

## Research Article

# Feeding ecology of the freshwater crab *Trichodactylus borellianus* (Decapoda: Trichodactylidae) in the floodplain of the Paraná River, southern South America

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**ABSTRACT.** Freshwater crabs are not commonly considered to be an important group in trophic webs, and this might be due to a lack of knowledge about their trophic roles in aquatic ecosystems. *Trichodactylus borellianus* is one of the most common and widely distributed freshwater crabs in the floodplains of the southern South American rivers. The main objective of the present study was to examine the trophic role of *T. borellianus*, in the floodplain of the Paraná River, and its relationships with the freshwater littoral community. The trophic spectrum of this species was characterized for both sexes and individuals of different sizes (adults and juveniles), throughout daily and seasonal cycles. Samples were collected from the aquatic vegetation of three shallow lakes. The diet composition and the feeding activity of *T. borellianus* were evaluated through the examination of the stomach contents and their degree of emptiness. This crab species consumed several plant and animal items, including amoebas, rotifers, oligochaetes, copepods, cladocerans, and insect larvae. Moreover, this species consumes filamentous and unicellular algae, diatoms, fungi, and macrophytic remains. The predatory habits varied with the season and time of day, and variations in the feeding activity of the juveniles and adults were detected and documented. The diversity of food items eaten by this crab suggests that its trophic role in the community as an omnivore and opportunistic predator provides a connection among several trophic levels from both aquatic and terrestrial communities.

**Keywords:** omnivore, trophic habits, stomach contents, detritus, macro-invertebrates.

## Ecología trófica del cangrejo dulceacuícola *Trichodactylus borellianus* (Decapoda: Trichodactylidae) en el valle de inundación del río Paraná, sur de Sudamérica

**RESUMEN.** Los cangrejos de agua dulce no son comúnmente considerados como un grupo importante en las redes tróficas, y esto podría ser debido a falta de conocimiento acerca de sus funciones tróficas en los ecosistemas acuáticos. *Trichodactylus borellianus* es uno de los cangrejos de agua dulce más comunes y ampliamente distribuido en llanuras de inundación del los ríos del sur de Sudamérica. El objetivo principal del presente estudio fue examinar el rol trófico de *T. borellianus* en la llanura de inundación del río de Paraná, y sus relaciones con la comunidad litoral de agua dulce. El espectro trófico de esta especie se caracterizó en ambos sexos e individuos de diferentes tamaños (adultos y juveniles), a través de los ciclos diarios y estacionales. Se tomaron muestras en la vegetación acuática de tres lagunas diferentes. La composición de la dieta y la actividad de alimentación de *T. borellianus* fueron evaluados mediante la observación de contenidos estomacales y grado de repleción. Esta especie consume plantas y animales, incluyendo amebas, rotíferos, oligoquetos, copépodos, cladóceros y larvas de insectos. Además, consume algas filamentosas y unicelulares, diatomeas, hongos y restos de macrófitas. Los hábitos de consumo variaron entre estaciones del año y según la hora del día. Las variaciones en la actividad trófica de juveniles y adultos fueron documentadas y analizadas. La diversidad de alimentos consumidos por este cangrejo sugiere que su rol trófico en la comunidad como un omnívoro y depredador oportunista, provee una conexión entre varios niveles tróficos de ambas comunidades, acuáticas y terrestres.

**Palabras clave:** omnivoría, hábitos tróficos, contenido estomacal, detrito, macroinvertebrados.

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## INTRODUCTION

Trophic webs are considered some of the main forces that structure aquatic communities (Pascual & Dunne, 2006). Moreover, studies of the feeding ecology of animals contribute to the knowledge of the nutritional requirements of species, interactions with other organisms, and community organization patterns over evolutionary time (Lampert *et al.*, 1992). According to previous studies, freshwater communities are complex assemblages influenced by the interactions and dynamics among the food web components (Kerfoot & DeMott, 1984). In such an habitat, assessing diversity is one possible way to analyze the condition of an environment. However, recent studies have utilized another method to evaluate this. Indeed, data on ecological interactions and functions of the species are considered as an alternative measurement for ecosystem studies (Woodward *et al.*, 2005; Woodward, 2009). Fulton *et al.* (2003), noted that information on predation is a crucial tool for modelling an ecosystem-level analysis because this parameter shows the direction of the flow of matter and energy that determines the organization of communities.

In the floodplain of the Paraná River, South America, aquatic vegetation is generally responsible for the coverage in shallow-lakes, and it is an important determinant of the physical and chemical properties of the water as well as the structuring of the littoral communities, providing potential food sites and shelter for organisms (Chen & Barko, 1988; Jeppesen *et al.*, 1998; Poi de Neiff & Neiff, 2006). Due to their abundance, freshwater decapods are an important zoological group in these littoral environments (Collins *et al.*, 2007); knowledge of the natural diet of macro crustaceans is one of the necessary factors for the understanding of trophic interactions.

