachium potiuna* no Arroio Sapucaia, Município de Gravataí, Rio Grande do Sul (Crustacea, Decapoda, Palaemonidae). Revista Brasileira de Biologia. 55:51–63.
- Sternberg RV, Cumberlidge N. 2003. Autapomorphies of the endophragmal system in trichodactylid freshwater crabs (Crustacea: Decapoda: Eubrachyura). Journal of Morphology. 256:23–28.
- Strayer DL. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology. 55:152–174.
- Taddei FG, Herrera DR. 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.
- Teodósio EAO, Masunari S. 2009. Estrutura populacional de *Aegla schmitti* (Crustacea: Anomura: Aeglidae) nos Reservatórios dos Mananciais da Serra Piraquara, Paraná, Brasil. Revista Brasileira de Zoologia. 26:19–24.
- Tsuchida S, Watanabe S. 1997. Growth and reproduction of the grapsid *Crab Plagusia dentipes* (Decapoda: Brachyura). Journal of Crustacean Biology. 17:90–97.
- Venâncio FA, Leme MHA. 2010. The freshwater crab *Trichodactylus petropolitanus* (Goeldi, 1886) (Decapoda, Trichodactylidae) associated with roots of *Hedychium coronarium* Koenig (Zingiberaceae). Pan-American Journal of Aquatic Sciences. 5:501–507.
- Vieira RRR, Rieger PJ, Cichowski V, Pinheiro MAA. 2013. Juvenile development of *Dilocarcinus pagei* Stimpson, 1861 (Crustacea, Brachyura, Trichodactylidae) in the laboratory, with emphasis in the setae morphology and topography. Crustaceana. 13:214–231.
- Vogt G. 2013. Abbreviation of larval development and extension of brood care as key features of the evolution of freshwater Decapoda. Biological Reviews. 88:81–116.
- Wear RG. 1974. Incubation in British Decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. Journal of the Marine Biological Association of the United Kingdom. 54:745–762.
- Williner V, Collins PA. 2002. Daily rhythm of feeding activity of the freshwater crab *Dilocarcinus pagei pagei* in the Rio Pilcomayo National Park, Formosa, Argentina. Modern approaches to the study of Crustacea. 23:171–178.
- Williner V, Carvalho DA, Collins P. 2014. Feeding spectra and activity of the freshwater crab *Trichodactylus kensleyi* (Decapoda: Brachyura: Trichodactylidae) at La Plata basin. Zoological Studies. 53:71–79.
- Yeo DCJ, Ng PKL, Cumberlidge N, Magalhães C, Daniels SR, Campos MR. 2008. Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater. Hydrobiologia. 595:275–286.
- Zanotto FP, Baptista BB. 2011. ATP pulse and calcium homeostasis in cells from hepatopancreas of *Dilocarcinus pagei*, a freshwater crab. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology. 158:432–437.