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Predation ability of freshwater crabs: age and prey-specific differences in *Trichodactylus borellianus* (Brachyura: Trichodactylidae)

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Freshwater crabs are rarely represented in food webs and their role in these ecosystems has been largely ignored. *Trichodactylus borellianus* is an omnivorous crab species that has a diverse natural trophic spectrum. This paper evaluates, in a laboratory assay, the ability of three ages of this crab to prey on three different organisms. The prey selectivity and relative importance of each prey item was also analyzed. Prey items (cladocerans, oligochaetes, and golden mussels) consisted of organisms of different shapes and mobility, representing the natural diet of this crab. Crabs were sorted according to size (juvenile, sub-adult, and adult) and increasing amounts of one prey was offered to each crab after 24 hrs of starvation. In the selectivity trial, all prey types were offered in a fixed set. Crabs in all three age categories were able to prey on all organisms. Cladocerans and oligochaetes were consumed in greater quantities compared to golden mussels when offered separately. However, only the consumption of oligochaetes exhibited a positive correlation with the crabs' size. When cladocerans and oligochaetes were offered together, more oligochaetes were consumed, both as percentage of volume and occurrence. Age-specific changes in consumption could be related to differences in the stomach capacity of the crab, the digestion time of each prey, and the predator–prey encounter probability. The selection of the most elongated prey with the lowest mobility indicated that the balance of the gain and loss of energy made it an advantageous species to prey on, as it was susceptible to predation. Additionally, the mussel, which is an invasive species, although not positively selected by *T. borellianus* in the present study, represented a new trophic resource for this crab.

Keywords: Trichodactylidae; freshwater crabs; prey selection; predation capacity

Introduction

Crabs are an important component of freshwater ecosystems but only a few aspects of their biology and ecology are known. The lack of study in these ecosystems may be the reason that this group is not included in classic trophic web models. The lack of inclusion of crabs in food web models leads researchers to ignore the role of crabs in the ecosystem and their capacity to interact with other members of freshwater community. *Trichodactylus borellianus* is a small and abundant species that belongs to the family Trichodactylidae, which is the only Brachyura in the continental freshwater systems in the La Plata system, Argentina (Collins et al. 2004). The distribution range of this species extends from the equator to

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35°S, with the Paraná and Paraguay rivers being the major regions of occurrence (Melo 2003). This crab is considered omnivorous because of its wide, natural trophic spectrum composed of a variety of prey types that inhabit the littoral–benthic zone (Collins et al. 2004, 2006; Williner and Collins forthcoming). Animal items include oligochaetes and insect larvae which are usually found in the digestive tract of these crabs along with macrophyte remains. Microcrustaceans and rotifers have also been found in the stomach contents. Algae and other groups are consumed to a lesser extent or even sporadically (Collins et al. 2007; Williner and Collins forthcoming). *T. borellianus* exhibits direct development meaning the hatched juvenile crabs have all of the characteristics of the adult (von Sternberg et al. 1999). Right from the moment of hatching, the digestive system of these crabs is functional, with capabilities similar to those of the adult crabs. Therefore, juvenile crabs can use the same trophic resources as the adult crabs (Williner and Collins forthcoming).

Trichodactylid species are usually found among the aquatic vegetation, primarily in the roots of common water hyacinth, *Eichhornia crassipes*. However, when the vegetation is scarce or during certain times of the day, this species can be found in the benthic zone, on sediment surface or among rocks or coarse wood (Poi de Neiff and Neiff 1980; Paporelo de Amsler 1987; Poi de Neiff and Carignan 1997; Collins et al. 2004). In both locations (aquatic vegetation and sediment), mobile and sessile prey are present. The vegetated area of a habitat decreases or disappears during low water levels or by senescence due to low temperatures during winter, establishing a more direct relationship between the open water body and the bottom. This promotes a closer relationship between the plankton and the littoral–benthic communities. In spring, the growth of aquatic vegetation enables a more direct interaction among the littoral–benthic organisms.

