

# Trophic analysis of two subtropical South American freshwater crabs using stable isotope ratios

Edward D. Burress · Michael M. Gangloff ·  
Lynn Siefferman

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**Abstract** Crustaceans with crayfish- and crab-morphologies do not co-occur often. However, the crab families Aeglidae (crayfish morphology) and Trichodactylidae (crab morphology) are sympatric in many subtropical South American streams. We investigated the trophic status of *Aegla uruguayana* (Aeglidae) and *Trichodactylus panoplus* (Trichodactylidae) in a South American subtropical piedmont river (Cuareim River, Uruguay) using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios. We estimated the relative importance of prey items using a five-source mixing model. Stable isotope analysis revealed that the two crabs have different trophic niches. Three fractionation rates ( $-1$ ,  $0$ , and  $+1$  ‰) influenced the estimated assimilation (%) of prey items to consumers. However, the relative importance of prey items was unaffected. *A. uruguayana* showed an ontogenetic shift from herbivore–detritivore to omnivore. Shared morphology between crayfishes and aeglids likely facilitates similar trophic roles; however, *A. uruguayana* occupies a much lower trophic position than is typical for crayfishes. *T. panoplus* is a

strict herbivore–detritivore. In contrast to tropical crabs, they do not engage in carnivory or exploit terrestrial subsidies. In subtropical South American streams, aeglids may be the functional equivalent of crayfishes, whereas trichodactylids may fill a trophic role atypical for freshwater crabs.

**Keywords** Mixing model · Trophic niche · *Aegla* · *Trichodactylus* · Crustacean

## Introduction

Invertebrate functional roles in stream ecosystems vary considerably across spatial and biogeographic gradients. In Northern Hemisphere streams, crayfish and caddisflies are often the major taxa driving detritivory (Wallace & Webster, 1996; Covich et al., 1999; Benke et al., 2001; Creed & Reed, 2004); however, shrimps or crabs are often the major detritivores in tropical streams (Covich & McDowell, 1996; Covich et al., 1999; Dobson et al., 2002; Zimmerman & Covich, 2003; Boulton et al., 2008; Cross et al., 2008; Lancaster et al., 2008). The trophic niches of many invertebrate taxa are well understood (reviewed in Wallace & Webster, 1996; Covich et al., 1999). However, invertebrate communities in many tropical and subtropical regions are poorly studied and information on basic ecology is lacking.

Crayfish are largely restricted to temperate zones, with most diversity occurring in Nearctic and Australasian regions (Crandall & Buhay, 2008).

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E. D. Burress · M. M. Gangloff · L. Siefferman  
Biology Department, Appalachian State University,  
572 Rivers Street, Boone, NC 28608, USA

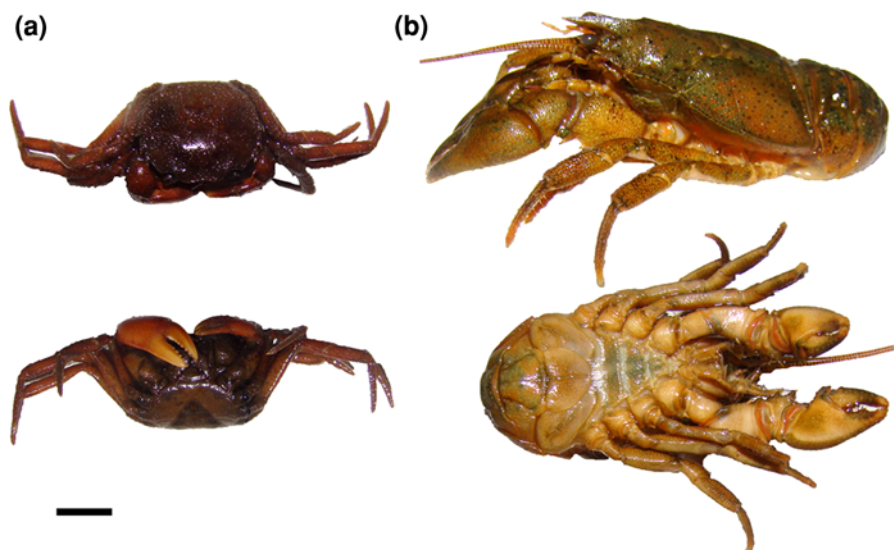
E. D. Burress (✉)  
Department of Biological Sciences, Auburn University,  
331 Funchess, Auburn, AL 36849, USA  
e-mail: burrested@appstate.edu; eb0014@auburn.edu

