

Reproductive behaviour of three species of freshwater crabs of the family Trichodactylidae (Crustacea: Decapoda) including forced copulation by males

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This report includes a detailed description of the reproductive behaviour of the freshwater crab *Zilchiopsis collastinensis* in the family Trichodactylidae and some observations on two other genera. It presents observations on the courtship, copulation, spawning, incubation and maternal care in *Z. collastinensis*. No discernible courtship behaviour occurred. We found instead that forced copulation is practised by males. *Z. collastinensis* copulations were observed in between April and October, for *Dilocarcinus pagei* between January and August, and throughout the year for *Trichodactylus borellianus*. The spawning behaviour of all of the species observed took place out of the water. Incubation lasted between 46 and 62 days in *D. pagei*, 37 and 41 days in *Z. collastinensis* and 8 and 12 days in *T. borellianus*. The number of juveniles carried by each ovigerous female ranged from 651 ± 172 in *Z. collastinensis*, through 582 ± 8 in *D. pagei* to 63 ± 33 in *T. borellianus*. The results support the proposition that members of the family Trichodactylidae, comprising exclusively endemic freshwater crabs, have evolved unusual adaptive reproductive behaviours to optimize their reproductive fitness in unstable environments.

Keywords: courtship; mating; maternal care; forced copulation; *Zilchiopsis collastinensis*; *Dilocarcinus pagei*; *Trichodactylus borellianus*

Introduction

The reproductive characteristics of each species or population are the result of the interactions between both endogenous and exogenous factors (Adiyodi & Adiyodi 1970; Sastry 1983; Conan 1985; Romero 2003). Endogenous components, such as genotypic characteristics and evolutionary history, determine the individual reproductive characteristics in each species. These are modelled by exogenous factors and are reflected by relationships between species density, availability and abundance of resources, and different environmental factors such as weather conditions (MacArthur & Wilson 1967; Pianka 1970; Ebert 1994; López-Greco 1997) and anthropic factors such as contamination, as we have described previously (Negro et al. 2014).

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The environmental conditions interact with each other and influence individuals, both by acting as a stimulus and by determining patterns of behaviour and development (Begon et al. 1999). Freshwater crabs have undergone morphological and behavioural adaptations to accommodate a unstable environment (Senkman et al. 2014), many of which are relevant to their reproductive characteristics. Habitat specialization, limited geographic range, endemism, low fecundity with small numbers of large eggs, brood protection, abbreviated larval phase and complete development are all reproductive characteristics of freshwater crabs and freshwater decapods associated with adaptation to an unstable environment (Hartnoll 1988; Anger 2013).

Sexual maturity in crustaceans is a process marked by morphological, physiological and behavioural transformations, each influencing the role of the individual in the population (Hartnoll 1985; Oliveira de Moura & Coelho 2004). The transition to adulthood is the primary process associated with achieving reproductive status (Oliveira de Moura & Coelho 2004). The numbers of sexually mature males and females influence to receptive partners (Emlen & Oring 1977; Borgia 1979), and thus, adding new individuals to a reproductive population is key in maintaining local populations (Oliveira de Moura & Coelho 2004).

These statements highlight the need to provide the basic information necessary to make comparisons with potentially related groups. Besides contributing information about which characteristics determine the continuity of populations, the results of this study could spur advances in applied sciences and predict the state of stocks with conservationist import that is at the centre of all our investigations. Relatively few studies have investigated the behaviour of freshwater tricodactylid crabs (Renzulli & Collins 2001; Alarcon et al. 2002; Mansur & Hebling 2002; Williner & Collins 2002; Zimmermann et al. 2009; Sant'Anna et al. 2014). Mating behaviour, spawning and maternal care during hatching have been described for other families of freshwater crabs *Geothelphusa dehaani* White 1847 (Minei 1976), *Spiralothelphusa hydrodroma* Herbest 1794 (Adiyodi 1988), *Potamon potamios palestinensis* Oliver 1804 (Gherardi & Micheli 1989), *Potamon fluviatile* Herbest 1785 (Micheli et al. 1990) and for other crustaceans (Andrews 1916; Mason 1970; Ingle & Thomas 1974; Barki & Karplus 1999; López Greco et al. 2004; Almerão et al. 2010).

Post-hatching maternal care in decapod crabs and freshwater lobsters is generally restricted (Li & Liu 2000). Maternal care has been described in *T. fluviatilis* Latreille 1828 (Alarcon et al. 2002), *Sylviocarcinus australis* Milne-Edwards 1853 (Magalhães & Türkay 1996; Mansur & Hebling 2002) and *Sylviocarcinus pictus* Milne-Edwards 1853 (Sant'Anna et al. 2013), and in other freshwater crab families such as potamoideos (Gherardi et al. 1988; Micheli et al. 1990; Cumberlidge 1999; Wehrtmann et al. 2010) and *Geosesarma notophorum* Ng and Tan 1995 (Ng & Tan 1995). Maternal care has also been observed in anomuran crabs of the genus *Aegla*, including *Aegla perobae* Hebling and Rodrigues 1977 (Rodrigues & Hebling 1978), *Aegla violacea* Bond Buckup and Buckup 1994 (Well Bond-Buckup et al. 1996) and *Aegla uruguayana* Schmitt 1942 (López Greco et al. 2004).

