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Trophic roles of tadpoles in tropical Australian streams

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Abstract

1. Tadpoles can be abundant consumers in stream ecosystems and may influence the structure and function of streams through their feeding activities and interactions with other organisms. To understand the contribution of tadpoles to stream functioning, and the potential impact of their loss, it is necessary to determine their diets and how they might influence food-web structure.

2. Using gut content analysis and stable isotope analysis of N and C, we determined the main food sources and trophic positions of tadpoles of five native frog species, invertebrates and fish in upland and lowland Australian Wet Tropics streams.

3. Omnivory was prevalent amongst the tadpoles and invertebrates. Tadpoles consumed different food according to availability and nutrient quality, but assimilated mainly biofilm and algae. Most tadpoles and invertebrates assimilated the same high-quality foods.

4. Food webs in upland riffles were simplified by local extinction of tadpoles, and were probably simplified in pools in the cooler months by seasonal decline in tadpole abundance. Food web complexity was increased in some pools by the presence of predatory fish and a greater number of basal sources.

5. As tadpoles are important seasonal components in stream food webs, their local extinction can greatly alter food web structure and complexity and, possibly, processes such as leaf litter breakdown and sediment accumulation.

Introduction

To understand functioning of stream systems, especially in the face of environmental change and species loss (Dudgeon *et al.*, 2006), we need community models that incorporate trophic interactions and roles of key taxa from diverse regions of the world (Pearson, Connolly & Boyero, 2015). These interactions and roles may be visualised in food webs that qualitatively or quantitatively illustrate important trophic networks. Trophic models for forested headwater streams, based on gut contents analysis of animals, typically indicate that terrestrial leaf litter provides the energetic and material base of the food web (e.g., Cummins, 1973; Vannote *et al.*, 1980; Cheshire, Boyero & Pearson, 2005; Neres-Lima *et al.*, 2017). However, stable isotope analyses of food web components suggest that algae are also important components of these food webs (Bunn, Davies & Mosisch, 1999; Mantel, Salas & Dudgeon, 2004; Dudgeon, Cheung & Mantel, 2010; Rosi-Marshall *et al.*, 2016), highlighting the importance of using a variety of methodological approaches to fully describe food webs.

Small streams are characterised by abundant and diverse invertebrates, but tadpoles can also be abundant and are likely to play key roles in food webs and ecosystem function (Allan & Castillo, 2007). Tadpoles feed on algae, sediments, detritus and other animals (Flecker, Feifarek & Taylor, 1999; Ranvestel *et al.*, 2004; Whiles *et al.*, 2006), with some species specialising at a single trophic level, some changing their diets according to resource availability, and others showing ontogenetic dietary shifts (Hocking & Babbitt, 2014). Food quantity and quality for tadpoles may differ among streams (Whiles *et al.*, 2010): thus, while heavily shaded streams are primarily heterotrophic, more open streams tend to be autotrophic, with abundant primary producers such as filamentous algae and diatoms (Anderson & Sedell, 1979). Food availability may also differ among habitats: for example, riffle-associated tadpoles may consume algae and fine detritus, whereas pool-dwelling species in the same stream may consume coarser detritus, which is more readily available in pools (Trenerry, 1988). Epilithic biofilm can also be an important basal food source for tadpoles in both riffles and pools (Trenerry, 1988; Cashins, 2009; Whiles *et al.*, 2010; Frauendorf *et al.*, 2013). Stable isotope analysis has shown that some tadpoles are generalist feeders that change their food sources based on availability (Francis, 2013; Huckembeck *et al.*, 2014), while others are more specialised (Verburg *et al.*, 2007).

Globally, research on the role of tadpoles in stream food webs is limited mainly to the Neotropics (e.g., Verburg *et al.*, 2007; Colon-Gaud *et al.*, 2010; Winemiller *et al.*, 2011; Barnum *et al.*, 2013; Frauendorf *et al.*, 2013). In the Australian Wet Tropics bioregion (hereafter "Wet Tropics"), tadpoles are conspicuous members of the stream fauna through the warmer months (Richards, McDonald & Alford, 1993), and may be major components of food webs. The gut contents of some species have been described (e.g., Trenerry, 1988), but we know little about their dominant food source or what they assimilate. Upland populations of many species, particularly riffle-dwellers, declined or disappeared during the late 1980s and early 1990s as a result of the fungal disease chytridiomycosis (Richards *et al.*, 1993; McDonald & Alford, 1999). These declines may have caused major changes to food webs, as reported for similar declines in the Neotropics (Ranvestel *et al.*, 2004; Colon-Gaud *et al.*, 2008; Connelly *et al.*, 2008; Colon-Gaud *et al.*, 2009).

We aimed to understand the trophic role of tadpoles in forested stream ecosystems in the Wet Tropics uplands and lowlands, and possible effects of their disappearance. We used stable isotope analysis to determine the basal food sources and the trophic positions of tadpoles and other consumers in riffle and pool communities. We hypothesised that (1) detritus would be the predominant basal food source, in common with other small forest streams; (2) tadpoles would therefore be mainly detritivores; (3) tadpoles would seasonally influence food web structure (in the summer months); and, therefore, (4) loss of tadpoles from riffle sites would greatly simplify food webs compared with adjacent pools.

Methods

Study species, sites, and sample collection

The Wet Tropics is a discrete, biodiverse region in north-eastern Queensland (Pearson *et al.*, 2015; Fig. S1) and has a seasonal climate with a distinct wet season during the summer months, from November to March. Sampling was conducted in Paluma Range National Park in

September 2012 and November 2013, and in Tully Gorge National Park in November 2013 (Fig. S1), to include representative upland and lowland streams (Pearson *et al.*, 2017). These streams have high diversity of invertebrates (Pearson & Boyero, 2009; Pearson *et al.*, 2017) and moderate diversity (up to seven species) of stream-breeding anurans (Cashins, 2009) (cf. 23 species at a Panamanian site; Lips, Reeve & Witters, 2003). Currently, frog species with stream-dwelling tadpoles recorded from Paluma uplands are the pool dwellers *Litoria serrata* and *Mixophyes coggeri*. Historically, two riffles species, *Litoria dayi* and *L. nannotis*, also occurred in this area, but they disappeared in the early 1990s as a result of chytridiomycosis (Richards *et al.*, 1993). Species recorded from Tully lowlands are *L. dayi*, *L. nannotis*, *L. rheocola* and *L. serrata*, which all remained following the declines in the uplands (C. Hoskin, pers. comm.). The conservation status of these species ranges from least concern (*L. serrata* and *M. coggeri*) to endangered (*L. nannotis, L. rheocola* and *L. dayi*) (Hoskin & Hero, 2008).

The study streams were perennial and flowed through closed rainforest ("simple notophyll vine forest"; Tracey, 1982). Six riffles and six pools were sampled in each of the study areas (Paluma and Tully). At Paluma, two pools and two riffles were sampled in each of three upland streams (sites P1, P2, and P3), while at Tully three pools and three riffles were sampled in each of two lowland streams (sites T1 and T2) (Table 1). The riffles and pools within a site were 100 – 200 m apart, with a reach length of approximately 10 m each. The streams comprised approximately 15 % riffles, 60 % runs and 25 % pools at Paluma and 30 % riffles, 50 % runs and 20 % pools at Tully. Physicochemical data recorded at each riffle or pool included: pH, conductivity and dissolved oxygen, measured using a Hydrolab Quanta; depth; and percent canopy cover and substratum composition, estimated visually. Current velocity was measured monthly using an Owen's River Hydroprop. Algal cover was estimated visually as percent cover in pools and riffles along a 150-m transect, each month between October 2011 and September 2013, as part of seasonal tadpole surveys in streams at Paluma and Tully (Schmidt, 2016).

Collection of food web components was undertaken in the late dry season, when streams were at base flow and frog breeding was in progress. In September 2012, we collected invertebrates, tadpoles, fish and basal food sources at the Paluma sites. In November 2013, we collected additional tadpoles at the Paluma sites, and tadpoles and basal sources at the Tully sites. Invertebrates and fish were not collected at Tully for logistic reasons.

Dip-net sweeps with a triangular net (mesh size 0.9 x 0.3 mm) were used to collect tadpoles and larger invertebrates from riffles, pools, and any submerged vegetation. The net was bounced along the substratum to force animals into the water column where they could be captured, and loose rocks were dislodged to expose sheltering tadpoles and invertebrates. Sampling commenced at the downstream end of each pool or riffle and continued without a time limit to the other end of the habitat, to ensure that sufficient material was collected for stable isotope analysis (SIA) (minimum 1 mg dry mass per item). Tadpoles were separated by species, weighed and euthanised in a solution of 0.02 % MS-222 buffered with sodium bicarbonate (Braunbeck *et al.*, 2007). Tadpoles not needed for SIA analysis were released. The tadpoles were between Gosner stages 25 and 31 (Gosner, 1960) and were grouped into small, medium and large length classes (Richards, 2002). For *M. coggeri* tadpoles these classes were: < 10 mm, 10 to < 22 mm, and ≥ 22 mm, respectively; for other species they were: < 7.5 mm, 7.5 to < 12 mm, and ≥ 12 mm, respectively. Invertebrates were rinsed with distilled water. A Smith-Root Model 12B backpack electrofisher was used to catch fish (the eel, *Anguilla reinhardtii*, and the gudgeon, *Mogurnda adspersa*) and large crustaceans (crayfish, *Cherax* sp., Parastacidae; and shrimp, *Macrobrachium* sp., Palaemonidae). Individuals of *A. reinhardtii* were weighed, fin-clipped, then released. Only small individuals of *M. adspersa* were caught, and were euthanised. These mobile species (fish and decapods) are locally resident for most of their lives (Whitehead, 1985; Coughlan, 1990; B. Pusey, pers. comm.). All faunal samples were placed on ice and returned to the laboratory.

