

Foregut ossicles morphology and feeding of the freshwater anomuran crab *Aegla uruguayana* (Decapoda, Aegliidae)

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Abstract

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The acquisition and processing of food is critical to animal survival and reproductive success. This work describes the foregut ossicles of *Aegla uruguayana*, which have been proposed to impart trophic characteristics. In addition, stomach contents were analysed using Index of Relative Importance and Weighted Result Index to characterize the diet. The Pearre index was applied to analyse trophic selectivity. We found *A. uruguayana* has a morphological foregut typical of macrophage organisms. Stomach contents included items typical of omnivorous, generalist and opportunistic feeding modes. Vegetal remains included algae (filamentous, unicellular and colonial morphotypes), insect larvae, oligochaetes, microcrustaceans (copepods and cladocerans), mites, tardigrades, juveniles of *A. uruguayana* and rotifers. Morphological descriptions of the foregut can reveal feeding habits and provide data on the possible trophic profile of a species, while guiding the selection of appropriate methodology for subsequent analysis. Our stomach content data corroborated the foregut description, but the presence of small prey suggested *A. uruguayana* utilizes both predation and detritivory trophic strategies.

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Introduction

Feeding in decapods is complex and requires integration by the external and internal apparatus. Externally, the maxillae, mandibles and maxillipeds play an important role in the success of crustaceans, which feed on a wide variety of food (Schembri 1982). The internal systems, principally the foregut ossicles, show interspecific variations that model the phylogeny and can reflect the evolutionary relationships of decapod taxa (De Jong-Moreau and Casanova 2001; Brösing *et al.* 2002, 2006). In addition, a description of ossicle morphology can reveal the feeding habits and trophic possibilities of decapods (Schaefer 1970; Caine 1975; Dall and Mortuary 1983).

Analysing the natural diet is a prerequisite for understanding the role of decapods in trophic webs and in the organization of ecosystems (Warren and Spencer 1996).

Understanding trophic structural patterns within the freshwater environment can be useful for interpreting processes such as depredation and the degree of diet specialization (Schmid-Araya *et al.* 2002). These studies are often hampered by the presence of ossicles in the foregut that limit the ability to observe stomach contents (Williams 1981). Some studies suggested that diet differentiation could imply a modification in the anatomy of the foregut, and affect the organism's ability to process food efficiently (Dall and Mortuary 1983; Felgenhauer and Abele 1989).

Aegla uruguayana is a freshwater anomuran crab that lives in lotic and lenitic freshwater environments of the southern state of Rio Grande do Sul in Brazil, and in Uruguay and central and northwest Argentina (Bond-Buckup and Buckup 1994). This decapod belongs to the unique family of anomurans that colonized freshwater environments (Schmitt 1942).

In Brazil, Castro-Souza and Bond-Buckup (2004) described the stomach morphology of *Aegla platensis* whereas Bueno and Bond-Buckup (2004) analysed natural diets of *Aegla ligulata*. Similarly, Castro-Souza and Bond-Buckup (2004) registered the trophic aspects of additional Brazilian species, including *Aegla leptodactyla* and *Aegla camargoi*.

In Argentina, extrataxonomic studies of this particular family are scarce (Giri and Collins 2004; López Greco *et al.* 2004; Devercelli and Williner 2006; Viau *et al.* 2006; Williner 2007; Giri and Loy 2008). The freshwater crab *A. uruguayana* has not been intensively studied (Giri and Collins 2004; Viau *et al.* 2006), and there are few references regarding the feeding aspects of this species (Devercelli and Williner 2006). In this study, we described the morphology of the major internal foregut ossicles and analysed the natural feeding habits of *A. uruguayana* adults.

Materials and Methods

Aegla uruguayana were obtained from Las Pencas Stream in Entre Ríos Province, Argentina (32°17'S, 60°26'W) during 2003–2004. Crabs were collected by hand from under rocks, principally in the littoral and shallow zones. Adults were identified according to Bond-Buckup and Buckup (1994). Carapace lengths (CL) were measured to the nearest 0.01 mm using a calliper under a stereomicroscope. All samples were preserved *in situ* in 70% alcohol.

