



## ECOSYSTEMS

# Structure, biomass, and secondary production of benthic macroinvertebrates in subtropical Andean rivers

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**Abstract:** Secondary production is the formation of heterotrophic biomass across time, which integrates several important ecological processes that affect the life of organisms, populations, communities and ecosystems, but its study has poor developed in South America. The objectives of this work were to describe the diversity of benthic macroinvertebrate assemblages in terms of abundance and biomass, and to quantify their secondary production for the first time in Andean rivers. A quantitative sampling scheme was implemented, using a Surber sampler, in three forested streams. Physical-chemical variables, nutrients, organic matter and chlorophyll were measured also. The macroinvertebrates were separated and identified mostly at the species level. Each taxon was assigned to a functional feeding group. Secondary production was estimated for 38 taxa, mostly Diptera, Trichoptera, Coleoptera, and Ephemeroptera. The annual production varied from 3769 to 13916 mg dry mass  $m^{-2} y^{-1}$ . Most abundant taxa were also those with higher production, dominated by Ephemeroptera (Baetidae), Trichoptera (Hydropsychidae) and Diptera (Chironomidae and Simuliidae). Density, biomass, and production of collectors and predators were much higher than the other feeding groups. We expect that our results will be useful to evaluate the effects on stream functioning produced by global warming and other anthropogenic disturbances in our region.

**Key words:** Aquatic insects, body mass, functional feeding groups, secondary production, size class.

## INTRODUCTION

Mountain streams usually present low temperatures, coarse sediments, high level of dissolved oxygen, and have a wide range of flow rates, dependent on regional rain and flood patterns (Allan & Castillo 2007). The low conductivity that characterizes them, with low nutrient content and scarce solar incidence (especially in forested ecoregions) entails one of the lowest ecosystems production on Earth (Jacobsen et al. 2008).

Secondary production (P) is the formation of heterotrophic biomass (B) across time, regardless of the taxon or trophic level (Benke 1993). The annual P/B rate represents the turnover rate for an entire year; that is, the number of times the biomass (annual average) is renewed during that period (Benke 1993). Generally, secondary production studies have been framed by bioenergetic theory (Odum 1968, Benke 2010), which deals with the transfer of energy between species and trophic levels in an ecosystem. Secondary production is a measure

of population fitness, i.e. represents a measure of “ecological success”. This parameter integrates several very important ecological factors and processes, such as individual growth, body size, development time, population mortality, intra- and interspecific competition, and predation, among others, that affect the life of an organism and of the population, and consequently the community and the ecosystem (Benke 1993, Dolbeth et al. 2012).

Secondary production is very useful to approach different types of ecological questions. Initially, to determine the carrying capacity in fish farming for commercial fishing (Waters & Crawford 1973). In recent decades, secondary production was a useful response variable to assess functional and ecological questions in aquatic ecosystems (Dolbeth et al. 2012). For example, secondary production allows differentiation between the ecosystems functioning of basins with different land use; or it's a useful tool for assessing and quantifying chemical flows (Benke 2010). For the tropical area of America, Ramírez & Pringle (1998) carried out the first study on the production of a stream macroinvertebrate assemblage in Costa Rica. They found a lower production than expected for a tropical stream, with a major contribution of shrimps. In lakes from Brazil, the issue was dealt with by Leal & de Assis Esteves (2000) and Dos Santos Lima & Pamplin (2017), focusing on the mayfly genus *Campsurus*. In streams from Argentina, the few studies we have found are focused on production and life cycles of one or two species or of a particular trophic guild, being also concentrated in Patagonia (Añón Suárez & Albariño 2001, Anderson & Rosemond 2007, Epele & Miserendino 2011, Epele et al. 2011, Brand & Miserendino 2011), except one study from our area (Molineri 2010). We did not find studies of secondary production for the entire assemblage of benthic macroinvertebrates in

Andean mountain rivers. Nevertheless, many studies focus on the structure and dynamics of the community in relation to seasonal changes or pollution effects (Fernández et al. 2001, Jacobsen 2003, Romero et al. 2010, Ríos-Pulgarín et al. 2016, Pero et al. 2019).

The study of secondary production in aquatic ecosystems is also a valid alternative to integrate taxonomic and functional feeding groups (FFG) approaches (Dolbeth et al. 2012). The FFG concept, since its introduction by Cummins (1973) has contributed to a better understanding of lotic ecosystems functioning (Reynaga 2009, Reynaga & Rueda Martín 2010, 2014, Cummins 2016). Both analyses are here combined for an integrated understanding of the system.

The objectives of this work were: 1) to describe the diversity of benthic macroinvertebrate assemblages in terms of abundance and biomass; 2) to quantify their secondary production; and 3) to assess how production is distributed among taxa and FFG.

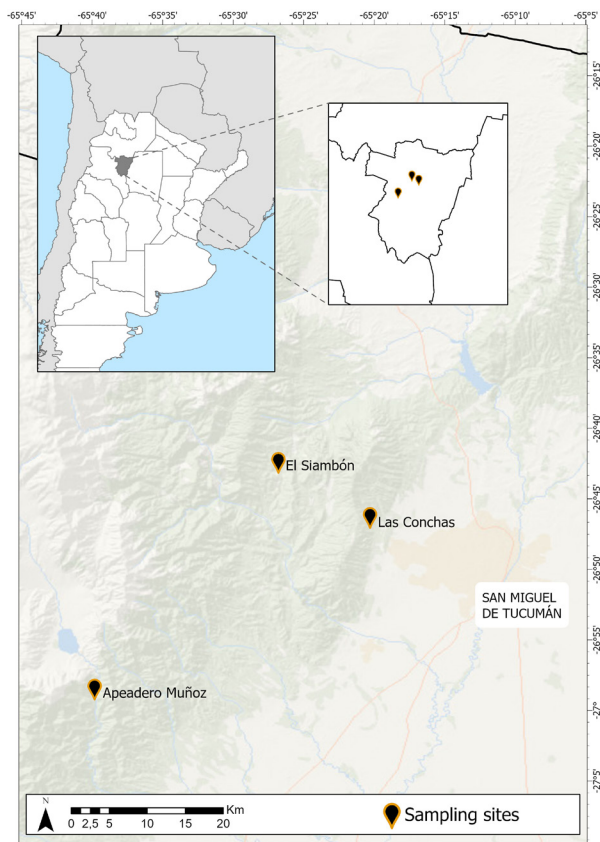
## MATERIALS AND METHODS

### Study area

Samplings were carried out in the province of Tucumán, Northwestern Argentina, a subtropical area profuse in mountain rivers. The climate is subtropical, with hot and wet summers and cooler and drier winters (Rodríguez & D'Urso 2005). The rains (annual average of 1141 mm) are unevenly distributed, with about 80% of it falling between November and April (summer-autumn, Sirombra & Mesa 2010), causing well-marked wet and dry seasons.

### Sampling sites

The field work was carried out in three mountain streams (Figure 1): Las Conchas (800 m a.s.l.), El Siambón (1100 m a.s.l.), and Apeadero Muñoz



**Figure 1. Sampled sites in the province of Tucumán, Northwestern Argentina. Sites coordinates: Las Conchas = 26° 47' 04.1"S, 65° 20' 17.9"W; El Siambón = 26° 43' 3.9"S, 65° 26' 47.6"W; Apeadero Muñoz = 26° 59' 14.0"S, 65° 39' 49.4"W. Map elaborated with QGIS 3.16.**

(1550 m a.s.l.). These streams have stony beds and clear waters and present a high frequency of disturbs (spates) during summer (January to March). They are covered by riparian vegetation (Yungas Cloud Forest), so the direct solar incidence is scarce, except in El Siambón with a more open canopy. Las Conchas stream is in the Yungas ecoregion, within the montane jungle altitudinal floor, within a protected area (the Parque Sierra de San Javier). El Siambón stream is in the transition zone between the Yungas and Chaco Serrano ecoregions, in a region of disperse rural population, with agricultural and recreational use. While, the Apeadero Muñoz stream is also found in the Yungas ecoregion, in the montane forest altitudinal floor, which is

almost a monospecific mountain alder forest (*Alnus acuminatus*), within a protected area (Reserva Provincial Los Sosa).