*Trichodactylus borellianus* is common in freshwater littoral communities and has a wide latitudinal distribution; this species extends from the Amazonas to Paraguay and the Paraná Basins in the south (0°-35°S) (Lopretto, 1995; Magalhães & Türkay, 1996; Magalhães, 2003, Collins *et al.*, 2006a). In addition, *T. borellianus* is part of the diet of many fish, amphibians, birds, and mammals (Bonetto *et al.*, 1963; Cabrera *et al.*, 1973; Massoia, 1976; Oliva *et al.*, 1981; Beltzer, 1983, 1984; Beltzer & Paporello, 1984; Bianchini & Delupi, 1987; Lajmanovich &

Beltzer, 1993; Lajmanovich *et al.*, 2005). Based on this information, the macro crustacean fauna can be considered as an important connector of matter and energy of the aquatic environment, aquatic-terrestrial transition zone (ATTZ) and terrestrial environment. Accordingly, it is necessary to generate information describing the early stage of these trophic connections, with one option being an analysis of the diet of this species.

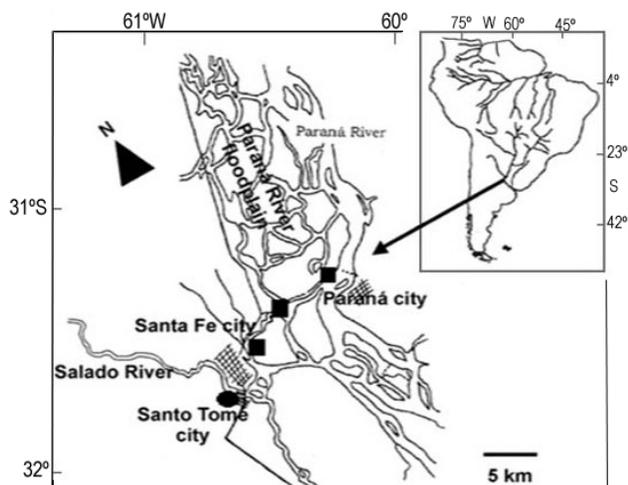
However, information on the biology and ecology of *T. borellianus* remains scarce (Magalhães, 2003). Therefore, this study focused on both the natural diet of *T. borellianus* with regard to variations over time, and the role of this crab in littoral freshwater communities. The main objective of this study was to evaluate the feeding activity of male and female and different-sized (adults and juveniles) *T. borellianus*, both daily and seasonally.

## MATERIALS AND METHODS

### Study area

This study was conducted in the Paraná River and its floodplain. This river is the largest channel of the La Plata Basin and southern South America, and contains 85% of the total freshwater in Argentina. The river is located within an alluvial valley that ranges from approximately 13 to 56 km in width, with a slope of 0.036 m km<sup>-1</sup>. In the study area, the main channel is located on the eastern margin and varies in width between 2 and 4.2 km (Paoli *et al.*, 2000). The western area of the river has several islands, secondary rivers, streams, and shallow lakes (Fig. 1).

Water runoff causes annual flooding during the spring and summer, whereas low flow occurs in the autumn and winter (Bonetto & Wais, 1995). The flood pulse of the Paraná River is one of the most dominant environmental factors which can change the chemical and physical conditions of the floodplain, and affect the crustacean populations (Collins *et al.*, 2006a, 2006b; Depetris & Pasquini, 2007). The littoral zones have free-floating and emergent macrophytes (*Eichhornia crassipes*) covering extensive areas. Other abundant aquatic plants are floating or emerging species, such as *Ludwigia peploides*, *Paspalum repens*, and *Salvinia herzogii* (Sabattini & Lallana, 2007).



**Figure 1.** Study area floodplain of Paraná River (Argentina) with the sites for seasonal (■) and circadian analyses (●).

### Crab collection and gut content analysis

To analyse the trophic spectrum of *Trichodactylus borellianus*, three selected ponds were sampled in four seasons (Fig. 1). Using a hand net (area of 0.9 m<sup>2</sup>, with a mesh size of 1 mm), three random points were sampled below the aquatic vegetation at each site (Williner & Collins, 2002). The assembly of macrophytes was the same at all sampling sites, and were mainly characterized by floating vegetation. The temperature, pH, conductivity, and dissolved oxygen were measured at each site. The river level was registered using a limnigraph in the Santa Fe Port.

A circadian activity analysis was conducted at a single sampling point in autumn. Specimens of *T. borellianus* were collected under the shoreline littoral vegetation. The crabs were collected using a 2 m<sup>2</sup> mouthed trawl, with a 1 mm mesh size net, on three days in the morning (9–10 am) and evening (6–7 pm), and the capture effort was kept constant. Immediately after being captured, the crabs were anesthetized by cooling, and preserved in 75% ethanol. This method of preserving the stomach contents has been used in previous studies (Abelló, 1989; Chande & Mgaya, 2004; Collins *et al.*, 2006b). The stomach contents were quickly removed, fixed, and stained with erythrosine to avoid the negative effect of digestion after the death of the organism.

The specimens of *T. borellianus* were classified as adult male, adult female, or juvenile according to their abdominal characteristics (Lopretto, 1976). The carapace width (CW), the distance between the two first spines next to the eyes, was measured to the

nearest 0.1 mm using a calliper under a stereomicroscope.