The distribution of Southern Hemisphere crayfishes is associated with the Gondwanan breakup (Toon et al., 2010). Crayfishes are often integral components of stream communities and have been shown to affect plant and animal community composition (Creed, 1994; Creed & Reed, 2004), organic matter processing (Parkyn et al., 2001), and transport of terrestrial resources into the aquatic food web (France, 1996). Crayfishes are generally considered omnivorous (Creed, 1994; Bondar et al., 2005) but often show ontogenetic shifts to carnivory (Gutiérrez-Yurrita et al., 1998) and may function as predators in some systems (Parkyn et al., 2001). In contrast, the global distribution of freshwater crabs is largely restricted to Neotropical and Oriental regions (Yeo et al., 2008). Crabs also influence organic matter processing (Hill & O'Keefe, 1992; Lancaster et al., 2008) and transport of terrestrial resources into the aquatic food web (Covich & McDowell, 1996; Lancaster et al., 2008). Crabs are typically omnivorous in tropical streams (March & Pringle, 2003; Lancaster et al., 2008), although ontogenetic shifts from carnivory to herbivory–detritivory may be common (Hill & O'Keefe, 1992; Marijnissen et al., 2009). Many species forage on land (Dobson, 2004) and often exploit unusual terrestrial resources such as ants (Lancaster et al., 2008) and palm fruits (A. P. Covich, personal communication). Both crayfishes and crabs are particularly key components of high-gradient stream communities (March & Pringle, 2003; Creed & Reed, 2004; Lancaster et al., 2008). Crayfishes and crabs have a conspicuously

allopatric distribution and share many functional roles in freshwater communities.

Freshwater crabs are found throughout South American subtropical rivers, one with typical crab morphology (Trichodactylidae) and the other with crayfish morphology (Aegliidae) (Fig. 1). In general, these two morpho-types are not thought to co-occur (Rodríguez, 1986), so this region provides a unique system for a comparative analysis of their trophic niches. In allopatry, crayfishes and crabs often exert similar trophic and functional roles. In sympatry, that scenario seems unlikely, particularly considering that these taxa occur in high densities (Collins et al., 2006, 2007), ensuring frequent interactions. The trophic roles of both groups are poorly understood. Bueno & Bond-Buckup (2004) described two aeglids in southern Brazil as omnivorous and noted increased carnivory in larger individuals. Collins et al. (2007) reported *Aegla uruguayana* and *Trichodactylus borellianus* in an Argentinean stream as herbivores–algivores. Castro-Souza & Bond-Buckup (2004) found that there was no seasonal variation in the trophic role of aeglids, perhaps due to the historically dry climate associated with subtropical South America (Iriondo, 1999) restricting seasonal resource fluxes. Furthermore, crabs are important prey items for a variety of aquatic and terrestrial animals in South American streams (Collins et al., 2006; Collins et al., 2007; Bond-Buckup et al., 2008) and are thus potentially important links between aquatic and terrestrial ecosystems.

**Fig. 1** Preserved specimens of **a** *Trichodactylus panoplus* and **b** *Aegla uruguayana* collected from the Rio Cuareim, Uruguay. Voucher specimens are deposited in the Auburn University Natural History Museum and Learning Center (Auburn, AL): *A. uruguayana* (AUM 22709) and *T. panoplus* (AUM 22710). Scale bar 1 cm



We investigated the trophic niche of two sympatric crabs, *Aegla uruguayana* and *Trichodactylus panoplus*, in the Rio Cuareim, a subtropical South American piedmont stream in northwestern Uruguay using stable isotope ratios. Our objectives were twofold. Our first goal was to compare the trophic niche of crabs with both morphologies (crayfish and crab) with prior literature in systems where they occur in allopatry, such as temperate streams (crayfishes) and tropical streams (crabs). Our second goal was to evaluate the trophic position of both crabs relative to the invertebrate food web. We hypothesized that aeglids and trichodactylids occupy distinct trophic niches and that the convergent morphology of aeglids and crayfishes would be conducive to occupying similar trophic niches.