Foregut ossicles description

Twenty empty foreguts were first cleaned with distilled water. Then, the foreguts were dissected and fixed in KOH solution (10%) to clarify and then stained with Alizarin-red (Brösing *et al.* 2002). Photographs of dorsal, ventral and lateral views were made with a stereo-microscope with a digital camera (Nikon Coolpix 7900). Ossicles were described according to the nomenclature proposed by Ngoc-Ho (1984) and Kunze and Anderson (1979). We emphasized describing those ossicles that have been implied to define trophic aspects, as well as those considered important from a methodological standpoint. The distance between teeth and thorns was measured by TPS (Rohlf 2004).

Trophic analysis

Samples of *A. uruguayana* and potential food sources were obtained during the 2 h after dawn, to optimize the stomach fullness (Williner 2007). Three benthic samples of 900 cm² each were collected with a Surber net (250 µm size net) using a CPUE of 5 min (Correia 2002), and plankton communities were collected by filtering 50 L of water with a net (20 µm size net). Three replicates were collected and preserved in 70% alcohol and then were stained with erythrosine.

Crabs that were in intermolt were used in this study, to improve the chances of a full foregut (Lipcius and Herrnkind

1982). The alimentary tracts were removed and individual foregut fullness was estimated according to a subjective scale, ranging from 0 to 3 (0 for empty; <30% full; 60% full; >60% full) (modified from Collins and Paggi 1998). The stomachs were opened and their contents were extracted and placed into erythrosine and alcohol in an Ependorf tube. At first, stereoscopic microscope viewing showed the stomach content was a dark, amorphous material, without identifiable structures. Therefore, we modified the procedure to observe the stomach content using a compound microscope binocular (Williner and Collins 2002). Five aliquots (approximately 50% of the content) per organism were analysed. The aliquots were mounted in a drop of glycerol (50%). Food items were sorted to taxonomic groups, measured, and counted under a compound microscope at 4× to 40×. The remains were identified according to a taxonomic key.

Subsamples (5 mL) of benthic resource availability were identified in a Borovov chamber. Plankton was enumerated in a Neubauer chamber of 0.1 mL and in a Sedgewick–Rafter chamber of 5 mL.

Food item volumes and potential food organisms were determined by approximation to regular geometric shapes or by converting them to volume data of weight reported in the literature (Collins 2000).

The Index of Relative Importance (IRI) was used to measure the incidence of food items, with $IRI = (C_v + C_n) \times F$ (Pinkas *et al.* 1971); where C_v is the volumetric content of prey, C_n the number of prey, and F the frequency of occurrence of each prey item. To assess the main contribution (volume or frequency) of the prey, we used the Weighted Result Index, $R_w = \left[\left[\frac{Q}{(v_i^2 + o_i^2)^{1/2}} \right] \cdot \left[\Phi - \frac{Q}{(v_i^2 + o_i^2)^{1/2}} \right]^{-1} \right] \cdot 100$, where v is a volume percentage of item₁, o is an occurrence percentage of item₁, Q takes into account the deviation of the angle Φ from the mid-way, while grading the importance of the food. The angle is determined as $\tan^{-1}(o/v_i)$ (Mohan and Sankaran 1988).

Potential food selectivity was determined by chi-squared formulation: $CI = [(a*b' - a'*b - n/2)2/A*B*C*D]$, where a is item₁ in the foregut, a' item₁ in the environment, b the rest of the items in the foregut, b' the rest of the items in the environment, A total of item₁, B total of the rest of the items, C total of the items in the foregut, D total of the items in the environment, n sum of the total of the items in the foregut and the environment. This index registered values from –1 for negative selectivity to +1 for positive selectivity. Values of 0 corresponded to neutral selectivity. Results were tested for significance by the Fisher's exact test with Yates' correction for continuity (Pearre 1982).

Results

Foregut ossicles description

The mean foregut size (CL) of twenty *A. uruguayana* specimens was 13.91 ± 2.54 mm (mean \pm SD).

The foregut was a thin-walled translucent organ with two well-differentiated chambers: a cardiac chamber with a high volume and a smaller pyloric chamber.