### Field sampling and laboratory work

A quantitative sampling scheme was implemented, using a Surber sampler (area = 0.09 m<sup>2</sup>, pore size = 300 μm). At each site, 3 Surber samples were taken from 3 individual riffles; each sample was collected at least 20 m above the previous one, in a 100 m reach. Las Conchas and Apeadero Muñoz sites were sampled, 12 and 9 times respectively, between June 2015 and July 2016. El Siambón was sampled 4 times between June 2016 and June 2017. Climatic conditions were similar among these years, so we did not expect important inter-annual differences among studied streams.

In each sampling date, the following environmental parameters were measured (Table 1): water temperature, pH, electrical conductivity, dissolved oxygen, turbidity, channel width, average depth, and current velocity. Measurements were taken with a multiparametric probe Horiba U-52 (Kyoto, Japan). Seasonally, water samples were taken to determine major ions and nutrients (with a Metrohm Ion Chromatograph 881 Compact IC pro). The depth and velocity data were measured (using a GlobalWater Flow Probe FP111, College Station, Texas) through transects across the stream, and then averaged and multiplied by the channel width to obtain the average flow rate.

**Chlorophyll a:** At each sampling event, five rocks exposed to the current were randomly collected in different riffles of the studied reach. For each rock, an acetate template was used and a 25 cm<sup>2</sup> (5 cm x 5 cm) surface was removed with a brush. The brushed material was placed in a container with 100 ml of distilled water and was kept cold (not more than 24 h). In the laboratory,

**Table I. Location, and physicochemical parameters of the sampling sites. The mean and range of each variable are given in brackets.**

Site	Las Conchas	El Siambón	Apeadero Muñoz
Latitude (S)	26° 47' 04.1"	26° 43' 03.9"	26° 59' 14.0"
Longitude (W)	65° 20' 17.9"	65° 26' 47.6"	65° 39' 49.4"
Altitude (m a.s.l.)	710	1126	1622
Number of sampling dates	12	4	9
Water temperature (°C)	16.6 (16.2-17)	14.2 (12.3-17)	10.4 (9.4-11.6)
pH	8.81 (8.3-9.6)	8.14 (6.5-8.7)	7.8 (7.2-8.3)
Electrical Conductivity ( $\mu\text{S cm}^{-1}$ )	344 (300-441)	230 (92-272)	68 (40-92)
Dissolved Oxygen ( $\text{mg l}^{-1}$ )	12.3 (6.3-14.3)	11.1 (9.2-14.3)	11.4 (7.5-15.8)
% O2 saturation	126 (69 - 141)	115 (93-153)	102 (73-141)
Turbidity (NTU)	0 (0)	0.4 (0-4.8)	0.25 (0-1.2)
Channel width (m)	1.4 (0.1-3.3)	1.8 (0.7-5.4)	3.5 (1.6-5.4)
Average depth (m)	0.08 (0.03-0.14)	0.09 (0.04-0.2)	0.17 (0.08-0.26)
Current velocity ( $\text{m s}^{-1}$ )	0.35 (0.05-0.8)	0.6 (0.2-1.5)	0.4 (0.2-0.7)
Discharge ( $\text{m}^3 \text{s}^{-1}$ )	0.06 (0.003-0.21)	0.2 (0.02-1.8)	0.28 (0.05-0.59)
Chlorophyll a ( $\mu\text{g cm}^{-2}$ )	4.85	6.65	4.8
NO <sub>3</sub> ( $\text{mg L}^{-1}$ )	3.5	1.9	9.1
NH <sub>4</sub> <sup>+</sup> ( $\text{mg L}^{-1}$ )	0.033	0.029	0.025
PO <sub>4</sub> <sup>3-</sup> ( $\text{mg L}^{-1}$ )	0.45	0.11	0.12
Alkalinity ( $\text{mg L}^{-1}$ )	177.5	102.7	44.2
Chloride ( $\text{mg L}^{-1}$ )	1.77	1.16	0.46
Sulphate ( $\text{mg L}^{-1}$ )	5.60	3.88	2.24
Calcium ( $\text{mg L}^{-1}$ )	43.5	29.8	10.8
Magnesium ( $\text{mg L}^{-1}$ )	14.5	5.79	2.74
Sodium ( $\text{mg L}^{-1}$ )	11.3	8.20	3.34
Potassium ( $\text{mg L}^{-1}$ )	3.16	2.51	2.62
BOM ( $\text{g DM m}^{-2}$ )	82.1	170.6	193.0

the original sample was homogenized using a vortex and 50 ml was separated and reserved for the quantification of chlorophyll a. To quantify chlorophyll a, the monochromatic spectrophotometric method was applied (Loez 1995). The 50 ml sample was filtered, using Whatman GF/C filters as recommended by Holm-Hansen & Riemann (1978) by means of an ECAM Aspirex diaphragm aspirator. To complete the cell lysis, the filters were frozen at -18 °C for 12 h. Subsequently, the filters were crushed and macerated in the dark, using methanol as a

solvent, because it has greater penetration power in the cell membranes of the algae. The extract obtained was filtered again and the reading was carried out by means of a spectrophotometer at the optical densities of 665 nm and 750 nm before and after acidification of 3 ml of the extract with 0.1 ml of 0.1 N HCl.

The concentration of chlorophyll a ( $\mu\text{g}$  of chlorophyll a/ $\text{cm}^2$ ) was calculated according to the formula of Talling & Driver (Ros 1979):

$$\text{chlorophyll a} = 2,43 \times (\text{Db}-\text{Da}) \times 1,33 \times \text{V}$$

B x L

Db: O.D.665-D. O.750 (before acidification).

Da: O.D. 665-D. O.750 (after acidification).

V: volume of methanol used in the extraction (in ml).

B: volume of filtered water (in liters and / or ml).

L: length of the cuvette (cm).

Surber samples were processed under a binocular stereomicroscope, separating the macroinvertebrates from the organic matter. These were identified down to the lowest possible taxonomic level (in most cases, genus or species), using dichotomous keys for this region (Domínguez & Fernández 2009, Domínguez et al. 2006, Merritt & Cummins 1996). We use “taxonomic operational units or OTUs” for data treatment because the taxonomic level was not the same in all groups; in this study, OTU refers to the lowest taxonomic level achieved in each group. While the macroinvertebrates were identified, each individual was measured and sorted into a size class. The size classes for each taxon were determined considering the minimum and maximum size range, dividing it into 4 (in species with small body range) to 6 (in those with larger body ranges) classes. To obtain dry mass of the specimens we used published length-body mass regressions (Benke et al. 1999, Miserendino 2001a). The assignment of each taxon to a FFG was made through stomach content analysis, except for some taxa, for which we used previous publications (Reynaga & Dos Santos 2012, Ramírez & Gutiérrez-Fonseca 2014). Benthic organic matter (BOM, g DM. m<sup>-2</sup>) was separated from the mineral fraction, and then dried in an oven for 24 hours at 60°C (Miserendino 2001b).