The oscillation of various abiotic factors, such as the water level, leads organisms to develop mechanisms that allow them to adapt to these conditions. In this context, food webs and their components, and the predation capacity of these species must develop along with the system to ensure the continuity of the population (Collins et al. 2006). These fluctuations likely favor the trophic generalism of species, which allows more flexibility in prey selection according to the feasibility of capture (shape, size, and mobility of prey) and the availability of prey in the environment. The consumption of certain prey supposes a positive selection of those prey that promote a greater gain in energy content and nutrition for the predator in a specific moment of life cycle (ecdysis cycle, reproduction, or development; Barnes et al. 1996; Collins 1999; Collins and Williner 2003; Collins et al. 2004). This tendency has been observed in some decapod species of the alluvial valley, such as *Dilocarcinus pagei*, *Macrobrachium borellii*, and *Palaemonetes argentinus* among others (Collins and Paggi 1998; Collins 1999; Collins et al. 2006). Maximizing the energy intake per unit time is the fundamental concept of optimal foraging behavior (MacArthur and Pianka 1966).

The aim of this study was to investigate, in a laboratory, the foraging behavior and predation capacity of three size categories (juveniles, subadults, and adults) of *T. borellianus*, with respect to prey organisms of different shapes, mobility, and hardness, representing the natural prey of the littoral, benthic and plankton communities. The observation of the search and capture behavior, and the analyses of a controlled predation assay were carried out to verify the predation capacity of this crab. Experiments evaluated the increase in the prey intake with the increase in the offered prey, and analyzed prey selection with respect to the importance of occurrence and volume of each prey. Three main alternative hypotheses regarding the predation capacity of this crab were formulated: (1) prey intake by juvenile, subadults, and adults varies by what prey are offered; (2) the consumption by juveniles, subadults, and adults is different for each prey type; and (3) juveniles, subadults, and adults have different prey preference when prey are offered together.

Methods

Samples of *T. borellianus* were collected during autumn in a variety of lentic environments of the Paraná River floodplain in Argentina (31°38′08.99″ S, 60°40′43.6″ W) among the aquatic vegetation, primarily in the roots of *E. crassipes*. These crabs were transferred immediately to the laboratory and placed in an aquarium with refugia (rocks and aquatic vegetation) for approximately one week, and were fed there with fish meat *ad libitum*. Species identification was performed with the aid of a species key (Melo 2003). The cephalothorax width (CW) of each individual was measured, and the gender was determined by assessing the shape of the abdomen and the presence of male pleopods. Crabs were then divided into the following age groups: juveniles (between 3 and 6 mm), subadults (between 6.1 and 9 mm), and adults (more than 9.1 mm), according to the relationship between sexual development and CW (V. Williner et al., unpublished). Gender was only determined for the age categories of subadults and adults. Thirty crabs (10 of each size category) in the intermolt phase were sorted according to size and placed individually in containers of 7.5 cm diameter and 0.1 L volume with dechlorinated water. Experiments began after 24 hrs of starvation at a controlled temperature (21°C) and photoperiod (16:8, light:darkness).

Three prey types were offered to each crab in two ways: (1) one prey type every 48 hrs in increasing amounts and (2) the three prey types together in a fixed amount. The three prey types represent the range of bioforms (shape, mobility, and hardness) of the natural prey in the littoral, benthic, and plankton communities (Collins et al. 2006; Williner and Collins forthcoming). Prey types supplied in the experiment were: (1) a prey type that was mobile and spherical (cladoceran: *Daphnia magna*); (2) a type that was slow moving and long (oligochaete: *Limnodrilus udekemianus*); and (3) a type that was hard and sessile (golden mussel: *Limnoperna fortunei*). The golden mussel and the oligochaete occur in the same environment as the crab and are common food resources. The cladoceran is an exotic that is not present in these ecosystems and only represents a prey bioform. The golden mussel was of particular interest for analysis because it is an invasive species that is native to Asia. It forms dense populations that adhere to water hyacinth roots (G. Musin, unpublished data) and is part of the trophic spectrum of native organisms that occur in the La Plata basin (Penchaszadeh et al. 2000; Sylvester et al. 2007). When evaluating this prey item, some care was taken because its volume could be greater than the other prey items. In some cases, mussels are even larger than the predator itself. Therefore, only individuals with a valve length between 0.5 and 0.9 cm were used.

