Ontogenetic predation capacity of *Macrobrachium borellii* (Caridea: Palaemonidae) on prey from littoral-benthic communities

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Abstract

Macrobrachium borellii is an abundant prawn of the Paraná River floodplain. Newly hatched juveniles have the general characteristics of adults, and they are proposed to have the same feeding habits. Its natural diet is composed mainly of animals' items rather than vegetals, of which dipteran larvae and oligochaetes are positively selected. However, the oscillations of the hydric cycle imply an adequacy of its selection according to prey availability in all seasons and moments of the ontogenetic development. This work verifies the predation behavior and the ontogenetic predation capacity of *M. borellii* feeding on three preys (cladoceran, dipteran larvae and oligochaetes) of different bioforms and mobility that represent its natural diet. The prawns were placed individually in containers where was offered one prey type in increasing amounts every 48 hours until any prawn ate the total amount offered. The predation behavior was recorded, and the amount consumed was verified after 24 hours. Both sizes of *M. borellii* were capable of preying on all food items used in this study. The search and catch was always made with the second queliped, suggesting a non-visual prey perception, and the handling was different for each prey. Cladoceran was the most consumed, followed by dipteran larvae and oligochaetes. The results show that, in both sizes, *M. borellii* has a trophic plasticity due to its capacity to prey on a variety of bioforms with differing mobility. This capacity could favor the ability of prawns to select the most profitable prey according to the changes in abiotic and ecological factors.

Key words: prawn, prey, cladoceran, dipteran larvae, oligochaetes

Introduction

Macrobrachium borellii (Nobili, 1896) is a widespread endemic prawn of the Paraná River system (Collins *et al.*, 2004). Its natural diet is characterized by the main presence of animals' items rather than vegetals that, like *M. borellii*, inhabit the littoral-benthic community (Collins and Paggi, 1998; Collins, 2005). The variety and availability of potential prey change with the unstable environment conditions of rivers with a floodplain. These fluctuations influence the interspecific relationship of predator-prey, and therefore, feeding plays an important role because prawns may supply their nutrient requirements in each stage of ontogenetic development during all hydric cycles (Collins *et al.*, 2006).

The oscillation of external conditions implies changes in search and capture behavior according to the prey availability and preference.

Moreover, the bioform and mobility of a prey implies different techniques of foraging and catching. In a previous work, Collins and Paggi (1998) found that *M. borellii* positively select oligochaetes and dipteran larvae, but, in winter, at low waters and low temperatures and in the absence of macrophytes, zooplankton might play an important nutritional role. Therefore, this prawn must to be able to hunt prey of different characteristics, such as shape and mobility, in all stages of its life cycle.

Macrobrachium borellii has an abbreviated larval development adapted to freshwater environments. The first instar young has the general characteristics of adults (Boschi, 1981; Jalihal *et al.*, 1993), and therefore, it was proposed to have the same feeding habits as adults (Collins and Paggi, 1998). However, there is little information about the ontogenetic predation capacity of this prawn. Some works have evaluated the predation capacity of palaemonid prawns on mosquito larvae as a biocontrol agent (Collins, 1998; Giri and Collins, 2003). Hence, the persistence of prey species within communities could be determined by predation (Paine, 1966). In this context, we proposed to verify the behavior and ontogenetic predation capacity of *M. borellii* on three preys of different bioforms and mobility of littoral-benthic communities that represent the natural diet of this prawn.

Material and Methods

Samples of *M. borellii* were taken using a hand net with a 1 mm mesh size among the vegetation of the lentic environments of the Paraná River system (31° 40´ 17.2"S - 60°34´07.4"W), and they were carried to the laboratory. The prawns were then sorted according to the length of the cephalothorax (LC) and measured with a caliper under a stereoscopic microscope. The range of size was: juveniles - less than 9 mm, adults - more than 9.1 mm (Collins and Petriella, 1999). The mean size and the standard error of the individuals used were 7.1 ± 0.6 mm to juveniles and 13.1 ± 0.3 mm to adults. Males and females were identified by visualization of the masculine appendix (Bond and Buckup, 1988) and were analyzed together. Only individuals in the intermolt period were used.