Basal sources collected from each habitat were: leaf litter (whole leaves); coarse and fine particulate organic matter (CPOM and FPOM, > 1mm or < 1mm, respectively); filamentous algae; biofilm; periphyton; and an iron matrix (Blanchette *et al.*, 2014), present only in one pool. The terms “biofilm” and “periphyton” are often used interchangeably to describe the organic layer growing on solid surfaces (Rasmussen, 2010; Ishikawa, Doi & Finlay, 2012;

Bunn, Leigh & Jardine, 2013), but we differentiated between them: periphyton comprised mainly algae, recognisable by its green colour, growing on sandy substrata at pool edges, and was removed directly to zip-lock bags; biofilm, which likely comprised a matrix of microorganisms, fine detritus and small amounts of algae (Lock *et al.*, 1984), was collected by scrubbing rocks and washing the material into plastic containers with distilled water. CPOM and FPOM did not accumulate in the riffles, but were collected from pools and washed through sieves of 1-mm and 250-µm mesh to produce samples of about 500 ml each. All material was placed on ice and frozen on return to the laboratory.

Sample processing for stable isotope and gut content analyses

In the laboratory, samples were rinsed with distilled water before processing. Tadpoles' guts were removed for gut content analysis. A sample of material from each gut was removed, mixed with a drop of water, placed on a glass slide and identified under a microscope at x 40 magnification. The proportion of each food type was estimated as a percentage of the total volume of particles present to the nearest 5 %, following Cheshire *et al.* (2005). For SIA we used whole bodies of small tadpoles (excluding the gut), but only the tail muscle for large individuals (Caut *et al.*, 2013). Tadpoles of different species, and size classes where possible, were kept separate for the analysis, as diet may vary with tadpole stage (Werner & Gilliam, 1984).

Invertebrates were separated to genus or higher taxon, depending on amount of material available, and into feeding groups (Merritt & Cummins, 1984; Gooderham & Tsyrlin, 2002; Cheshire *et al.*, 2005); taxa from the same feeding group and habitat within an order were combined if necessary to achieve an adequate sample size (Table S5). For most invertebrates, the whole body was analysed because individuals were small. For crustaceans, only the tail muscles were analysed. Fin clips of *A. reinhardtii* were used whole, while *M. adspersa* were analysed with the axial skeleton, scales and guts removed. Isotopic analyses were based on samples of 106 tadpoles (Paluma: 50 *L. serrata*, 14 *Mixophyes coggeri*; Tully: 13 *L. serrata*, 11 *L. nannotis*, 12 *L. rheocola*, 6 *L. dayi*), 5365 invertebrates, 3 *A. reinhardtii* and 8 *M. adspersa*.

CPOM and FPOM samples were rinsed with distilled water and whole leaves were rinsed, dried and homogenised using a coffee grinder. All samples were oven-dried at 60°C for 48 hours and weighed. The invertebrates were weighed to provide estimates of dry mass per taxon. Tadpole wet mass was converted to dry mass using regressions based on samples of 8 to 14 individuals per species. For fish, body length measurements were used to estimate dry mass (Pusey, Kennard & Arthington, 2004). All samples were ground to a fine powder using a mortar and pestle, except for some very small samples, which were sent for analysis intact.

Analysis for δ^{15}N, δ^{13}C, % N and % C was conducted by the Stable Isotope Laboratory at the University of Hong Kong using a continuous flow stable isotope ratio mass spectrometer (Nu Instruments, Perspective series) connected to an elemental analyser (Eurovector EA3028). Isotope values were normalised with a certified acetanilide reference standard. Vienna Pee Dee Belemnite and atmospheric nitrogen were used as standard references for carbon and nitrogen respectively (Peterson & Fry, 1987).

Data analyses

We used ^{13}C as a measure of basal food source and ^{15}N as an indicator of trophic position (Peterson & Fry, 1987). Mean δ^{15}N and δ^{13}C ratios of basal sources and consumers were plotted across sites using raw isotopic data (Whiles *et al.*, 2006). For fish with a C:N ratio greater than 3.5, lipid correction was applied to the isotopic carbon values using the equation $\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99\ (C{:}N_{bulk})$, where *normalised* refers to tissues that are lipid-extracted and *untreated* refers to bulk tissues (Post *et al*. (2007). For tadpoles with a C:N ratio greater than 3.5, the correction used the equation $\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 1.11 + 0.37\ (C{:}N_{bulk})$, which was derived for tadpoles (Caut *et al.*, 2013). Correction is unnecessary for invertebrates (Kiljunen *et al.*, 2006; Logan *et al.*, 2008).

The C:N ratio of basal sources was calculated to compare their nutritional quality (Iwai & Kagaya, 2007), with a lower C:N ratio generally indicating higher quality food (Gulis *et al.*, 2004; Iwai, Kagaya & Alford, 2012). Standard deviations for C:N ratios and basal-source contributions were calculated using data per stream site or data from all sites per area if the basal source was found in only one pool or riffle within an area. Standard deviation was not included for the iron matrix C:N ratio because it was found in only one pool. However, for the basal-source contribution of the iron matrix, the mean standard deviation of the other basal sources from the same stream was used to facilitate inclusion in the model (Blanchette *et al.*, 2014). Where appropriate, C:N ratios were compared using ANOVA in S-Plus.

The relative contribution of basal sources to consumer isotopic signature was modelled with a two-source mixing model using Stable Isotope Analysis in R (SIAR, version 3.2.5). This enables analyses of several basal sources simultaneously to produce the most likely dietary scenarios (Parnell *et al.*, 2010). The model was run using one of two commands, with 500,000 iterations, of which the first 50,000 were discarded: we used “siarmcmcdirichletv4” when multiple data points were available for each consumer taxon, and “siarsolomcmcv4” for single data points. Riffle and pool samples of basal sources were combined within sites, but sites were kept separate, and only sources found at a site were included.

Basal sources within a site were combined if their carbon isotope signatures differed by less than 1.0 ‰, except that allochthonous and autochthonous sources were always kept separate (Table S1). Other studies have used a threshold of 2.0 ‰ (e.g., Blanchette *et al.*, 2014), but as the signatures of most sources differed by less than this, a smaller threshold was required. Where basal sources within a stream site were combined, the overall average isotopic signatures and standard deviations were used for the mixing models.

SIAR requires the input of trophic enrichment factor (TEF) values, which represent the change in ratio of heavy to light isotopes from resource to consumer (Peterson & Fry, 1987), to place the consumers within the source geometry. We used tadpole TEF values of 3.80 ± 0.46 ‰ for $\Delta^{15}N$ and 1.19 ± 0.31 ‰ for $\Delta^{13}C$, following Caut et al. (2013). For invertebrates, the $\Delta^{15}N$ values used were 0.6 ± 1.7 ‰ for herbivores and 1.2 ± 1.3 ‰ for predators (Bunn *et al.*, 2013). A $\Delta^{15}N$ value of 3.7 ± 2.2 ‰ for predatory fish (Bunn *et al.*, 2013) was used for *M. adspersa* and *A. reinhardtii*, which are known predators (Sloane, 1984; Hortle & Pearson, 1990; Pusey *et al.*, 2010). For $\Delta^{13}C$, a TEF value of 0.4 ± 1.3 ‰ was used for invertebrates and fish (Post, 2002; Blanchette *et al.*, 2014).

Consumers that fell outside the SIAR isotopic mixing space were excluded from analyses and their models were considered to be unresolved (see Blanchette *et al.*, 2014). Sources with a minimum contribution of 20 % were considered “likely” contributors, and sources with a minimum contribution of less than 20 %, and a maximum of greater than 50 % were considered “possible” contributors (Blanchette *et al.*, 2014).

The variability of $\delta^{15}N$ in basal sources was standardised by obtaining a baseline relationship between $\delta^{15}N$ and $\delta^{13}C$ for primary consumers, which was used to calculate isotopic trophic position for higher consumers (Vander Zanden & Rasmussen, 1999; Blanchette *et al.*, 2014). The baseline equation was obtained from invertebrates usually considered to be primary consumers (grazers, gatherers, filterers or shredders) (Cheshire *et al.*, 2005). Tadpoles are likely to be omnivores (Alford, 1999) and were therefore not included in the equation estimate. The baseline equation for primary consumers was $\delta^{15}N_{base} = 14.224 + (0.344 * \delta^{13}C)$, $r^2 = 0.388$, $n = 33$, $P < 0.0001$.

Consumer isotopic trophic position (ITP) was calculated using the equation: $ITP = [(\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta^{15}N] + 2$, where $\delta^{15}N_{consumer}$ is the isotopic measure of the consumer in question, $\delta^{15}N_{base}$ is calculated from the $\delta^{13}C$ of the consumer using the baseline equation (above), and $\Delta^{15}N$ is the mean trophic fractionation of $\delta^{15}N$ between basal sources and consumers (Winemiller *et al.*, 2011). For $\Delta^{15}N$, a value of 3.8 ‰ was used for tadpoles (Caut *et al.*, 2013), 3.7 ‰ for predatory fish (Bunn *et al.*, 2013), and 1.2 ‰ for invertebrates (Bunn *et al.*, 2013). ITPs approximating integer values were allocated to that trophic level. Values of 1.9 - 2.1 indicated primary consumers and values of 2.9 - 3.1 indicated secondary consumers, while ITPs that were not close to an integer indicated omnivory (Thompson *et al.*, 2007). ITPs were compared using one-way ANOVA followed by Tukey’s post-hoc tests in S-Plus, using pooled samples from all sites within each consumer group for tadpoles, herbivorous invertebrates, predatory invertebrates and fish.