Other behaviours have been observed in the Trichodactylidae family. Zimmermann et al. (2009) described the repertoire of *T. panoplus* von Martens 1869. Renzulli and Collins (2001) characterize the nycthemeral rate of *Dilocarcinus pagei* Stimpson 1861 and *T. borellianus* Nobili 1896, and Sant'Anna et al. 2014 described the behavioural repertoire and substrate choice of *D. pagei*. This study provides the first record of courtship, mating and maternal care for *Zilchiopsis collastinensis* Pretzmann 1968, *D. pagei* and *Trichodactylus borellianus* Until this point, studies have been limited to growth

(Taddei 1999), fecundity (Mansur & Hebling 2002), feeding behaviour (Williner & Collins 2002), some experimental anatomy in relation to the gills (Onken & McNamara 2002; Weihrauch et al. 2004), fecundity (Senkman et al. 2014) and toxicology (Negro et al. 2012a, 2012b, 2013, 2014).

Members of this family are native to the rivers of South America and, as amphibious species, can stay out of the water for long periods of time, though these excursions are mostly nocturnal. *Z. collastinensis*, *D. pagei* and *T. borellianus* are the most abundant and widely distributed freshwater crabs in Argentina (unpublished data) and are good candidates for the study of reproductive behaviour in the family. The purpose of this study was to describe courtship, mating, spawning, incubation and maternal care in the freshwater crabs *D. pagei*, *Z. collastinensis* and *T. borellianus* in the Paraná River.

Materials and methods

Study species

Ninety *Z. collastinensis*, *D. pagei* and *T. borellianus* individuals were obtained from the coast of the Paraná River, Santa Fe, Argentina, between 2010 and 2012. After capture, the animals were transported to the Macrocrustacean Laboratory at the National Institute of Limnology, Argentina, a journey of approximately one hour. To minimize stress, animals were transported in darkened buckets containing water from the collection site, with a depth of approximately 5 cm. A total of 107 crabs were collected, and the number and size are detailed in Table 1. The size (cephalothorax width) was recorded in each individual using a retractable flexible ruler (precision of ± 0.1 mm). The species was determined according to Melo (2003).

Experimental design

Courtship, copulation, spawning, incubation and maternal care in *Z. collastinensis*, *D. pagei* and *T. borellianus* were recorded and analysed in the laboratory. Mating and courtship tests were conducted monthly over the course of a year.

The animals were isolated for a week in aquaria at 20 ± 2 °C and a photoperiod of 12:12. Animals were fed fish muscle daily. Waste disposal and water replacement were carried out every third day. Observations were made using reproductively mature animals, as defined by Taddei (1999) and Senkman (2014) and included complete chelipeds and pereopods and a hard carapace relative to the state of the moult cycle. For courtship and copulation trials, a male and a female of the same species were placed in 72-L aquaria measuring 30 cm by 60 with a depth of 40 cm.

Table 1. Size range and number of individuals of *Z. collastinensis*, *D. pagei* and *T. borellianus* used in laboratory assays.

| Species | Size (mm) | |
|--------------------------|------------------------|------------------------|
| | Females | Males |
| <i>Z. collastinensis</i> | (<i>N</i> = 13) 51–58 | (<i>N</i> = 13) 54–61 |
| <i>D. pagei</i> | (<i>N</i> = 12) 48–55 | (<i>N</i> = 12) 43–50 |
| <i>T. borellianus</i> | (<i>N</i> = 20) 9–13 | (<i>N</i> = 20) 9–11 |

Courtship and mating

Based on courtship and copulation observations, we defined pre-mating, mating and post-mating phases, as well as movement patterns that occur at each stage and the time spent on each. The test endpoint was defined as the moment the crabs were separated. The pre-copulation phase was established as the moment that interaction between the crabs began. This phase was defined as the interval between the male touching the female with pereopods or chelipeds and the initiation of mating. During copulation, crabs were observed with abdomens facing and the male in a physically superior position with pleopods inserted into the female genitalia until the female was released. Crabs were also observed during post-copulation, a 10-min period after the female, to see whether further interactions would take place (Li & Liu 2000). The courtship and copulation tests were performed throughout the year to observe seasonal variation in these behaviours.

Actions and time intervals were recorded with a Sony H9 digital camera. Recordings were digitally analysed with the Video Edit Magic 4.3 program to assess movement patterns and evaluate the time of each event in minutes.

Spawning and maternal care

Assays were performed according to the reproductive size of *Z. collastinensis*, *D. pagei* and *T. borellianus* females. Immediately after copulation, females were isolated until they were visibly ovigerous. Crabs were placed in aquaria of the same specifications as above, fitted with rocks beyond the level of water and a water plant (*Eichhornia crassipes*). This enabled the crab to leave the water a necessary consideration because ovigerous females were observed out of the water in the field (unpub.obs). Additionally, 10 *T. borellianus* and 10 *Z. collastinensis* ovigerous females carried stage 0 eggs at the time of collection (Senkman 2014). Each female was monitored daily to determine the duration of incubation and maternal care. The daily monitoring process involved opening the abdomen, a procedure done rapidly with extreme care. The behaviour of females and their brood were observed daily in their aquaria. Control films were made to reduce stress. Each female was filmed every other day for 30 min, during the first hours of daylight, at which time the females in their environment are refugees (unpubb.obs). Ventilation, cleaning of egg masses and juvenile behaviour were recorded and analysed from the films as were the movements made by small crabs after hatching. Juveniles were counted when found outside the mother's abdomen.