### **Data treatment**

To describe the benthic assemblages in terms of individual abundance and biomass, we used Whittaker curves. The following diversity metrics and indices were calculated using the annual average abundance: taxa richness (S), Shannon’s index (H’), Simpson’s diversity index (expressed as 1-D), and evenness (J’). These indices were calculated using the Vegan package (Oksanen et al. 2019) in R software (R Core Team 2018).

Body size data (length) of each specimen were turned into tables by OTU to perform the secondary production calculations (available at <https://ibn.conicet.gov.ar/recursos/>). Annual production (P) was calculated using the size-frequency method (Benke 1984). The production interval of the cohort (CPI) was estimated using the method developed by Marchant & Yule (1996). Production values were informed as dry mass by area and time (mg DM m<sup>-2</sup> y<sup>-1</sup>). Although Trichoptera were diverse and an important component of the biomass, they were not abundant, so the calculation of production was limited to a few groups. We calculate the secondary production only for OTUs that exceeded 60 individuals in the sampling time (a year). This minimum number of individuals (an arbitrary limit) to be included in the production calculation and produce consistent results is not established or reported in the literature. However, at the time of assembling the spreadsheets to make the calculations, it was detected that with a smaller number of individuals, the productivity values were not consistent (they do not coincide with other groups of similar size and growth). Pearson correlations between production vs. physicochemical parameters and nutrients were performed, using the soft R (R Core Team 2018).

## RESULTS

### Physico-chemical characterization

All sites showed low conductivities, being higher in Las Conchas (Table I). In the same way, all streams showed well oxygenated and alkaline waters. Regarding the composition of major ions, Las Conchas, El Siambón, and Apeadero Muñoz presented calcium-bicarbonate waters. Apeadero Muñoz and El Siambón presented similar BOM values, doubling that present in Las Conchas (Table I).

### Structure and biomass of the communities

A total of 32526 specimens of benthic macroinvertebrates were separated and identified, classified into 90 OTUs (including 49 families). The total annual abundance (all specimens collected in all sampling dates) was similar in the three rivers: 10815 in Las Conchas, 9960 in El Siambón, and 11751 in Apeadero Muñoz. El Siambón presented the highest density and richness (Table II). The Shannon, Simpson, and Pielou indices pointed to the Apeadero Muñoz as the site with the greatest diversity, while Las Conchas presented the lowest values. The Whittaker abundance curves (Figure 2), also showed that the assemblage with the greatest evenness was that of Apeadero Muñoz (i.e., the curve presents a moderate slope). The general structure was similar in all sites, with Ephemeroptera being the most abundant taxon representing about 50% of total abundance in each site. The most abundant taxon at all sites was a small mayfly inhabiting riffles, *Baetodes huaico* (Baetidae). Diptera was the second

taxon in importance, followed by Trichoptera. In Apeadero Muñoz, Oligochaeta (mostly *Pristina*, Naididae) was the third important component. Plecoptera (*Anacroneuria*, Perlidae) was important in El Siambón and Apeadero Muñoz, but not in Las Conchas. The maximum abundances in all sites were recorded during winter (June to August), coinciding with the low water period.

Biomass followed the abundance pattern, with maximum records from June to October, and minimum in January and February; except for El Siambón (with a minimum in May). Trichoptera and Ephemeroptera were the most important groups, reaching both combined, more than 50% of the annual biomass in each site. The Whittaker curves for biomass (Figure 3) showed *Leptonema* (Hydropsychidae) as the largest contributor in Las Conchas and Apeadero Muñoz, and *Baetodes huaico* in El Siambón. Other relevant groups include: Odonata and Decapoda in Las Conchas; Coleoptera in El Siambón, and Megaloptera at Apeadero Muñoz.

### Secondary production

It was possible to estimate the secondary production for 38 OTUs, those most frequent and abundant: 14 Diptera (mostly Chironomidae), 11 Ephemeroptera, 5 Coleoptera, 5 Trichoptera, 2 Odonata, and 1 Plecoptera. The complete list of production (P) values estimated is in the Appendix. For the Apeadero Muñoz, P was calculated for 23 OTUs, reaching 9034 mg DM m<sup>-2</sup> y<sup>-1</sup>. In Las Conchas, it was calculated for 18 OTUs, totaling 3769 mg DM m<sup>-2</sup> y<sup>-1</sup>. Finally, in El Siambón

**Table II. Density (mean annual, individuals m<sup>-2</sup> y<sup>-1</sup>) and Diversity indices for each site are shown (mean and SD): S (Richness), H' (Shannon), 1-D (Simpson), J' (Pielou, evenness).**

Site	Density	S	H'	1-D	J'
Las Conchas	3341 (2133)	31 (9)	2.22 (0.47)	0.78 (0.14)	0.65 (0.13)
El Siambón	9210 (4572)	46 (8)	2.24 (0.31)	0.79 (0.08)	0.63 (0.06)
Apeadero Muñoz	4688 (2954)	41 (9)	2.64 (0.30)	0.87 (0.05)	0.72 (0.07)

16 OTUs produced 13916 mg DM m<sup>-2</sup> y<sup>-1</sup> (Table III). This represents, on average, 40% of the OTUs and 71% of the biomass.

The FFG with the highest contribution to secondary production in all the sites was that of collectors (CG, around 70% on average, Figure 4) followed by predators (PR, around 25%). In Las Conchas there was also a contribution to production by shredders (SH, 16.7%) and scrapers (SC, 4.2%).

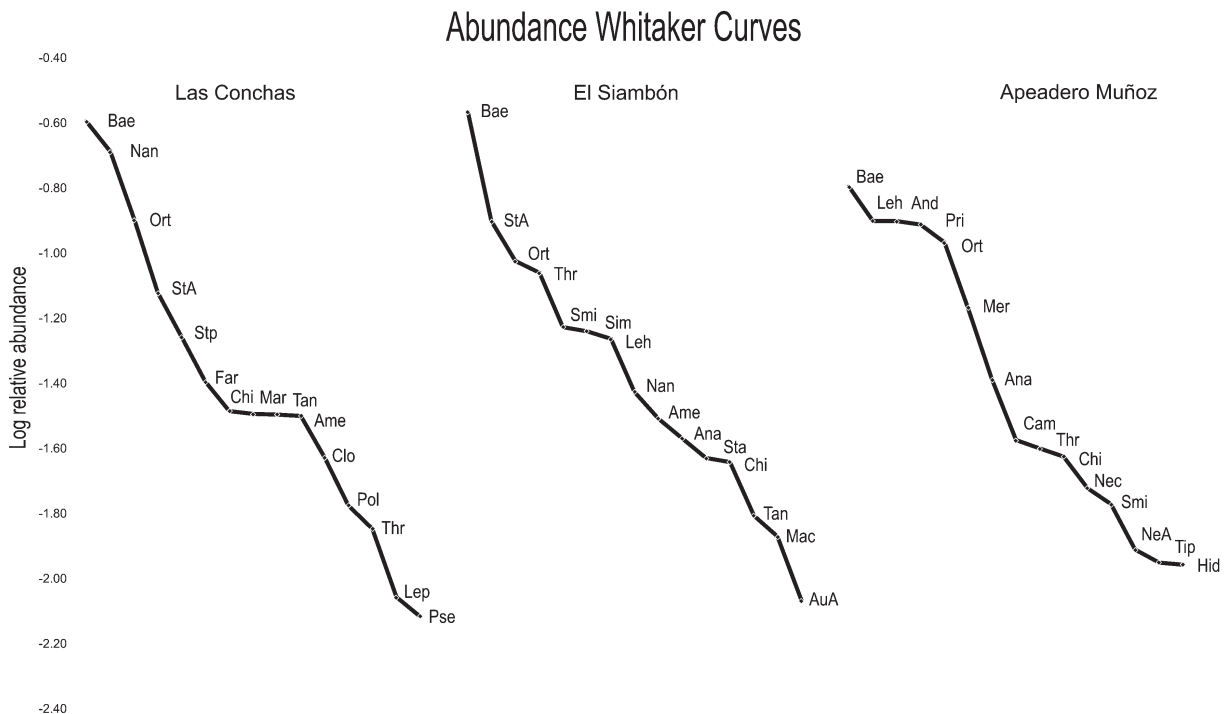
Secondary production in the three sites was dominated by Baetidae (Appendix): in Las Conchas, *Baetodes huaico* (P = 998.6 mg DM m<sup>-2</sup> y<sup>-1</sup>) and *Nanomis galera* (801.3 mg DM m<sup>-2</sup> y<sup>-1</sup>). In El Siambón, *Baetodes huaico* (5356.8 mg DM m<sup>-2</sup> y<sup>-1</sup>); and, in Apeadero Muñoz *Andesiops peruvianus* (1779.9 mg DM m<sup>-2</sup> y<sup>-1</sup>). The correlation