Food webs

Food webs were constructed for pools and riffles for Paluma sites only, as invertebrates and fish were not collected at Tully. Invertebrate consumers were categorised according to their feeding behaviours (Merritt & Cummins, 1984; Gooderham & Tsyrlin, 2002; Cheshire *et al.*, 2005; Whiles *et al.*, 2013). The tadpoles of the two pool species, *L. serrata* and *M. coggeri*, were grouped together in the food webs because they had similar isotopic trophic positions. Trophic positions were assigned using the stable isotope data for consumers, and links were added according to the SIAR analysis. The isotopic trophic positions for invertebrates were variable so were used in combination with information from the literature (e.g., Cheshire *et al.*, 2005) to construct food webs.

The relative importance of basal resources to the primary consumers was estimated using the mean probability value of the 95 % CI obtained from the SIAR model (basal sources were not combined for this analysis). The values were calculated separately for each primary consumer group and the mean value (per consumer group from all the sites) was calculated as a measure of importance. This was only done for primary consumers because it was not clear whether predators fed on basal sources directly.

Results

At the time of sampling, all streams were at base flow. The in-stream habitats differed between Paluma and Tully sites (Table 1), with a larger proportion of boulders, less shade and greater algal growth at Tully. Water quality was similar among streams, except that pH, temperature and nutrient concentrations were lower at Paluma than Tully.

Isotopic values of consumers and basal sources across sites

Overlap of δ^{13}C signatures of basal resources potentially affected the ability to distinguish source contributions to diets (Fig. 1). At Paluma, most of the tadpole and invertebrate groups had δ^{13}C signatures similar to the basal sources, whereas at Tully, the carbon signatures of tadpoles overlapped only with the autochthonous sources. Consumers were generally δ^{15}N-enriched in comparison to basal sources. Generally, the δ^{15}N composition ranged from about 2 ‰ to 6 ‰ for invertebrates and clustered around 6 ‰ for most tadpoles. The fishes *M. adspersa* and *A. reinhardtii* had the highest δ^{15}N values at Paluma, and *A. reinhardtii* was the most carbon enriched.

Tadpole isotopic signatures varied between sampling occasions: they were more δ^{15}N depleted in 2013 than in 2012 at Paluma, and tadpoles from 2013 exhibited more differences in isotopic signatures among species and size classes at both Paluma and Tully (Fig. S2). Isotopic signatures of most invertebrate groups at Paluma were variable: predators and herbivores overlapped in their δ^{15}N and δ^{13}C measures, but gatherers were generally more nitrogen-enriched than grazers (Fig. S3).

Source contribution to consumer diets and nutritional quality

Eighteen percent of consumers had unresolved isotopic mixing models due to source overlap and/or omnivory, and 21 % were outside the source mixing space. These included small *L. serrata* tadpoles and *A. reinhardtii* from P2 (Table 2), and a number of invertebrates from all Paluma sites (Table 3). For some consumers, the models were unresolved despite the animals being within the source mixing space – for example, tadpoles at P3 and large *M. coggeri* tadpoles at P1 (Table 2), and several invertebrate taxa, especially at P1 and P3, where more basal sources were available (Table 3).

Biofilm was a possible or likely contributor for most tadpoles at P2, but was less evident as a source at P1 and P3 (Table 2). At Tully, the tadpoles were linked to more than one source. Biofilm, algae and/or particulate organic matter were possible or likely sources at T1, whereas filamentous algae, leaves and FPOM were the main sources at T2. Biofilm and filamentous algae had the highest nutritional quality of the basal sources available for consumers (low C:N ratio – Table S2). The iron matrix at P3 was not a possible or likely source contribution to tadpole diets. Particulate organic matter (leaves and FPOM) was a possible contributor for several size groups of several species at Tully, although leaves had the highest C:N ratio, indicating low nutritional quality (Table S2). Moss was a possible food source for tadpoles at Paluma. Periphyton (on sand) was a possible contributor at P1, but had lower nutrient quality than epilithic biofilm at the same site (Table S2). For invertebrates at Paluma, 48 % of the SIAR mixing models were unresolved (Table 3), although resolved models indicated biofilm as a possible source.

Comparison of the gut content analysis of tadpoles with the results from the stable isotope models suggests that the material assimilated did not correspond closely with that consumed (Tables 2 and 4). High proportions of FPOM or CPOM were found in tadpole guts, with some algae or diatoms, but SIA revealed that tadpoles assimilated mostly biofilm and filamentous algae, depending on availability. The gut content analysis also indicated that some *L. nannotis* tadpoles consumed trichopteran larvae.

Isotopic trophic position for consumers

Tadpoles from Paluma in 2012 were all categorised as omnivores (ITP 2.2 – 2.8), whereas in 2013 some were categorised as primary consumers (ITP ~ 2), along with most tadpoles at Tully (Table S3). Both fish species were secondary consumers with ITPs of approximately 3 (Table S4). The ITPs for invertebrates at Paluma were variable both spatially and taxonomically (0.4 - 3.2 for invertebrates generally regarded as herbivores and 1.5 - 4.8 for predators – Table S4). Most of the nominal herbivores were classified as omnivores, but a few were classified as primary consumers (ITP near 2) or secondary consumers (ITP near 3). Most of the crayfish and shrimps were secondary consumers or omnivores. The majority of nominal predators were classified as secondary consumers, but SIA indicated that some fed as omnivores or primary consumers. The ITPs differed among the consumer groups ($F_{4,85}$ =7.74, $P < 0.001$; Fig. 2), with predatory invertebrates having higher ITPs than the herbivorous invertebrates and Tully tadpoles, and fish having higher ITPs than the Tully tadpoles (Tukey's test, $P < 0.05$). There were no differences between Paluma tadpoles and any other group, fish and predatory invertebrates, or herbivorous invertebrates and tadpoles.

Food webs

Omnivory was prevalent in the food webs, with primary consumers feeding on various food sources, and secondary consumers feeding across trophic levels (Fig. 3). SIA indicated that grazers, filter-feeders and shredders fed on both autochthonous and allochthonous material, while gatherers and tadpoles consumed a combination of autochthonous and animal material. Predatory invertebrates and fish formed the top trophic level and were linked to all other consumers.

The food-web structure at Paluma was more complex (with more links) in pools than in riffles, because tadpoles and fish occurred in pools only (Fig. 3). The biomass of invertebrate shredders and gatherers was higher in pools, that of filterers and grazers was higher in riffles, and predatory invertebrates had similar biomass in both habitats. Food-web structure also differed among the three sites due to varying numbers of basal sources – five at P2 and seven at P1 and P3. Total fish biomass was 1.5 kg at P2 (three *A. reinhardtii* individuals) and 0.011 kg at P3 (six *M. adspersa* individuals). Tadpole biomass (mean dry mass = 10.9 g per sample) was greater than that of the invertebrate consumer groups (mean dry mass = 2.2 g per sample) in the pools of all three sites.

Discussion

Food sources and trophic positions

Generally, the basal sources were the most δ^{15}N depleted, invertebrates and tadpoles were intermediate, and predatory invertebrates and fish were the most enriched, as expected (e.g., Minagawa & Wada, 1984; Fry, 1988). However, the main sources of assimilated food identified for all consumers (fish, tadpoles and invertebrates) appeared to be biofilm and algae (autochthonous resources), contrary to hypotheses 1 and 2. While this result might be expected for the more open, lowland sites, it was also true of the most shaded, upland sites. We confirmed that biofilm and filamentous algae were the highest quality basal sources (lowest C:N ratios) (Cross *et al.*, 2005), contrasting with allochthonous leaves (highest C:N ratio), and appeared to have been selected whenever available. However, tadpoles and many invertebrates also consumed allochthonous particulate organic matter and were therefore generalist omnivores, feeding across trophic levels (Pimm & Lawton, 1978). Resource use at Paluma overlapped between tadpoles and invertebrates, so competition for food may occur (Morin, Lawler & Johnson, 1988; Pearson *et al.*, 2015), especially if high quality food is in short supply. However, the influence of tadpoles on invertebrate assemblages in Wet Tropics streams is unclear (see below). Omnivory allows tadpoles and invertebrates to maximise resource use (Lancaster *et al.*, 2005) and may be particularly common in tropical streams, in which availability of different food sources may vary with seasonal rainfall (Frauendorf *et al.*, 2013). For example, particulate organic material accumulates during the dry season, but is removed by wet-season floods (Dudgeon, 2000).

While gut contents analysis suggests that allochthonous resources are the major food source for consumers in headwater streams (Cummins & Klug, 1979; Cheshire *et al.*, 2005), our results confirm the conclusions of other studies using SIA that autotrophic production may also play an important role (Bunn *et al.*, 1999; Mantel *et al.*, 2004; Dudgeon *et al.*, 2010), although not universally (Neres-Lima *et al.*, 2017). Diets of tadpoles in neotropical streams are similarly generalist, incorporating CPOM, periphyton and non-algal biofilm (Verburg *et al.*, 2007; Barnum *et al.*, 2013).

Relative importance of sources can be difficult to assess because of unresolved models, and because we have no estimate of quantity or type of material that is metabolised but not assimilated. Additionally, consumers may selectively assimilate components from a complex mixture of materials such as biofilm, so that the stable isotope signatures of sources and consumers do not completely overlap (Dodds *et al.*, 2014). The isotopic trophic positions of tadpoles at Tully indicated that they were closer to being primary consumers than those at Paluma, probably because the more open canopy of the lowland Tully streams enhanced primary productivity. Invertebrates (analysed for Paluma only), including nominal specialists such as shredders and predators, assimilated a range of sources, but again biofilm and algae were important, as in streams elsewhere (e.g., Jardine *et al.*, 2012; Frauendorf *et al.*, 2013; Hayden, McWilliam-Hughes & Cunjak, 2016). The fish at Paluma were predatory, but their isotopic trophic positions were lower than the predatory invertebrates, possibly indicating short food chains (Jardine, 2016).