Once the prey items were offered, the search and capture behavior of the crabs was observed and recorded with a digital camera (Sony™ Cyber-shot, 12.1 mpx) over the time necessary to verify a common pattern of behavior. All assays began after 24 hrs of starvation, and the number of consumed prey was always determined after 24 hrs. Thus, each trial had a duration of 48 hrs. The six-day experiment was carried out over three trials, increasing the amount of prey each day. The maximum amount of prey corresponded to the number that was not totally consumed by any crab. On the first day, 10 prey individuals were offered to each crab (with the exception of *L. fortunei*), followed by 20 on the second day, and 30 on the third day. The mussels were offered to each crab in a smaller amount (3 individuals per crab) due to its large volume, as mentioned before. In the preference experiment, all three prey types were offered at once in a fixed set (20 cladocerans, 20 oligochaetes, and 3 mussels) to each crab and their consumption within 24 hrs was observed (two-day experiments).

A Spearman's rank correlation coefficient was used to test the relationship between the size of *T. borellianus* and the consumed prey in all offers. A nonparametric

Kruskal–Wallis (KW) test was performed to check, on the one hand, consumption differences among different offers within the same age (hypothesis 1), and on the other hand, consumption differences among different ages within the same offer (hypothesis 2). The preference trial was also analyzed with a KW test to verify the differences in the prey consumption of each age-class of the crab. A Mann–Whitney post-test was used to identify differences between groups when necessary (Zar 1996). All of these tests were conducted using the PAST$^{®}$ statistical package (Hammer et al. 2001).

When the three prey types were offered together, a weighted resultant index (R_w) was applied to compare the food components and to evaluate if a particular item had a higher or lower degree of importance. To each item, an angle was assigned that represented the volume or frequency contribution in the selection. Values between 0 and 45 indicated a greater volume than those between 45 and 90. Therefore, it helped define the relative representation of these parameters (Mohan and Sankaran 1988). The prey volume was assessed by liquid displacement for *L. fortunei* and *D. magna*, and through the approximations of geometric shapes for *L. udekemianus* (Edmonson and Winberg 1971; Dumont et al. 1975; Collins 2000).

Results

Search and capture behavior

When prey was placed into the aquaria, *T. borellianus* reacted to the presence of prey almost immediately. Although not all crabs began an active search for the prey, all of the crabs consumed the prey within 24 hrs. The behavior of crabs during the capture was different for each prey. When a cladoceran (a prey that was difficult to catch because of its mobility, sphericity and small size) was offered, the crab showed a sit-and-wait predation behavior, waiting until a cladoceran swam nearby. Then, the crab generally reacted in two ways: (1) the crab captured the cladoceran with one chela and transferred it directly to the mouthparts, or (2) the crab made a circular movement with the chelae and produced a flow of water which helped to bring the prey into its mouth.

In the case of elongated and slow moving prey, crabs searched for and caught the prey at the bottom of the aquarium using the chelae. After the prey was found, it was transferred to the maxillipeds, where it was further handled before it was put in the mouth. While an oligochaete was held by the third maxillipeds, the maxillae tore open the material that was introduced into the mouth. During this process, *L. udekemianus* was held by its most distal part and untangled by the chelae.

In contrast, when the mussel was offered, the crab did not move and stayed close to its prey. When the valves of *L. fortunei* opened and the mollusc exposed its foot or internal organs, the crab tried to hold the mussel with the chelae. If it could be grasped, the foot was transferred to the mandibles of the crab. Handling of the foot led to the rupture of soft parts and caused the death of the prey. In some instances, the crab could break the mussel valves at the middle. If this was achieved, the crab could then eat the whole prey.

