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Feeding spectra and activity of the freshwater crab *Trichodactylus kensleyi* (Decapoda: Brachyura: Trichodactylidae) at La Plata basin

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Abstract

Background: In inland water systems, it is important to characterize the trophic links in order to identify the 'trophic species' and, from the studies of functional diversity, understand the dynamics of matter and energy in these environments. The aim of this study is to analyze the natural diet of *Trichodactylus kensleyi* of subtropical rainforest streams and corroborate the temporal variation in the trophic activity during day hours.

Results: A total of 15 major taxonomic groups were recognized in gut contents. The index of relative importance identified the following main prey items in decreasing order of importance: vegetal remains, oligochaetes, chironomid larvae, and algae. A significant difference was found in the amount of full stomachs during day hours showing a less trophic activity at midday and afternoon. The index of relative importance values evidenced the consumption of different prey according to day moments. Results of the gut content indicate that *T. kensleyi* is an omnivorous crab like other trichodactylid species. Opportunistic behavior is revealed by the ingestion of organisms abundant in streams such as oligochaetes and chironomid larvae. The consumption of allochthonous plant debris shows the importance of this crab as shredder in subtropical streams. However, the effective assimilation of plant matter is yet unknown in trichodactylid crabs.

Conclusions: This research provides knowledge that complements previous studies about trophic relationships of trichodactylid crabs and supported the importance of *T. kensleyi* in the transference of energy and matter from benthic community and riparian sources to superior trophic levels using both macro- and microfauna.

Keywords: Decapoda; Omnivorous crab; Shredder; Subtropical forest; Streams

Background

The trophic ecology of brachyuran crabs has been widely studied in marine crabs probably because of their ecological and economic importance (Wear and Haddon 1987; Freire 1996; Cannicci et al. 1996; Mantelatto and Petracco 1997; Balasubramanian and Suseelan 1998; Frick et al. 2001; Mantelatto and Christofeletti 2001; Josileen 2011). However, among freshwater crabs, the research effort in this area is more recent with little emphasis in trichodactylid crabs (Collins et al. 2007; Carvalho et al. 2013a; Williner and Collins 2013; Pirela

and Rincón 2013). Knowledge about trophic ecology aspects of any species is essential to understand the nutritional requirements and how species interact with the environment and with other organisms. In inland water systems, it is important to characterize the trophic links in order to identify the 'trophic species' and, from the studies of functional diversity, understand the dynamics of matter and energy in these environments (Woodward 2009).

Trichodactylidae is a family of crabs associated to river basins of Center and South America with exception of the Pacific slope rivers (Magalhães 2003; César et al. 2004). The genus *Trichodactylus* is composed of nine species in the Neotropical region of which almost 50% inhabits aquatic environments of Argentina. Among these species, *Trichodactylus kensleyi* has a geographical distribution associated to the Paraná and

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Uruguay Rivers and restricted to the subtropical forest of Argentina, Paraguay, Brazil, and Uruguay (Magalhães 2003). Capture records of this freshwater crab in Argentina range from 200 to 600 m above sea level in streams of subtropical rainforest, where they can be trapped in the bottom under rocks, clay, and sand (Collins 2005).

Trophic ecology studies (e.g., behavior, feeding habits) on trichodactylid crabs in Argentina have reported a variety of aquatic environments (e.g., in subtropical savannah and alluvial valley of temperate rivers) and feeding habits (Williner and Collins 2002; Collins et al. 2006; Collins et al. 2007; Williner and Collins 2013; Carvalho et al. 2013a, 2013b). In general, these crustaceans are omnivorous with a wide trophic spectrum that ranges from algae and plant remains to insect larvae and even vertebrates (Collins et al. 2006). In this way, they can play a functional role as shredders and predators. On the other hand, they are prey of many vertebrates like fishes, amphibians, reptiles, birds, and mammals (Bonetto et al. 1963; Beltzer 1983; 1984; Beltzer and Paporello 1984; Lajmanovich and Beltzer 1993; Massoia 1976; Bianchini and Delupi 1993; López et al. 2005), emphasizing the importance of this species in aquatic systems.

Despite the ecological significance of trichodactylid crabs, there are little information about the biology and ecology of some species such as *T. kensleyi*. This endemic distribution and the progressive habitat modification where they occur make any research about this decapod important. Considering this background, the aim of this study is to analyze the natural diet of *T. kensleyi* of subtropical rainforest streams and verify the daily variation in the feeding activity during light hours.