The food material enters the stomach from the ventral portion of the oesophagus. Two oesophageal valves regulate the entrance to the stomach (Fig. 1A,C). In the ventral view, the outstanding structures were located in the cardiac chamber, at the junction of the two chambers and the ampullae in the

pyloric region. In the dorsal view, the mesocardiac and propyloric ossicles were the most evident structure, in the cardiac and pyloric chamber, respectively.

The cardiac chamber was situated in the cardiopyloric position, and was composed of mesocardiac, urocardiac, zygocardiac and pterocardiac ossicles. The mesocardiac ossicles formed a central unique triangular structure, with a vertical and horizontal axis. The horizontal axis is a flattened structure that is strongly calcified, whereas the vertical structure is the main support of the cardiac camera (Fig. 1C,G). In the posterior region, these ossicles articulated to urocardiac ossicle. The second dominating structure forming the gastric mill was the zygocardiac ossicle, with nine teeth that increased progressively in size, and four thorns (Fig. 1B,C,G). The distance between the first and the second tooth was 0.15 ± 0.02 mm (mean \pm SD) and the distance between the first and second thorn was 0.23 ± 0.02 mm (mean \pm SD). The urocardiac ossicle, also called the median tooth, was articulated with the previous ossicles. The urocardiac ossicle was formed by five ends that are located three-dimensionally, in two levels (Fig. 1B,C,F–H). The superior level was formed by three ends and the inferior level consisted of the remaining two ends. This central structure occupied approximately 80% of the longitudinal section of the cardiac chamber. The basal section of the structure articulated with the propyloric ossicle. The dorsal portion of the cardiac camera was supported by the pyloric and exopyloric ossicles. Pectinal and pospectinal ossicles, structures implicated in the mechanical action of processing food, were paired in the lateral wall. The pectinal ossicle appeared as an elongated and teathed rod located laterally to the zygocardiac ossicles (Fig. 1D,G). These ossicles both had an accessory tooth in the proximal end. The pospectinal ossicles served to support the foregut chamber and had a series of moderately hardened thorns (Fig. 1C,G). The remaining ossicles of the cardiac chamber did not have annexed structures (teeth, thorns), and some were fused and do not function in maceration of food, so they probably serve in support roles. The cardiopyloric valve was located in the ventral area (Fig. 1E,G). This configuration was supported by a pair of ossicles that were separated in the anterior ends. A semicircular structure with a peak and sclerotized and separate ridges and silks was located in the dorsal view. The channel between both the chambers was 0.19 ± 0.02 mm (mean \pm SD) and 0.11 ± 0.01 mm (mean \pm SD) wide in the anterior and posterior positions, respectively (Fig. 1E).