Predation capacity

The mean CW (mean value ± standard deviation) of crabs used in the assays was 4.7 ± 0.6 mm for juveniles, 7.2 ± 0.8 mm for subadults, and 10.6 ± 1.0 mm for adults. Crabs in all size categories consumed the three offered prey types. However, the consumption varied according to the prey type and the predator age-class, indicating changes in the predation capacity. In the case of the golden mussel, *T. borellianus* of all sizes consumed very few individuals (Table 1). Hence, no analysis of the predation capacity could be

Table 1. Mean values and standard errors of the maximum number of prey consumed during one day in three size categories of *T. borellianus*.

	Mean values		
Prey	Juveniles	Subadults	Adults
D. magna	15.7 ± 5.1	17.7 ± 9.7	17.6 ± 9.5
L. udekemianus	7.5 ± 7.8	10.5 ± 7.3	25.2 ± 4.3
L. fortunei	0.1 ± 0.3	0.1 ± 0.3	0.2 ± 0.4

made. Nevertheless, it is noteworthy that both juvenile and adult crabs could prey on *L. fortunei* (Table 1). In contrast, the predation capacity of the other two prey species was substantial and similar between males and females in the subadult and adult classes (cladocerans: subadults – $KW_{0.05; 6; 4} = 1.15$, $p = 0.29$; adults – $KW_{0.05; 5; 5} = 0.534$, $p = 0.46$; oligochaetes: subadults – $KW_{0.05; 6; 5} = 0.43$, $p = 0.52$; adults – $KW_{0.05; 5; 5} = 0.935$; $p = 0.35$). Because of this, the following statistical analyses were made without considering gender differences between the subadults and the adults.

When the cladoceran *D. magna* was the prey, crabs of all sizes consumed a similar number of organisms regardless of the number of prey offered (Table 1), indicating a predation capacity with no significant correlation between size and the number of prey consumed (Spearman's correlation coefficient $r_s = 6.7 \times 10^{-4}$; $p = 0.997$; Figure 1(a)). This indicates that crabs of all size groups ate with the same intensity when the offer was
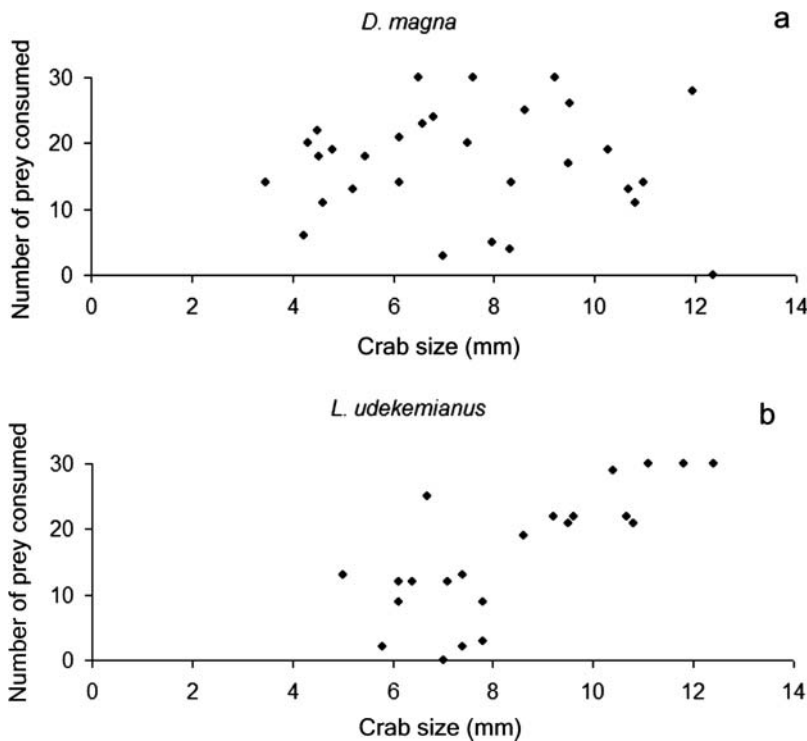

Figure 1. Relationship between the size of *T. borellianus* and the consumption of cladocerans (a) and oligochaetes (b).

Table 2.   Results of the KW test (H: test statistic, *p*: significance) performed on the differences in the prey consumption among the predator size categories (juveniles, subadults, and adults) of *T. borellianus* fed with an increasing number of prey (10, 20, and 30).