## Methods

Our study area, the Rio Cuareim, is located in subtropical South America (Iriondo, 1999) and drains northwestern Uruguay and southwestern Brazil and is a major tributary to the middle Rio Uruguay (Fig. 2). We manually sampled crabs and potential food items from the upper Rio Cuareim, Uruguay, in November 2010. We recorded carapace length (CL) for *Aegla* and carapace width (CW) for *Trichodactylus* (according to convention for their respective morphologies). We fasted specimens for 72 h to allow for gut clearing and

then froze specimens in the field and later stored them at  $-80^{\circ}\text{C}$ . Biofilm and debris were rinsed from macrophytes, and algae were cleaned of debris using a microscope. Leaf litter was rinsed of debris and invertebrates, but our samples are considered inclusive of associated microbes.

Whole specimens were lyophilized until dry and ground into a homogenous mixture (Anderson & Cabana, 2007). Weighed samples (0.6–1.2 mg) were then transferred into Ultra-Pure tin capsules (Costech Analytical Technologies, Valencia, CA). Stable isotope ratios were analyzed at the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, AZ). Isotope values are expressed in delta notation (‰), which represents deviation from universal standards. Delta notation is calculated as  $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$  (see DeNiro & Epstein, 1978; Post, 2002).

We use a three factor (juvenile and adult *A. uruguayana*, and *T. panoplus*) one-way analysis of variance (ANOVA) and Tukey's post-hoc tests separately for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope ratios. We did not encounter small *T. panoplus*. Their densities may either be extremely low due to predation (Collins et al., 2006; Collins et al., 2007; Bond-Buckup et al., 2008) or they may utilize different habitats (e.g., deep water) that were not surveyed.

The most abundant prey items were sampled based on preliminary surveys and with consideration to the

**Fig. 2** The Rio Uruguay Drainage and the study site, the Rio Cuareim basin (**bold**) located in subtropical South America. *Aegla uruguayana* and *Trichodactylus panoplus* were collected in the headwaters of the Rio Cuareim, along the border of Uruguay and Brazil



prey items described by Bueno & Bond-Buckup (2004). All potential prey items were collected from littoral zones where aeglids and trichodactylids were abundant. Detritus samples are primarily terrestrial leaf based (*Casearia sylvestris*). The only common macrophyte in the Rio Cuareim was *Hydrilla*, which has a patchy distribution. We sampled filamentous green algae from rock surfaces using a scalpel. Filament lengths were 1–3 cm and had a patchy distribution. We sampled seven invertebrates assumed to be representative of the invertebrate food web.

We used a five-source  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  mixing model (Phillips & Gregg, 2003) to estimate percent contribution of potential prey items (Table 1) to *A. uruguayana* and *T. panoplus* diets. Mass balance tolerance was set to 0.3 ‰ and source increment was set to 1 ‰ (Hoeinghaus & Davis, 2007). Fractionation is the relative change in stable isotope ratios across a trophic transfer (from prey to consumer) and is possibly the primary assumption involved in stable isotope interpretation (reviewed in Gannes et al., 1997; Post, 2002). We corrected for  $\delta^{15}\text{N}$  fractionation using the mean rate of 2.54 ‰ reported from a meta-analysis of fractionation rates (Vanderklift & Ponsard, 2003) and accepted for marine crabs (Hoeinghaus & Davis, 2007). Mixing models are particularly sensitive to the fractionation value incorporated into the model. Additionally, isotopic fractionation has been shown to be variable in marine crabs, particularly  $\delta^{13}\text{C}$  fractionation (Frantle et al., 1999). Therefore, we report mixing model estimations based on three  $\delta^{13}\text{C}$  fractionation corrections (+1, 0, and  $-1$  ‰). These rates encompass accepted fractionation rates for marine crabs (0 ‰; Hoeinghaus & Davis, 2007) and liberal enrichment (+1 ‰) and depletion ( $-1$  ‰) alternatives that span the variation reported in marine crabs (Frantle et al., 1999). Variation in fractionation results from consuming items with high- (i.e., plants) and low- (i.e., animals) C/N ratios (Rudnick & Resh, 2005; Lancaster et al., 2008). Because aeglids and trichodactylids do not consume all