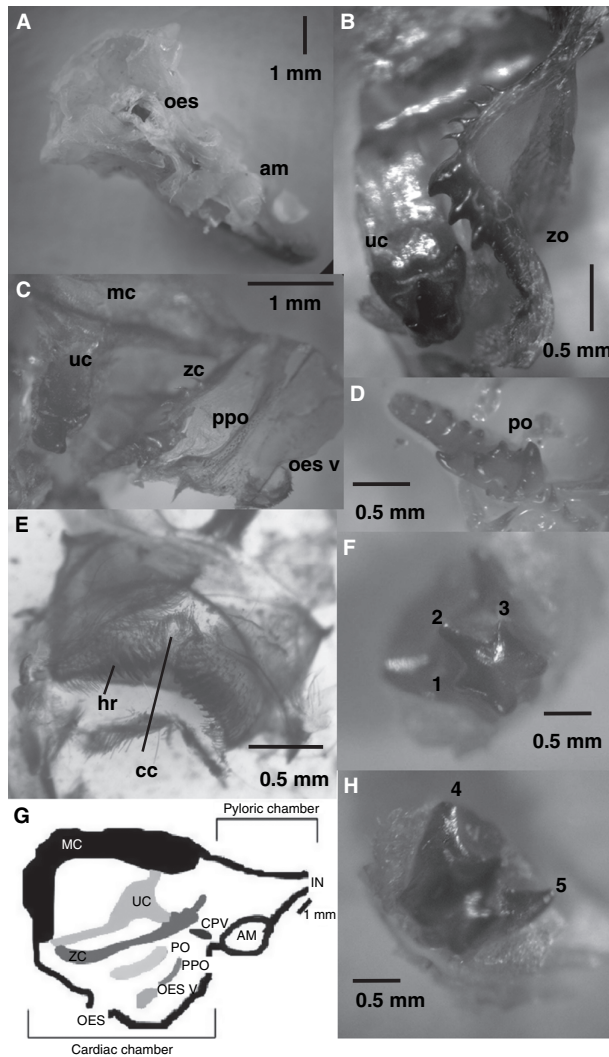


Fig. 1—Main foregut ossicles of *Aegla uruguayana*. — **A**. Ventral view of foregut; *oes*, oesophagus; *am*, ampullae. — **B**. *uc*, urocardiac ossicle; *zo*, zygocardiac ossicle. — **C**. Roof and lateral wall of foregut; *mc*, mesocardiac ossicle; *uo*, urocardiac; *zo*, zygocardiac ossicle; *ppo*, pospectinal ossicle; *oes v*, oesophageal valve. — **D**. *po*, pectinal ossicle. — **E**. Cardiopyloric valve; *hr*, hardened ridges; *cc*, cardiopyloric channel. — **F,H**. Median tooth of urocardiac ossicle; 1, 2, 3 ends of the superior level; 4 and 5 ends of inferior levels. — **G**. Scheme of main foregut ossicle; *in*, intestine.

Trophic analysis

Crabs used in this study had a minimum size of 4.8 mm (CL) and a maximum size of 24.8 mm (CL) and about 75% were males. Of the crabs used, 49% had full foreguts, whereas 10% had empty foreguts. Twenty-two separate food items were identified in the foreguts of the analysed population and

Table 1 List of food items recorded in the foregut of *Aegla uruguayana*

Item	Item	Item
ALGAE	<i>Pinnularia</i> sp.	Copepoda
Cyanophyceae	<i>Pleurosigma</i> sp.	Calanoidea
<i>Aphanothece</i> sp.	<i>Roicosphenia</i> sp.	<i>Notodiatomus</i> sp.
<i>Coelosphaerium</i> sp.	<i>Rhopalodia</i> sp.	Not identified
<i>Chroococcus</i> sp.	<i>Stauroneis</i> sp.	Larvas nauplii
<i>Hapalosiphon</i> sp.	FUNGI	Ostracoda
<i>Microcystis</i> sp.	Ascomycetes	Not identified
<i>Nostoc</i> sp.	Mixomicete	Decapoda
<i>Spirulina</i> sp.	PROTOZOA	<i>Aegla</i> sp.
Chlorophyceae	Rhizopoda	Palaemonidae
<i>Chaetophora</i> sp.	<i>Arcella</i> sp.	INSECTA
<i>Cladophora</i> sp.	<i>Centropyxis</i> sp.	Chironomidae
<i>Coleochaete</i> sp.	<i>Diffugia</i> sp.	Chironominae
<i>Dicranochaete</i> sp.	Ciliophora	<i>Cryptochironomus</i> sp.
<i>Eudorina</i> sp.	<i>Coleps</i> sp.	<i>Procladius</i> sp.
<i>Hydrodictyon</i> sp.	PORIFERA	Orthocladinae
<i>Microthamion</i> sp.	Not identified	<i>Cricotopus</i> sp.
<i>Mougeotia</i> sp.	BRIOZOA	<i>Pseudosmittia</i> sp.
<i>Oedogonium</i> sp.	Not identified	Not identified
<i>Ulothrix</i> sp.	ROTIFERA	Ephemeroptera
Zygophyceae	Bdelloidea	Baetidae
<i>Cosmarium</i> sp.	No identificado	Not identified
Euglenophyceae	Lecanidae	Leptophlebiidae
<i>Trachelomonas</i> sp.	<i>Lecane</i> sp.	Caenidae
<i>Phacus</i> sp.	Brachionidae	Not identified
Dinophyceae	<i>Brachionus</i> sp.	Trichoptera
<i>Peridinium</i> sp.	Notommatidae	Hidroptiliidae
Xanthophyceae	<i>Cephalodella</i> sp.	Not identified
<i>Tribonema</i> sp.	<i>Mytilina</i> sp.	Terrestrial insect
Not identified	TARDIGRADA	Not identified
Bacillariophyceae	Macrobotidae	Formicidae
<i>Amphiprora</i> sp.	<i>Dactylobiotus</i> sp.	Not identified
<i>Amphora</i> sp.	Not identified	ARACHNIDA
<i>Attheya</i> sp.	ANNELIDA	Acari
<i>Cyclotella</i> sp.	Oligochaeta	Hydrachnidia
<i>Cymbella</i> sp.	Naididae	<i>Arrenurus</i> sp.
<i>Diploneis</i> sp.	<i>Allonais</i> sp.	Not identified
<i>Eunotia</i> sp.	<i>Dero</i> sp.	Vegetal remain
<i>Gomphonema</i> sp.	<i>Nais</i> sp.	POLLEN GRAINS
<i>Gyrosigma</i> sp.	<i>Pristina</i> sp.	SAND AND MUD
<i>Luticola</i> sp.	<i>Melosira</i> sp.	
<i>Meridion</i> sp.	CRUSTACEA	
<i>Nistchia</i> sp.	Cladocera	
<i>Navicula</i> sp.	<i>Ilyocryptus</i> sp.	