Offer	10		20		30	
	H	*p*	H	*p*	H	*p*
D. magna	3.679	0.159	3.45	0.842	0.761	0.684
L. udekemianus	10.55	5.1×10^{-3}	15.1	5.3×10^{-4}	12.81	1.6×10^{-3}

equal, leading to acceptance of null hypothesis 2 (Table 2; Figure 2(a)). However, when the consumption of the three offers in one size category was compared, it was observed that consumption increased with prey abundance in all sizes, indicating that null hypothesis 1 was not supported (Table 3; Figure 2(a)). The Mann–Whitney post-test identified differences in the consumption between the offers of 30 and 10 for all age categories (juveniles: $U = 7, p = 3.6 \times 10^{-3}$; subadults: $U = 23.5, p = 5.6 \times 10^{-3}$; adults: $U = 8, p = 4.7 \times 10^{-3}$).

However, when the oligochaete *L. udekemianus* was the prey, only adult crabs increased their consumption with the increase in the offer (Table 1), which meant null
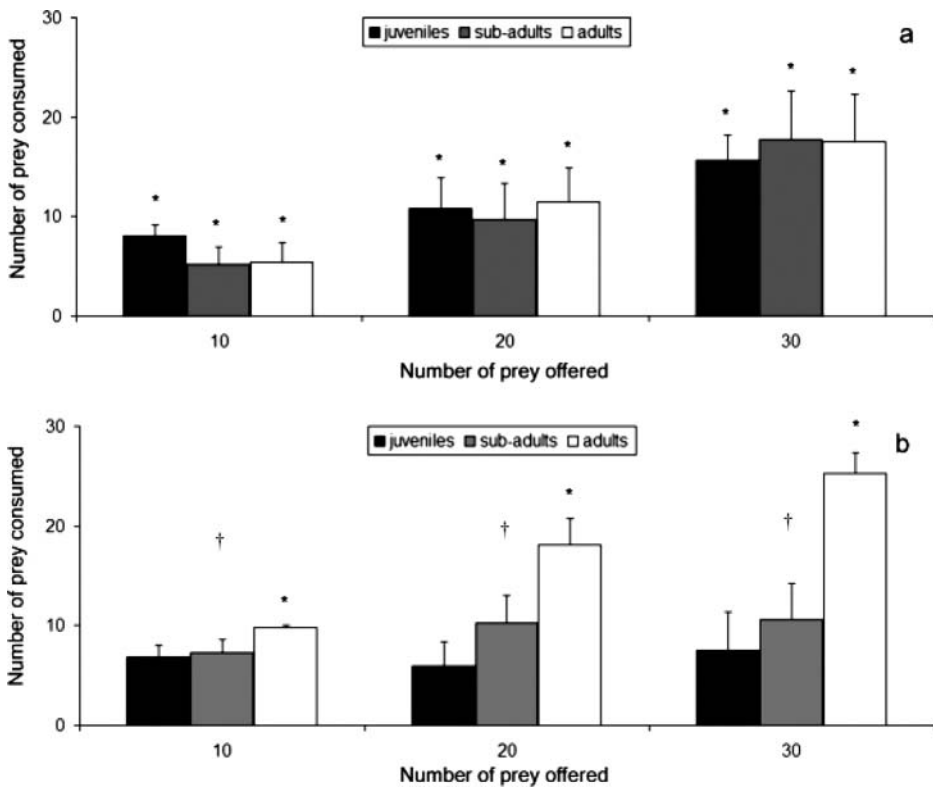

Figure 2.   Number (mean value and standard deviation) of cladocerans (a) and oligochaetes (b) consumed over 24 hrs by *T. borellianus* among the three size categories (juveniles, subadults, and adults) fed with 10, 20, and 30 prey. Symbols represent significant differences within the same size (*) and within the same amount of prey offered (†).

Table 3. Results of the KW test (H: test statistic, p: significance) performed on the differences in the prey consumption among the three prey offers (10, 20, and 30 individuals) of *T. borellianus* sorted among the size categories (juveniles, subadults, and adults).