Results

We observed mating at the cave entrance in the field. Coupling time could not be calculated because crabs coupled before the observations began. We observed the male superior position and lack of interaction during post-copulation. Ovigerous females were observed on *E. crassipes* plants and inside caves with shallow water. It was not possible to observe spawning females or calculate the time of maternal care, courtship and mating.

Courtship and mating

The courtship patterns observed in *Z. collastinensis* and *T. borellianus* were similar and short (lasting between 5 and 15 min). In all three species, the courtship is composed of a series of movements in which the male recognizes the female and grasps her pereopods.

D. pagei courtship was different from that of the other two species studied in that females made erratic movements before mating until the initiation of copulation.

Copulations recorded in the field and in the laboratory were performed by crabs with hard cephalothoraxes.

A pattern of aggressive behaviour was observed during courtship and copulation in all three species (Video 1). The male controlled the reproductive event, and the female position was below the male:

- (1) Movements during copulation were similar and generally adhered to the following sequence. The male rotated the female to the position in which their ventral surfaces came into contact and in this way maintained a position above the female. Coupling was performed in this position.
- (2) The male helped open the female's abdomen with his pereopods and inserted the gonopods into the female genitalia. Once in this position, the female maintained the tips of her chelae horizontal and inward facing, while the male kept his chelae down to restrain the female.
- (3) After mating, the male released the female and the pair separated. Males did not hold the females after separation. The crabs were not easily disturbed during copulation.

Thirteen *Z. collastinensis* copulations were observed between April and October; each lasted between 300 and 960 min. Three were observed in the field during the month of July. Twelve *D. pagei* copulations were observed between January and August: each lasted between 50 and 65 min. Of the total number of observed copulations, two were observed in the natural environment in the month of May. Twenty *T. borellianus* copulations were distributed throughout the year. These lasted between 50 and 90 min, and all occurred under laboratory conditions.



Video 1. Erratic movements and forced copulation in *Dilocarcinus pagei*. [Please see the full text version to access Video 1. Alternatively, the video can be accessed via the article's Supplemental material tab: <http://dx.doi.org/10.1080/10236244.2015.1021556>]

Spawning and maternal care

Spawning behaviour took place out of the water. Ovigerous females remained out of the water during much of this phase. *Z. collastinensis* tended to stay in a cave that was sealed with a plug of mud and vegetation throughout incubation. *T. borellianus* and *D. pagei* ovigerous females were found on aquatic plants. During the incubation period, significantly more ovigerous females of all three species were found out of the water than submerged: 43:26, respectively. There was, however, no preference for any particular out of the water substrate. Females were observed on the stones and plants supplied. The preference for land ended when the brood hatched. From that moment, females were observed out of the water for short periods, until the last young left the maternal abdomen.

Under laboratory conditions, the incubation lasted between 46 and 62 days in *D. pagei*, 37–41 in *Z. collastinensis* and 8–12 days in *T. borellianus*. In *Z. collastinensis* and *D. pagei*, eggs were not glued or attached to the female pleopods, as observed in *T. borellianus*. Instead, they formed a cohesive mass in the mother's abdomen when they were not submerged in water. The structure of the tricodactylid crab abdomen and pleopods forms a kind of "incubation chamber" where the eggs remain during incubation.

During incubation maternal care was observed in the form of ventilation and cleaning of the egg mass. "Lateral", "up-down" and "oblique" movements are the three types of abdominal pleopod movements identified (Table 2). Asynchronous hatching was observed in *Z. collastinensis* and *D. pagei*, with three to five days between the hatching of the first and last crabs. We were unable to make comparative determinations regarding *T. borellianus*.

The small crabs were maintained on the maternal abdomen over a period of 30 ± 3 days in *Z. collastinensis*, 34 ± 4 days in *D. pagei* and 10 ± 2 days in *T. borellianus*.


A yolk reserve was observed in the carapace of the newly hatched juveniles in each of the three species. *D. pagei* and *Z. collastinensis* young consumed the reserve during the first week after hatching and in *T. borellianus* young during the first day. The mean number of hatched juveniles per female was 651 ± 172 in *Z. collastinensis*, 582 ± 8 in *D. pagei* and 63 ± 33 in *T. borellianus*.

No oophagy or cannibalism by the mother was observed in any of the three species.

Discussion

During courtship, the tricodactylid males were observed vigorously approaching females. This behaviour could imply sexual recognition, as in the case of *Procambarus clarkii* Girard 1852, *Homarus americanus* Milne Edwards 1837 and *Callinectes sapidus* Rathbun 1896, who observed that the time before intercourse is used by the male to distinguish the state of the female's sexual maturity (Gleeson 1980; Ameyaw Akumfi 1981; Waddy & Aiken 1991).

The aggressive approach behaviour that was observed during tests with tricodactylid crabs would be included in the "search and interception" mating type described by

Table 2.  Ventilation movements made by ovigerous females of *Z. collastinensis*, *D. pagei* and *T. borellianus* during egg incubation.