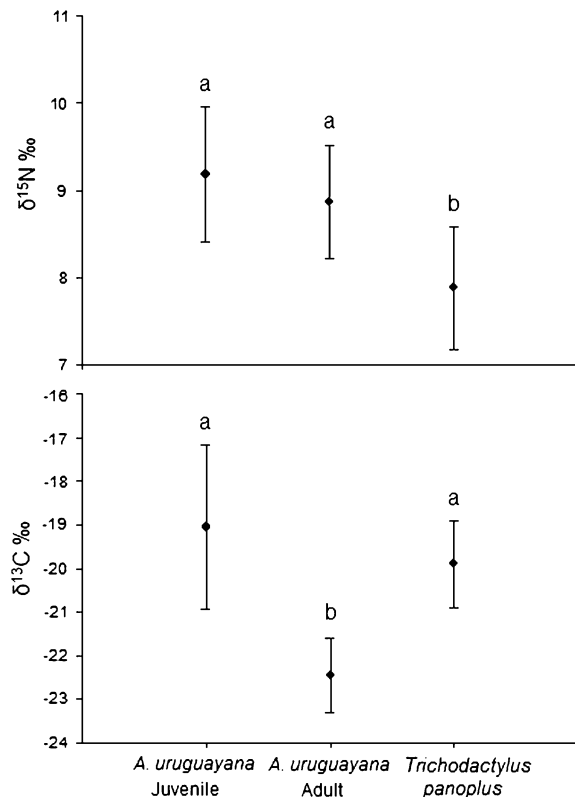
invertebrates we sampled (e.g., belostomatids; Bueno & Bond-Buckup, 2004; Collins et al., 2007), we included only the most representative prey items in our model (leptophlebiids and hydropsychids; Bueno & Bond-Buckup, 2004; Collins et al., 2007). Because these two prey items display different  $\delta^{15}\text{N}$  signatures, we did not pool them (i.e., Phillips et al., 2005). Collectively, they should represent the spatial range between grazers and collectors and provide an estimation of invertebrate contributions to aeglid and trichodactylid diets. For all additional statistical analyses, we used SPSS (ver. 17.0; SPSS, Inc., Chicago, IL). Species were identified using meristics outlined in Martin & Abele (1988) for *A. uruguayana* and Magalhaes (2003) for *T. panoplus*. Voucher specimens are deposited in the Auburn University Natural History Museum and Learning Center (Auburn, AL): *A. uruguayana* (AUM 22709) and *T. panoplus* (AUM 22710).

## Results

Potential food sources (algae, leaf litter, macrophytes, and benthic invertebrates) displayed distinct isotopic signatures (Table 1) allowing for high-source discrimination by the mixing model. Juvenile (CL  $10.8 \pm 1.1$  mm) and adult *A. uruguayana* ( $27.27 \pm 1.8$  mm) displayed significantly different  $\delta^{13}\text{C}$  ratios ( $P < 0.0001$ ; Fig. 3), suggesting a shift in the relative importance of C sources. There was no significant difference in  $\delta^{15}\text{N}$  ratios of juveniles and adults ( $P > 0.05$ ; Fig. 3), suggesting *A. uruguayana* feeds within the same trophic level in both life stages. Mixing model results suggest that generally two prey items are obligate for each class regardless of the  $\delta^{13}\text{C}$  fractionation rate used in the model (Table 2). Aquatic macrophytes were the only primary food item of juvenile *Aegla* but they secondarily assimilated algae, detritus, and larval insects (Table 2). Adult *Aegla* primarily assimilated detritus and larval insects. *T. panoplus* (CW  $12.6 \pm 2.7$  mm) displayed

**Table 1** Stable isotope ratios (mean  $\pm$  SD) of potential prey items of *Aegla uruguayana* and *Trichodactylus panoplus* in the Rio Cuareim, Uruguay

Sources	<i>n</i>	C/N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Filamentous algae	5	12.1 $\pm$ 0.1	$-20.6 \pm 0.4$	7.5 $\pm$ 0.6
Leaf Litter	3	22.9 $\pm$ 1.4	$-23.5 \pm 0.1$	3.1 $\pm$ 0.3
<i>Hydrilla</i>	3	23.0 $\pm$ 2.2	$-16.9 \pm 0.5$	6.6 $\pm$ 0.6
Hydropsychidae	20	5.4 $\pm$ 0.1	$-21.1 \pm 0.4$	10.5 $\pm$ 0.3
Leptophlebiidae	16	5.7 $\pm$ 0.7	$-20.8 \pm 0.6$	9.3 $\pm$ 0.2