Size	Juveniles		Subadults		Adults	
	H	p	H	p	H	p
D. magna	8.99	1.2×10^{-2}	9.901	7.1×10^{-3}	8.84	1.2×10^{-2}
L. udekemianus	0.850	0.653	3.38	0.184	8.84	1.3×10^{-5}

hypothesis 1 was rejected only for adults (Table 3). A positive and significant correlation between the predator size and the amount of prey offered was confirmed by Spearman's rank correlation ($r_s = 0.721$; $p = 1.5 \times 10^{-4}$; Figure 1(b)). Indeed, the post-test analysis found that consumption differences in the adult crabs were found mainly in three offers: 10 vs. 20 ($U = 10$, $p = 2.8 \times 10^{-3}$); 20 vs. 30 ($U = 0$, $p = 2.8 \times 10^{-4}$); and 10 vs. 30 ($U = 0$, $p = 2.8 \times 10^{-4}$; Figure 2(b)). Prey consumption among the age groups fed with the same number of organisms was different in all cases, indicating the rejection of null hypothesis 2 (Table 2). However, the post-test identified differences only between adults and the other two size categories in the three offered amounts (10: adult vs. juveniles: $U = 9$, $p = 8.7 \times 10^{-4}$ and adults vs. subadults: $U = 30$, $p = 3.2 \times 10^{-2}$; 20: adult vs. juveniles: $U = 9$, $p = 8.7 \times 10^{-4}$ and adults vs. subadults: $U = 17$, $p = 3.2 \times 10^{-3}$; 30: adult vs. juveniles: $U = 0$, $p = 4.5 \times 10^{-2}$ and adults vs. subadults: $U = 5$, $p = 8.3 \times 10^{-4}$).

Results of the KW test for the preference experiment demonstrate that *T. borellianus* had differential consumption in all age groups (juveniles: KW: 17.57, $p = 1.2 \times 10^{-4}$; subadults: KW: 38.15, $p = 2.99 \times 10^{-9}$; adults: KW: 25.12, $p = 1.71 \times 10^{-6}$), indicating the rejection of null hypothesis 3. The calculation of the prey volume utilized in the assays showed that *D. magna* was the organism with the lowest volume per individual (0.5 mm^3) compared to *L. udekemianus* (1.96 mm^3) and *L. fortunei* (3.3 mm^3). When the three prey types were offered together, crabs of all sizes directly focused on the elongated and slow moving prey, consuming it first. The other two prey were captured sporadically. The calculated percentage of volume and occurrence were very similar among all sizes (Table 4). Evaluating the importance of each prey as a part of the diet for the three size categories after 24 hrs of consumption, the R_w index exhibited the highest values for

Table 4. Values of R_w index, percentage of volume, and percentage occurrence of each prey in the three size categories of *T. borellianus*.

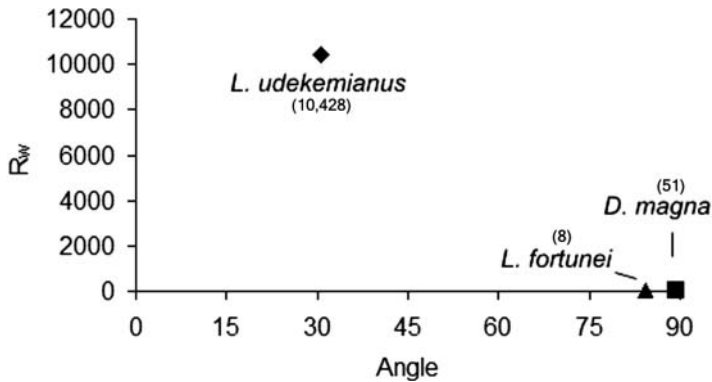|	Juveniles	Subadults	Adults
D. magna			
R_w	39	50	58
% volume	0.41	0.56	0.68
% occurrence	32.25	39.41	43.58
L. udekemianus			
R_w	10909	10501	10193
% volume	99.53	99.39	99.16
% occurrence	67.09	60.13	54.86
L. fortunei			
R_w	5	4	14
% volume	0.05	0.04	0.16
% occurrence	0.64	0.45	1.55

Figure 3.   Angle and values of the R_w index among the three size categories of *T. borellianus*, indicating the volume and occurrence importance of each prey. Note: The number in parentheses indicates the R_w value.

oligochaetes, in percentage of both volume (99.32%) and occurrence (58.89%). The prey *D. magna* had a percentage of 0.58% in volume and 40.15% in occurrence, while *L. fortunei* corresponded to 0.092% and 0.95%, respectively (Figure 3).