Methods

Study area

The study was conducted in the subtropical rainforest of southern South America (Misiones Province, Argentina), in streams with drainage to the Uruguay and Paraná Rivers such as Zamambay, El Trébol, Cuña Pirú, and Yaguarundí streams (Figure 1). This area covers the subregion of Paranaense forest and is characterized by great biological diversity, unique in southern South America (Myers et al. 2000). It is located in the upper zone of the Paraná basin. In the west, it is limited by the Paraná River, in the east by the Uruguay, San Antonio, and Pepirí Guazú Rivers, and in the north by the Iguazú River (Figure 1). This region has a subtropical climate without drought season with an annual rainfall between 1,600 and 2,000 mm and an annual average temperature of 20°C. Environmental oscillations are mainly related to the rainfall regime. The so-called gallery forest bordered the streams' shoreline with dominance of hydrophilic vegetation. The streams of sampling are shallow, have high transparency and water velocity, and have scarce submerged vegetation, and the

bottom is composed of clay, sand, and rocks. The input of organic matter in these streams mainly comes from allochthonous source.

Field sampling

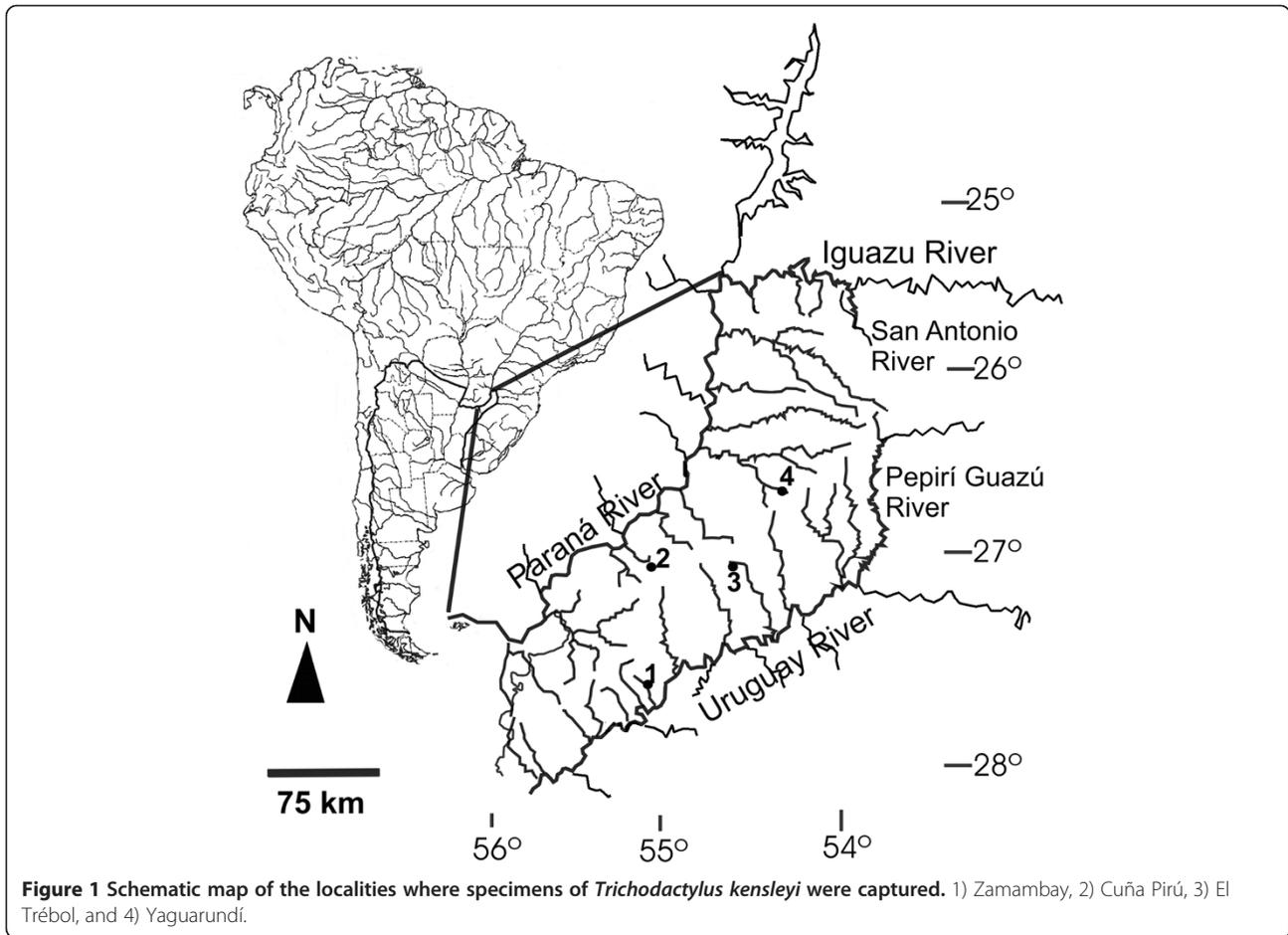
Crabs were collected and separated from the bottom and below rocks manually and with a hand net with a pore size of 500 µm. The crabs were placed in containers with cold water and ice to reduce their metabolism, to inhibit maceration by the gastric mill, and to avoid regurgitation. After a few minutes, the crabs were fixed by adding 96% alcohol to the cold water. This humane way of sacrificing these animals was used in the absence of an approved ethical procedure in the jurisdiction where the study was carried out. The same procedure was repeated in each stream during the light hours of a day (8:00, 12:00, 15:00, and 19:00). Crabs of the same sample hour were pooled to fit the statistical analysis. To characterize the water quality, some physicochemical parameters such as temperature, dissolved oxygen, pH, and conductivity were measured with digital sensors (HANNA HI 98129, HANNA instruments, Woonsocket, RI, USA).