Oblique Swimmerets are moved at an oblique angle to its initial position so that they make a "surround" movement of the egg mass plane

Christy (1987). In this type of mating, the male intercepts the female by force without first determining the state of receptivity. In this model, there is no competition between males for females. Because agonistic behaviour was observed between tricodactilid males, their mating behaviour could also be described by the “male dominance” mating type, which is characterized by significant competition between males for access to females (Christy 1987).

In many species of crabs, including *G. dehaani*, *Candidiopotamon rathbunae* De Man 1914 and *P. fluviatile*, a more subtle courtship is observed; the male takes the female with strength and then adjusts the position until the appropriate copulation position is reached (Minei 1976; Warner 1977; Micheli et al. 1990; Li & Liu 2000). The use of chelipeds to control females before copulation is a feature shared with other crustaceans, particularly portunids (Ryan 1966; Fielder & Eales 1972; Berrill & Arsenault 1982; Campbell 1982). This type of control has also been observed in other marine crabs (Edwards 1964; Bigford 1979; Elner et al. 1987; Donaldson & Adams 1989; Perez & Bellwood 1989; Claxton et al. 1994), shrimp (Seibt & Wickler 1979; Nakashima 1995), locusts (Lipcius et al. 1983; Atema 1986; Waddy & Aiken 1991) and freshwater lobsters (Mason 1970; Ingle & Thomas 1974; Stein 1976; Snedden 1990).

During *D. pagei* courtship, females were observed making a series of erratic movements with their pereopods. These movements may be related to the mobilization of the genital pore structure, allowing reception of the male and indicating female sexual maturity. Similarly, *Aegla platensis* Schmitt 1942 females exhibit a series of contractions of the body and abdomen during courtship. In these anomurans, such movements could be related to the mobilization of oocytes from the ovary to the genital pores before intercourse (Almerão et al. 2010). The positioning of the female below the male has also been observed in other crab species, such as *P. fluviatile* (Micheli et al. 1990), *C. rathbunae* (Li & Liu 2000), *Austropotamobius pallipes* Lereboullet 1858 (Ingle & Thomas 1974) and *C. sapidus* (Gleeson 1991; Jivoff et al. 2007). The superior position of the male may facilitate transfer of sperm by gravity to the female seminal receptacles, and it is also necessary to maintain the correct position and complete copulation, since the ability to maintain physical control of females is critical to mating success (Jivoff et al. 2007).

The short duration of copulation recorded for *D. pagei* and *T. borellianus*, which is measured in minutes, contrast with the behaviour of *Z. collastinensis*. It is not unusual that copulation times are measurable in minutes (Hartnoll 1969), especially when it comes to hard copulations, which do not involve cuddling or post-copulation interactions (Sastry 1983; López Greco 1997), as noted in *Z. collastinensis*. This time between decapod species, ranging between 12 min and 21 days, such as in *C. sapidus* (Gleeson 1991), *A. pallipes* (Ingle & Thomas 1974), *P. fluviatile* (Micheli et al. 1990) and *Orconectes limosus* Rafinesque 1817 (Bechler 1981). The time range associated with different species is related to the condition of the female relative to the moult cycle when mating (Hartnoll 1969).

The tricodactilids studied have different seasonal strategies regarding copulation, incubation and maternal care, for example *T. borellianus* lays egg several times per year, unlike *D. pagei* and *Z. collastinensis*, which lay eggs only once. The freshwater crab *C. rathbunae* has been observed spawning out of the water (Li & Liu 2000). This behaviour could be particular to the tricodactilid crabs studied. Although the decent of eggs was not directly observed, one can speculate that spawning also took place out of the water even though the immediate aftermath was not observed. This unusual behaviour could be a strategy to reduce damage caused by water movements during egg

extrusion (Li & Liu 2000). The completion of egg fertilization, which took place 60 and 90 min after extrusion (McLay & López Greco 2011), may also be involved. The rapid hardening of the corium wall in freshly extruded eggs may also form part of this behavioural strategy. Given the hyperosmotic medium, this would help to isolate the egg and prevent excessive water intake. This has been observed in other decapods, where the embryo sac is changed and layers are formed in the corium wall within the first hours after oviposition (Sandifer & Lynn 1980; Lynn & Clark 1983; Talbot & Goudeau 1988; Goudeau et al. 1991; Lynn et al. 1993; Glass et al. 1997).

During the incubation period, in contrast to the mating period, females were highly susceptible to interruption by external stimuli. Recently, ovigerous females spontaneously released eggs in events during which they had to dive throughout the incubation period, though less so at the end of the period. This was also observed by in ovigerous *D. pagei* females (Mansur & Hebling 2002).

Based on our observations and those of Taddei (1999) and Mansur and Hebling (2002), we hypothesize that in the relative vulnerability of the incubation period, females show refuge habits. It is therefore difficult to find ovigerous females in the field, particularly in the case of *D. pagei*. The post-hatching yolk reserves in juvenile tricodactylid species could represent a food source used to complete calcification of the mouthparts. This lecitotrófica strategy could be beneficial in environments with significant variation in food availability and would give the newly hatched juveniles trophic independence (Anger 1995) and may be reflected in an “extra” time for full development. This “extra” step of maternal care to juveniles is called extended parental care. During this type of parental care, juvenile-like, fully developed adults are kept in the “incubation chamber” for a period well after hatching (Thiel 1999). As we observed in *T. borellianus*, the maternal care generally last several days (Li & Liu 2000; Swiech-Ayoub & Masunari 2001; López-Greco et al. 2004). Unlike *T. borellianus*, this period lasted nearly two months in *D. pagei* and *Z. collastinensis*, as in *S. hydrodroma* (Pillai & Subramoniam 1984). This could be a strategy to cope with the effects of the hyperosmotic environment until the hatchling’s bodies are sufficiently hardened to avoid excessive water intake.