between secondary production and alkalinity was negative (p= 0.01, r = -0.99).

The annual P/B ratios, for the entire assemblage ranged 4.5-8.6 in the studied sites (Table III). Highest ratios for each site corresponded to Staphylinidae (35.1), and *Maruina* (34.4, Diptera, Psychodidae) in Las Conchas; and for *Simulium* (Simuliidae) in El Siambón (30.7) and Apeadero Muñoz (18.5).

### DISCUSSION

This is the first study to assess the structure, diversity, and secondary production of macroinvertebrate assemblages in three mountain streams in the Subtropical Andes. The high diversity of the streams from Las Yungas



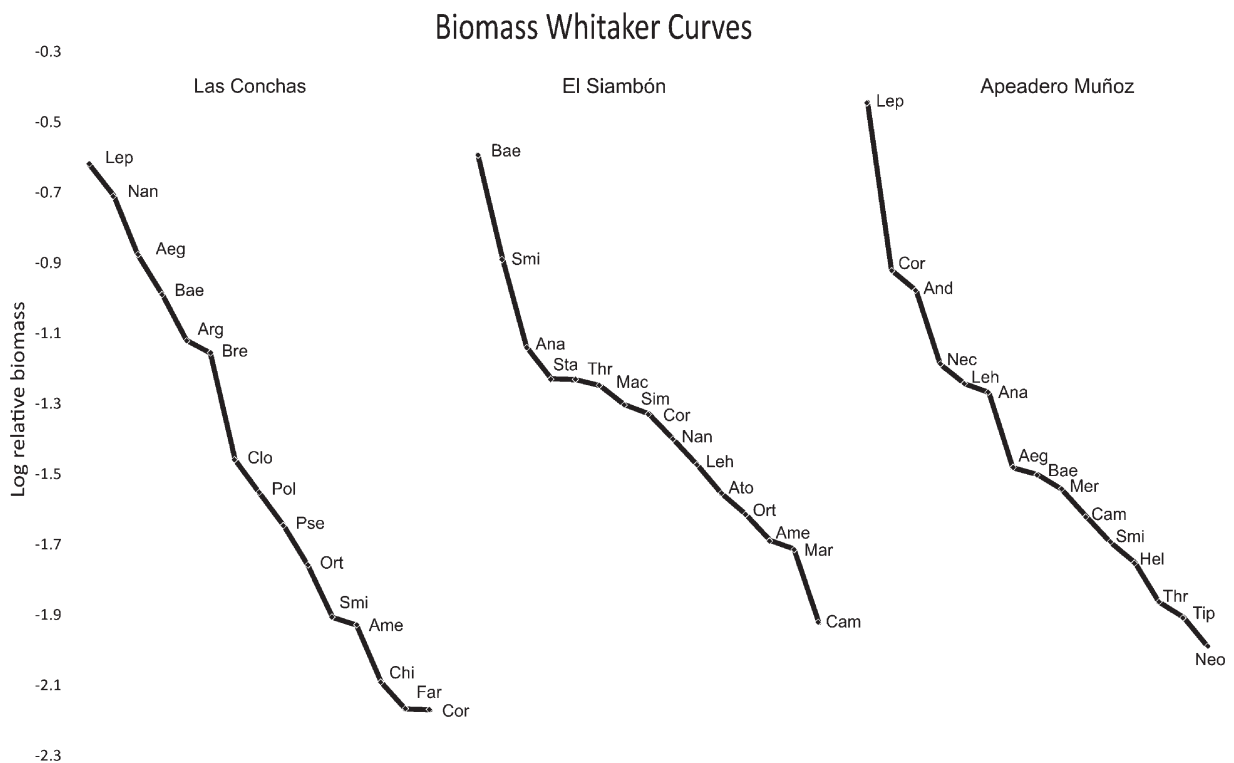
**Figure 2.** Rank-abundance curves showing taxon abundance for the three sites. Codes for the species: Aeg= Aegla, Ame= Americabaetis alphas, Ana= Anacroneuria, And= Andesiops peruvianus, Arg= Argia joergenseni, Ato= Atopsyche, AuA= Austrelmis (adulto), Bae= Baetodes huaico, Cam= Camelobaetidius penai, Chi= Chironominae, Clo= Cloeodes penai, Cor= Corydalus, Far= Farrodes yungaensis, Hel= Helicopsychidae, Hid= Hydroptilidae, Leh= Leptohyphes eximius, Lep= Leptonema, Mac= Macrelmis (larva), Mar= Maruina, Mer= Meridialaris tintinnabula, Nan= Nanomis galera, NeA= Neoelmis (adulto), Nec= Nectopsyche, Neo= Neoelmis (larva), Ort= Orthoclaadiinae, Pol= Polycentropus, Pri= Pristina, Pse= Psephenidae, Sim= Simuliidae, Smi= Smicridea, StA= Staphylinidae (adult), Stp= Staphylinidae (larva), Tan= Tanypodinae, Thr= Thraulodes consortis, Tip= Tipulidae.

rain forest (von Ellenrieder 2007, Molineri et al. 2009, Romero et al. 2011, Pero et al. 2019) was correctly included by our sampling design. Biomass and secondary production, much less studied parameters in these streams, was dominated by Ephemeroptera and Trichoptera. Macroinvertebrate production values were low (in the order of 10 g DM m<sup>2</sup> for an entire year), but this is commonly reported in mountain streams with very low nutrient contents (ranging 3 to 50 g DM m<sup>-2</sup> y<sup>-1</sup>, Huryn & Wallace 2000, Ramírez & Pringle 1998). Collectors and predators were the most important FFG in all three parameters (abundance, biomass and production), shredders were almost absent in spite of high quantities of coarse particulate organic matter (leaf packs and twigs), that is almost entirely decomposed by microorganisms (Molineri et al. 2009, Romero et al. 2010).

Some taxa were not available for production calculation (ranging 22-36% of the total

biomass sampled) because their frequency and abundance were not enough to estimate it with the method used. This happened in Las Conchas and Apeadero Muñoz, with *Aegla* (Decapoda) and *Corydalus* (Megaloptera), both with large body sizes but low frequency, what prevented production calculations with the frequency size method. Similar limitations were found by Ramírez & Pringle (1998) whose production study covered only 30% of the total biomass of their site, because they could not include shrimps. Other studies in tropical streams have shown that shrimps and other crustaceans can be a very important component (Jacobsen et al. 2008).