The relative degree of stomach fullness was determined immediately after removing the stomach from the crabs. Each foregut was visually assessed by a subjective scale ranked from 0 (empty) to 5 (full) (Collins & Paggi, 1998); this visual assessment was possible because the stomach of *T. borellianus* is a thin-walled, translucent organ. After this analysis, the entire stomach content was mounted on a slide on a drop of glycerol (50%). The stomach contents were then examined, using a stereomicroscope, and the food items were measured, counted at 150x–600x resolution power, and classified into the lowest possible taxonomic group. We searched for the presence of intact or empty filaments and for isolated cells to identify different groups of algae. Diatoms were recognised by their frustules, whereas the presence of small fragments of leaves was useful in detecting macrophytic remains. Fungi were recognised by the presence of hyphae, and amoebas were determined by shells or shell fragments. Oligochaetes were recognised by their setae. Cladocerans were identified by their carapace remains, post abdomens, antennae, and spines; copepods were recognised by their appendages. Chironomids were identified by their head capsules, antennae, mandibles, ligula, paraglossa, and posterior regions. Material in decomposition was included in a category entitled "detritus," but this material was not quantified.

The minimum number of crab stomachs needed for the analysis of the trophic diversity for each sampling period was determined by the Chao estimation of species richness (Colwell, 2006), and the means of the accumulative Shannon-Weaver function (Krebs, 1996). The diversity index was calculated after observing the contents of each stomach. Thus, a cumulative diversity curve was constructed to determine the minimum number of stomachs required to ensure the representativeness of the sample.

The dietary patterns of *T. borellianus* were analysed using the Weighted Result Index (Rw) (Mohan & Sankaran, 1988), applying the following formula:

$$Rw = \frac{Q \sqrt{(vi^2 + oi^2)}}{\Phi Q \sqrt{(vi^2 + oi^2)}} \cdot 100$$

where  $v$  is the volume percentage of food items and  $o$  is the percentage of occurrence in the stomach contents of each crab.  $Q$  takes into account the deviation of  $\Phi$  from the mean. The food items were ranked in their order of importance using the following formula:

$$Q = \frac{(45 - |\Phi - 45|)}{45}$$

The value  $\Phi$  was calculated as  $\tan^{-1} \frac{oi}{vi}$ .

The volume of the food items was calculated by an approximation to geometrical shapes using the size of the items preyed upon from direct measurements and/or data in the literature (Edmonson & Weinberg, 1971; Dumont *et al.*, 1975; Ruttner-Kolisko, 1977). A graphical representation of  $R_w$  index helped to elucidate the relative contribution of the occurrence or volume of every food item present in the stomach contents. The index values allow comparisons among the items following their order of importance (Mohan & Sankaran, 1988). When the value of  $\Phi$  ranged from 0 to 45, the food item comprised much of the volume of the sample; in contrast, when the value of  $\Phi$  ranged from 45 to 90, the food item occurred more frequently in the sample.

### Statistical analysis

The normality and homoscedasticity of the data were examined prior to performing statistical tests. The differences in the crab size among the seasons were analysed using a one-way analysis of variance (ANOVA) test, and the circadian samples were analysed using Student's t-test. The detected differences were tested using the post-hoc Bonferroni test. Comparisons of sex ratio deviations from the expected 1:1 rate were determined using the Chi-square test at a 95% significance level (Zar, 1996).

The distribution resulting from the degree of stomach fullness was compared between juveniles and adults; the degree of stomach fullness was also compared between seasons and circadian samples, using the Wilcoxon and Kruskal-Wallis test. The coefficient of correlation was applied to evaluate the feeding differences among size classes. The significance of the Weighted Result Index was tested among samples, using an adaptation of the Student t-test, with the value of the tangent used for the comparison (Zar, 1996).

## RESULTS

### Environmental conditions

All of the sampling sites showed aquatic vegetation, including *Eichhornia crassipes*, *E. azurea* (85% approximately), and *Salvinia* sp. (7%), with the remainder represented by *Limnobium* sp., *Azolla* sp., *Pistia* sp., *Ludwigia* sp., *Paspalum repens*, and *Hydrocotyle ranunculoides*. The observed seasonal fluctuations in the floodplain water level (1.3 to 4.4 m)

and temperature (4°C to 43.4°C) corresponded to the natural cycle. The conductivity oscillated between 90  $\mu\text{S cm}^{-1}$  (*e.g.*, the environments of the Paraná River floodplain) and 3,000  $\mu\text{S cm}^{-1}$  (*e.g.*, the environments near the Salado River). The pH ( $7.4 \pm 0.102$  SD) and dissolved oxygen ( $7.23 \pm 0.544$  mg L<sup>-1</sup>SD) showed relatively constant values over time and were similar among the sites.