Although there are still many unknowns regarding the biology of tricodactylid crabs, including their origin and mechanisms of adaptation, this study is a step towards a better understanding of the behaviour of freshwater crabs and particularly those in the Paraná River. The reproductive strategies of a species are the basis for its persistence in a given habitat, so understanding the mechanisms and adaptations involved in this process are essential for conservation of natural populations of these freshwater crabs.

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Supplemental material

Supplemental data for this article can be accessed here: <http://dx.doi.org/10.1080/10236244.2015.1021556>

References

- Adiyodi RG. 1988. Reproduction and development. In: Burggren WW, McMahon BR, editors. Biology of the land crabs. Cambridge: Academic Press; p. 139–185.

- Adiyodi KG, Adiyodi RG. 1970. Endocrine control of reproduction in decapod Crustacea. *Biol. Rev.* 45:121–165.
- Alarcon DA, de Leme MH, Cobo VJ. 2002. Population structure of the freshwater crab *Trichodactylus fluviatilis* Latreille, 1828 (Decapoda, Trichodactylidae) in Ubatuba, northern coast of Sao Paulo State, Brazil. In: Escobar-Briones E, Alvarez F, editors. Modern approaches to the study of Crustacea. New York (NY): Kluwer Academic/Plenum publisher; p. 179–182.
- Almerão MG, Bond-Buckup G, de S. Mendonça Jr. M. 2010. Mating behavior of *Aegla platensis* (Crustacea, Anomura, Aeglidae) under laboratory conditions. *J Ethol.* 28:87–94.
- Ameyaw-Akumfi C. 1981. Courtship in the crayfish *Procambarus clarkii* (Girard) (Decapoda, Astracidae). *Crustaceana.* 40:57–64.
- Andrews EA. 1916. The attached young of the crayfish *Cambarus clarkii* and *Cambarus diogenes*. *Am Nat.* 41:253–271.
- Anger K. 1995. The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics. *J Exp Mar Biol Ecol.* 193:119–145.
- Anger K. 2013. Neotropical Macrobrachium (Caridea: Palaemonidae): on the biology, origin, and radiation of freshwater-invading shrimp. *J Crustacean Biol.* 33:151–183.
- Atema J. 1986. Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. *Can J Fish Aquat Sci.* 43:2283–2290.
- Barki A, Karplus I. 1999. Mating behavior and a behavioral assay for female receptivity in the red-claw crayfish *Cherax quadricarinatus*. *J Crustacean Biol.* 19:493–497.
- Bechler DL. 1981. Copulatory and maternal-offspring behavior in the hypogean crayfish, *Orconectes inermis inermis* Cope and *Orconectes pellucidus* (Tellkamp) (Decapoda, Astacidea). *Crustaceana.* 40:136–143.
- Begon M, Harper JL, Townsend C. 1999. *Ecología. Individuos, Poblaciones y Comunidades* [Ecology. Individuals, populations and communities]. Barcelona: Ediciones Omega; p. 1147
- Berrill M, Arsenault M. 1982. Mating behaviour of the green shore crab *Carcinus maenas*. *Bull Mar Sci.* 32:632–638.
- Bigford TE. 1979. Synopsis of biological data on the rock crab, *Cancer irroratus* Say. FAO Synopsis 123 NOAA Washington, DC. Technical Report NMFS Circular 426, p. 25.
- Bond-Buckup G, Bueno AAP, Keunecke KA. 1996. Primeiro estágio juvenil de *Aegla prado* Schmitt (Crustacea, Decapoda, Anomura, Aeglidae). *Rev Bras Zool.* 13:1049–1061.
- Borgia, G. 1979. Sexual selection and the evolution of mating systems. In: Blum MS, Blum NA, editors. *Sexual selection and reproductive competition*. New York (NY): Academic Press, University of Michigan; p. 19–80.
- Campbell GR. 1982. A comparative study of adult sexual behaviour and larval ecology of three commercially important portunid crabs from the Moreton Bay region of Queensland, Australia [PhD Dissertation]. Brisbane: University of Queensland, p. 253.
- Christy JH. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. *Bull Mar Sci.* 4:177–191.
- Claxton WT, Govind CK, Elner RW. 1994. Chela function, morphometric maturity, and the mating embrace in male snow crab, *Chionoecetes opilio*. *Can J Fish Aquat Sci.* 51:1110–1118.
- Conan GY. 1985. Periodicity and phasing of molting. In: Wenner AM, editor. *Factors in adult growth*. Rotterdam: A. A. Balkema; p. 73–99.
- Cumberlidge N. 1999. The freshwater crabs of West Africa. Family Potamonautidae. *Faune et Flore Tropicales* 35. Paris: Institut de Recherche Pour le Developpement IRD (ex-ORSTOM), p. 382.
- Donaldson WE, Adams AA. 1989. Ethogram of behavior with emphasis on mating for the tanner crab *Chionoecetes bairdi* Rathbun. *J Crustacean Biol.* 9:37–51.
- Ebert D. 1994. A maturation size threshold and phenotypic plasticity of age and size at maturity in *Daphnia magna*. *Oikos.* 69:309–317.
- Edwards E. 1964. Mating behaviour in the European edible crab (*Cancer pagurus* L.). *Crustaceana.* 10:23–30.
- Elner RW, Hurley Geoffrey V, Koshio Shunsuke. 1987. Mating behavior of the deep-sea red crab, *Geryon quinquedens* Smith (Decapoda, Brachyura, Geryonidae). *Crustaceana.* 52:194–201.

- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*. 197:215–223.
- Fielder DR, Eales AJ. 1972. Observations on courtship, mating and sexual maturity in *Portunus pelagicus* (L., 1766) (Crustacea, Portunidae). *J Nat Hist*. 6:273–277.
- Gherardi F, Micheli F. 1989. Relative growth and population structure of the freshwater crab, *Potamon potamios palestinensis*, in the dead sea area (Israel). *Israel J Zool*. 36:133–145.
- Gherardi F, Micheli F, Monaci F, Tarducci F. 1988. Note sulla biologia ed ecologia del granchio di fiume *Potamon fluviatile* [Notes on the biology and ecology of the river crab *Potamon fluviatile*]. *Bollettino del Museo di Storia Naturale della Lunigiana*. 6–7:169–174.
- Glass ADM, Erner Y, Kronzucker HJ, Schjoerring JK, Siddiqi MY, Wang M-Y. 1997. Ammonium fluxes into plant roots: energetics, kinetics and regulation. *Z. Pflanzenernähr. Bodenkd*. 160:261–268.
- Gleeson RA. 1980. Pheromone communication in the reproductive behaviour of the blue crab, *Callinectes sapidus*. *Mar Behav Physiol*. 7:19–134.
- Gleeson RA. 1991. Intrinsic factors mediating pheromone communication in the crab *Callinectes sapidus*. In: Bauer RT, Martin N, editors. *Crustacean sexual biology*. New York (NY): Columbia University Press; p. 17–32.
- Goudeau M, Goudeau H, Guillaumin D. 1991. Extracellular Mg²⁺ induces a loss of microvilli, membrane retrieval, and the subsequent cortical reaction, in the oocyte of the prawn *Palaemon serratus*. *Dev Biol*. 148:31–50.
- Hartnoll RG. 1969. Mating in the Brachyura. *Crustaceana*. 16:161–181.
- Hartnoll RG. 1985. Growth, sexual maturity and reproductive output. Factors in adult growth. In: Wenner AM, editor. *Crustacean issues 3*. Rotterdam: A. A. Balkema; p. 101–128.
- Hartnoll RG. 1988. Growth and molting. In: Burggren WW, McMahon BR, editors. *Biology of the land crabs*. New York (NY): Cambridge University; p. 186–210.
- Ingle RW, Thomas W. 1974. Mating and spawning of the crayfish *Austropotamobius pallipes* (Crustacea: Astacidae). *Jpn J Zool*. 173:525–538.
- Jivoff PR, Hines AH, Quackenbush S. 2007. Blue crab reproductive biology. In: Kennedy VS, Cronin LE, editors. *Biology of the blue crab*. College Park (MD): College Press; p. 181–223.
- Li C-W, Liu H-C. 2000. Reproduction in the fresh-water crab *Candidiopotamon rathbunae* (Brachyura: Potamidae) in Taiwan. *J Crustacean Biol*. 20:89–99.
- Lipcius RN, Edwards ML, Herrnkind WE, Waterman SL. 1983. In situ mating behavior of the spiny lobster *Panulirus argus*. *J Crustacean Biol*. 3:217–222.
- López-Greco LS. 1997. Acquisition of sexual maturity and characterization of the pattern of growth and reproduction of *Chasmagnathus granulata* Dana (Brachyura, Grapsidae, Sesarninae) Samborombón Bay, Buenos Aires, Argentina [Doctoral Thesis]. Aires: University of Buenos; p. 244.
- López Greco LS, Viau V, Bond-Buckup G, López Greco LS, Lavolpe M. 2004. Juvenile hatching and maternal care in *Aegla Uruguayana* (Anomura, Aeglidae). *J Crustacean Biol*. 24:309–313.
- Lynn JV, Clark WH. 1983. A morphological examination of sperm-egg interaction in the freshwater prawn, *Macrobrachium rosenbergii*. *Biol Bull*. 164:446–458.
- Lynn JW, Glas PS, Lin Q, Green JD. 1993. Assembly of extracellular envelopes around the eggs and embryos of the marine shrimp, *Sicyonia ingentis*. *J Reprod Develop*. 39:90–91.
- MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton (NJ): Princeton University Press.
- Magalhães C, Türkay M. 1996. Taxonomy of the neotropical freshwater crab family Trichodactylidae II. The genera *Forsteria*, *Melocarcinus*, *Sylviocarcinus*, and *Zilchiopsis* (Crustacea: Decapoda: Brachyura). *Senck biol*. 75:97–130.
- Mansur C, Hebling NJ. 2002. Análise comparativa entre a fecundidade de *Dilocarcinus pagei* Stimpson e *Sylviocarcinus australis* Magalhães & Türkay (Crustacea, Decapoda, Trichodactylidae) no Pantanal do Rio Paraguai, Porto Murinho [Comparative analysis between fertility *Dilocarcinus pagei* Stimpson and *Sylviocarcinus australis* Magalhães & Türkay (Crustacea,