El Siambón (with only 16 OTUs available for P calculation) showed the highest annual production, almost doubling that of Apeadero Muñoz and Las Conchas, both with more OTUs included in the analysis. The high densities of algae, mainly epilithic and represented mostly



**Figure 3.** Rank-abundance curves showing biomass for the three sites. Codes for the species as in Fig. 2.



by diatoms (M.A. Taboada, unpublished data) at El Siambón, could be one of the factors that favored higher secondary production (Krueger & Waters 1983). El Siambón stream presented a more open canopy allowing some direct incidence of solar radiation in the bottom, generating a greater development of algae in the dry season, in spite of low nutrient concentrations (Guasch et al. 1995). It will be important to continue monitoring long-term changes to better understand the dynamics of these systems and prevent eutrophication processes.

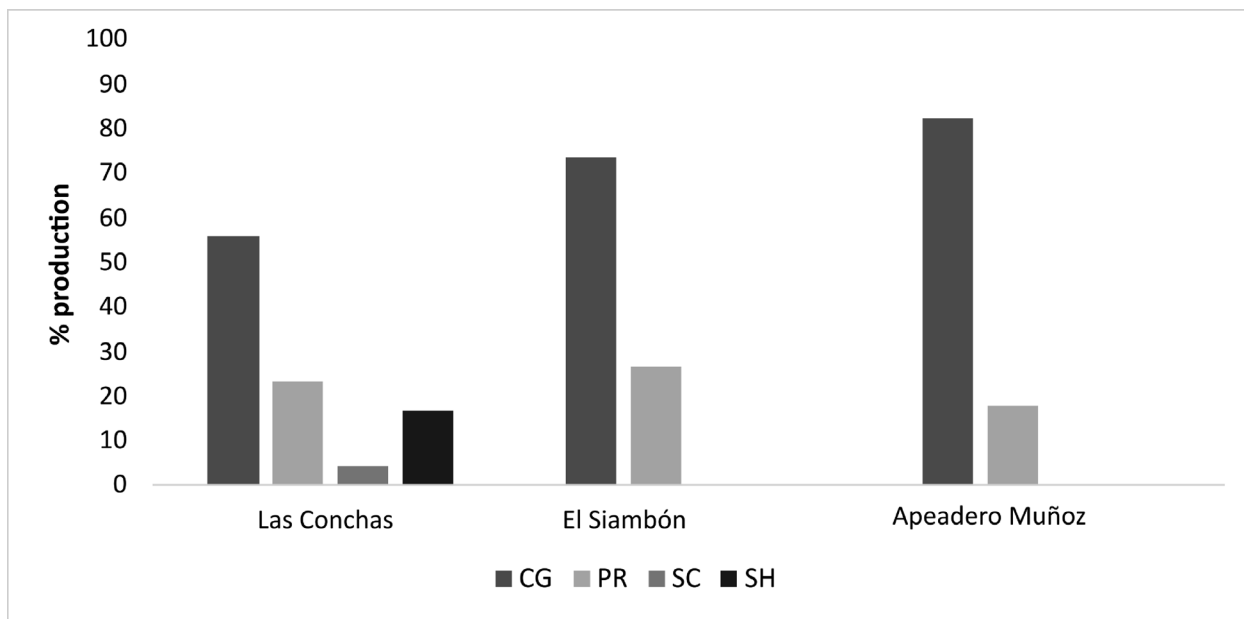
During low water period, the stability of the water column, that reduced detachment and sediment removal (Horner & Welch 1981, Horner et al. 1990) favored the increment of algal and macroinvertebrate biomass. This was reported in different studies in tropical and subtropical rivers and streams (Huertas-Farías et al. 2019, Godoy-Lozada & Pelaez-Rodríguez 2020). Although the samplings of benthic communities were developed in two consecutive years, we consider that this did not influence our production estimates, because there were no extraordinary events that affected differently the water regime of each stream. In this work we have not focused on the seasonal variation of biomass and productivity, however, in concordance with a previous study (Molineri 2010) our results point to a significant reduction of both parameters during the flood season.

There are no estimates of secondary production for macroinvertebrate assemblages in mountain streams for other regions of

Argentina or subtropical South America. However, there are numerous studies from temperate zones, especially from North America, and some from Central America with which we can make comparisons. For example, annual production estimates in the present study were one order of magnitude higher than those found by Ramírez & Pringle (1998) in a stream in Costa Rica & Colón-Gaud et al. (2009) in streams from Panama. Numerous studies coincide with the results mentioned here in pointing to the orders Ephemeroptera, Trichoptera, Diptera, Odonata, and Plecoptera as the main ones responsible for secondary production (Fisher & Gray 1983, Benke 1993, Grubaugh et al. 1996, Ramírez & Pringle 1998, Stagliano & Whiles 2002, Rosas et al. 2019, Ríos-Touma et al. 2022). P/B ratios indicate the frequency with which biomass is renewed in the system; higher values are associated with shorter life cycles (Benke 1993). As shorter life cycles are associated with higher water temperatures it is not surprising that our warmer sites presented higher P/B ratios. Krueger & Waters (1983) estimated the production for three mountain streams in Minnesota (USA) with different alkalinity conditions (range 34-245 mg L<sup>-1</sup>), of which only one (with the higher alkalinity) presented higher production (22.5 g DM m<sup>-2</sup> y<sup>-1</sup>) than that found by us. Griffith et al. (1994) also found a positive correlation between production (they only evaluated shredders) and alkalinity, in four sites with alkalinity ranging between 0-40 mg L<sup>-1</sup>. Instead, we obtained a negative correlation between alkalinity and secondary production, with similar alkalinity values to the

**Table III. Annual mean biomass (B, in brackets standard deviation), annual secondary production (P), and total P/B rate at the sampled sites.**

Site	B (mg DM m <sup>-2</sup> )	P (mg DM m <sup>-2</sup> y <sup>-1</sup> )	P/B
Las Conchas	559.4 (367.6)	3769.3	6.7
El Siambón	1616.6 (670.4)	13916.4	8.6
Apedero Muñoz	1980.9 (146.4)	9034.2	4.5



**Figure 4. Secondary production according to feeding functional groups in the three sampled sites. CG: collectors-gatherers, PR: predators, SC; scrapers, SH: shredders.**

referred studies. In our study region, Fernández et al. (2019) reported strong calcite precipitation on algal masses (*Cladophora* sp.) facilitated by epiphytic diatom metabolism (mainly *Gomphonema* spp.), resulting in a thick layer of microbiolites that may prevent herbivory. Since alkalinity and calcite precipitation are related, more research is necessary to elucidate the relationship between them and production.

In relation to the production of the different FFG, our results (collectors and predators being the principal contributors ) coincide with many other studies (Krueger & Waters 1983, Lugthart & Wallace 1992, Grubaugh et al. 1996, Ramírez & Pringle 1998, Meyer & Poepperl 2003, Frauendorf et al. 2013). The major difference with those previously cited studies is that scrapers exceeded shredders in production; which is common in Yungas, because of a natural shortage of both groups (Molineri et al. 2009, Romero et al. 2010), due to the shady nature of the rivers, and competition with decomposing

microorganisms (Dudgeon 2000). Aquatic top predators in our systems are 3 species of small catfishes (*Trichomycterus* and *Heptapterus*) and introduced rainbow trout. Their top-down effect affecting macroinvertebrate production is still under study, but it seems small because of low fish density and biomass.

The study of trophic relationships, biomass, and production has important general implications for the conservation and management of water courses and the services they provide to our societies. These parameters are complex outcomes of an ecosystem evidencing its correct function and health. We expect that our results will serve as a baseline for future monitoring of global warming in our region, and its effects on stream functioning. We hope that this is the first step to increasing studies of this type, including other ecoregions and river types.