The preys used in the experiments were selected according to the forms that represent potential food sources for *M. borellii*, according to previous work (Collins and Paggi, 1998). The cladoceran *Daphnia magna* represent a zooplanktonic organism characterized by a cilindric form and fast swimming; the oligochaete *Limnodrilus udekemianus* is a cilindric prey with scarce movement; and the dipteran larvae *Culex pipiens* are an insect larvae with active movement. The size of prey used in this work was: cladocerans (size: 3.03 ± 0.09 mm); oligochaetes (size: 10.5 ± 0.9 mm) and dipteran larvae (size: 7.26 ± 0.2 mm). Fifteen individuals that represents the size of each prey used in this work were photographed and the total length were obtained with the free morphometric software TpsDig2 (Rohlf, 1997). The prey species were cultived at "Instituto Nacional de Limnología" and were offered only if they were alive.

A total of 3 essays were performed to each prey. The experiment was simultaneous to juveniles and adults. All essays began with 25 juvenile prawns and 30 adults. This number varied because some individuals molted and were not counted in the day's results; another reason for this variation was the feasibility of counting the prey offered (Tab. 1). For example, counting 160 cladocerans to 30 prawns, 4800 in total, is time-consuming and difficult. Therefore, in this type of case, we used 9 juveniles and 10 adults to improve the observing efficiency. The same procedure was

Table 1: Mean values and the standard error of the maximum consumption, volume of prey species offered to *M. borellii* during 24 hours. * This value is overestimated because the juveniles prawn did not eat the entire mosquito larvae.

	Size	*D. magna*	*C. pipiens*	*L. udekemianus*
Number	Juveniles	288 ± 3.6	31 ± 1.1	10.8 ± 0.9
	Adultos	840 ± 16.3	78.6 ± 6.6	36.1 ± 4.4
Volume (mm^3)	Juveniles	144 ± 1.8	39 ± 1.6*	23 ± 1.9
	Adultos	420 ± 8.1	117.9 ± 20.3	70.8 ± 8.6

done with the other prey taking into account the methodological ease of separation and counting each one.

The experiments were performed in containers of 500 ml (at 21°C and a photoperiod of 12:12) where the prawns were placed individually and kept for 24 hours without food. The essays were then started with one type of prey. Firstly, were offered oligochaetes, followed by mosquitoe larvae and cladocerans, respectively, without sequential purpose. After the placement of the prey in each aquarium, the behavior was observed for at least 5 minutes and recorded with a camera (Sony Cyber Shot, 12.1 mpx). Another prawn was placed in a transparent tube and filmed while it ate each prey item. This process was performed to better visualize the *M. borellii* behavior. The prawns were then left, and after 24 hours, the consumption was verified. Those preys that were not consumed were removed and counted, and the prawns were kept in starvation during 24 hours again. After 48 hours (24 hours of consumption and 24 hours of starvation) of the last offer, the amount of the same prey was placed in an increasing number (1:2:5:10:20:40:80:160:320:640:1280). If the offer was entirely consumed for at least one prawn, the experiment was continued. When none of the prawns could consume the total offered, the trial was suspended.

This procedure was not entirely possible for *D. magna* because the counting effort became unfeasible after reaching 640 cladocerans per prawn. For this reason were used 6 juveniles (7.1 ± 0.3 mm of LC) and 5 adults (13.2 ± 0.8 mm of LC) individually separeted in a recipient. To each prawn was offered 200 cladocerans, and after 30 minutes, the total consumption was verified. This amount of prey and time was sufficient to completely fill the prawns´ stomach. The mean value of consumption was then multiplied by the maximum number of trophic cycles (12) that *M. borellii* can have during a day. According to a recent work (Carvalho *et al.*, 2011), the stomach emptying of this prey occurs at approximately the second hour after ingestion, allowing a new trophic event. The estimated result was defined as the maximum consumption in 24 hours. These data were then transformed in volume for all prey using the methodology of approximation to regular geometric shapes or water displacement (Edmondson and Winberg, 1971; Collins, 2000).

The Mann-Whitney test was used to identify differences in the maximum prey consumption between sizes. The statistical tests were conducted with the PAST statistical package (Hammer *et al.*, 2001)