Laboratory analysis

The cephalothorax width (CW), considered as the length between postorbital spines, was measured with a caliper under a stereomicroscope to the nearest 0.01 mm, and the sex was determined by the presence of the masculine appendix and abdominal characteristics (Lopretto 1976). To acquire the degree of stomach fullness, the crabs were dissected, the stomach was removed, and the muscular remains were cleaned to facilitate the visualization of the gut content. A subjective scale from 1 to 5 (1: empty, 2: 1% to 25% full, 3: 25% to 50% full, 4: 50% to 75% full, and 5: 75% to 100%) was used to categorize the total stomach repletion. Then, each stomach was opened and the content placed in an Eppendorf tube with alcohol 96% and stained with erythrosine. After at least 1 day, contents were mounted on slides on a drop of glycerol and examined under a compound microscope with ×100 and ×400 of magnification. Prey items were identified as precisely as possible.

Data analysis

The minimum number of crabs needed to reach a representative sample of the trophic diversity was estimated for every sample hour by the Chao estimation of species richness (Colwell 2013). The index of relative importance (IRI) was applied to analyze gut contents with the following formula: $IRI = (C_v + C_n) \times F$ (Pinkas et al. 1971), where C_v is the volumetric content of prey, C_n is the number of prey, and F is the frequency of occurrence of each prey item. The volume of items was calculated by approximation to a geometric shape or water displacement or transformed from values obtained from



the literature (Edmonson and Winberg 1971; Dumont et al. 1975; Ruttner-Kolisko 1977; Williner 2007). In order to compare IRI values of each sample hour among food items, a non-parametric analysis of variance (Kruskal-Wallis) was performed. The degree of stomach repletion was compared for each sample hour using a non-parametric analysis of variance (Kruskal-Wallis) while the cephalothorax width was tested for significance with a parametric analysis of variance (Kruskal-Wallis) (Zar 1996).

Results

Physicochemical parameters of water in the sampling period showed average values of $21.7^{\circ}\text{C} \pm 2.28^{\circ}\text{C}$ for temperature, $44.8 \pm 15.24 \mu\text{S}$ for conductivity, 7.2 ± 0.3 for pH, and $5.5 \pm 0.8 \text{ mg/l}$ for dissolved oxygen. The proportion of males and females was 50% and 40.5%, respectively. The highest sex ratio (males/females) was recorded during the warmest time of the day (15:00) while during the midday and sunset, these values were close to one. The averages of cephalothorax width were similar (ANOVA, $F = 0.306$, $p = 0.821$) in all sample hours with a maximum of 21.5 mm and a minimum of 4.7 mm (Table 1).