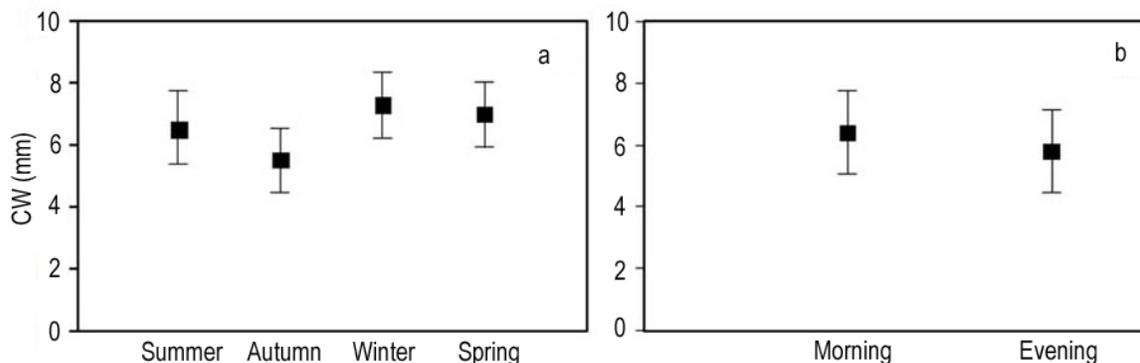
### Characterization of crab populations

Of the 695 crabs sampled during the study, 142 random specimens (55 males, 59 females, and 28 juveniles), were used to analyze the feeding habits. A total of 80 crabs were subsampled to observe the stomach contents for each season (20 for each one), and 62 crabs were evaluated to reveal the circadian differences in the diet (27 in the morning and 35 in the evening). These numbers were derived from the implementation of the diversity index for each stomach, and a cumulative diversity curve was generated to determine the minimum number necessary to analyze. To ensure the representativeness of the results, the quantity of observed stomachs was two times more than those given by the cumulative diversity curve. The carapace width of all of the organisms collected ranged from 2.5-11.3 mm (Fig. 2). The size of the crabs differed between autumn and the other seasons (one-way ANOVA<sub>(3; 79)</sub>: 3.13;  $P = 0.036$ ) in that smaller specimens were common in autumn. However, the size of the specimen did not differ according to the time of day (Test  $t_{(2; 61)}$ : 0.47;  $P = 0.496$ ) or sex (Test  $t_{(2; 113)}$ : 0.15;  $P = 0.700$ ). Moreover, the number of males and females was similar during the day (Chi-square test  $\chi^2_{(2; 2)}$ : 1,  $P = 1$ ) and throughout the seasons (Chi-square test  $\chi^2_{(2; 4)}$ : 1.3,  $P = 0.779$ ).

### Trophic spectrum

The spectrum of food items consumed by *T. borellianus* was wide, consisting of many plant and animal items (Table 1), and with high  $R_w$  values for oligochaetes, insects, and chironomid larvae (Fig. 3). For certain food items (*e.g.*, plant remains, cladocerans, copepods, amoebas) the  $R_w$  index indicated significant differences across the seasons and times of day (morning and evening) (Fig. 3). However, differences between males and females were not observed.

When the food items were correlated with the size of the crabs (adults and juveniles), a trend in the feeding behaviour was observed (Fig. 4). Plant remains, amoebas, and insect larvae were mainly preyed upon by larger individuals (6 to 10 mm of carapace width), whereas filamentous algae, unice-



**Figure 2.** a) Size frequency of *Trichodactylus borellianus* samples from seasonal, and b) circadian analyses.

llular algae, chironomid larvae, and fungi were mostly consumed by the small individuals (less than 6 mm of carapace width). Other items, such as allochthonous arachnids and ants, occurred sporadically along the food spectrum of *T. borellianus*.

### Feeding activity

The stomachs were analysed according to a fullness index, which indicated variations in the feeding activity of the crabs throughout the year (Fig. 5). Lower values were recorded in winter, and higher values were found in spring (Kruskal-Wallis test,  $H = 8.30$ ;  $P = 0.0403$ ). Moreover, differences existed between morning and evening periods (Wilcoxon test,  $W = 2.20$ ;  $P = 0.0001$ ) (Fig. 5): in the evening, adult crabs had higher values of stomach fullness than juveniles. In addition, the stomach fullness of adults differed significantly between morning and evening (Wilcoxon test  $W = 2.02$ ;  $P = 0.0005$ ), whereas the stomach fullness of juveniles did not (Wilcoxon test,  $W = 1.15$ ;  $P = 0.1390$ ).

The minimum number of stomachs necessary for the analysis was different throughout the seasons and the two daily sampling times: more stomachs needed to be collected in the spring and evening than in the winter and morning (Fig. 6). According to the Shannon-Weaver function ( $H'$ ), the trophic diversity of the stomach contents was higher in the evening ( $H' = 0.93$ ) than in the morning ( $H' = 0.76$ ). However, there were no significant differences (Test  $t_{(2; 258)}$ :  $0.15$ ,  $P = 0.8822$ ) between the index values among the stomachs sampled in the morning and evening. According to the Shannon index, it was necessary to analyze at least eight stomachs from the morning collection, whereas a minimum of twelve was required for the evening. The Chao estimate indicated that between 9 and 13 stomach observations were required for the seasonal samples (Fig. 6).

### DISCUSSION

The wide spectrum of food items found in the stomach of *T. borellianus* indicates that this crab acts as an omnivorous and opportunistic predator. Crabs of both sexes prey mainly upon animals that move slowly, such as oligochaetes, chironomids, and other insect larvae. Indeed, preying on evasive, slow-moving prey could be a way to optimise the energy expended in capturing food (Collins & Paggi, 1998). Among these prey, the oligochaete plays an important role in the diet of crabs, as it does in others animals, due to its high protein content (50% of their dry weight) (Popchenko, 1971; Ciancio *et al.*, 2007).