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## REFERENCES

- ALLAN JD & CASTILLO MM. 2007. Stream Ecology: Structure and function of running waters. Springer Science & Business Media.
- ANDERSON CB & ROSEMOND AD. 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* 154(1): 141-153.
- AÑÓN SUÁREZ D & ALBARIÑO RJ. 2001. Life cycle and annual production of *Caenis* sp (Ephemeroptera, Caenidae) in Lake Escondido (Bariloche, Argentina). In: DOMÍNGUEZ E (Ed). Trends in research in Ephemeroptera and Plecoptera. Boston: Springer, MA, p. 67-75.
- BENKE AC. 1984. Secondary production of aquatic insects. In: RESH VH & ROSENBERG DM Eds. The ecology of aquatic insects. New York: Praeger Scientific, p. 289-322.
- BENKE AC. 1993. Concepts and patterns of invertebrate production in running waters. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 25(1): 15-38.
- BENKE AC. 2010. Secondary production as part of bioenergetic theory-contributions from freshwater benthic science. *River Res Appl* 26(1): 36-44.
- BENKE AC, HURYN AD, SMOCK LA & WALLACE JB. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J N AM Benthol Soc* 18(3): 308-343.
- BRAND C & MISERENDINO ML. 2011. Life history strategies and production of caddisflies in a perennial headwater stream in Patagonia. *Hydrobiologia* 673(1): 137-151.
- COLÓN-GAUD C, WHILES MR, KILHAM SS, LIPS KR, PRINGLE CM, CONNELLY S & PETERSON SD. 2009. Assessing ecological responses to catastrophic amphibian declines: patterns of macroinvertebrate production and food web structure in upland Panamanian streams. *Limnol Oceanogr* 54(1): 331-343.
- CONTADOR T & KENNEDY J. 2016. The life histories of *Meridialaris chiloeensis* (Demoulin, 1955) (Ephemeroptera: Leptophlebiidae) and *Gigantodax rufescens* (Edwards, 1931) (Diptera: Simuliidae) on a Magellanic sub-Antarctic island (55°S). *Aquat Insects* 37(2): 145-158.
- CUMMINS KW. 1973. Trophic relations of aquatic insects. *Annu Rev Entomol* 18: 183-206.
- CUMMINS KW. 2016. Combining taxonomy and function in the study of stream macroinvertebrates. *J Limnol* 75(S1): 235-241.
- DOLBETH M, CUSSON M, SOUSA R & PARDAL MA. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. *Can J Fish Aquat Sci* 69(7): 1230-1253.
- DOMÍNGUEZ E & FERNÁNDEZ HR. 2009. Macroinvertebrados Bentónicos Sudamericanos. *Sistemática y biología*. Tucumán: Fundación Miguel Lillo, Argentina, p. 656.
- DOMÍNGUEZ E, MOLINERI C, PESCADOR ML, HUBBARD MD & NIETO C. 2006. Ephemeroptera of South America. *Aquatic Biodiversity in Latin America (ABLA)*, Vol. 2.
- DOS SANTOS LIMA JC & PAMPLIN PAZ. 2017. Life cycle and secondary production of two species of *Campsurus* (Ephemeroptera, Polymitarcyidae) in reservoirs of southeastern Brazil. *Stud Neotrop Fauna Environ* 52(1): 1-10.
- DUDGEON D. 2000. The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annu Rev Ecol Evol Syst* 31: 239-263.
- EPELE LB & MISERENDINO ML. 2011. Life cycle, production and habitat selection of *Notoperla fasciata* and *N. magnaspina* (Plecoptera: Gripopterygidae) in a headwater Patagonian stream. *Fundam Appl Limnol / Archiv für Hydrobiologie* 178: 219-229.
- EPELE LB, MISERENDINO ML & PESSACQ P. 2011. Life history, seasonal variation and production of *Andesiops torrens* (Lugo-Ortiz and McCafferty) and *Andesiops peruvianus* (Ulmer) (Ephemeroptera: Baetidae) in a headwater Patagonian stream. *Limnologica* 41(1): 57-62.
- FERNÁNDEZ HR, GONZÁLEZ ACHEM AL, CORREA M & ALBARRACÍN VH. 2019. Microbialite-like structures in *Cladophora* sp.(Ulvophyceae) mats from a subtropical Andean basin: ecological implications. *Rev Biol Trop* 67(1): 83-93.
- FERNÁNDEZ HR, ROMERO F, PERALTA M & GROSSO L. 2001. La diversidad del zoobentos en ríos de montaña del noroeste de Argentina: comparación entre seis ríos. *Ecol Austral* 11(1): 9-16.
- FISHERSG & GRAYLJ. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* 64(5): 1217-1224.
- FRAUENDORF TC, COLÓN-GAUD C, WHILES MR, BARNUM TR, LIPS KR, PRINGLE CM & KILHAM SS. 2013. Energy flow and

the trophic basis of macroinvertebrate and amphibian production in a Neotropical stream food web. *Fresh Biol* 58: 1340-1352.

GAINES WL, CUSHING CE & SMITH SD. 1992. Secondary production estimates of benthic insects in three cold desert streams. *Great Basin Nat* 52(1): 11-24.

GODOY-LOZADA D & PELAEZ-RODRIGUEZ M. 2020. Diversidad y distribución de la comunidad fitoperifítica presente en un río andino amazónico y su relación con variables ambientales. *Rev Aca Col Cs Exactas, Físicas y Naturales* 44(171): 437-451. DOI: 10.18257/raccefyn.1098.

GRIFFITH SA, PERRY SA & PERRY WB. 1994. Secondary production of macroinvertebrates shredders in headwater streams with different baseflow alkalinity. *J N Am Benthol Soc* 13(3): 345-356.

GRUBAUGH JW, WALLACE JB & HOUSTON ES. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Can J Fish Aquat Sci* 53(4): 896-909.

GUASCH H, MARTÍ E & SABATER S. 1995. Nutrient enrichment effects on biofilm metabolism in Mediterranean streams. *Freshw Biol* 33: 373-383.

HOLM-HANSEN O & RIEMANN B. 1978. Chlorophyll a determination: improvements in methodology. *Oikos* 30: 438-447.

HORNER RR & WELCH EB. 1981. Stream periphyton development in relation to current velocity and nutrients. *Can J Fish Aquat Sci* 38: 449-457.

HORNER RR, WELCH EB, SEELEY MR & JACOBY JM. 1990. Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshw Biol* 24: 215-232.

HUERTAS-FARIAS K, PARRA YT & REINOSO G. 2019. Aspectos ecológicos de la comunidad fitoperifítica en el río Anchique, Cuenca andina colombiana. *Rev Acad Col Cs Exactas, Físicas y Naturales* 43(166): 98-107. DOI: 10.18257/rCCAefyn.722.

HURYN AD & WALLACE JB. 2000. Life history and production of stream insects. *Annu Rev Entomol* 45(1): 83-110.

JACKSON JK & SWEENEY BW. 1995. Egg and Larval Development Times for 35 Species of Tropical Stream Insects from Costa Rica. *J North Am Benthol Soc* 14(1): 115-130.

JACOBSEN D. 2003. Altitudinal changes in diversity of macroinvertebrates from small streams in the Ecuadorian Andes. *Archiv fur Hydrobiologie* 158(2): 145-168.

JACOBSEN D, CRESSA C, MATHOOKO JM & DUDGEON D. 2008. Macroinvertebrates: composition, life histories and production. In: DUDGEON D. editor. *Tropical stream ecology*. London: Academic Press, p. 65-105.

KRUEGER CC & WATERS TF. 1983. Annual production of macroinvertebrates in three streams of different water quality. *Ecology* 64(4): 840-850.