The degree of stomach repletion was statistically different throughout the day (Kruskal-Wallis (KW), $H = 30.28$, $p = 5.54 \times 10^{-7}$), and the stomach fullness reaches the highest values at the afternoon and dawn period (Figure 2). The minimum number of stomachs necessary for the analysis was quite similar throughout the day to reach a representative sample. However, the content diversity is greater in the evening and morning than in the midday and afternoon (Figure 3).

The analyses of stomach content indicate that this crab fed on benthic organisms, riparian vegetation remains, and drifting terrestrial fauna, with a wide trophic spectrum (Table 2). Food was found completely shredded, and grains of sand were observed in the stomach content. The most important food items were autotrophic organisms with predominance of vegetation remains. Macroinvertebrates such

Table 1 Sex ratio (males/females) and CW (mean and standard deviation) of *T. kensleyi* at each sample hour

	08:00	12:00	15:00	19:00
M/F	1.5	0.9	3	0.9
CW (mm)	12.53 ± 3.78	11.92 ± 4.13	12.92 ± 5.89	11.43 ± 4.91

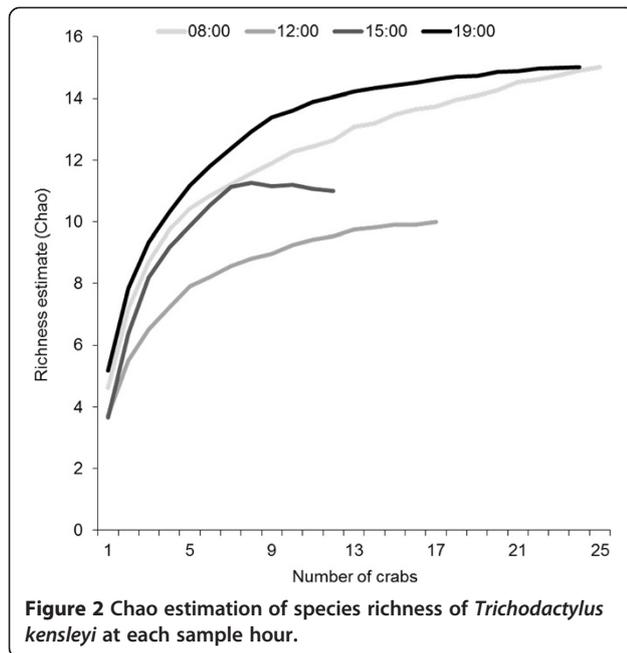


Figure 2 Chao estimation of species richness of *Trichodactylus kensleyi* at each sample hour.

as Oligochaeta and Chironomidae larvae had also a high IRI (Figure 4).

The analysis of IRI values evidenced statistical differences among food items (KW, $H = 41.8$, $p = 0.0001$; Figure 5). The presence of unicellular algae, diatoms, ostracods, and insect larvae in the stomach content of crabs caught at 8:00 and 12:00 evidenced the consumptions of these prey during the early morning until the midday. A reverse pattern was observed with filamentous algae, fungus, cladocerans, adult insects, and arachnids, which were more important in the diet in the last day hours. Microorganisms such as protozoans, rotifers, copepods, and also oligochaetes were preyed with more intensity during the afternoon. On the other hand, chironomid larvae and vegetal remains had two peaks of consumptions: one in the morning and the other in the evening.

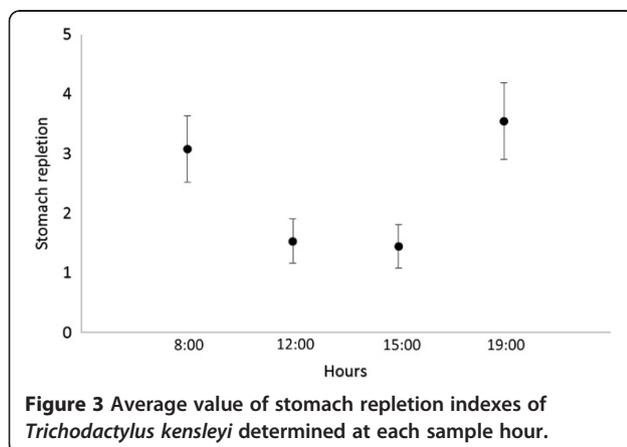


Figure 3 Average value of stomach repletion indexes of *Trichodactylus kensleyi* determined at each sample hour.