Food webs and tadpole loss

Different occurrences of consumers and basal sources among our sites and habitats led to spatial variability in food-web structure and complexity (links among consumers and basal sources). For example, the food webs at Paluma were less complex in riffles than in pools because of the absence of tadpoles and fish. The food webs described here are for spring/summer, the period when tadpoles are most abundant. It is probable that declining tadpole abundance in the cooler months also simplifies the food web. During the warmer months, tadpole biomass was greater than that of the invertebrates, suggesting their likely greater importance in the food web and their possible influence on invertebrate assemblages by reducing food availability and/or causing physical disturbance to invertebrates and sediments (Ranvestel *et al.*, 2004; Colon-Gaud *et al.*, 2008; Connelly *et al.*, 2008; Colon-Gaud *et al.*, 2009). However, invertebrate assemblages at Paluma do not differ greatly between seasons (Cheshire *et al.*, 2005), suggesting that fluctuations of tadpole abundance have little effect on invertebrate assemblage composition in pools; similar conclusions cannot be drawn for riffles as riffle tadpoles were locally extinct.

Tadpoles were a major seasonal influence on food web structure in the summer months, confirming our hypothesis 3. Loss of tadpoles through disease or habitat destruction may thus have a significant impact on community complexity, as suggested by hypothesis 4, and possibly on associated ecosystem processes, especially energy and materials transfer and bioturbation (Ranvestel *et al.*, 2004; Barnum *et al.*, 2013; Frauendorf *et al.*, 2013). Experimental studies are required to further investigate feeding and assimilation by tadpoles, and their interactions with other consumers.

Stream food webs are only reliable up to the primary consumer level, after which they consist of a tangled web of omnivores (Thompson *et al.*, 2007). Many studies have used gut content analysis to draw detailed food webs, enabling identification of prey species as well as autochthonous or allochthonous food sources (Mantel *et al.*, 2004; Cheshire *et al.*, 2005; Barnum *et al.*, 2015). Such food webs therefore incorporate consumers at more detailed taxonomic levels, but are unable to show what the consumers assimilate. Our food-web diagrams are simpler representations of the webs that actually exist, given that various nodes include multiple species and given the prevalence of omnivory (Cheshire *et al.*, 2005); however, they benefit from incorporating information on food consumed and assimilated, using SIA and gut content analysis.

Our research has demonstrated widespread omnivory among tadpoles and the prevalence of omnivory in Wet Tropics streams. We also highlighted the importance of using both gut content analysis and SIA to construct food webs by indicating the importance of autochthonous food sources to the stream assemblages. In this case, tadpole gut contents did not necessarily indicate what they assimilated, and isotopic trophic position did not always concur with the expected trophic position. Our findings also indicate that absence of tadpoles can greatly alter food webs, which is a major management concern in the light of local extinctions of some stream-dwelling anuran species in the Wet Tropics uplands and globally.

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Table 1. Characteristics of habitats and sampling sites at Paluma and Tully with ranges where appropriate. The substratum size distribution is presented as proportions (%) of sand/gravel, cobbles and boulders/bedrock, averaged within habitats. Substratum cover, canopy cover, stream depth and temperature measurements were taken at the time of sampling in November 2013. Conductivity, dissolved oxygen and pH readings were measured during the time of sampling in September 2012 (only in pools at Tully). Current velocity and algal cover estimates were obtained from monthly surveys at sites P1, P2, P3, T1 and T2 between October 2011 and September 2013. Nutrient measurements were obtained from water samples collected in February 2012 at Paluma and November 2011 at Tully. No water samples were collected from P1 at Paluma.

	PALUMA						TULLY			
	P1		P2		P3		T1		T2	
Stream characteristics	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle
Location	19.00°S, 146.18°E		18.98°S, 146.17°E		18.97°S, 146.17°E		17.77°S, 145.65°E		17.75°S, 145.61°E	
Altitude (m above sea level)	859		795		766		102		237	
Current velocity (ms^{-1})	0.00-0.06	0.05-1.10	0.0-0.09	0.24-1.30	0.00-0.07	0.05-1.30	0.00-0.45	0.25-2.03	0.00-0.41	0.37-1.85
Stream temperature	18.9		20.0		20.0		22.5		22.5	
Conductivity (µScm^{-1})	30	30	31	31	26	26	29	-	35	-
Dissolved oxygen (% saturation)	76.7	78.5	84.2	85.9	80.5	81.1	96.0	-	88.7	-
pH	6.35	6.45	6.70	6.70	6.35	6.40	8.40	-	8.10	-
Filterable Reactive Phosphorus (µgL^{-1})	-		4		4		3		3	
Nitrate and nitrite N (µgL^{-1})	-		46		17		136		226	
Stream depth (cm)	43	10	55	13	62	9	37	29	50	22
Substratum composition – Sand/gravel: cobbles: boulders/bedrock (%)	72:15:13	72:15:13	40:15:45	52:18:30	87:5:8	82:18:0	16:22:62	10:28:62	16:34:50	10:20:70
Canopy cover (%)	50-75	50-75	50-75	50-75	75-100	25-50	25-50	0-25	0-25	25-50
Algal cover (%)	0-25	0-25	0-25	0-75	0-25	0-25	0-100	0-25	0-100	0-25

Table 2. Stable isotope mixing model results for tadpoles at Paluma in 2012 and 2013, and Tully in 2013. Basal source abbreviations: A = filamentous algae, B = biofilm, C = coarse particulate organic matter, F = fine particulate organic matter, Fe = iron matrix, L = leaves, M = moss, and P = periphyton. Sources not separated by commas were combined for analysis. Boldface source = likely source contribution (minimum contribution ≥ 20 %), regular type = possible contribution (minimum contribution > 0 % and maximum contribution ≥ 50 %), nr = unresolved (equal source contribution or isotopic source overlap), and nr[1] = consumer outside the basal source mixing space (not analysed using SIAR). Tadpole size classes were: for *Mixophyes coggeri*, small (< 10 mm), medium (≥ 10 to < 22 mm) and large (≥ 22 mm) tadpoles; for other species, small (< 7.5 mm), medium (≥ 7.5 to < 12 mm) and large (≥ 12 mm).

Species	Size class	PALUMA						TULLY	
		P1		P2		P3		T1	T2
		2012	2013	2012	2013	2012	2013	2013	2013
L. serrata	Large	-	-	B	-	-	-	B, A, LF	-
	Medium	M	CF	**B**	M, LCF	nr	A	-	-
	Small	-	-	nr[1]	**B**	-	-	-	-
	Small/ medium	-	-	-	-	nr	**LCF**	-	**A**, LF
M. coggeri	Large	nr	-	B	-	nr	-	-	-
	Medium	BP	-	M*	-		-	-	-
L. nannotis	Large	-	-	-	-	-	-	B, A, LF	A, LF
	Small/ medium	-	-	-	-	-	-	B, LF	-
L. rheocola	Large	-	-	-	-	-	-	**B**, A	-
	Medium	-	-	-	-	-	-	B, A, LF	-
	Small	-	-	-	-	-	-	B, A**	
L. dayi	Large	-	-	-	-	-	-	B, LF	-
	Small/ medium	-	-	-	-	-	-	**B**, LF	-

* Sample from sites P2 and P3

** Sample from sites T1 and T2

Table 3. Stable isotope mixing model results (using SIAR) for invertebrates and fishes at Paluma stream sites P1, P2 and P3 in 2012. Basal source abbreviations: A = filamentous algae, B = biofilm, C = coarse particulate organic matter, F = fine particulate organic matter, Fe = iron matrix, L = leaves, M = moss, and P = periphyton. Sources not separated by commas were combined for analysis. Boldface source = likely source contribution (minimum contribution ≥ 20 %), regular type = possible contribution (minimum contribution > 0 % and maximum contribution ≥ 50 %), nr = unresolved (equal source contribution or isotopic source overlap), and nr^1 = consumer outside the basal source mixing space (not analysed using SIAR). Several taxa were combined within feeding groups to produce sufficient material for analysis, as indicated.

Major taxon	Family or species	Feeding group	P1	P2	P3
Diptera	Simuliidae	Filterer	BP	-	nr
	Mixed	Filterer	-	B, LCF	-
Several gatherer/filterers	Mixed	Gatherer/filterer	nr^1	B	-
Parastacidae, large		Gatherer	nr^1	nr^1	nr^1
Parastacidae, medium		Gatherer	nr	nr^1	nr^1
Parastacidae, small		Gatherer/predator	nr^1	nr^1	nr^1
Palaemonidae		Grazer	-	-	**B**
Coleoptera	Psephenidae	Grazer	A	nr	-
Ephemeroptera	Leptophlebiidae	Grazer/shredder/gatherer	nr	B, M, LCF	nr
	Mixed	Grazer	nr	M	A
Plecoptera	Gripopterygidae	Predator/grazer	-	M	A
Trichoptera	Mixed	Grazer/gatherer/filterer	BP	-	-
	Philopotamidae	Grazer/gatherer/filterer	-	B	-
	Mixed	Shredder	CF, BP	B, LCF	B
Lepidoptera		Grazer/shredder	-	B, M, LCF	-
Several predators	Mixed	Predator	M	B	-
Coleoptera	Dytiscidae	Predator	-	B	nr
	Mixed	Predator	BP		-
Ephemeroptera	Ameletopsidae	Predator	nr	B	-
Plecoptera	Mixed	Predator/grazer	A	-	-
Hemiptera	Gelastocoridae	Predator	-	nr^1	-
	Mixed	Predator	nr^1	B	B
Megaloptera	Corydalidae	Predator	nr^1	-	B
Arachnida	Pisauridae	Predator	nr^1	-	nr^1
Zygoptera	Synlestidae	Predator	nr^1	B	-
	Mixed	Predator	nr^1	B	nr
Epiproctophora	Gomphidae	Predator	-	B	-
	Synthemistidae	Predator	-	B	-
	Telephlebiidae	Predator	-	B	-
	Mixed	Predator	nr	-	nr
Trichoptera	Mixed	Predator	nr	B	-
Pisces	*Mogurnda adspersa*	Predator	-	-	B
	Anguilla reinhardtii	Predator	-	nr^1	-

Table 4. Gut contents of tadpoles at Paluma, collected in 2012 and 2013, and Tully, collected in 2013. The proportions of the various sources are presented as a percentage of overall gut content. Algae and diatoms were not differentiated. Tadpole size classes as in Table 1. FPOM = fine particulate organic matter, CPOM = coarse particulate organic matter.