Results

Predatory behavior

Macrobrachium borellii are shown to be a predator capable of preying on organisms of different bioforms and mobility in both sizes analyzed. When the preys were placed in the container, the prawn started the search almost immediately. More mobile prey, like the dipteran larvae and cladocerans, began to escape when they felt the predator's movements. The mosquito larvae hanging at the water surface moved to the bottom. This escape response often resulted in a collision and capture by a prawn. Then the larvae were seized and kept with the second queliped while the first quelipeds and the third maxilipeds settled it with the posterior part of the body into the mouth to be handled with the first and second maxiliped. The capture of cladocerans was made in the water column, and it failed on some occasions due to their fast swimming. However, the handy movement of the second queliped could take the prey and pass it directly to the mouthparts. In the case of oligochaetes, the search was made at the bottom of the aquarium. The prawn was fingering with the second quelipeds until it found the prey and then passed it to the first quelipeds. With the help of the third maxilipeds, the prawn unrolled the oligochaete and ingested it as if it were a noodle. A general characteristic of the capture behavior of all prawns was the search and catch of the prey with the second queliped. The first thoracic appendages, before the second queliped, were more involved in the handling of the prey rather than its capture, whereas the last were most involved in the prawn's locomotion. The visual search of the prey was not evident in *M. borellii*, and it was shown to be nearly tactile after a probable chemical and/or mechanical perception.

Predation capacity

Although both sizes of prawn were capable of catching all prey, the predation capacity increased with size, and it was significantly different between juveniles (7.1 ± 0.3 mm LC) and adults (13.1 ± 0.3 mm LC) for all prey (Mann-Whitney, cladoceran: U = 0, p = 8.1 x 10^{-3}; dipteran larvae: U = 0, p = 6.7 x 10^{-5}; oligochaete: U = 4, p = 3.9 x 10^{-5}). Both sizes consumed the three offered prey with different intensities (Fig. 2). Cladoceran was the most consumed prey in 24 hours, followed by mosquito larvae and oligochaete (Tab. 1). The transformation of the maximum consumption in volume and dry weigth showed the same sequential result (Tab. 1). Although *D. magna* was the prey with the lower volume per individual (0.5 mm^3), compared with *C. pipiens* (1.5 mm^3) and *L. udekemianus* (1.96 mm^3), its consumption values offset the volume. An inverse relation can be established for the other two preys. Is appropriate clarify that the estimated result of maximum consumption of *D. magna* in 24 hours could be overestimated once is considered that the prawn eat every two hours regardless the circadian trophic rhythm.

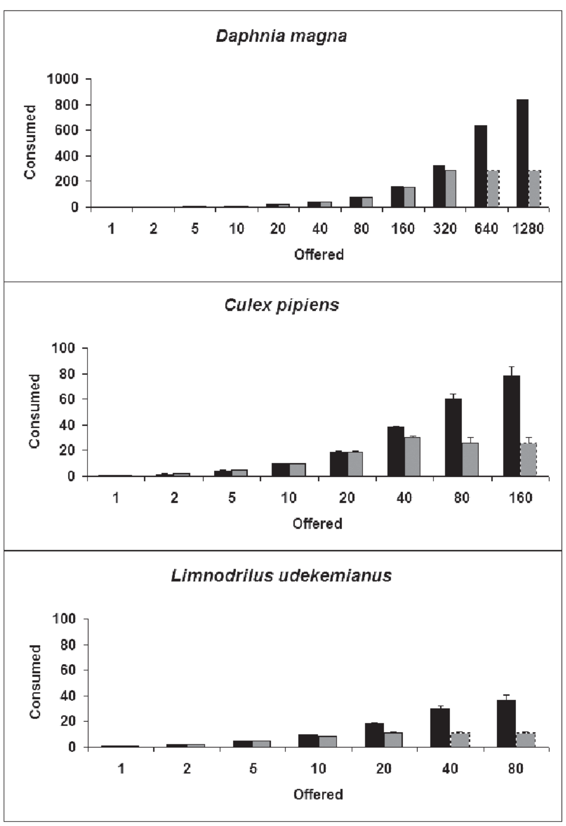

Figure 2: Mean consumption values of three preys in relation to the amount of prey offered during 24 hours. Black columns: adults. Gray columns: juveniles. Dotted lines represent the consumption asymptote. **Note**: The error bar in the figure of *D. magna* prey can not be seen in some values due to a scale problem. The deviation is to low to be seen in the figure size.

An important observation was that the smaller prawns could only eat the abdominal parts of the dipteran larvae. The head and thoracic segments were left almost intact. Both parts of the 13 larvaes were measured, and it was shown that the juvenile prawns (7.1 ± 0.15 mm LC) could not eat the whole mosquito when it had more than 1.13 ± 0.04 mm of thoracic segment. The head had a smaller size than the thorax (0.92 ± 0.01 mm). Therefore, the transformation in volume of the consumed prey, in this particular case, was overestimated due to the inability to ingest the whole larvae body.