Discussion

The analysis of gut content of *T. kensleyi* revealed that this crab shares similar aspects to the diet of other crabs of the same genus and family. Trichodactylid crabs are reported to have opportunistic and omnivorous feeding habits, with a high consumption of vegetal matter, but animal items represent an important fraction of the trophic spectrum (Williner and Collins 2002; Collins et al. 2006; Pirela and Rincón 2013; Williner and Collins 2013). The presence of omnivorous organisms can contribute to understand the dynamics of aquatic systems and provide elements to analyze the stability of these species (Long et al. 2011; Kratina et al. 2012).

In the present study, it is observed that animals of low movement such as oligochaetes and quironomid larvae constituted the most important items in the diet of this crab species. On the other hand, the presence of algae was relevant in the gut content while microorganisms like rotifers, protozoans, and microcrustaceans had a minor relative importance. These results conform with the previous finding of Williner and Collins (2013) who reported that a crab of the same genus, *T. borellianus*, had a high relative importance of oligochaetes and insect larvae in the diet. However, in contrast to the generalizations made by Burress et al. (2013) that 'trichodactylids do not appear to engage in carnivory', it is evident in this study and in the previous literature that trichodactylid species often use animal resources, hunting them and eating dead animals (Williner and Collins 2002; Collins et al. 2006; Carvalho et al. 2013a, Pirela and Rincón 2013; Williner and Collins 2013).

Despite the importance of animal items, the prominence of vegetal component in the diet of trichodactylid crabs is indubitable. In the case of *T. kensleyi*, this type of food is provided mainly from allochthonous source. This fact open two main issues of discussion: the importance of this crab as shredder in subtropical streams and the effective nutrient assimilation of plant matter. The paucity of shredders in tropical (Dobson et al. 2002) and subtropical (Neiff and Poi de Neiff 1990; Ezcurra de Drago et al. 2007) zones suggested that the leaf processing could be done by alternative decomposition pathways, such as microbial activity, which is favored by higher temperatures (Irons et al. 1994). However, there is evidence that shredders are not scarce in these systems (Cheshire et al. 2005) and decapod crustaceans have been reported to bear a strong impact as macroconsumers on the leaf detritus processing (Mancinelli and Alessandro Scalzo 2013). In this way, *T. kensleyi* can play an important role in subtropical streams of southern South America influencing energy flow at multiple trophic levels.

The other issue is related to the effective assimilation of energy derived from vegetal matter. Plant litter is of

Table 2 Items recorded in the stomach contents of *Trichodactylus kensleyi* sampled in streams of subtropical rainforest

	Species
Algae	
Euchlorophyceae	<i>Coelastrum</i> sp. <i>Selenastrum</i> sp. <i>Scenedesmus</i> sp. <i>Ankistrodesmus</i> sp.
Zygothryxaceae	<i>Staurostrum</i> sp. <i>Zignema</i> sp. <i>Cosmarium</i> sp. <i>Euastrum</i> sp. <i>Closterium</i> sp. <i>Spirogyra</i> sp.
Bacillariophyceae	<i>Navicula</i> sp. <i>Chaetoceros</i> sp. <i>Gyrosigma</i> sp. <i>Cymbella</i> sp. <i>Fragillaria</i> sp. <i>Anphipleura</i> sp. <i>Bacillaria</i> sp.
Ulothricophyceae	<i>Bacillaria</i> sp. <i>Oedogonium</i> sp. <i>Ulotrix</i> sp. <i>Bulbochaeta</i> sp.
Vegetal remains	
Fungi	
Protozoa	
Rotifera	<i>Brachionus</i> sp. <i>Keratella</i> sp.
Oligochaeta	
Crustacea	
Cladocera	<i>Diaphanosoma</i> sp. <i>Daphnia</i> sp. <i>Bosminopsis</i> sp. <i>Ilyocryptus spiniger</i> <i>Macrothrix</i> sp. <i>Chydorus</i> sp.
Copepoda: Calanoida	<i>Notodiaptomus</i> sp. <i>Diaptomus</i> sp. <i>Bockella</i> sp.
Nauplii	
Ostracoda	

Table 2 Items recorded in the stomach contents of *Trichodactylus kensleyi* sampled in streams of subtropical rainforest (Continued)