consisted of animal prey and vegetal material, ranging in size from small (e.g. diatoms), to big (e.g. ephemeropterans and calanoids copepods) (Table 1).

Diatoms and vegetal remains had the largest IRI indices; 978 and 879, respectively. This was followed by oligochaetes and chironomid larvae at 44 and 30, respectively (Fig. 2). The RW showed a high value for the vegetal remains (Fig. 3). Oligochaetes, cladocerans, copepods, ostracods, mites and ephemeropterans larvae contributed the most to the total in volume (left side of figure). Other prey included bryozoans,

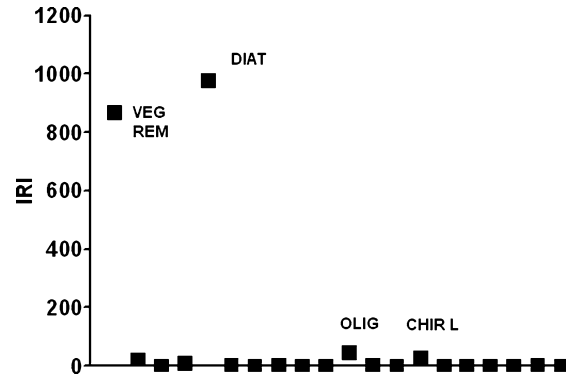


Fig. 2—Index of relative importance (IRI) of major food items found in *Aegla uruguayana*. DIAT, diatoms; VEG REM, vegetal remains; OLIG, oligochaetes; CHIR L, chironomids larvae. The rest of the items showed a low value (between 1.13 and 44.81), in order from left to right: filamentous algae, colonial algae, unicellular algae, fungi, ciliates, testaceous amoeba, rotifers, water bears, cladocerans, copepods, nauplii, ostracods, terrestrial insect, mites, ephemeropterans larvae, caddisflies larvae, *A. uruguayana* juveniles, palaemonids shrimps.