We were interested in the nutritional value of the macrophytic remains, which are an important item in the floodplains of large rivers. Mattson (1980) stated that energy would be more readily available from plant matter than from animal matter, even though the former has a lower content of nitrogen (*e.g.*, aquatic macrophytes may contain 0.9-4% of their dry weight) (Karasov & Martinez del Rio, 2007). The nitrogen content can vary among the plant species throughout seasons and ontogenetic development. The high value of the Weighted Result Index might indicate that *T. borellianus* eats much volume of macrophytes to obtain a sufficient nutritional quality. From an evolutionary viewpoint, plant consumers have developed many solutions to the problem of nitrogen shortage. Crustaceans have evolved to host certain endosymbiotic organisms in their digestive tracts (Zimmer *et al.*, 2001). Additionally, some crabs could have consumed individuals capable of metabolising cellulose, as reported for the shrimp *Palaemonetes pugio* and freshwater crab *Aegla uruguayana*, which assimilates cellulose from plant stems and algae (Devercelli & Williner, 2006). Nevertheless, the energy from plant consumption can vary according to

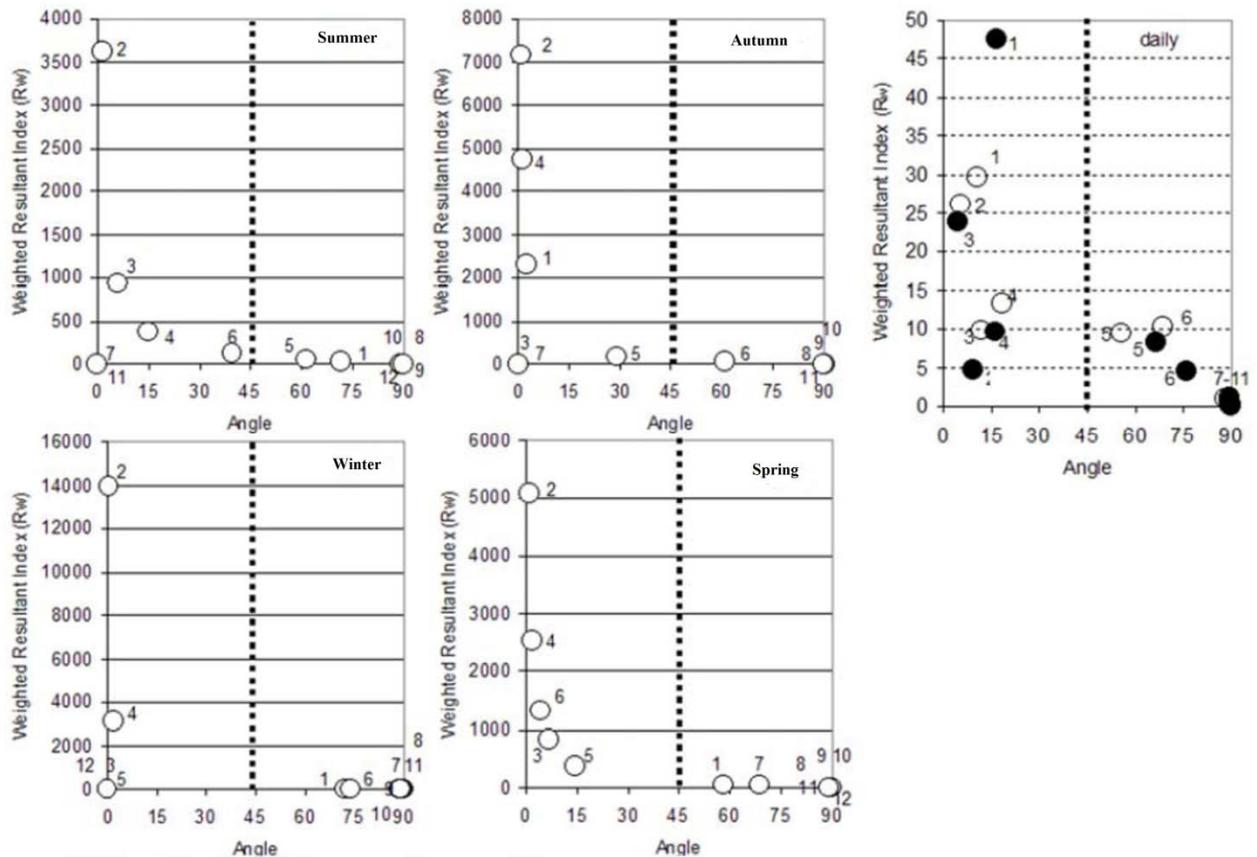
**Table 1.** List of food items recorded in the stomach contents of *Trichodactylus borellianus* from the floodplain of Paraná River, Argentina, with a comparison of the Weighted Result index calculated on the elements eaten by specimens sampled in the morning and evening.  $S = RW_{\text{morning}} - RW_{\text{evening}}$ ;  $df = \text{degrees of freedom}$ ;  $T'S = RW_{\text{morning}} \cdot RW_{\text{evening}}$ ; \* statistical difference between Weighted Result Index from morning and evening samples; + not quantified.