Insecta	
Ephemeroptera	
Trichoptera	
Diptera	<i>Chironomus</i> sp. <i>Parachironomus</i> sp.
Araneae	

lower quality, contains a high proportion of fiber (cellulose and hemicellulose), has high C:N ratio, and typically contains secondary compounds such as tannins. On the other hand, cellulose is the major source of carbohydrates in the Earth, and traditionally, textbooks indicated non-animal organisms (e.g., bacteria and fungi) as the primary cellulase synthesizers. The widespread belief that animals cannot produce cellulase is now being rejected (Lo et al. 2003), and there are studies that prove the endogenous synthesis of these enzymes in decapods (Linton et al. 2006). The important amount of vegetal matter in the gut content of *T. kensleyi* implies some kind of metabolic way for the digestion of cellulose, either by an endogenous capacity or by carrying endosymbiotic organisms as reported for other crustaceans (Zimmer et al. 2001). The low nutritional quality of plant debris is known; however, it could be improved by the colonization of decomposer microorganisms after leaves have fallen (Nordhaus et al. 2006; Linton and Greenaway 2007). The high amount of vegetal matter ingested by *T. kensleyi* suggests a way to enhance the energy supply derived from a poor nutritional food. On the other hand, the high values of IRI

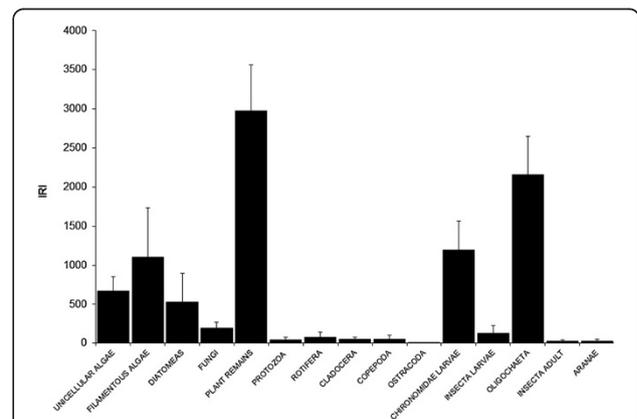


Figure 4 IRI of food items identified in all stomach contents of *Trichodactylus kensleyi* captured in subtropical streams.