**Fig. 3** Results of ANOVA post-hoc (Tukey HSD) comparisons (for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) between juvenile ( $n = 9$ ) and adult ( $n = 8$ ) *Aegla uruguayana* and *Trichodactylus panoplus* ( $n = 6$ ) from the Rio Cuareim, Uruguay. Stable isotope ratios are mean  $\pm$  SD. Letters denote significant comparisons

significantly different  $\delta^{15}\text{N}$  ratios than juvenile ( $P = 0.004$ ) and adult ( $P = 0.036$ ) *A. uruguayana* (Fig. 3). There was a significant difference in  $\delta^{13}\text{C}$  ratios between *T. panoplus* and adult *A. uruguayana* ( $P = 0.005$ ), but not between *T. panoplus* and juvenile *A. uruguayana* ( $P > 0.05$ ; Fig. 3). Because there were not distinct size classes for *Trichodactylus* (CW 9.1–15.5 mm), we could not adequately analyze ontogenetic diet shifts. However, using regressions, we found no significant relationship between carapace width and  $\delta^{13}\text{C}$  ( $R^2 = 0.06$ ,  $F_{2,6} = 0.33$ ,  $P = 0.59$ ) or  $\delta^{15}\text{N}$  ratios ( $R^2 = 0.18$ ,  $F_{2,6} = 1.12$ ,  $P = 0.34$ ), nor did we find a significant relationship between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios ( $R^2 = 0.08$ ,  $F_{2,6} = 0.42$ ,  $P = 0.55$ ). Compared to other invertebrate taxa, both crabs displayed relatively low-trophic positions (Fig. 4).

Our data demonstrate that the proportion (%) of estimated assimilation was influenced by the

fractionation rate incorporated into the mixing model. Prey item assimilation often varied 20–30 % and up to 50 % depending upon assumed fractionation rates (Table 2). However, the relative importance of prey items was unaffected by fractionation assumptions. The most important or obligate (i.e., 1st–99th percentile does not zero) items were conserved across multiple fractionation rates (Table 2). For example, *T. panoplus* displayed obligate assimilation of macrophytes and detritus in all models.

## Discussion

Stable isotopes reveal that aeglids and trichodactylids have different trophic niches in the Rio Cuareim, but that there is an ontogenetic component to their trophic relationship. *A. uruguayana* shifts from herbivore–detritivore as juveniles to omnivore as adults. *A. uruguayana* share many trophic characteristics with crayfishes and may be functional equivalents in subtropical South American streams. *T. panoplus* are superficially similar to shrimps and crabs in tropical systems in that they are herbivore–detritivores. However, in contrast to many tropical crabs, trichodactylids do not appear to engage in carnivory. Both subtropical crabs also have lower trophic positions than their temperate or tropical counterparts. Mixing models indicate that fractionation correction influences the relative assimilation (%) of prey items by freshwater crabs but does not change the relative importance of prey items.

*Aegla uruguayana* exhibit ontogenetic diet shifts and assimilate a larger proportion of invertebrates in later life stages, a pattern also shared with subtropical *A. platensis* and *A. ligulata* (Bueno & Bond-Buckup, 2004) and temperate crayfish (Gutiérrez-Yurrita et al., 1998). *A. ligulata* shift from consuming ~8 % invertebrates (by volume) to 20 % throughout ontogeny and *A. platensis* from 8.5 to 10.5 % (Bueno & Bond-Buckup, 2004). This is lower than the estimated 16.5–43 % for *A. uruguayana* according to our isotopic analyses. However, in crayfish, estimated assimilation of invertebrates can be higher than consumption (Hollows et al., 2002). This is likely due to preferential assimilation of invertebrates compared to lower quality foods (Whiteledge & Rabeni, 1997), such as detritus, which is the primary diet item for *A. uruguayana*. The contribution ranges (1st–99th

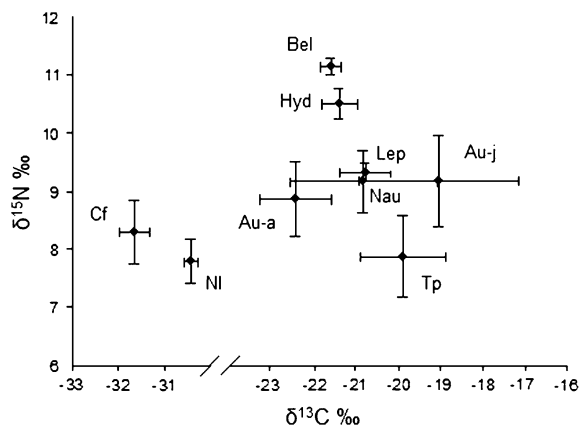
**Table 2** Percent contribution of food items to *Aegla uruguayana* and *Trichodactylus panoplus* diet estimated by a five-source  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  mixing model after three  $\delta^{13}\text{C}$

fractionation corrections: +1: enrichment, 0: no enrichment, -1 ‰: depletion relative to prey