Species	Size	Area	FPOM (%)	CPOM (%)	FPOM/ CPOM (%)	Algae/ diatoms (%)	Invertebrates (%)
L. serrata	Large	Paluma			100		
		Tully			60	40	
	Medium	Paluma	65	25		10	
		Tully			75	25	
	Small	Paluma			90	10	
		Tully			75	25	
M. coggeri	Large	Paluma		75	20	5	
	Medium			75	25		
L. nannotis	Large	Tully	58	20		20	2
	Small/medium	Tully	85	10		5	
L. rheocola	Large	Tully	50	30		20	
	Medium	Tully	60	30		10	
	Small	Tully	60	20		20	
L. dayi	Large	Tully	80	10		10	
	Small/medium	Tully	80	10		10	

Figure legends

Figure 1. Mean (± s.d.) $\delta^{15}N$ and $\delta^{13}C$ ratios of food-web components in (a) Paluma and (b) Tully streams. Abbreviations: A = filamentous algae, B = biofilm, C = CPOM, F = FPOM, Fe = iron matrix, L = leaves, M = moss, P = periphyton (basal sources), and E = *Anguilla reinhardtii* (eel), Ma = *Mogurnda adspersa* (fish). Each consumer point represents a taxon of a specific feeding group for invertebrates, a species of fish, or a size class of a species for tadpoles.

Figure 2. Isotopic trophic positions (calculated as per Winemiller *et al.*, 2011) of tadpoles (all species) at Tully (Tadpoles Tul) and Paluma (Tadpoles Pal); invertebrates at Paluma – herbivores including all non-predators (Herb inverts) and predators (Pred inverts); and fish (both species combined) at Paluma. Groups that were not significantly different are indicated by vertical lines (Tukey's test with $\alpha = 0.05$). The left and right boundaries of the boxes represent the 25th and 75th percentiles respectively, the central bar represents the median, the whiskers represent the 10th and 90th percentiles, and the dots indicate outliers.

Figure 3. Food webs linking major community components for riffles and pools at three sites (P1, P2 and P3) at Paluma in 2012-13. The boldface letters at the base of each figure represent basal sources that were present at each site and analysed for $\delta^{15}N$ and $\delta^{13}C$ content. Weighted links were drawn between primary consumers and basal sources. The line thickness of links between primary consumers and basal sources is based on the relative importance of sources to consumers, using four categories: 1 (≤ 10 %), 2 (11-25 %), 3 (26-50 %) and 4 (> 50 %). Components (boxes) and links that were absent are shown in grey. Boxes are scaled in proportion to biomass of each component in the streams. Basal sources: A = filamentous algae, B = biofilm, C = CPOM, F = FPOM, Fe = iron matrix, L = leaf litter, M = moss and P = periphyton. Invertebrate consumer groups: FF = filter feeders, Ga = gatherers, Gr = grazers, Sh = shredders, and Pr = predators. Other consumers: Fish = *Anguilla* + *Mogurnda*, and T = tadpoles.

Supplementary information

Figure S1. Location of study streams in the Queensland Wet Tropics.

Figure S2. Mean (± s.d.) δ^{15}N and δ^{13}C ratios of tadpoles at (a) Paluma in 2012 and 2013, and (b) Tully in 2013.

Figure S3. Mean (± s.d.) δ^{15}N and δ^{13}C ratios of invertebrate herbivores and predators at Paluma in 2012.

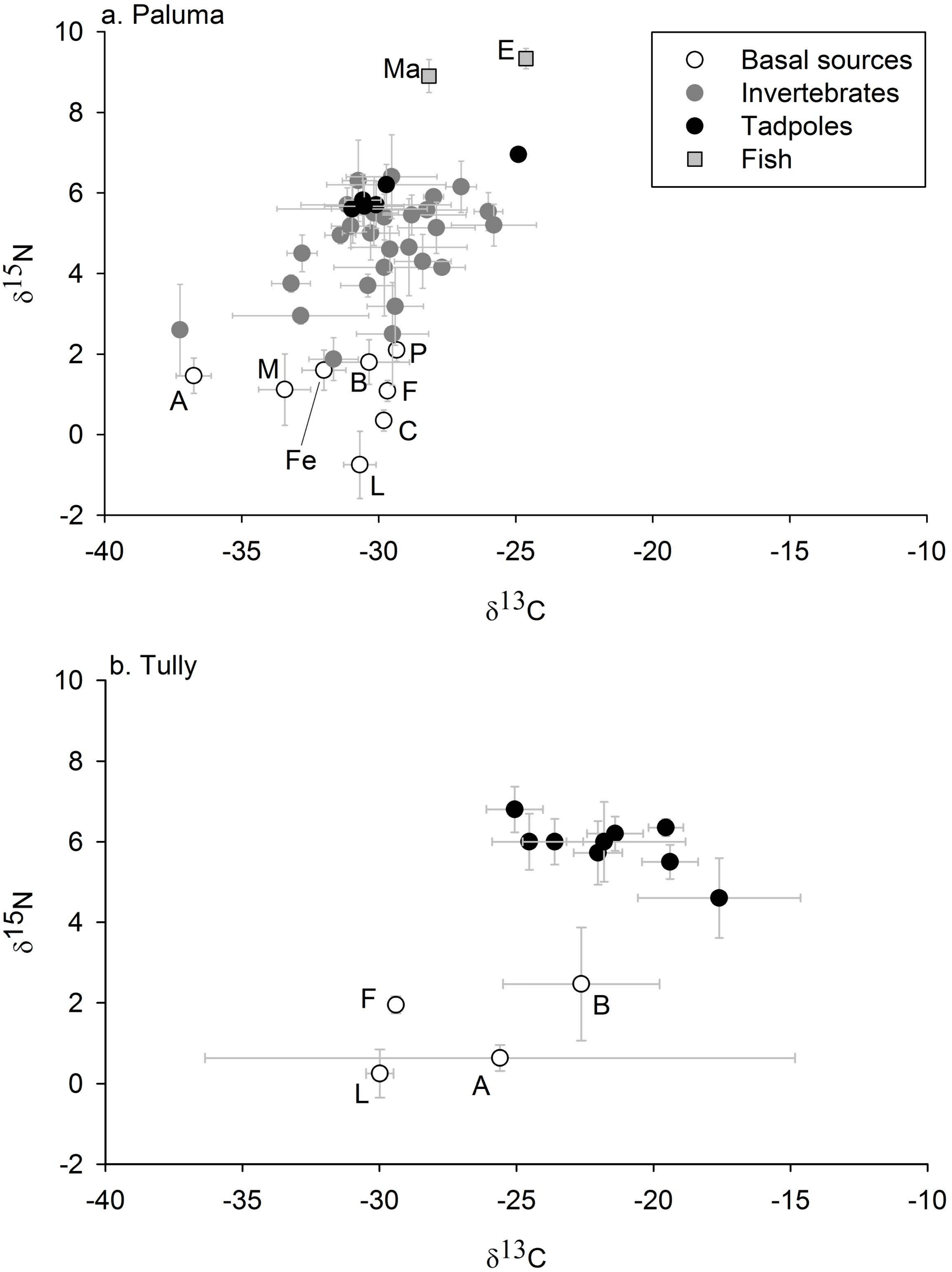
Table S1. Basal sources present in the streams at Paluma and Tully.