Food Items	S	df	T'S	P	Food Items	S	df	T'S	P
Algae					Protozoa	0.047	51	3.75*	0.01
Unicellular algae	0.002	62	-0.58	0.21	Rhizopoda				
Desmidiaceae					<i>Centropyxis</i> sp.				
<i>Triploceras</i> sp.					<i>Diffflugia</i> sp.				
<i>Desmidium</i> sp.					Rotifera	0.015	56	-0.62	0.32
<i>Closterium</i> sp.					Ord. Ploima				
Filamentous algae	0.015	51	1.20	0,09	Brachionidae				
Nostocaceae					<i>Brachionus</i> sp.				
<i>Nodularia</i> sp.					Notommatidae				
<i>Nostoc</i> sp.					<i>Cephalodella</i> sp.				
Charaphyceae					Ord. Bdelloideo				
<i>Chaetophora</i> sp.					Not identified				
Ulotricophyceae					Oligochaeta	0.164	54	-130.64*	0.00000006
<i>Basicladia</i> sp.					Not identified				
<i>Oedogonium</i> sp.					Hirudinea				
<i>Bulbochaeta</i> sp.					<i>Helobdella</i> sp.				
Xantophyceae					Copepoda	0.121	62	-47.03*	0.0003
<i>Tribonema</i> sp.					Calanoida				
Rivulariaceae					Cyclopoida				
<i>Rivularia</i> sp.					<i>Macrocyclops</i> sp.				
Euchlorophyceae					Cladocera	0.138	56	-8.18*	0.005
<i>Cladophora</i> sp.					Chydoridae				
<i>Rizoclonium</i> sp.					<i>Moina</i> sp.				
Bacillariophyceae	0.006	39	-6.36*	0.008	Arachnida (terrestrial)+				
<i>Cyclotella</i> sp.					Insecta (aquatic larvae)				
<i>Bacillaria</i> sp.					Diptera				
<i>Nitzschia</i> sp.					Chironomidae	0.197	40	70.59*	0.000005
<i>Navicula</i> sp.					<i>Chironomus</i> sp.				
<i>Chaetoceros</i> sp.					<i>Larissa</i> sp.				
Macrophyte Remains	0.286	47	62.63*	0.0000001	Other insects (not identified)	0.154	59	-23,91*	0.0047
Fungi					Ephemeroptera				
Hyphomycetes					Tricoptera				
Ditritus +					ANTS +				

the presence of bacteria in the gut (Foulds & Mann, 1978; Morgan, 1980; Fleeger *et al.*, 1999). However, decapods might also decompose cellulose in their hepatopancreatic cells, similar to the process in crayfish (Brown, 1995). In *Cherax quadricarinatus*, a functional endoglucanase indicates that cellulose substrates can be a source of energy for this species (Crawford *et al.*, 2004). In addition, as plant debris

decomposes, the material contains greater amounts of associated microorganisms, such as bacteria and fungi, providing improved nutritional quality (Nordhaus *et al.*, 2006; Linton & Greenaway, 2007).

The microalgae ingested by *T. borellianus* may be associated with sediment or other substrates because the algae identified were mainly periphytic and benthic algae (Vélez & Maidana, 1995). Their



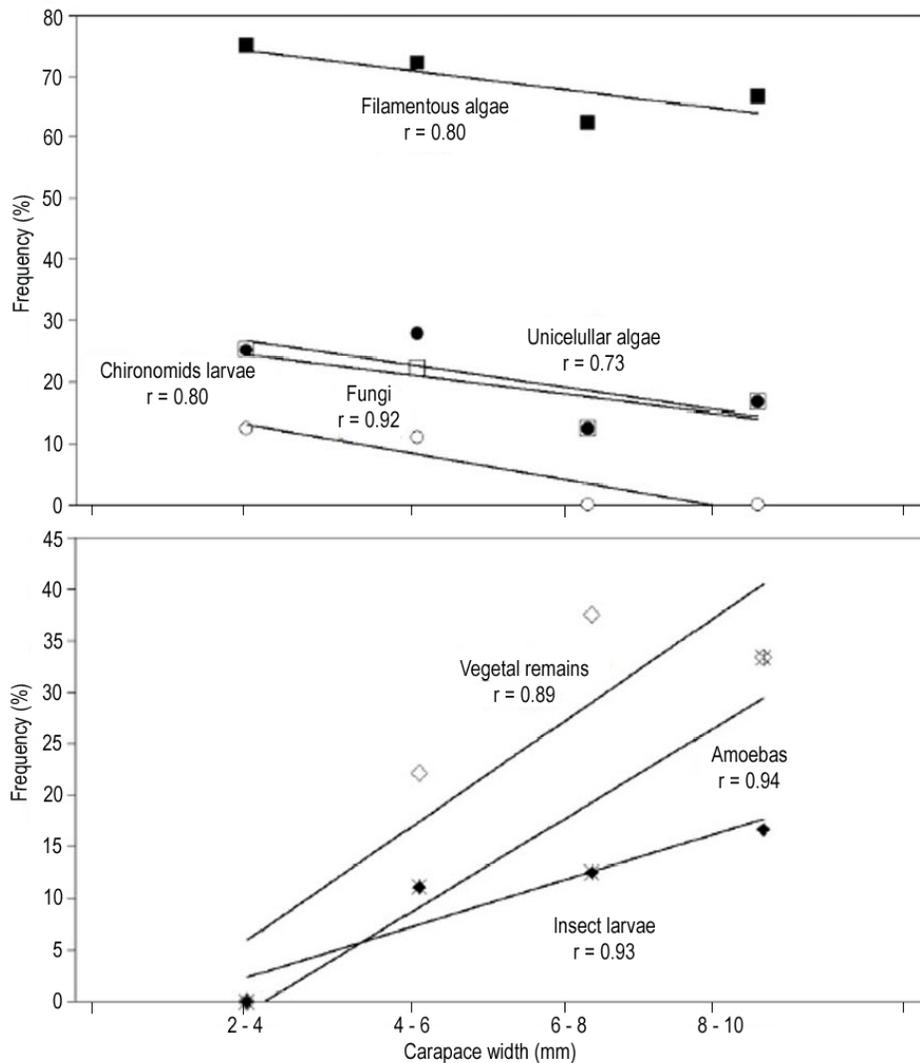
**Figure 3.** Weighted result index (RW) of food items from the stomach content of *Trichodactylus borellianus* according to the angle of preponderance from season and circadian samples. 1. Plant Remains, 2. Oligochaetes, 3. Chironomid larvae, 4. Insect larvae, 5. Cladocerans, 6. Copepods, 7. Amoebas, 8. Rotifers, 9. Filamentous algae, 10. Unicellular algae, 11. Diatoms, 12. Fungi. ● Morning, ○ Evening.