LEAL JFF & DE ASSIS ESTEVES F. 2000. Life cycle and production of *Campsurus notatus* (Ephemeroptera, Polymitarcyidae) in an Amazonian lake impacted by bauxite tailings (Pará, Brazil). *Hydrobiologia* 437(1-3): 91-99.

LOEZ CR. 1995. Determinación de clorofila a. In: TELL G & LOPRETTO EC (Eds), *Ecosistemas de aguas continentales. Metodología para su estudio*, Vol. I, 263-269 p.

LUGTHART GJ & WALLACE JB. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. *J N Am Benthol Soc* 11(2): 138-164.

MARCHANT R & YULE CM. 1996. A method for estimating larval life spans of aseasonal aquatic insects from streams on Bougainville Island, Papua Nueva Guinea. *Freshw Biol* 35: 101-107.

MERRITT RW & CUMMINS KW. 1996. *An introduction to the Aquatic Insects of North America*. 3rd. edition. Dubuque: Kendall/Hunt Publishing Company.

MEYER EI & POEPPERL R. 2003. Secondary production of invertebrates in a Central European mountain stream (Steina, Black Forest, Germany). *Archiv für Hydrobiologia* 158(1): 25-42.

MISERENDINO ML. 2001a. Length-mass relationships for macroinvertebrates in freshwater environments of Patagonia (Argentina). *Ecol Austral* 11(1): 3-8.

MISERENDINO ML. 2001b. Macroinvertebrate assemblages in Andean Patagonian rivers and streams: environmental relationships. *Hydrobiologia* 444(1): 147-158.

MOLINERI C. 2010. The influence of floods on the life history of dominant mayflies (Ephemeroptera) in a subtropical mountain stream. *Stud Neotrop Fauna Environ* 45(3): 149-157.

MOLINERI C, ROMERO VF & FERNÁNDEZ HR. 2009. Diversidad y conservación de invertebrados acuáticos. In: BROWN AD, BLENDINGER P, LOMÁSCOLO T & BES PG (Eds). *Selva pedemontana de las Yungas. Historia natural, ecología y manejo de un ecosistema en peligro*. Tucumán: San Miguel de Tucumán: Ediciones del Subtrópico, Argentina, p. 121-148.

ODUM EP. 1968. Energy flow in ecosystems: a historical review. *Am Zool* 8(1): 11-18.

- OKSANEN J ET AL. 2019. Vegan: Community Ecology Package. R package version 2.5-5. <https://CRAN.R-project.org/package=vegan>.
- PERO EJI, HANKEL GE, MOLINERI C & DOMÍNGUEZ E. 2019. Correspondence between stream benthic macroinvertebrate assemblages and ecoregions in northwestern Argentina. *Freshw Sci* 38(1): 64-76.
- R CORE TEAM. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- RAMIREZ A & GUTIERREZ-FONSECA P. 2014. Functional feeding groups of aquatic insect families in Latin America: a critical analysis and review of existing literature. *Rev Biol Trop* 62(2): 155-167.
- RAMIREZ A & PRINGLE CM. 1998. Structure and production of a benthic insect assemblage in a Neotropical stream. *J N Am Benthol Soc* 17: 443-463.
- REYNAGA MC. 2009. Hábitos alimentarios de larvas de Trichoptera [Insecta] de una cuenca subtropical. *Ecol Austral* 19(3): 207-214.
- REYNAGA MC & DOS SANTOS DA. 2012. Rasgos biológicos de macroinvertebrados de ríos subtropicales: patrones de variación a lo largo de gradientes ambientales espacio-temporales. *Ecol Austral* 22(2): 112-120.
- REYNAGA MC & RUEDA MARTÍN P. 2010. Trophic analysis of two species of *Atopsyche* (Trichoptera: Hydrobiosidae). *Limnologia* 40(1): 61-66.
- REYNAGA MC & RUEDA MARTÍN PA. 2014. Trophic analysis of three species of *Marilia* (Trichoptera: Odontoceridae) from the neotropics. *Rev Biol Trop* 62(2): 543-550.
- RÍOS-PULGARIN MI, BARLETTA M, ARANGO-JARAMILLO MC & MANCERA-RODRIGUEZ NJ. 2016. The role of the hydrological cycle on the temporal patterns of macroinvertebrate assemblages in an Andean foothill stream in Colombia. *J Limnol* 75(S1): 107-120. [10.4081/jlimnol.2016.1394](https://doi.org/10.4081/jlimnol.2016.1394).
- RÍOS-TOUMA B, ENCALADA AC & PRAT N. 2022. Life history and secondary production of *Anomalocosmoecus illiesi* Marlier, 1962 (Trichoptera, Limnephilidae) in a small stream in the northern Ecuadorian Paramo. *ZooKeys* 1111: 381-388.
- RODRÍGUEZ GV & D'URSO CH. 2005. Estudio hidrogeológico y de calidad de agua en el sector oriental de la Sierra de San Javier entre las localidades de Yerba Buena y el Manantial. Provincia de Tucumán, República Argentina. *Estud Geol* 61(3-6): 197-206.
- ROMERO F, FERNÁNDEZ HR, MANZO V, MOLINERI C, CORREA M & NIETO MC. 2011. Estudio integral de la cuenca del Río Lules (Tucumán): aspectos biológicos. In: FERNÁNDEZ HR & BARBER HM (Eds), *La Cuenca del río Lules. Una aproximación multidisciplinaria a su complejidad*. EDUNT. San Miguel de Tucumán, Tucumán, Argentina, p. 111-135.
- ROMERO F, FERNÁNDEZ HR, MOLINERI C & DOMÍNGUEZ E. 2010. Ecología de ríos y arroyos de la Sierra de San Javier. In: GRAU R (Ed), *Ecología regional de una interfase natural - urbana. La Sierra de San Javier y el Gran San Miguel de Tucumán*. Tucumán: Editorial de la Universidad Nacional de Tucumán, p. 77-92.
- ROS J. 1979. *Prácticas de Ecología*. Ed. Omega. Barcelona.
- ROSAS KG, COLÓN-GAUD C & RAMÍREZ A. 2020. Trophic basis of production in tropical headwater streams, Puerto Rico: an assessment of the importance of allochthonous resources in fueling food webs. *Hydrobiologia* 847(8): 1961-1975.
- SIROMBRA MG & MESA LM. 2010. Composición florística y distribución de los bosques ribereños subtropicales andinos del Río Lules, Tucumán, Argentina. *Rev Biol Trop* 58(1): 499-510.
- STAGLIANO DM & WHILES MR. 2002. Macroinvertebrate production and trophic structure in a tallgrass prairie headwater stream. *J N Am Benthol Soc* 21(1): 97-113.
- SUÁREZ DAA & ALBARIÑO RJ. 2001. Life Cycle and Annual Production of *Caenis* sp (Ephemeroptera, Caenidae) in Lake Escondido (Bariloche, Argentina). In: Dominguez E (Ed), *Trends in Research in Ephemeroptera and Plecoptera*. Boston: Springer, p. 67-75.
- VON ELLENRIEDER N. 2007. Composition and structure of aquatic insect assemblages of Yungas mountain cloud forest streams in NW Argentina. *Rev Soc Entomol Argent* 66(3-4): 57-76.
- WATERS TF & CRAWFORD GW. 1973. Annual production of a stream mayfly population: a comparison of methods. *Limnol Oceanogr* 18(2): 286-296.