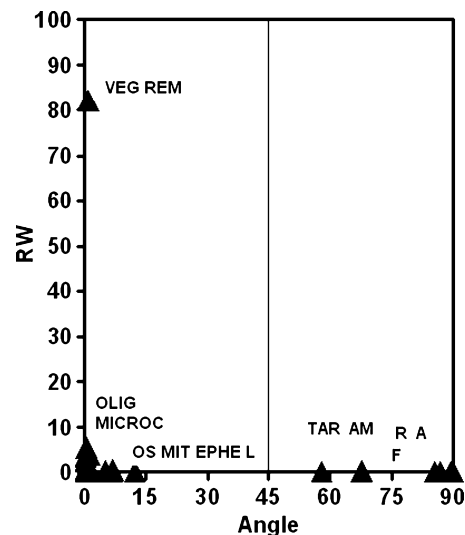


Fig. 3—Weighted Result Index (RW) of major food items found in *Aegla uruguayana*. VEG REM, vegetal remains; OLIG, oligochaetes; MICROC, microcrustaceans; OS, ostracods; MIT, mites, EPHE L, ephemeropterans larvae; TAR, tardigrades; AM, amoebas; R, rotifers; F, fungi; A, algae. The points plotted from the midline to the left correspond to the items that build the index making a greater contribution in volume. The points in the right side correspond to the items making a greater contribution in frequency.

terrestrial insects and sponges, but these were only found infrequently in a few stomachs.

Positive values of selectivity were determined for prey, and cladocerans and rotifers were statistically significant (Fisher's test, $P < 0.05$) (Fig. 4).

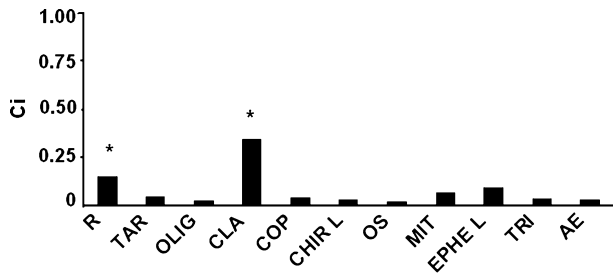


Fig. 4—Selectivity index (C_i) of main food items recorded in the foregut of *Aegla uruguayana*. R, rotifers; TAR, tardigrades; OLIG, oligochaetes; CLA, cladocerans; COP, copepods; CHIR L, chironomids larvae; OS, ostracods; MIT, mites; EPHE L, ephemeropterans larvae; TRI, caddis flies; AE, juveniles of *A. uruguayana*. The asterisk represents those items that showed a statistically significant positive selectivity.

Discussion

Foregut ossicles description

Aegla uruguayana general foregut armature adjusts by a progressive increase in robustness. Mainly ossicles are heavily calcified (Icely and Nott 1992). This same tendency has been observed in the infraorders Astacidea, Thalassinidea, Palinura and Anomura, and finally in Brachyura. In agreement with a previous report (Castro-Souza and Bond-Buckup 2004), the oesophageal valve was found in *A. uruguayana* to be a dish-shaped expansion that connects the oesophagus and the foregut.

The gastric mill is the most conspicuous structure of the cardiac chamber, and is located in the cardiopyloric section. This position is uniform in decapods (De Jong-Moreau and Casanova 1997). King and Alexander (1994) argued that the absence of silk, channels and furrows provided evidence of macrophagy. The *A. uruguayana* cardiac chamber also lacks these features and the gastric mill ossicles were similar with those described by Castro-Souza and Bond-Buckup (2004) for *A. platensis*.

The urocardiac and mesocardiac ossicles are the main structures supporting the roof of the cardiac region. This characteristic is also observed in other groups of decapods, such as hermit crabs (Kunze and Anderson 1979). Food processing is carried out chiefly by movements that are dorsomedial of the zygo-cardiac ossicle and anteroventral of the urocardiac ossicle (Icely and Nott 1992). The registered thorns in the zygo-cardiac ossicle are peculiar structures that have not been observed in other anomurans. *Aegla uruguayana* presented nine teeth and four thorns, while e.g. *A. platensis* had a series of thorns, but the quantity was not specified (Castro-Souza and Bond-Buckup 2004). The foregut morphology of anomurans species may have systematic and phylogenetic implications (Brösing *et al.* 2006). The hardness and prominence of the teeth and the thorns provide evidence of the intensity of the

mechanical action and could suggest the potentiality of prey. The distances between teeth or thorns can be an indicator of the size of the identifiable pieces likely to be found during analysis of the stomach contents. In addition, specific dimensions can contribute information about the types of organisms that can pass through without mechanical destruction (Devercelli and Williner 2006).