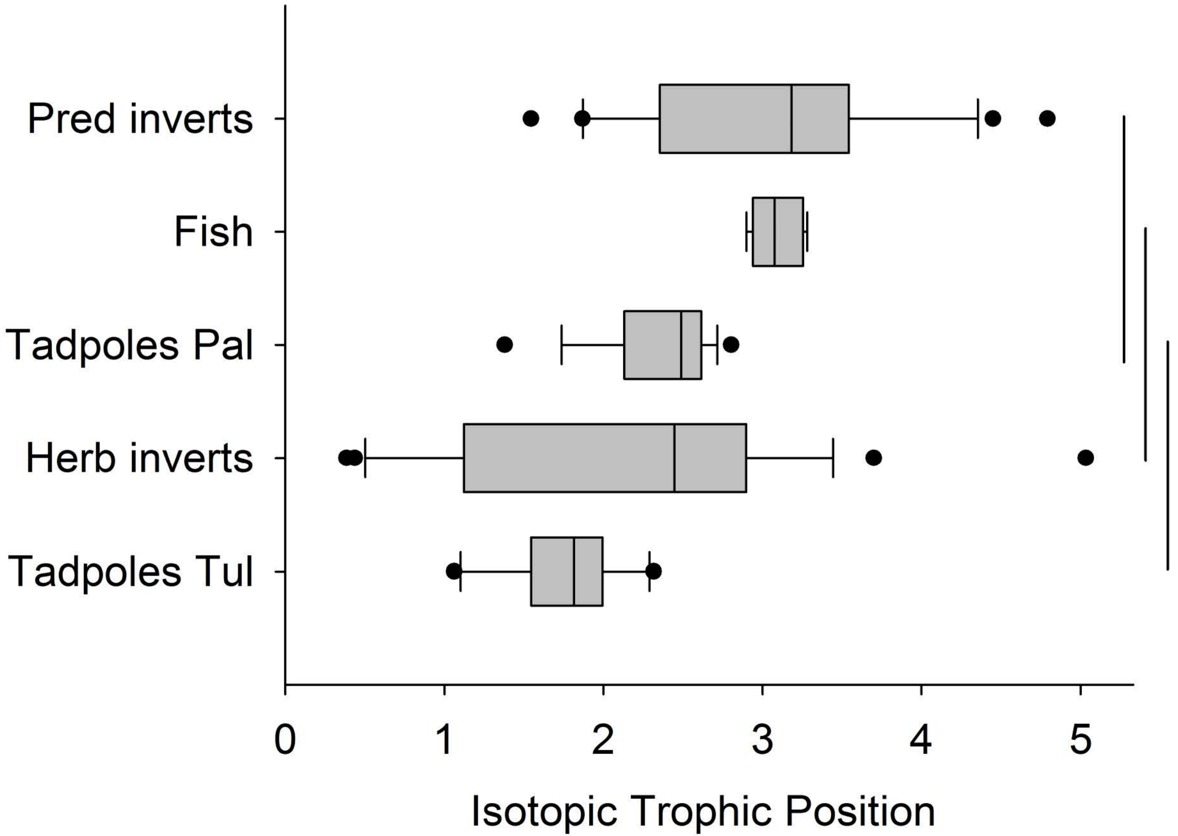
Table S2. The C:N ratio ± SD of basal sources in the streams at Paluma and Tully.

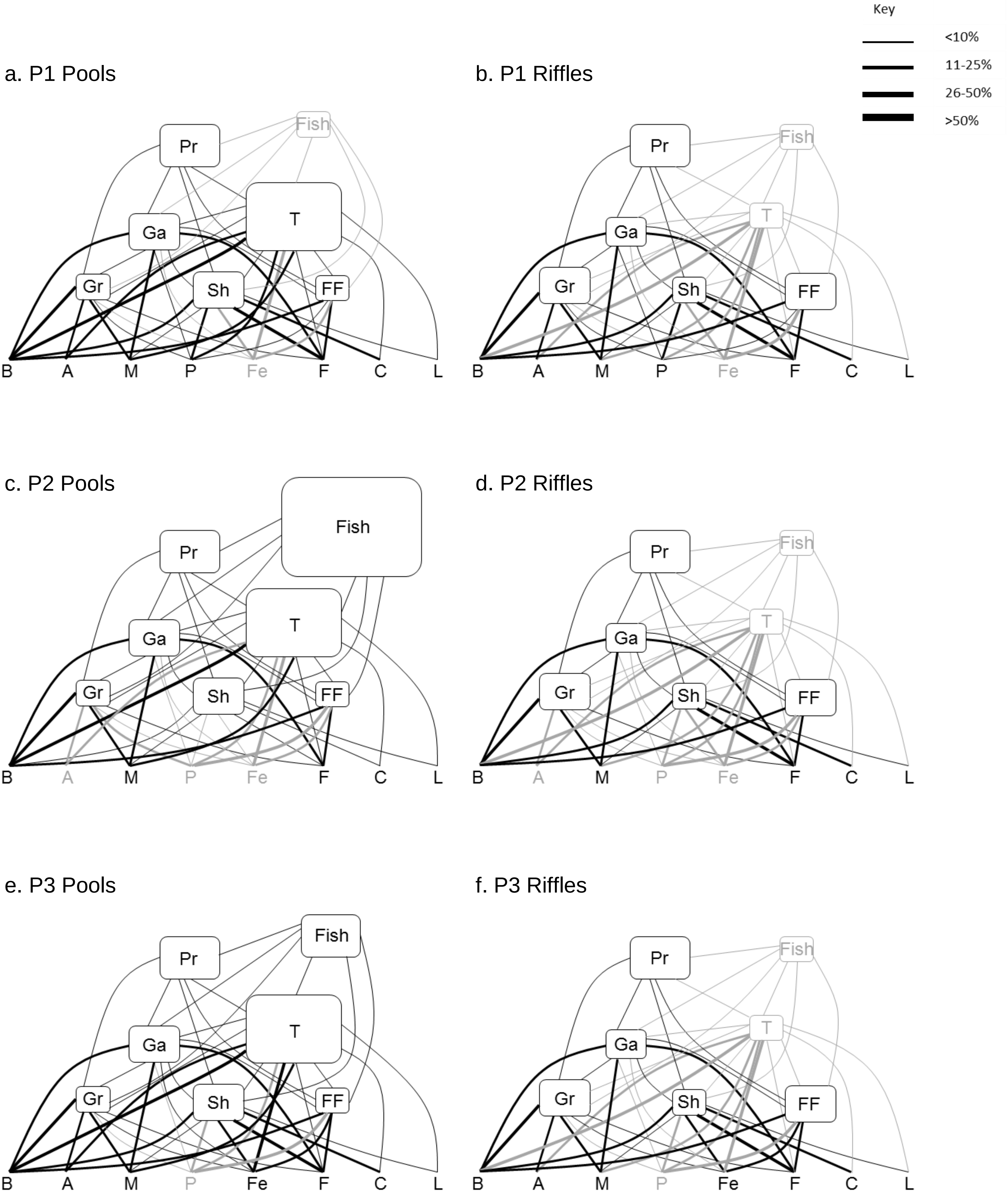
Table S3. Isotopic trophic positions (ITPs) for tadpoles at Paluma in 2012 and 2013, and Tully in 2013.

Table S4. Isotopic trophic positions (ITPs) for invertebrates and fishes at Paluma in 2012.

Table S5. Assignment of invertebrates to consumer feeding groups.


a. Paluma
Basal sources
Invertebrates
Tadpoles
Fish
Ma
E
A
M
Fe
B
P
F
C
L
$\delta^{15}N$
$\delta^{13}C$
10
8
6
4
2
0
-2
-40
-35
-30
-25
-20
-15
-10
b. Tully
F
B
L
A
$\delta^{15}N$
$\delta^{13}C$


Pred inverts
Fish
Tadpoles Pal
Herb inverts
Tadpoles Tul
0
1
2
3
4
5
Isotopic Trophic Position



a. P1 Pools

b. P1 Riffles

c. P2 Pools

d. P2 Riffles

e. P3 Pools

f. P3 Riffles

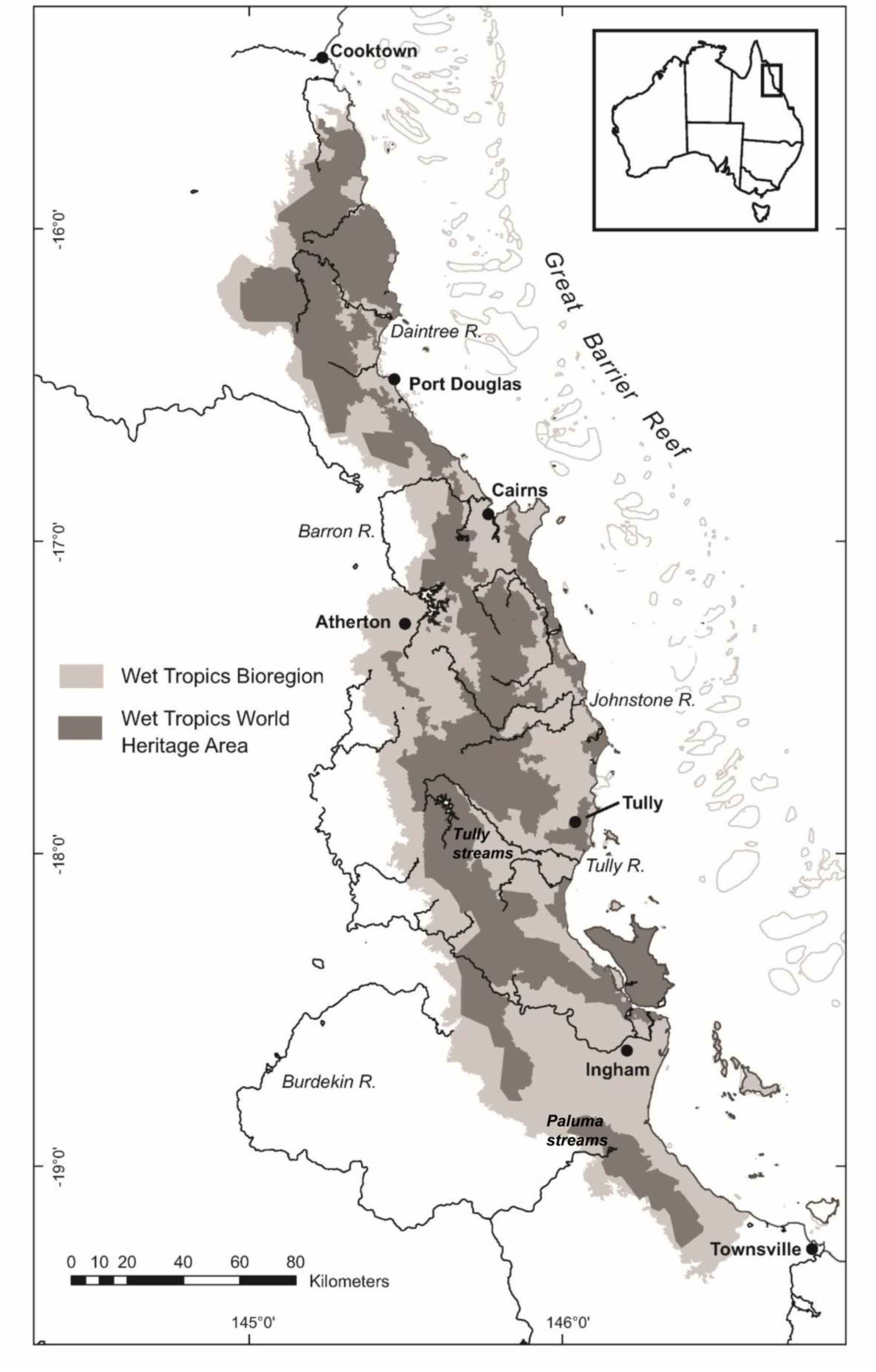


Figure S1. Location of study streams in the Queensland Wet Tropics. Map drawn by Adella Edwards.