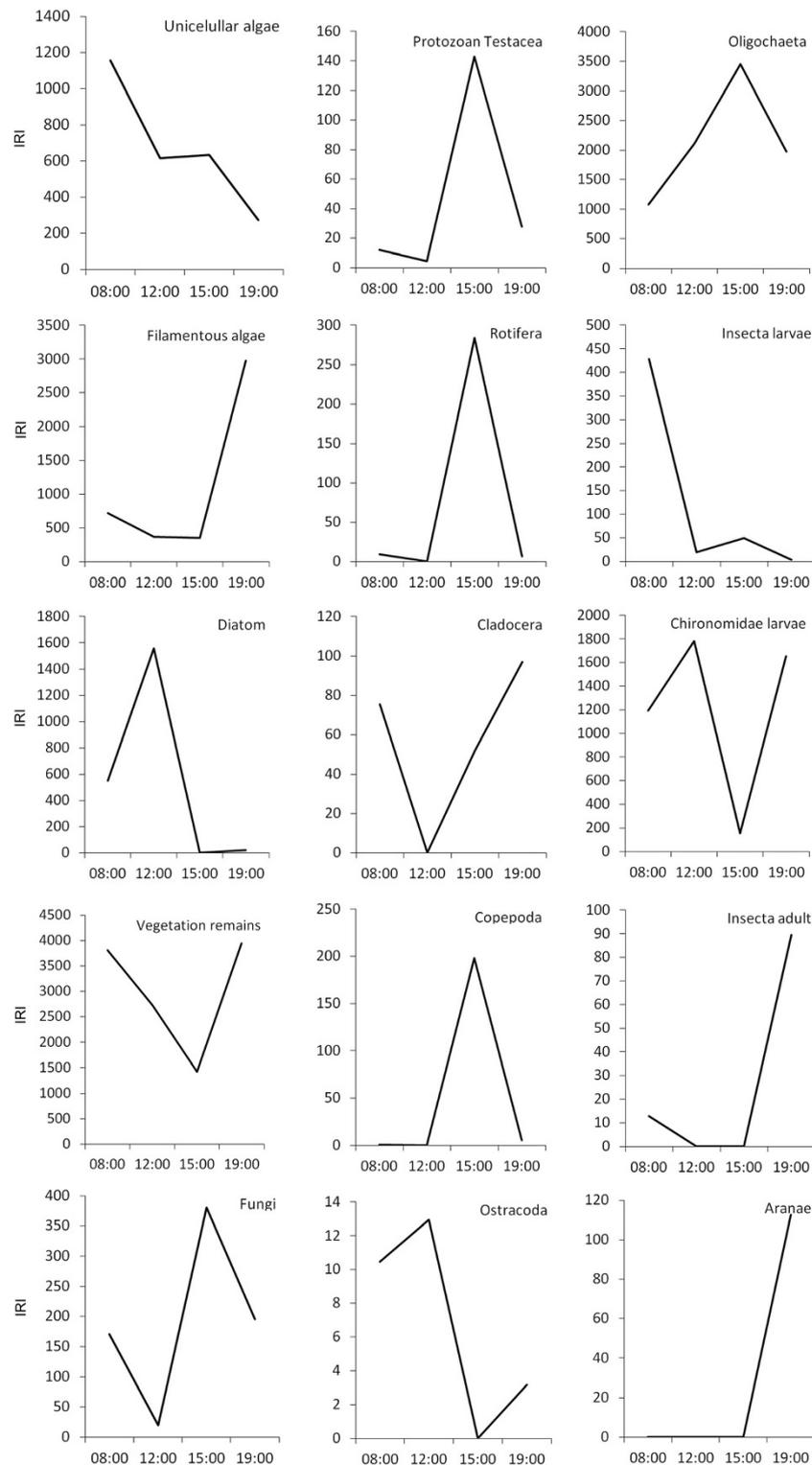


Figure 5 IRI of food items identified in stomach contents of *Trichodactylus kensleyi* at each sample hour.

could be masking the long time of digestion needed to process plant tissue, as suggested previously for *Aegla platensis* (Colpo et al. 2012).

Williner and Collins (2013) verified that adults of *T. borellianus* ate more vegetal components than juveniles. It is possible that the same may happen with

T. kensleyi, since the average of cephalothorax width of specimens captured in this study corresponded to the adult specimens (12.2 ± 2.2 mm). However, further studies of juveniles' diet are still necessary to corroborate this hypothesis. Juveniles need a protein-rich diet for growth while adult crabs require energy for maintenance, ingesting the poorest nitrogen food such as vegetal tissue (Mancinelli and Alessandro Scalzo 2013). In addition, *T. kensleyi* and *T. borellianus* are small-sized crabs, which implies a high metabolic rate than large species, requiring extracting more energy per unit of ingesta due to higher respiration losses (Mattson 1980). Then, this requirement is even higher in juveniles. In this way, the nutritional improvement of the diet should be supplied with nitrogen-rich food such as animal items and even algae.

Oligochaetes and chironomid larvae were the most important items in the diet of *T. kensleyi* following vegetal remains. In terms of nutritional content, oligochaetes and insect larvae contain a high proportion of protein relative to their biomass (Hepher 1989). In addition, these organisms are in general abundant in streams (Cushing and Allan 2001), indicating the opportunistic trophic behavior of this crab species. On the other hand, algae, another important item in the diet, are considered truly as the grasses of the stream waters and can be present in varying numbers and kinds attached to solid objects such as rocks (Cushing and Allan 2001). All these prey items, together with those of less relative importance in the diet (e.g., microcrustaceans, rotifers, and protozoans) should be nutritionally essential for the crabs' growth and reproduction, contributing with protein, lipid, vitamin, and mineral requirements. However, the ingestion of different kinds of food can be variable and modulated by endogenous factors and environmental influences (Aréchiga and Rodríguez-Sosa 1997). In this study, *T. kensleyi* showed moments of major trophic activity and uses different kinds of trophic sources throughout the day.

The diel rhythm of feeding activity of organisms is primarily a response to the most constant external stimulus, the light–dark phase. However, there are other ecological factors in nature, both positive and negative stimuli, which determine the temporal distribution of behavior patterns (Daan and Aschoff 2001). Some of the most adaptive temporal shift in the rhythm behavior is related to the co-existence of species and ecological interaction such as predation-prey systems and competition (Kronfeld-Schor and Dayan 2003). *T. kensleyi* co-exist in subtropical streams with other decapod anomurans such as *Aegla singularis* (Melo 2003). Both decapods are found in the stream bottom, under sediments and rocks, and have similar diet (Williner 2007), suggesting a potential niche overlap between these decapods. In this way, it is feasible to think that these sympatric species could

facilitate the co-existence through the partitioning of time. However, this hypothesis is speculative since there is no additional information about the feeding activity of *A. singularis*, although studies of other aeglids propose a more nocturnal activity (Sokolowicz et al. 2007).