ingestion might indirectly occur while the crabs are cropping plant remains or other items. Furthermore, the zooplankton consumed by *T. borellianus* confirms that the studied community belongs to the littoral-benthic community. Chironomid cladocerans are organisms that climb on the substrate or riparian vegetation. Within the rotifer population, *Brachionus* spp. comprises some species occupying littoral habits, whereas *Cephalodella* sp. is a benthic species (José de Paggi & Paggi, 2007).

Although our results could be masked by the residence time of the food items in the stomach, it is possible to assume that the diet composition could not be influenced by this phenomenon. In the shrimp *Palaemonetes argentinus*, another member of the fauna of the Parana River, the mean residence time of the stomach contents was 9 h (Giri *et al.*, 2002), and the total time required for the stomach of *Jasus edwardsii* to empty was 10 h (Simon & Jeffs, 2008). The time required in crabs might be less due to the higher number of sclerotic structures in the stomach (Icely & Nott, 1992).

### Feeding activity

Differences in the trophic activity between juvenile and adult crabs would indicate some type of temporal segregation brought about to avoid competition; this is caused by aggressive interactions in other decapods, particularly when food or shelter is scarce or unavailable (Lodge & Hill, 1994). These patterns could suggest that *T. borellianus* adults feed on the surface of macrophytes, whereas the juveniles prey mainly at the bottom of the shoreline. Smaller specimens search for food at the bottom of the littoral zone. This pattern was evident in the differences in the diet spectrum (Fig. 4). Other authors have similarly suggested that the trophic habits of decapods change with the ontogenetic stages. In marine crabs, adults of *Callinectes ornatus* consumed more plants, crustaceans, and fish than juveniles (Mantelatto & Christofolletti, 2001). In the floodplain of the Paraná River, juveniles of *Palaemonetes argentinus* feed only on algae and plant remains, whereas adults have a greater feeding item diversity (Collins, 1999).

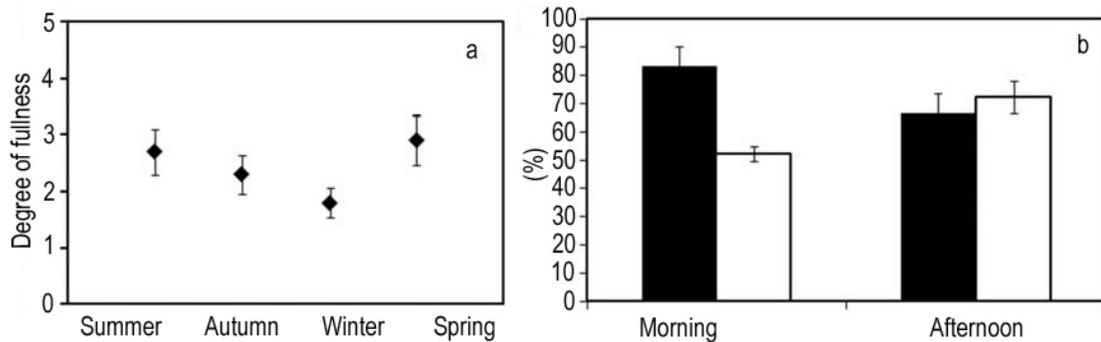


**Figure 4.** Variations in frequency percentage of main preyed items as a function of size of *Trichodactylus borellianus* ( $r$ : correlation coefficient,  $n$ : 462). ◇ Plant remains, \* Amoebas, ◆ Insect larvae, ■ Filamentous Algae, ● Unicellular algae, □ Chironomid larvae, ○ Fungi).