Food source	Juvenile <i>A. uruguayana</i>	Adult <i>A. uruguayana</i>	<i>T. panoplus</i>
-1 $\delta^{13}\text{C}$ ‰			
Algae	21.2 (0–61)	0.3 (0–1)*	11.3 (0–35)
Macrophyte	<b>34.6 (21–46)</b>	0 (0–0)*	<b>29.7 (20–39)</b>
Detritus	<b>22.5 (11–32)</b>	<b>60 (59–61)*</b>	<b>47.8 (40–55)</b>
Hydropsychidae	9.3 (0–27)	<b>39.3 (39–40)*</b>	4.8 (0–15)
Leptophlebiidae	12.3 (0–36)	0.3 (0–1)*	6.5 (0–20)
0 $\delta^{13}\text{C}$ ‰			
Algae	15.3 (0–45)	4.9 (0–18)	6.1 (0–21)
Macrophyte	<b>53.8 (43–63)</b>	0.9 (0–4)	<b>48.3 (41–56)</b>
Detritus	<b>14.5 (5–22)</b>	<b>51.2 (47–55)</b>	<b>39.4 (34–46)</b>
Hydropsychidae	7.6 (0–23)	<b>29.9 (3–47)</b>	2.9 (0–43)
Leptophlebiidae	8.9 (0–27)	13.1 (0–43)	3.4 (0–12)
+1 $\delta^{13}\text{C}$ ‰			
Algae	9.5 (0–30)	23.6 (0–65)	2.0 (0–8)
Macrophyte	<b>73.9 (65–82)</b>	10.5 (0–22)	<b>65.3 (61–71)</b>
Detritus	6.9 (0–14)	<b>38.5 (26–48)</b>	<b>31 (28–34)</b>
Hydropsychidae	4.1 (0–14)	11.8 (0–33)	0.7 (0–3)
Leptophlebiidae	5.6 (0–18)	15.5 (0–43)	1.0 (0–4)

Values are mean contribution (1st–99th percentile in parenthesis). Items with obligate assimilation (contribution ranges do not zero) are indicated in *bold*

\*Undefined using -1  $\delta^{13}\text{C}$  ‰ correction because the mixture fell out of bounds (i.e., outside the polygon of sources) therefore, listed contributions are after -0.5  $\delta^{13}\text{C}$  ‰ correction



**Fig. 4** Mean ( $\pm$ SD) stable isotope ratios of invertebrates in the Rio Cuareim, Uruguay. Abbreviations are as follows: Cf—*Corbicula fluminea*, NI—*Neocorbicula limosa*, Bel—Belostomatidae, Hyd—Hydropsychidae, Lep—Leptophlebiidae, Nau—Naucoridae, Au-a—adult *A. uruguayana*, Au-j—juvenile *A. uruguayana*, and Tp—*Trichodactylus panoplus*

percentile) of invertebrates also suggest that mean contribution data may overestimate assimilation rates. Large contribution ranges provide for ambiguous interpretation of mixing model results (Phillips & Gregg, 2003; Benstead et al., 2006). However, with subtropical crabs, obligate prey items explain a large proportion of the diet (60–90 %) and have constrained contribution ranges (max–min contributions <20 %), thus allowing for strong inference about dietary patterns.

Enriched  $\delta^{15}\text{N}$  ratios are often associated with increased carnivory (Post, 2003). However, although the  $\delta^{15}\text{N}$  difference is not statistically significant, larger *A. uruguayana* display lower average  $\delta^{15}\text{N}$  signatures than juveniles despite higher assimilation of invertebrates. This phenomenon has also been shown in crayfishes (Parkyn et al., 2001; Bondar et al., 2005). We assume that the incorporation of a larger proportion of  $\delta^{15}\text{N}$ -enriched invertebrates is mitigated by a larger proportion of  $\delta^{15}\text{N}$ -depleted detritus.