In *T. kensleyi*, the presence of full stomachs was registered throughout the day, but with a higher proportion during the early morning and late afternoon. This pattern is similar to other decapod species from inland waters, which indicates a crepuscular (dawn and dusk) feeding rhythm (Collins 1997; Williner and Collins 2002; Aguzzi et al. 2005; Zimmermann et al. 2009). However, there are many evidences that the presence of food at any time of the day can trigger the locomotion in decapod crustaceans even in periods of low activity (Fernandez de Miguel and Aréchiga 1994; Reigada 2002; Pontes and Arruda 2005; Sokolowicz et al. 2007; Zimmermann et al. 2009). Indeed, in *T. kensleyi*, the presence of prey items in the gut content suggests a continuous food intake and can provide clues of the movement of crabs in streams throughout the day.

As mentioned, higher proportion of full stomachs were registered at 8:00 and 19:00. In these moments, the presence of chironomid larvae, vegetal remains, unicellular green algae, and diatoms was more abundant in the early morning while oligochaetes and meiofauna organisms (e.g., protozoans, rotifers, copepods, cladocerans) reach higher IRI values during the dusk period. Chironomidae genera (*Chironomus* Meigen and *Parachironomus* Lenz), identified in crabs' gut contents, are categorized as gatherers-collectors. Oligochaetes also belong to this functional feeding group (Zilli et al. 2008). These benthic organisms are commonly found within the sediment or above stones where they obtain their food, collecting fine particulate organic matter (FPOM) in deposit zones and under rocks (Cushing and Allan 2001). In this way, it is possible to infer that *T. kensleyi* foraged mainly these zones during crepuscular hours. During the forage of these areas, crabs could ingest meiofauna together with the ingestion of sand and sediment particles in the stream bottom. In the dawn period, the ingestion of algae might be indirectly related to the cropping of vegetal debris, since the algae identified were mainly periphytic and benthic (Vélez and Maidana 1995). On the other hand, algae could be actively consumed by the grasping of rocks. The consumption of food during those moments of lower activity (midday and afternoon) could be related to the availability of such items nearby shelter sites. When analyzing consumer relations, it is relevant also to delve into those unexplored as may be facilitating habitat (Hart and Marshall 2013). This type of interaction has been registered in the anomuran *A. uruguayana* (Schmitt 1942), wherein the step of diatoms to the digestive tract results in an increase in their rate of reproduction (Devercelli and Williner 2006).

Although results suggest general movements during feeding activity, there are some factors that could influence the evaluation of the effective trophic spectrum and the exact moment when each kind of food was ingested. Initially, brachyuran decapods have the most complex foregut armature with a robust gastric mill (Icely and Nott 1992) that contributes to an efficient trituration process and, consequently, difficult gut content identification. In addition, the residence time can vary greatly according to the type of food (McGaw and Curtis 2013). For example, the complete gut clearance of prey such as oligochaetes and dipteran larvae could lead at least 10 h at 21°C in *Macrobrachium borellii* (Nobili, 1896), a caridean freshwater prawn (Carvalho et al. 2011). However, the absence of a robust gastric armature in caridean prawns implies that crabs may have a lesser time of foregut evacuation. Digestive efficiency is ultimately influenced by transit times and tends to be higher in diets composed of animal items than in those based on vegetable matter (McGaw and Curtis 2013). This leads to an underestimation of prey with rapid digestion, like those of soft body, and an overestimation of those with slow digestion, like plant debris.

Conclusions

There are many biological and ecological aspects of crustacean decapods that still must be studied for a better understanding of their role in freshwater systems. This research provides knowledge that complements previous studies about trophic relationships of trichodactylid crabs. The generalist and opportunistic trophic behavior together with the carnivore and shredder feeding habitats indicates that *T. kensleyi* directs the flow of energy and matter from benthic community and riparian sources to superior trophic levels using both macro- and microfauna.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

VW and PAC designed the study. PAC participated in the field trips for sampling. VW and PAC carried out the laboratory analyses and data analyses. DAC made the figures and wrote the manuscript. VW, DAC, and PAC made intellectual contributions and reviewed the manuscript. All authors read and approved the final manuscript.

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