Discussion

Both crabs and prey of the littoral–benthic communities coevolved in high temporal and spatial environmental heterogeneity, which was primarily controlled by alternating dry and wet seasons. This dynamic, as experienced in the Paraná River floodplain, led to oscillating changes in the richness and abundance of species, as well as in the existence of refugia (Marchese et al. 2002; Collins et al. 2006). Thus, organisms had to adapt to these cyclical modifications to establish sustainable populations. In this way, potential and effective trophic webs can vary according to external (abiotic: hydrologic cycle, photoperiod, and temperature; biotic: predation risk, competitive ability, and prey availability) and internal factors (nutritional requirements and molt cycle) for each organism and environment (Begon et al. 1996; Collins et al. 2012). In this context, it is important that crabs can respond to environmental changes and prey on the available organisms, ensuring their ontogenetic development. This study demonstrated that all analyzed group sizes of *T. borellianus* were capable of preying on a variety of organism types that represented its natural diet. This makes *T. borellianus* a crab with plastic diet, being able to feed on a variety of trophic resources of the littoral, benthic, and plankton communities at any time of the year.

Although the studied crab was capable of preying on the three prey types, the consumption of the golden mussel was low and happened only when the golden mussel was more vulnerable or when it kept its soft parts exposed. This mussel has a rigid shell that protects it and makes predation by *T. borellianus* more difficult and costly. It is likely that the size range of the mussels used in this study was too large to allow for valve manipulation and rupture. Therefore, crabs must employ strategies other than just net energy gain in order to select mussels as prey. The risk of damaging the chelipeds could influence this selection (Smallegange and van der Meer 1994). Other common, larger-size trichodactylid crabs of the La Plata system (*Zilchiopsis collastinensis*) have been shown to be capable of preying on different sizes of this invasive mussel; however, they generally prefer

large animals (Torres et al. 2012). Unpublished data observing *T. borellianus* gut content indicated that this mollusc represented a new trophic resource for this crab (Carvalho unpublished). The mussel's nutritional content could provide proteins, lipids, and mineral substances that are important for successful ecdysis and the formation of a new exoskeleton (Lordi and Collins 2004). The occurrence of decapods in regions where populations of *L. fortunei* developed (Sylvester et al. 2007) corroborated the fact that *T. borellianus* uses this mussel as a food source.

In contrast, the consumption of the cladoceran *D. magna* was high when it was offered separately, and there was no correlation between the crab size and the amount of prey consumed. This means that consumption increased with the increase in the prey amount in all age categories. The encounter probability between the prey and the crab was enhanced with increasing prey density, which also reduced the predator search effort. In contrast, when the cladocerans were offered with the other two prey species, their importance as a part of the diet was lower. Nevertheless, it was reported previously that zooplanktonic organisms can be a nutritionally important item in the natural diet of other decapods species, such as the crayfish *Procambarus clarkii* (Brown et al. 1992), the caridean prawn *M. borellii* (Collins and Paggi 1998) and the sergestid shrimp *Acetes paraguayensis* (Collins and Williner 2003). Despite the small size and swimming ability of cladocerans, *T. borellianus* has the ability to prey on this organism and consume microcrustaceans at certain times of the year when other, more preferred prey are not available (Williner and Collins forthcoming).