Discussion

Macrobrachium borellii has the capacity to prey on a variety of organisms of different bioforms and mobility, both in the adult and juvenile stages. The search for food can be guided through chemical, mechanical and visual cues (Derby *et al.*, 2001; Graso and Basil, 2002). However, the observation of the prawns' behavior indicates that this species may use the first two signals more than the last one. This makes sense if, in its natural environment, the water is usually cloudy. Therefore, the movements of the prey or cues that are released in the water (or even a mix of both) are perceived by the prawn and activate the forage behavior. Then *M. borellii*; with the second pairs of pereiopods, starts a constant groping at the bottom or in the water column to catch its prey.

The prawns' ability to prey on different organisms provides a more plastic diet to this predator and allows it to prey within various zones of a lake. All bioforms represented by the three prey in this work can be distributed in the littoral, pelagic and benthic zones of a lake (zooplankton: Lopretto, 1995; Paggi, 1995; Jose de Paggi, 1995; Battistoni, 1995; Moguilevsky and Whatley, 1995; dipteran larvae: Angrisano and Trémouilles, 1995; oligochaete: Marchese, 2009). In this way, the swimming capacity of *M. borellii* allows its displacement to all of these zones, enabling a wider trophic spectrum. This generalism could favor the ability of the prawn to adjust its trophic circadian rhythm to the changes in the hydric cycle and to the presence of predators and competitors. Although in this work we do not consider the trophic circadian rhythm at the beginning of the essay, prey was available 24 hours and the prawns were able to capture all of them. However, is probable that the consumption was not continuous throughout the day and could be more intense during those periods of more activity.

Both the adults and juveniles demonstrated the ability to prey on all prey types analyzed. The overlap of the trophic spectrum could lead to the overlap of the niche resulting in intraspecific competition. In this way, the population must have mechanisms that allow coexistence. Previous studies have shown that *M. borellii* is a more aggressive predator than sympatric species (Collins, 2005) and even other malacostraceans (Collins, 1998). This aggressiveness also implies predation between individuals of the same species, and this cannibalism is most intense on juveniles (Williner and Collins, 2000). Therefore, it is common to observe the differential use of space by adults and juveniles (Williner and Collins, 2000) and, in this case, the trophic generalism could favor the ability of the smaller individuals to reach the subsequent stages of development.

The predation capacity could be more effective if the predator has a "search-image" of the prey (Ramalho and Anastácio, 2011; Ishii and Shimada, 2010). In this work, all prey represented the natural diet, and the prawn may have come from its environment with this image already formed. However, it is possible that the repeated instances of exposure to the prey helped the prawn consolidate this image and increase its rate of predation. This learning ability could also help the prawn recognize exotic prey after a period of contact. The mussel *Limnoperna fortunei* was introduced in the Paraná System from Asia in 1991 (Pastorino *et al.*, 1993) and is now a potential prey of decapods of the Paraná River (Williner *et al.*, unpublished).

Learning provides an adaptive mechanism for behavioral plasticity (Ishii and Shimada, 2010), but the spatial and temporal variability of prey species requires that the predator forage optimally. To prey on suitable organisms, the prawn should be able to distinguish the prey with the greatest cost-benefit ratio. Collins and Paggi (1998) have already verified that *M. borellii* has a positive selection on oligochaetes and dipteran larvae when they are available. In fact, both prey contain a high proportion of protein (Hepher, 1989), which brings more net energy and decreases vulnerability to predators, making them a more advantageous choice. However, these prey have a lengthy digestion compared with that for cladocerans (Carvalho *et al.*, 2011), which implies that the number of consumed prey will be less within 24 hours. The rates of foregut evacuation are related to the return of appetite (Loya-Javellana *et al.*, 1995; Simon and Jeffs, 2008). Therefore, the high number of preyed cladoceran can be explained by the faster foregut clearance of the prawns (Carvalho *et al.*, 2011).

Macrobrachium borellii is abundant in lentic environments and, due to the high amount of ingested prey per individual by both juveniles and adults, this prawn could regulate the prey population in nature. Although it has not been considered as a biocontrol agent of *Culex pipiens* (Collins, 1998), it is important to recognize that this prawn is an important natural enemy of all of the studied prey. It is obvious that the laboratory experiment does not reflect the total reality of the natural habitat, but it provides accurate information due to the control of some parameters (Pascual and Dunne, 1996). Therefore, this work is important for understanding certain aspects of the predator-prey relationship of *M. borellii*, and it provides a basis for future works related to the ecology of this prawn species.

Acknowledgments

We thank Agencia (PICT 2007 N°01360) for research support and Instituto Nacional de Limnología where this work was conducted.

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Submitted 24 March 2011
Accepted 24 July 2011