On the basis of the morphology and characterization provided by Schaefer (1970), Caine (1975) and Kunze and Anderson (1979), our work was adjusted to consider *A. uruguayana* as both a predatory and macrophagous organism. The tendency towards macrophagy was predicted by the sharpness of the teeth and thorns of the ossicles and by the quantity of crests that presented in the cardiopyloric valve. However, in *A. uruguayana*, there is a large quantity of silks alongside the ridges of the cardiopyloric valve, a feature that typifies the filtering organisms. This could be attributed to ancestral attributes or could be functional for processing micro-organisms (unicellular algae and others planktonic animals). The cardiopyloric valve does not possess a projection of silk in other anomurans (Caine 1975). The presence of silk and teeth in the cardiopyloric valve of *A. uruguayana* suggests multiple functions in retention and movement of particles, and also in chewing the food. According to Caine (1975), the presence of silk and the distances between them suggest macrophagic habits, and crushing jointly with the remainder of the ossicles. In addition, Kunze and Anderson (1979) stated that a progressive increase in distances among the silks increases the level of macrophagic feeding. The valve structure of *A. uruguayana* is similar with that of *Dardanus setifer*, considered by Kunze and Anderson (1979) as macrophagous. Our results substantiate the findings of Kunze and Anderson (1979) and showed the distances among silk did not vary among crabs with different feeding habits; in general, the width of the central channel of the valve ranged from 1 to 2 μm . The prepectineal ossicles were not observed with clarity, so they may be fused next to the pectineals, as occurs in *A. platensis* (Castro-Souza and Bond-Buckup 2004).

Trophic analysis

Bueno and Bond-Buckup (2004) reported that *A. ligulata* consumed mainly macrophytes and insect larvae. Here, we found that in addition to these items *A. uruguayana* consumes small organisms (diatoms, rotifers and others). In *A. platensis*, *A. ligulata*, *A. camargoi* and *A. leptodactyla*, small prey have little significance to the diet. In contrast, *A. uruguayana* showed a significant presence of diatoms in the stomach contents (Devercelli and Williner 2006). This disparity in results may reflect the environment in which these organisms live, but also point to methodological differences in nature. The point method, used to examine trophic Brazilian species, does not require microscopic observation (Hynes 1950). The method does not include the volume of prey, which can

influence differences among data from indexes that are built from volumetric data (IRI and RW).

The omnivorous diet attributed to these *Anomura* agree with previous studies that analysed the diet of other decapod crustaceans in continental hydrosystems (Collins and Paggi 1998; Collins 1999; Williner and Collins 2002; Collins and Williner 2003; Collins *et al.* 2006).

Woodward and Hildrew (2002) emphasized the importance of omnivores in increasing the cross-linking in food web, thus promoting stability and complexity of the system. With more links the system has a wider range of possible responses available. Omnivory is considered a key component of how benthic decapod crustaceans regulate the flow of energy and recycling of nutrients (Evans-White *et al.* 2001; Buck *et al.* 2003). From a functional point of view, omnivory is favourable within systems, combining resources of different conversion efficiency (Krivan and Diehl 2005). The intake of plant debris is common in freshwater lobsters, crabs and shrimps (Pérez-Bote 2005) and the origin of this material has been studied. In four species of Brazilian anomurans, the origin of plant material is attributed to macrophytes (Bueno and Bond-Buckup 2004; Castro-Souza and Bond-Buckup 2004). Unlike other species of freshwater decapods, such as *Trichodactylus borellianus* and *Dilocarcinus pagei*, the population of *A. uruguayana* analysed in this study was not from environments with macrophytes (Williner and Collins 2002; Williner, personal observations). This suggests that the origin of vegetation ingested is alloctonous, fulfilling in these decapods a role in processing leaves, while not affecting the primary productivity of the stream. However, this effect should be considered for the case of filamentous algae and diatoms. Algae found in the stomachs of the *Anomura* could be classified as benthic and periphytic. The diatoms were an item of importance (IRI) in *A. uruguayana*. In the laboratory, browsing on diatom decreased living cells by 12%, which could potentially play an important role in structuring the algal assemblage (Devercelli and Williner 2006). For these *Anomura*, bacillariophyceae were identified as the main component in the stomach according to trophic descriptions provided by Burns (1972). With IRI, the filamentous algae were found to be the second most important item. Puccio *et al.* (2006) suggested that the presence of filamentous algae was likely due to their tendency to create thick felts, from which the crab easily obtains polyspecific food items, and potential prey items, especially invertebrates.