In crayfishes, assimilation efficiencies are higher for invertebrates than plant detritus (Whiteledge & Rabeni, 1997). Diets consisting of protein-rich invertebrates also result in faster growth rates (Bondar et al., 2005) demonstrating a benefit to consuming animal material rather than plant material. Thus, increased consumption of detritus in adults could be an inadvertent side effect of foraging for invertebrates. This observation is consistent with aeglids affinity to habitats rich in leaf fragments and twigs (Bücker et al., 2008).

Aeglids, like crayfishes, appear to be omnivorous. Ontogenetic shifts to carnivory and reductions in  $\delta^{15}\text{N}$  ratios are also shared characteristics with crayfishes (Gutiérrez-Yurrita et al., 1998; Parkyn et al., 2001; Bondar et al., 2005). The convergent morphology between crayfishes and aeglids may be key in these shared functional roles. However, aeglids have distinctly lower trophic positions than crayfishes. Crayfishes typically have higher trophic positions (based on  $\delta^{15}\text{N}$  ratios) than other invertebrates such as mayflies and caddisflies (Parkyn et al., 2001; Bondar et al., 2005), suggesting that they can function as top invertebrate predators in some systems. In contrast, we found that aeglids have lower trophic positions than mayflies and caddisflies. Indeed, of all invertebrate taxa sampled, only bivalves and trichodactylids had lower trophic positions. Assimilation of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  may be decoupled in crabs (Lancaster et al., 2008), thus aeglids may preferentially assimilate detrital  $\delta^{15}\text{N}$  relative to crayfishes, particularly considering crayfishes are known to preferentially assimilate invertebrates relative to plants (Whiteledge & Rabeni, 1997).

*Trichodactylus panoplus* displays trophic characteristics of an herbivore–detritivore. This is similar to the trophic roles of crabs in tropical systems (Dobson et al., 2002; Dobson, 2004). However, crabs are often opportunistically carnivorous (Dobson, 2004) and, depending on the extent, may be functional omnivores (March & Pringle, 2003) or top-predators (Marijnissen et al., 2009) in their respective invertebrate communities. Based on mixing model estimations and their low-trophic position relative to other invertebrates, it is unlikely that *T. panoplus* engages in carnivory. Furthermore, trichodactylids do not appear to exploit terrestrial prey (Collins et al., 2007) and we did not observe *T. panoplus* on land. Thus, crabs in subtropical South America appear to deviate from their

tropical counterparts. Fidelity to in situ resources may prevent these crabs from transporting some terrestrial resources into the aquatic food web. However, predation by numerous terrestrial predators including birds, mammals, reptiles, and amphibians (Collins et al., 2007 and references therein) provides transport of autochthonous resources to the terrestrial food web. This difference in food web connectivity suggests further contrasts to tropical systems, where crabs frequently forage on land (Dobson, 2004) and predation is often low (Dobson et al., 2007; Lancaster et al., 2008). This difference is likely because wet tropical montane environments are more conducive to overland excursions by crabs (Dobson et al., 2007; Lancaster et al., 2008). The arid prairie environment of Uruguay and southern Brazil (Iriondo, 1999) likely prohibits this behavior.

Although their feeding behavior is infrequently studied, freshwater crabs are likely important components of many subtropical South American stream ecosystems. *A. uruguayana* has trophic characteristics that mirror those observed in Northern Hemisphere temperate crayfishes (Cambaridae, Astacidae; Gutiérrez-Yurrita et al., 1998; Bondar et al., 2005; Stenroth et al., 2008) and Southern Hemisphere temperate crayfishes (Parastacidae; Parkyn et al., 2001). These patterns are also consistent with other aeglid taxa (Collins et al., 2007; Santos et al., 2008). Future studies are needed to determine whether like crayfish, aeglids are ecosystem engineers and keystone species (Feminella & Resh, 1989; Creed, 1994; Usio, 2000; Creed & Reed, 2004; Dorn & Wojdak, 2004; Bengtson et al., 2008). Furthermore, herbivory in streams can have dramatic effects on competitors as well as on taxa that rely on macrophytes for cover or reproduction (reviewed in Feminella & Hawkins, 1995). Thus, the effects of trichodactylids in South American stream ecosystem processes are likely important ecologically and deserve further study, especially now that their distributions and evolution are increasing being documented (Pérez-Losada et al., 2002; Pérez-Losada et al., 2004; Campos 2005; Pérez-Losada et al., 2009).

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