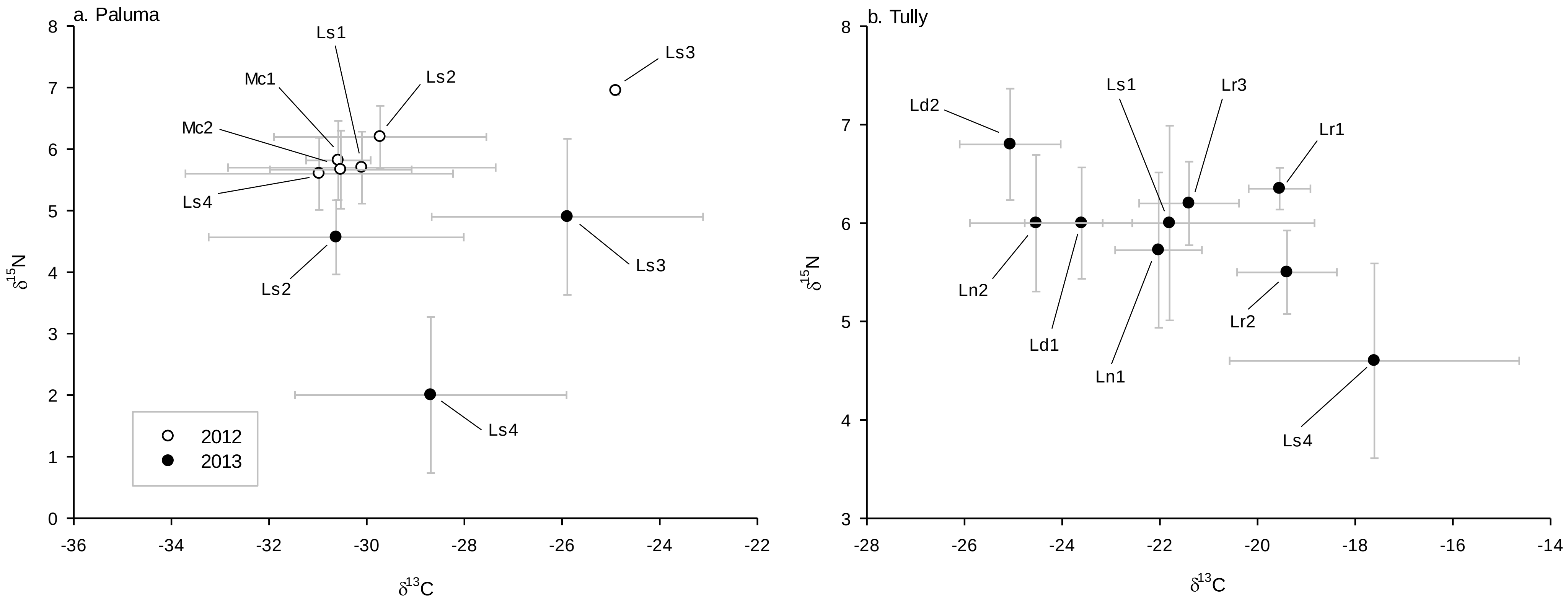


Figure S2. Mean (± s.d.) $\delta^{15}N$ and $\delta^{13}C$ ratios of tadpoles at (a) Paluma in 2012 and 2013, and (b) Tully in 2013. Each point represents a specific size class of a species. Species codes: Ld = *Litoria dayi,* Ln = *L. nannotis,* Lr = *L. rheocola,* Ls = *L. serrata,* Mc = *Mixophyes coggeri.* Size classes: 1 = large, 2 = medium, 3 = small, 4 = small and medium tadpoles combined.

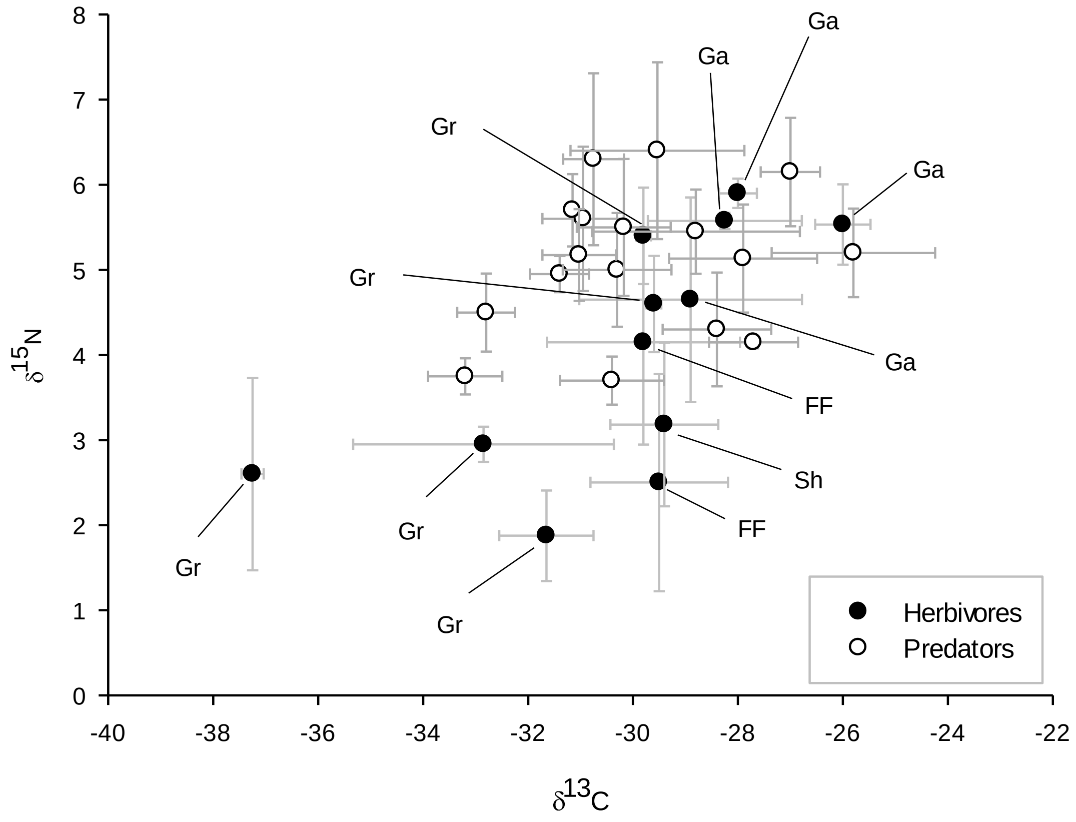


Figure S3. Mean (± s.d.) $\delta^{15}N$ and $\delta^{13}C$ ratios of invertebrate herbivores and predators at Paluma in 2012. Each point represents a taxon of a specific feeding group. Feeding group codes for herbivores: FF = filterer, Ga = gatherer, Gr = grazer and Sh = shredder. See Table 2 for invertebrate taxa identified and grouped according to feeding mode.

Table S1. Basal sources present in the streams at Paluma and Tully. Sources were combined (indicated by hyphenation) when the $\delta^{13}C$ measures differed by less than 1.0 ‰.

Area	Stream reach	Basal sources
Paluma	P1	Filamentous algae, moss, leaves, biofilm-periphyton, CPOM-FPOM
	P2	Biofilm, moss, leaves-CPOM-FPOM
	P3	Biofilm, filamentous algae, moss, iron matrix, leaves-CPOM-FPOM
Tully	T1	Biofilm, filamentous algae, leaves-FPOM
	T2	Biofilm, filamentous algae, leaves-FPOM

Table S2. The C:N ratio ± SD of basal sources in the streams at Paluma and Tully. A lower C:N ratio indicates a higher nutrient quality. For basal sources that were collected in only one riffle or pool in a stream site, the standard deviations were calculated using data from all the riffles and pools sampled within an area (except for the iron matrix, which was found in only one pool at Paluma). Differences between overall ratios indicated by different letters under TUKEY (Tukey test, $P < 0.05$, following ANOVA, $F_{7,75} = 50.83$, $P < 0.0001$).