- Decapoda, Trichodactylidae) in the Pantanal of the Paraguay River, Port Murtinho, Mato Grosso do Sul]. *Mato Grosso Rev Bas Zoo*. 19:797–805.
- Mason JC. 1970. Maternal-offspring behavior of the crayfish, *Pacifastacus trowbridgi* (Stimpson). *Am Midl Nat*. 84:463–474.
- McLay CL, López-Greco LS. 2011. A hypothesis about the origin of sperm storage in the Eubrachyura, the effects of seminal receptacle structure on mating strategies and the evolution of crab diversity: how did a race to be first become a race to be last? *Zool Anz*. 250:378–406.
- Melo GAS. 2003. Manual de identificação dos Crustacea Decapoda de água doce do Brasil [Identification manual of freshwater Crustacea Decapoda in Brazil]. Museu de Zoologia Universidade de São Paulo. São Paulo: Edições Loyola; p. 429.
- Micheli F, Gherardi F, Vannini M. 1990. Growth and reproduction in the freshwater crab, *Potamon fluviatile* (Decapoda, Brachyura). *Freshwater Biol*. 23:491–503.
- Minei H. 1976. Ecology of the freshwater crab *Geothelphusa dehaani*. *Animal*. 41:10–15.
- Moura NF, Coelho PA. 2004. Maturidade sexual fisiológica em *Goniopsis cruentata* (Latreille) (Crustacea, Brachyura, Grapsidae) no Estuário do Paripe, Pernambuco, Brasil. *Rev Bas Zool*. 21:1011–1015.
- Nakashima Y. 1995. Can small male shrimps achieve copulation in the presence of larger ones? *J Ethol*. 13:9–16.
- Negro CL, Sekman LE, Collins P. 2012. Metabolic responses of burrowing and pleustonic freshwater crabs exposed to endosulfan. *Fresenius Environ Bull*. 12:216–222.
- Negro CL, Senkman LE, Vierling J, Repetti MR, Garcia SR, Collins P. 2012. Bioaccumulation in fresh-water crabs. Endosulfan accumulation in different tissues of *Zilchiopsis collastinensis* (Decapoda: Trichodactylidae). *Bull Environ Contam Toxicol*. 89:1000–1003.
- Negro CL, Castiglioni M, Senkman LE, Loteste A, Collins P. 2013. Cost of reproduction. Changes in metabolism and endosulfan lethality caused by reproductive behaviour in *Hyalella curvispina* (Crustacea: Amphipoda). *Ecotoxicol Environ Saf*. 90:121–127.
- Negro CL, Senkman LE, Marino F. 2014. Effects of chlorpyrifos and endosulfan on different life stages of the freshwater burrowing crab *Zilchiopsis collastinensis* P.: protective role of chorion. *Bull Environ Contam Toxicol*. 92:625–630.
- Ng PKL, Tan CGS. 1995. *Geosesarma Notophorum* sp. Nov. (Decapoda, Brachyura, Grapsidae, Sesarminae), a terrestrial crab from sumatra, with novel brooding behaviour. *Crustaceana*. 68:390–395.
- Onken H, McNamara JC. 2002. Hyperosmoregulation in the red freshwater crab *Dilocarcinus pagei* (Brachyura, Trichodactylidae): structural and functional asymmetries of the posterior gills. *J Exp Biol*. 205:167–175.
- Perez OS, Bellwood DR. 1989. Observations on the mating behaviour of the indo-pacific sandy shore crab *Matuta lunaris* (Forskål), with notes on the reproductive behaviour of the matutinae (Decapoda, Brachyura, Calappidae). *Crustaceana*. 57:1–8.
- Pianka ER. 1970. On r and K-selection. *Am Nat*. 104:592–597.
- Pillai CK, Subramoniam T. 1984. Monsoon-dependent breeding in the field crab *Parathelphusa hydrodromus* (Herbst). *Hydrobiologia*. 119:7–14.
- Renzulli P, Collins PA. 2001. Ritmo nictimeral de la actividad locomotora de los cangrejos dulcicuicolas *Dilocarcinus pagei pagei* Simpson, 1861 y *Trichodactylus borellianus* Nobili, 1896 [Nictimeral locomotor activity rhythm of freshwater crabs *Dilocarcinus pagei pagei* Simpson, 1861 and *Trichodactylus borellianus* Nobili, 1896]. *FABICIB*. 5:145–153.
- Rodrigues W, Hebling NJ. 1978. Estudos biológicos em *Aegla perobae* Hebling & Rodriguez, 1977 (Decapoda, Anomura) [Studies on biological *Aegla perobae* Hebling & Rodriguez, 1977 (Decapoda, Anomura)]. *Rev Bas Biol*. 38:383–390.
- Romero L. 2003. Comportamiento reproductivo y mutilaciones en el cangrejo de las rocas *Grapsus grapsus* (Linnaeus, 1758) (Crustacea, Decapoda) [Reproductive behavior and mutilation crab rocks *Grapsus grapsus* (Linnaeus, 1758) (Crustacea, Decapoda)]. *Revista Peruana de Biología*. 10:2–10.
- Ryan EP. 1966. Pheromone: evidence in a decapod crustacean. *Science*. 151:340–341.