The consumption of plant material provides energy at the expense of similar aspects. The palatability of the plant debris ingested depends on physical factors (hardness of tissues) and chemical factors (nutritional value, presence of toxic compounds) of plants (Bolser *et al.* 1998). The observation of fungi, primarily ascomycetes, in the stomachs of crabs could relate to their need to ingest micro-organism decomposers that make plant energy available (Zimmer and Topp 2000). By including plants as a food source, *A. uruguayana* display a strategy that utilizes readily available food in the environment,

and eliminates the need to search for other food sources (Wolcott and O'Connor 1992).

The oligochaetes, copepods, ostracods and insect larvae (mainly chironomids and ephemeropterans) did not show a high value index, however, their contribution was significant in terms of overall volume. The high nutritional value and energy expenditure could encourage consumption of prey with slow movements, such as oligochaetes and chironomid larvae, which were the most abundant resource in the environment. Cannibalism (consumption of juveniles) occurred and provided a prominent protein intake (Collins 2000). This phenomenon has been observed in other decapod crustaceans (Collins and Paggi 1998; Collins 1999; Pérez-Bote 2005) and regulates the population dynamics (Lovrich and Sainte-Marie 1997). Cannibalism was reported previously in the Brazilian crab species (Bueno and Bond-Buckup 2004; Castro-Souza and Bond-Buckup 2004).

The remaining stomach contents included rotifers, tardigrade and mites, albeit with low index values, and were therefore characterized as rare resources that provide occasional but certain essential nutrients (Collins and Paggi 1998; Collins 1999; Williner and Collins 2002). Occasional consumption of other prey as it was encountered could affect the stability of the system and play a role in energy flow from the riparian zone, coupled with the contribution of vegetation sources (Cloe and Garman 1996). In *A. uruguayana*, the cladocerans and rotifers are items that could be considered key for development. Capturing fast-moving prey, such as the cladocerans, requires greater energy expenditure that limits the benefit and highlights the value of selective foraging.

Trophic studies characterized *Anomura* as detrital organisms, although some species may be characterized as macrophages. Nicol (1932) concluded that the carnivore habit is typical of decapods and is secondarily modified, so that in *Anomura*, detrital and planktonic feeding habits predominate in the marine environment. *Aegla uruguayana* combines two food strategies (Romero *et al.* 2004), detritivorous and predator. The evolutionary history of Aegliidae is still recent and some authors believe the species is currently in the process of speciation (D'Amato and Corach 1997).

Conclusions

Digestive tract morphology can affect digestive efficiency and is closely related to food habits. One premise of the studies that relate morphological and ecological aspects is that the first of them are heavily influenced by the second ones (Wainwright and Reilly 1994). The data from this work provide the basis to reject earlier statements about correspondence between morphology and eating habits (Schaefer 1970), while corroborating relationships proposed by Caine (1975). While *A. uruguayana* ossicle descriptions fit a macrophagous pattern it is possible to argue that organisms make certain adjustments to ambient pressures, incorporating in this case micro-organisms and larger prey in the diet. These results, along with

trophic spectrum and selectivity data contribute to the widespread rejection of the theory that morphology acts as a determinant of diet.

Identification of stomach contents allowed us to characterize *A. uruguayana* as omnivore generalists that preferentially consume plant debris and algae, along with a smaller variety of animal items. Within the animal food, the diet is characterized by macroscopic and microscopic prey. Applying the selected indices to stomach content data showed that these anomurans utilize an opportunistic food strategy and highlighted the rare or occasional presence of a significant number of prey items. *Aegla uruguayana* presented two trophic strategies, combining the effects of predation with detritivory. The second strategy is focused mainly on the consumption of altonous plant debris. Future research should focus on determining the usability of plant resources and establish whether crabs can act as shredders or have the ability to degrade cellulose.

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