The consumption of the oligochaete *L. udekemianus* was high when it was offered in conjunction with and separately from other prey. However, the increase in the consumption of *L. udekemianus* with the amount of prey offered was only verified in adult crabs. The increasing prey density and encounter probability between oligochaetes and crabs was not significant enough to enhance the predation rate by juveniles and subadults. When different prey types were accessible, *T. borellianus* preferred slow moving organisms. This observation corroborates the results of Williner and Collins (forthcoming), who found significant values for the occurrence and volume of oligochaetes and insect larvae in the gut content of the studied crab. A preference for slow moving prey was also observed in two sympatric freshwater prawns, *P. argentinus* (Collins 1999) and *M. borellii* (Collins and Paggi 1998). In terms of nutritional content, oligochaetes contain a high concentration of protein (59%) relative to their biomass (Hepher 1989). The nutritional composition of other species of *Daphnia* demonstrated that this genus also has a high proportion of protein in its biomass (57% to 64%) (Riccardi and Mangoni 1999). However, crabs must capture and ingest a higher number of cladocerans than oligochaetes to receive the same amount of net energy. Moreover, the elongated form and slow moving behavior of oligochaetes indicates a possible positive balance between the gain and loss of energy during foraging behavior. This makes it an advantageous prey that is susceptible to predation by many aquatic organisms (Popchenko 1971; Bouguenec and Giani 1989).

Predation capacity can be viewed from two perspectives: (1) whether the predator is able to prey on a particular organism and (2) the number of individuals of a species that the predator is able to eat within a day. All size groups of crabs were able to capture prey, but the consumption of oligochaetes varied with the predator's age group. The capacity to prey on different organisms at each size was related both to the capacity of the stomach to store a predetermined number of prey items and to the time of the foregut evacuation. Oligochaetes have a greater individual volume than cladocerans (Collins 2000), yielding a lower number of stocked prey in the crabs' stomach. Furthermore, the digestion time of oligochaetes was observed to be slower than cladocerans in the prawn *M. borellii*

(Carvalho et al. 2011). Therefore, the return of appetite, which is closely related to the rates of foregut evacuation (Loya-Javellana et al. 1995; Simon and Jeffs 2008), is faster and allows for higher daily consumption of a diet that consists of microcrustaceans. Because the digestion of oligochaetes is slower, the positive correlation between size and consumption must be related to the capacity of the crab stomach to store prey. Changes in the prey type and the amount of ingested food have already been observed both in freshwater and marine decapods (Jayachandran 2001; Collins et al. 2006).

Mechanical and chemical receptors in decapods enable the recognition of potential prey and determine the ability of crabs to identify and capture their food (Derby et al. 2001; Graso and Basil 2002). These receptors may be located on the antennae where vibration sensors (Felgenhauer 1992) can detect microflows of water caused by prey movements, such as cladoceran swimming. The mechanoreceptors activate the action of the predator (search and encounter), while prey that moves slowly or is immobile can be detected through their secretions. This detection is carried out by chemoreceptors located in the antennules (Govind 1992), which induce the hunting activity of crabs. The location and perception of prey could also occur through visual receptors. However, the natural environment of this crab is constantly clouded due to the large amount of suspended solids at the bottom and thus, would not favor this type of perception.

Each prey has a nutritional value that not only depends on its chemical compound composition but also on its ease of capture, size, and shape characteristics, digestibility, risk of damage, energy content, and essential nutrient concentrations, which are specific to each prey organism (Collins et al. 2004). In this work, the oligochaete was the prey that was selected most, by all sizes, and had features that make it a desirable prey, according to the optimum foraging theory (MacArthur and Pianka 1966). However, all age groups of the crab species were capable of preying on all of the organisms that represented their natural diet. Therefore, it is probable that their niches overlap, and an intraspecific competition takes place during those moments when prey availability is scarce. Because of this, further studies regarding the predator–prey relationship are needed to elucidate whether there is niche displacement or resource partitioning during the crab's life cycle.

T. borellianus is an important member of the littoral–benthic community and therefore, must be considered to be a part of the trophic web models of the Paraná River system. The ability of *T. borellianus* to prey on a wide variety of bioforms makes it a generalist species that is capable of adjusting its diet according to food availability and variations in environmental conditions. Moreover, at the earliest stages of development, this crab can capture prey similar to those captured by adults. This feature could favor its growth, increase the probability of achieving the next stages of its development, and result in an abundant population.

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