**Appendix. Cohort productive interval (CPI), mean annual biomass (B, mg DM m<sup>-2</sup>), annual secondary production (P, mg DM m<sup>-2</sup> y<sup>-1</sup>) and annual P/B rate for macroinvertebrates community of the three studied sites. CPI is expressed in days. CPI from other works are provided for comparison when available.**

**Las Conchas:**

Family	Genus or species	CPI literature	CPI	B	P	P/B
Psephenidae	<i>Psephenus</i>		136.0	17.5	204.5	11.7
Staphylinidae	-		60.7	1.9	66.8	35.1
Chironomidae	Chironominae	24 <sup>g</sup>	84.1	4.5	116.1	25.6
Chironomidae	Orthoclaadiinae	24 <sup>g</sup>	75.0	9.7	250.7	25.7
Chironomidae	Tanypodinae	24 <sup>g</sup>	45.4	2.8	76.8	27.1
Psychodidae	<i>Maruina</i>		49.4	0.6	20.0	34.4
Baetidae	<i>Americabaetis alphus</i>	51 <sup>f</sup>	152.0	6.6	87.5	13.3
Baetidae	<i>Baetodes huaico</i>		142.6	88.1	998.6	11.3
Baetidae	<i>Cloeodes penai</i>		143.4	10.1	158.5	15.7
Baetidae	<i>Nanomis galera</i>		183.2	49.7	801.3	16.1
Caenidae	<i>Caenis ludicra</i>	365 <sup>e</sup>	140.1	1.5	18.0	12.1
Leptohyphidae	<i>Leptohyphes eximius</i>	74 <sup>a</sup>	88.6	0.4	6.4	17.5
Leptophlebiidae	<i>Farrodes yungensis</i>		105.9	8.0	141.7	17.6
Leptophlebiidae	<i>Thraulodes consortis</i>	124 <sup>a</sup>	147.4	4.3	68.4	15.9
Caenogrionidae	<i>Argia joergenseni</i>		390.3	42.3	128.9	3.0
Libellulidae	<i>Brechmorhoga nubecula</i>		519.0	39.0	120.1	3.1
Hydropsychidae	<i>Leptonema</i>	365 <sup>d</sup>	286.9	56.7	389.4	6.9
Polycentropodidae	<i>Polycentropus joergenseni</i>		217.6	15.4	115.7	7.5
Total				359.2	3769.3	6.7

**El Siambón:**

Family	Genus or species	CPI literature	CPI	B	P	P/B
Perlidae	<i>Anacroneuria</i>	120 <sup>f</sup>	414.7	121.8	586.3	4.8
Baetidae	<i>Baetodes huaico</i>		86.8	373.4	5356.8	14.4
Baetidae	<i>Nanomis galera</i>		226.2	68.1	688.7	10.1
Baetidae	<i>Americabaetis alphus</i>	51 <sup>f</sup>	181.9	33.0	433.38	13.1
Leptohyphidae	<i>Leptohyphes eximius</i>	74 <sup>a</sup>	350.6	54.2	536.8	9.9
Leptophlebiidae	<i>Thraulodes consortis</i>	124 <sup>a</sup>	506.8	84.9	576.2	6.8
Simuliidae	<i>Simulium</i>	30 <sup>g</sup>	11.2	75.2	2307.9	30.7
Hydropsychidae	<i>Smicridea</i>	365 <sup>d</sup>	182.3	152.9	990.5	6.5
Elmidae	<i>Austrelmis</i>		68.0	4.9	78.58	16.2
Elmidae	<i>Macrelmis</i>		124.0	91.2	807.1	8.9
Staphylinidae	<i>Staphylinidae</i>		37.5	68.8	857.8	12.5
Chironomidae	<i>Pentaneura</i>	24 <sup>g</sup>	24.3	6.6	120.5	18.2
Chironomidae	<i>Rheotanytarsus</i>	35 <sup>f</sup>	52.9	3.8	72.8	19.0
Chironomidae	<i>Cricotopus</i>	24 <sup>g</sup>	22.8	14.1	267.8	19.0
Chironomidae	<i>Paramectrionemus</i>	35 <sup>f</sup>	8.5	12.9	225.9	17.5

**Appendix. Continuation.**

Chironomidae	<i>Onconeura</i>	24 <sup>g</sup>	0.6	0.4	9.3	23.6
Total				1166.1	13916.4	8.6

**Apeadero Muñoz:**

Family	Genus or species	CPI literature	CPI	B	P	P/B
Perlidae	<i>Anacroneuria</i>	120 <sup>f</sup>	420.1	148.5	622.2	4.2
Baetidae	<i>Baetodes huaico</i>		275.9	69.7	694.4	10.0
Baetidae	<i>Andesiops peruvianus</i>	365 <sup>b</sup>	221.7	260.1	1779.9	6.8
Baetidae	<i>Americabaetis alphus</i>	51 <sup>f</sup>	226.9	2.0	26.8	13.3
Baetidae	<i>Camelobaetidius penai</i>		185.9	68.5	468.7	6.8
Baetidae	<i>Leptohyphes eximius</i>	74 <sup>a</sup>	413.8	138.1	1038.5	7.5
Leptophlebiidae	<i>Meridalaris tintinnabula</i>	218 <sup>c</sup>	486.6	80.9	452.0	5.6
Leptophlebiidae	<i>Thraulodes consortis</i>	124 <sup>a</sup>	387.3	37.3	208.3	5.6
Simuliidae	<i>Simulium</i>	30 <sup>g</sup>	43.8	5.0	91.6	18.5
Tipulidae	-		239.3	24.2	171.9	7.1
Elmidae	<i>Austrelmis</i>		100.3	1.9	19.3	10.0
Elmidae	<i>Neoelmis</i>		112.8	2.3	18.5	8.0
Chironomidae	<i>Onconeura</i>	24 <sup>g</sup>	35.8	0.6	10.1	17.1
Chironomidae	<i>Paramectronemus</i>	35 <sup>f</sup>	13.0	10.0	129.8	13.0
Chironomidae	<i>Cricotopus</i>	22 <sup>f</sup>	43.0	5.1	70.6	14.0
Chironomidae	<i>Corynoneura</i>	24 <sup>g</sup>	29.3	0.2	3.1	18.2
Chironomidae	<i>Tanytarsus</i>	35 <sup>f</sup>	81.3	1.6	21.9	14.0
Chironomidae	<i>Rheotanytarsus</i>	35 <sup>f</sup>	107.2	2.2	30.3	14.0
Ceratopogonidae	<i>Bezzia</i>		33.4	8.3	104.1	12.6
Helicopsychidae	<i>Helycopsyche</i>	86 <sup>f</sup>	162.3	30.2	151.3	5.0
Leptoceridae	<i>Nectopsyche</i>	365 <sup>d</sup>	305.7	162.2	795.0	4.9
Hydropsychidae	<i>Leptonema</i>	365 <sup>d</sup>	169.0	878.1	1903.6	4.7
Hydropsychidae	<i>Smicridea</i>	365 <sup>d</sup>	251.9	44.1	222.4	5.0
Total				1980.9	9034.2	3.6

<sup>a</sup>Molineri (2010) <sup>b</sup>Epele et al. (2011) <sup>c</sup>Contador & Kennedy (2016) <sup>d</sup>Brand & Miserendino (2011) <sup>e</sup>Suárez & Albariño (2001) <sup>f</sup>Jackson & Sweeney (1995) <sup>g</sup>Gaines et al. 1992.

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GH and CM designed the work. GH, CN, FR, MLG, MCR, MT, PRM, JR, VM and CM collected and generated the data. GH, CM, MLG, CN and MT analyzed and interpreted the data. GH and CM drafted the article. GH, CN, FR, MLG, MCR, MT, PRM, JR, VM and CM critically revised and approved the final version.