- Sandifer PA, Lynn JW. 1980. Artificial insemination of caridean shrimp. In: Clark WH Jr, Adams TS, editors. *Advances in invertebrate reproduction Vol. II*. New York (NY): Elsevier, North Holland, p. 271–288.
- Sant'Anna B, Takahashi E, Hattori G. 2013. Parental care in the freshwater crab *Sylviocarcinus pictus* (Milne-Edwards, 1853). *OJE*. 03:161–163.
- Sant'Anna BS, Andrade DR, Watanabe TT, Hattori GY. 2014. Behavioral repertoire and substrate choice of the freshwater crab *Dilocarcinus pagei* Stimpson, 1861 (Decapoda, Trichodactylidae). *Global Diversity, Behavior and Environmental Threats*, 57.
- Sastry AN. 1983. Ecological aspects of reproduction. In: Vernberg FJ, Vernberg WB, editors. *The biology of crustacea. Environmental adaptations*. New York (NY): Academic Press; p. 179–270.
- Seibt U, Wickler W. 1979. The biological significance of the pair-bond in the shrimp *Hymenocera picta*. *Zier Tierpsychology*. 50:166–179.
- Senkman LE. 2014. *Biología reproductiva de cangrejos tricodactílicos en el río Paraná Medio [Reproductive biology of tricodactylid's crabs in the Middle Paraná River] [Tesis doctoral]*. La Plata, Argentina: Facultad de Ciencias Naturales y Museo UNLP.
- Senkman E, Williner V, Negro L, König N, Collins P. 2014. Fecundity and oxygen consumption of freshwater crab *Trichodactylus borellianus* (Decapoda: Trichodactylidae) in the alluvial valley of Middle Paraná (Argentina). *Hidrobiológica*. 3:287–296.
- Snedden WA. 1990. Determinants of male mating success in the temperate crayfish *Orconectes Rusticus*: chela size and sperm competition. *Behaviour*. 115:100–113.
- Stein RA. 1976. Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. *Can Jpn J Zool*. 54:220–227.
- Swiech-Ayoub BP, Masunari S. 2001. Flutuações temporal e espacial de abundância e composição de tamanho de *Aegla castro* Schmitt (Crustacea, Anomura, Aeglididae) no Buraco do Padre, Ponta Grossa, Paraná, Brasil [Temporal and spatial fluctuations of abundance and composition of size *Aegla castro* Schmitt (Crustacea, Anomura, Aeglididae) in the Hole Father, Ponta Grossa, Paraná, Brazil]. *Rev Bras Zool*. 18:1003–1017.
- Taddei FG. 1999. *Biologia populacional e crescimento do caranguejo de água doce Dilocarcinus pagei* Stimpson, 1861 (Crustacea, Brachyura, Trichodactylidae) da Represa Municipal de São José do Rio Preto [Population biology and freshwater crab growth *Dilocarcinus pagei* Stimpson, 1861 (Crustacea, Brachyura, Trichodactylidae) of the Municipal Dam of São José do Rio Preto]. SP: Dissertação de Mestrado, Universidade Estadual Paulista, Botucatu, Brasil; 107 p.
- Talbot P, Goudeau M. 1988. A complex cortical reaction leads to formation of the fertilization envelope in the lobster *Homarus*. *Gam Res*. 19:1–18.
- Thiel M. 1999. Duration of extended parental care in marine amphipods. *J Crustacean Biol*. 19:60–71.
- Waddy SL, Aiken DE. 1991. Mating and insemination in the American lobster, *Homarus americanus*. In: Bauer RT, Martin JR, editors. *Crustacean sexual biology*. New York (NY): Columbia University; p. 126–144.
- Warner GF. 1977. *The biology of crabs*. New York (NY): Van Nostrand Reinhold; p. 129.
- Wehrtmann IS, Magalhães C, Hernáez P, Mantelatto FL. 2010. Offspring production in three freshwater crab species (Brachyura: Pseudothelphusidae) from the Amazon region and Central America. *Zoologia*. 27:965–972.
- Weihrauch D, Morris S, Towle DW. 2004. Ammonia excretion in aquatic and terrestrial crabs. *J. Exp. Biol*. 207:4491–4504.
- Williner V, Collins P. 2002. Daily rhythm of feeding activity of a freshwater crab *Dilocarcinus pagei pagei* in National Park Río Pilcomayo, Formosa, Argentina. In: Escobar-Briones E, Alvarez F, editors. *Modern approaches to the study of Crustacea*. Argentina: Kluwer Academic and Plenum Publishers; p. 103–113.
- Zimmermann BL, Aued AW, Machado S, Manfio D, Scarton LP, Santos S. 2009. Behavioral repertoire of *Trichodactylus panoplus* (Crustacea: Trichodactylidae) under laboratory conditions. *Zoologia*. 26:5–11.