	PALUMA			TULLY		TUKEY
Basal source	P1	P2	P3	T1	T2	
Leaves	44.5 ± 10.3	53.0 ± 15.3	45.2 ± 6.2	68.7 ± 9.3	53.9 ± 11.1	a
CPOM	31.4 ± 1.2	31.8 ± 1.5	33.0 ± 1.4	-	-	b
FPOM	25.5 ± 1.0	25.2 ± 0.5	25.6 ± 0.9	20.3 ± 0.7	18.8 ± 1.1	b
Moss	22.5 ± 5.7	25.0 ± 1.2	28.2 ± 2.8	-	-	b
Periphyton	27.8 ± 12.3	-	-	-	-	bc
Iron matrix	-	-	19.6	-	-	bc
Biofilm	12.5 ± 2.0	10.5 ± 2.7	10.2 ± 4.3	10.6 ± 0.2	10.3 ± 0.2	c
Filamentous algae	9.2 ± 0.5	-	8.9 ± 0.9	11.6 ± 0.6	7.8 ± 1.7	c

Table S3. Isotopic trophic positions (ITPs) for tadpoles at Paluma in 2012 and 2013, and Tully in 2013. The tadpoles were categorised as primary consumers if ITP was close to 2 (1.9 - 2.1), as secondary consumers if ITP was close to 3 (2.9 – 3.1), and as omnivores if ITPs were not centred on an integer. Tadpole size classes were: small (< 10 mm), medium (10 to < 22 mm) and large (≥ 22 mm) for *Mixophyes coggeri* tadpoles, and small (< 7.5 mm), medium (7.5 to < 12 mm) and large (≥ 12 mm) for other species.

Species	Size class	PALUMA						TULLY	
		P1		P2		P3		T1	T2
		2012	2013	2012	2013	2012	2013	2013	2013
L. serrata	Large	-	-	2.5	-	-	-	1.8	-
	Medium	2.8	2.0	2.4	2.1	2.6	2.6	-	-
	Small	-	-	2.3	1.9	-	-	-	-
	Small/ medium	-	-	-	-	2.5	1.4	-	1.1
M. coggeri	Large	2.7	-	2.6	-	2.5	-	-	-
	Medium	2.5	-	2.5*	-		-	-	-
L. nannotis	Large	-	-	-	-	-	-	1.8	1.6
	Small/ medium	-	-	-	-	-	-	2.1	-
L. rheocola	Large	-	-	-	-	-	-	1.7	-
	Medium	-	-	-	-	-	-	1.5	-
	Small	-	-	-	-	-	-	1.8**	
L. dayi	Large	-	-	-	-	-	-	2.0	-
	Small/ medium	-	-	-	-	-	-	2.3	-

* Sample from P2 and P3

** Sample from T1 and T2

Table S4. Isotopic trophic positions (ITPs) for invertebrates and fishes at Paluma in 2012. Invertebrates were categorised as primary consumers if ITP was close to 2 (1.9 - 2.1), as secondary consumers if ITP was close to 3 (2.9 – 3.1), and as omnivores if ITPs were not centred on an integer.

Taxon	Family	Feeding group	P1	P2	P3
Diptera	Simuliidae	Filterer	2.5	-	1.8
	Mixed	Filterer	-	0.7	-
"Several"	Mixed	Gatherer/filterer	2.6	2.0	-
Parastacidae	Large	Gatherer	1.9	2.5	2.5
	Medium	Gatherer	3.4	2.7	2.8
	Small	Gatherer/predator	3.1	3.2	3.0
Palaemonidae	Medium	Grazer	-	-	5.0
Coleoptera	Psephenidae	Grazer	3.7	2.3	-
Ephemeroptera	Leptophlebiidae	Grazer/shredder/gatherer	0.4	1.0	0.8
	Mixed	Grazer	1.3	2.4	2.2
Plecoptera	Gripopterygidae	Grazers	-	2.5	3.1
Trichoptera	Mixed	Grazer/gatherer/filterer	3.2	-	-
	Philopotamidae	Grazer/gatherer/filterer	-	2.5	-
	Mixed	Shredder	0.9	1.5	0.4
Lepidoptera		Grazer/shredder	-	0.5	-
"Several"	Mixed	Predator	4.3	3.0	-
Coleoptera	Dytiscidae	Predator	-	1.9	2.0
	Mixed	Predator	1.5	-	-
Ephemeroptera	Ameletopsidae	Predator	3.3	3.3	-
Plecoptera	Mixed	Predator/grazers	3.3	-	-
Hemiptera	Gelastocoridae	Predator	-	1.9	-
	Mixed	Predator	2.3	3.1	1.9
Megaloptera	Corydalidae	Predator	2.8	-	3.1
Arachnida	Pisauridae	Predator	2.4	-	3.3
Zygoptera	Synlestidae	Predator	4.8	3.6	-
	Mixed	Predator	4.4	3.5	3.9
Epiproctophora	Gomphidae	Predator	-	1.9	-
	Synthemistidae	Predator	-	3.0	-
	Telephlebiidae	Predator	-	3.4	-
	Mixed	Predator	3.3	-	3.5
Trichoptera	Mixed	Predator	4.1	3.6	-
Fishes	*Mogurnda adspersa*	Predator	-	-	3.2
	Anguilla reinhardtii	Predator	-	3.0	-

Table S5: Assignment of invertebrates to consumer feeding groups (according to Merritt & Cummins, 1984; Gooderham & Tsyrlin, 2002; Cheshire, Boyero & Pearson, 2005), including assignment to broader mixed groups (right column) for when invertebrates were combined for stable isotope analysis.

Consumer feeding group	Filterer	Gatherer	Grazer	Shredder	Predator	Combined invertebrate groups
Ameletopsidae	·	·	·	·	•	·
Athericidae	·	·	·	·	•	Predators mixed
Baetidae	·	•	•	·	·	Ephemeroptera grazers mixed
Caenidae	·	•	•	·	·	Ephemeroptera grazers mixed
Calamoceratidae	·	·	·	·	·	
Anisocentropus sp.	·	·	·	•	·	Trichoptera shredders mixed
Ceratopogonidae	·	•	·	·	•	Predators mixed
Chironomidae	•	•	·	·	·	Gatherers/filterers mixed
Chorismagrionidae	·	·	·	·	•	Zygoptera predators mixed
Cordulephyidae	·	·	·	·	•	Epiproctophora predators mixed
Corydalidae	·	·	·	·	•	
Culicidae	•	·	·	·	·	Diptera filterers mixed
Diphlebiidae	·	·	·	·	•	Zygoptera predators mixed
Dixidae	•	·	·	·	·	Diptera filterers mixed
Dolichopodidae	·	·	·	·	•	Predators mixed
Dytiscidae	·	·	·	·	•	
Ecnomidae	·	·	·	·	•	Trichoptera predators mixed
Eustheniidae	·	·	·	·	•	Plecoptera predators/grazers mixed
Gelastocoridae	·	·	·	·	•	
Gerridae	·	·	·	·	•	Hemiptera predators mixed
Gomphidae	·	·	·	·	•	
Gripopterygidae	·	·	•	·	·	
Gyrinidae	·	·	·	·	•	Coleoptera predators mixed
Helicopsychidae	·	·	•	·	·	Trichoptera grazers/gatherers/filterers mixed
Hydrobiosidae	·	·	·	·	•	Trichoptera mixed predators
Hydrometridae	·	·	·	·	•	Hemiptera predators mixed
Hydropsychidae	•	·	·	·	·	Trichoptera grazers/gatherers/filterers mixed
Hypolestidae	·	·	·	·	•	Zygoptera predators mixed
Lepidoptera	·	·	•	•	·	
Leptoceridae	·	·	·	·	·	
Lectrides sp.	·	·	·	•	·	Trichoptera shredder mixed
Oecetis sp.	·	·	·	•	·	Trichoptera shredder mixed
Triplectides sp.	·	·	·	•	·	Trichoptera shredder mixed
Triplexa sp.	·	·	·	•	·	Trichoptera shredder mixed
Leptophlebiidae	·	·	·	·	·	
Atalophlebia sp.	·	•	•	•	·	Ephemeroptera grazers/gatherers/ shredders mixed
Genus Q	·	•	•	•	·	Ephemeroptera grazers/gatherers/ shredders mixed
Jappa sp.	·	•	•	•	·	Ephemeroptera grazers/gatherers/ shredders mixed

Consumer feeding group	Filterer	Gatherer	Grazer	Shredder	Predator	Combined invertebrate groups
Leptophlebiidae	·	·	·	·	·	
Koornonga sp.	·	●	●	●	·	Ephemeroptera grazers/gatherers/ shredders mixed
Neboissophlebia sp.	·	●	●	●	·	Ephemeroptera grazers/gatherers/ shredders mixed
Nousia sp.	·	●	●	●	·	Ephemeroptera grazers/gatherers/ shredders mixed
Leptophlebia sp.	·	●	●	●	·	Ephemeroptera grazers/gatherers/ shredders mixed
Ulmerophlebia sp.	·	●	●	●	·	Ephemeroptera grazers/gatherers/ shredders mixed
WT sp 2/4	·	●	●	●	·	Ephemeroptera grazers/gatherers/ shredders mixed
Lindeniidae	·	·	·	·	●	Epiproctophora predators mixed
Nevrorthidae	·	·	·	·	●	Predators mixed
Notonectidae	·	·	·	·	●	Hemiptera predators mixed
Oxygastridae	·	·	·	·	●	Epiproctophora predators mixed
Parastacidae	·	·	·	·	·	
large	·	●	·	·	·	
medium	·	●	·	·	·	
small	·	●	·	·	●	
Philopotamidae	●	●	●	·	·	
Pisauridae	·	·	·	·	●	
Pleidae	·	·	·	·	●	Hemiptera predators mixed
Polycentropodidae	·	·	·	·	●	Trichoptera mixed predators
Psephenidae	·	·	●	·	·	
Pseudocorduliidae	·	·	·	·	●	Epiproctophora predators mixed
Scirtidae	●	·	·	·	·	Gatherers/filterers mixed
Simuliidae	●	·	·	·	·	
Stratiomyidae	·	●	·	·	·	Gatherers/filterers mixed
Synlestidae	·	·	·	·	●	
Synthemistidae	·	·	·	·	●	
Telephlebiidae	·	·	·	·	●	
Veliidae	·	·	·	·	●	Hemiptera predators mixed