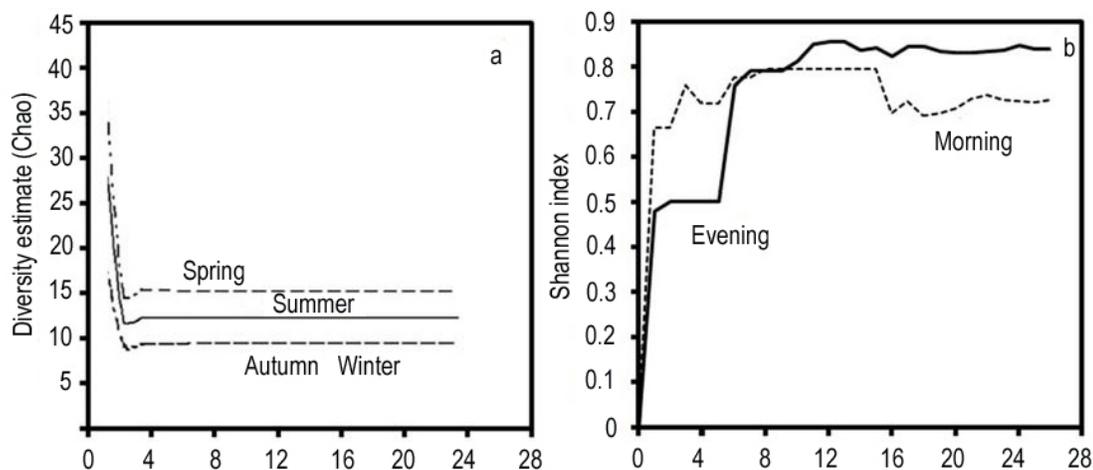
Fungal consumption was mainly associated with small crabs, and less consumption was observed in large individuals. However, the incorporation of detritus may be due to the inability of small crabs to crush their prey, possibly as a result of less mouthpart calcification, thus restricting their ability to capture, cut, manipulate, and digest food. Furthermore, crabs that were larger in size were found to have a greater quantity of plant remains in their stomachs. Therefore, it appears that adult specimens may eat macrophytes more frequently than young crabs (Collins, 1999). Similar ontogenetic differences in dietary habits have been found in species with larval stages, and the morphological changes during ontogeny lead to the differential exploration of habitats and food sources (Lumasag *et al.*, 2007).

Differences in the diet composition among the size classes of *T. borellianus* might be explained by changes in the hardening and degree of calcification of the gastric mills, feeding appendages, endosymbiotic diversity, and/or time of endosymbiotic development in the stomach and gut (Caine, 1975; Kunze & Anderson, 1979; Factor, 1989; Zimmer & Topp, 1997, 1998). Although larger crabs tended to consume less algae, this behaviour was not shown to be significant in this study; however, this behaviour may reflect some differences among size classes in their preference for certain foods and their ability to detect and capture these foods.

*Trichodactylus borellianus* consumed autochthonous and allochthonous material from the aquatic environment. Terrestrial ants and arachnids may be



**Figure 5.** a) Degree of stomach repletion of stomachs of *Trichodactylus borellianus* from seasonal samples (means and standard deviation), b) Fullness index (%) values of juveniles (black columns) and adults (white columns) from morning and evening samples. Bars represent standard deviation.



**Figure 6.** a) Chao estimation of species richness to determine the minimum number of stomach observations of *Trichodactylus borellianus* in each season, b) Shannon-Weaver trophic diversity index from morning and evening samples.

considered an important material from neighbouring habitats because they were consumed and, thereby, incorporated into the food web. Woodward & Hildrew (2002) suggested that the magnitude of external contributions to the feeding preferences of the consumers may influence the stability of food webs. Because of its polytrophic habits, *T. borellianus* could function as an energetic transformer at several trophic levels throughout the year.

Our results were similar to those obtained from the analysis of the natural diets of the sympatric Neotropical crab, *Dilocarcinus pagei* (Williner & Collins, 2002). Other decapods, such as *Macrobrachium borellii* and *Palaemonetes argentinus*, have demonstrated similar roles in the trophic web of the Río de La Plata system, by being important energy carriers from the bottom to the top levels of the web (Collins & Paggi, 1998; Collins, 1999; Collins *et al.*, 2007). As generalists, decapods can increase the

pathways within the food web, improving their stability (Woodward & Hildrew, 2002) and the connections between different communities (Collins *et al.*, 2006b). Moreover, similar to other decapods in the floodplains of rivers with abundant aquatic vegetation, this species could be the transformer of the abundant vegetation that develops in these environments because *T. borellianus* consumes this production using alternative methods. Based on this characterisation of omnivory, it must be emphasised that these crabs would cross the trophic relationships, thus promoting the stability and complexity of the system (Diehl, 2003; Eubanks *et al.*, 2003; Krivan & Diehl, 2005; Thompson *et al.*, 2009).

Although there are still large gaps in our knowledge of many aspects of the Neotropical decapod fauna, such as the predator-prey relationships, digestion mechanisms, and nutrient absorption, this study constitutes a step toward a better understanding

of the trophic relationships of the littoral aquatic communities in the Río de La Plata System.

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