







Composition, life-history, and population dynamics of the Chironomidae from a tropical high-altitude stream (Saltana River, Ecuador)

Composição, história de vida e dinâmica populacional de Chironomidae de um riacho tropical de alta altitude (Rio Saltana, Equador)

Narcís Prat i Fornells^{1*} , Andrea C. Encalada² , Christian Villamarín³  and Blanca Ríos-Touma^{3*} 

¹Freshwater Ecology and Management Research Group, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Faculty of Biology, University of Barcelona, Av. Diagonal, 643, 08028, Barcelona, Catalonia, Spain

²Laboratorio de Ecología Acuática, Instituto BIOSFERA, Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Vía Pampite, s/n, Cumbayá, Quito, Ecuador

³Grupo de Investigación en Biodiversidad, Medio Ambiente y Salud – BIOMAS, Facultad de Ingenierías y Ciencias Aplicadas, Ingeniería Ambiental, Universidad de las Américas, Vía a Nayón, 170124, Campus UDLAPARK, Quito, Ecuador

*e-mail: nprat@ub.edu; blanca.rios@udla.edu.ec

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Abstract: Aim: To study the composition and population dynamics of Chironomidae (Diptera) from a high-altitude tropical stream in Ecuador. **Methods:** Samples were taken at Saltana River between April 2009 and November 2010. Physico-chemical parameters, such as flow, dissolved oxygen, conductivity, pH, and temperature, were measured in each sampling campaign. Larvae and pupae sampling was conducted with a Hess sampler in different substrates. During each sampling campaign, adults were sampled using amphibious emergence traps for 24 hours. All materials collected were separated and classified in the laboratory. The biomass was calculated using the individual weight of the larvae of different instars multiplied by the density of each instar at each sample. **Results:** A total of 18 larval taxa were found in 14 different genera in the benthic samples. The subfamily Orthoclaadiinae showed the highest richness (12 genera), followed by Podonominae, Diamesinae, and Chironominae, with two genera each. The most frequent taxa were *Cricotopus* sp.3, *C. (Oliveiriella) rieradevallae*, and Genus 1 sp.a. Total densities fluctuate very much from one month to another following the changes of the most abundant species, and only one species showed a relationship with the substrates. Biomass values are lower from June to August of both years, which matches the high flow season. **Conclusions:** The Saltana River's cold temperature (6-7 °C) and the flow variability determine the low richness, density and biomass throughout the year. It is unclear if individuals showed very short or long-life cycles due to constant temperature throughout the year. However, there is a clear asynchrony in life cycles due to the presence of emerging adults throughout the year.

Keywords: chironomids; mountain stream; community composition; Andes.

Resumo: Objetivo: estudar a composição e a dinâmica populacional de Chironomidae (Diptera) de um riacho tropical de altitude no Equador. **Métodos:** As amostras foram coletadas no rio Saltana entre



abril de 2009 e novembro de 2010. Os parâmetros físico-químicos como fluxo, oxigênio dissolvido, condutividade, pH e temperatura foram medidos em cada campanha de amostragem. Larvas e pupas foram coletadas com um amostrador Hess em diferentes substratos. Já os adultos foram amostrados com armadilhas anfíbias de emergência por 24 horas durante cada campanha de amostragem. Todo o material coletado foi triado e identificado no laboratório. A biomassa foi calculada usando o peso individual das larvas de diferentes instares multiplicado pela densidade de cada instar em cada amostra. **Resultados:** Um total de 18 táxons larvais foi encontrado em 14 gêneros diferentes nas amostras bentônicas. A subfamília Orthocladiinae apresentou a maior riqueza (12 gêneros), seguida por Podonominae, Diamesinae e Chironominae, com dois gêneros cada. Os táxons mais frequentes foram *Cricotopus* sp3, *C. (Oliveiriella) rieradevallae* e Genus 1 sp a. As densidades totais flutuaram muito de um mês para outro, seguindo as mudanças das espécies mais abundantes, e apenas uma espécie mostrou relação com os substratos. Os valores de biomassa são mais baixos de junho a agosto em ambos os anos, o que corresponde à estação de alto fluxo. **Conclusões:** A temperatura fria do rio Saltana durante todo o ano (6-7 °C) e a variabilidade do fluxo determinam os baixos valores de riqueza e densidade. Não está claro se os indivíduos apresentaram ciclos de vida muito curtos ou longos devido à temperatura constante durante todo o ano. No entanto, há uma clara assincronia nos ciclos de vida devido à presença de adultos emergentes ao longo do ano.

Palavras-chave: quironomídeos; riachos de montanhas; composição de comunidades; Andes.

1. Introduction

The life history and population dynamics of macroinvertebrates in tropical regions are relatively unknown compared with the work done in temperate areas despite recent advances in their taxonomy (Hamada et al., 2018). Jacobsen et al. (2008) reviewed the topic and concluded that most of the taxa have asynchronous emergence and multivoltine life cycles due to elevated temperatures in the lowland tropical areas, although data on Chironomidae in these studies are scarce, especially in the Neotropical region. The life cycle in such conditions may be less than a week in some Chironomidae (Jackson & Sweeney, 1995) and up to 175 days in some Ephemeroptera (Jacobsen, 2008; Jacobsen et al., 2008). Data on the biomass of insects and the secondary production in tropical streams were nearly inexistent for midges, with a few studies (Ramírez & Pringle, 1998), but differentiating only between Tanypodinae and non-Tanypodinae. In high Andean streams and rivers (above 2 500 m.a.s.l.), where midges usually dominate the community (Acosta & Prat, 2010; Ríos-Touma et al., 2014; Villamarín et al., 2021), the situation is even worse (Jacobsen et al., 2008) because there is no data on life cycles, population dynamics, biomass, and production for individual species or even families. More studies have been done in the Argentinian mountain streams, even in extreme environments (Torrejon et al., 2022), but communities are not the same as in the Neotropical high-altitude zone (Rodríguez et al., 2020).

The main reason for such a lack of knowledge of the biology and ecology of midges in the high-altitude Andean rivers is that very few papers have

studied Chironomidae at the genera or species level of the high-altitude streams in the Andes. Roback & Coffman (1983) published an article that, until a few years ago, was unique about the taxonomy and distribution of midges in this region. Recently, some papers were published on the altitudinal and seasonal changes of midges in Perú (Acosta & Prat, 2010) and keys on larvae (Prat et al., 2011, 2018b) and pupae (Prat et al., 2014) of Chironomidae that allow distinguishing the genera and some species groups. A recent key on Neotropical midges (Silva et al., 2018) made possible a better identification of larvae below 2000 m.a.s.l., but not for some dominant genera in the high Andean streams (like *Cricotopus*) that may be identified in the key of Prat et al. (2018b) and Hamerlik et al. (2018). In the last five years, the number of papers on midges in high-altitude Andean streams has increased (Rojas-Sandino et al., 2018; González-Trujillo et al., 2019) and this demonstrates the importance of classifying at genera or species level the midges, which is not usual.

The use of molecular methods contributes to clarifying some genera' taxonomy, systematics, and ecology, as in the case of *Barbadocladius* (Cranston & Krosch, 2011; Prat et al., 2013), *Stictocladius* (Krosch & Cranston, 2013) or *Podonomopsis* (Cranston & Krosch, 2015). A new species from the Saltana River was described: *Cricotopus (Oliveiriella) rieradevallae* (Prat et al., 2018a), while other works on the taxonomy and ecology of biting midges remain unpublished (Villamarín, 2012). A recent paper pointed out the difficulties of midge taxonomy of genus *Polypedilum*, when morphological and barcoding species delimitation is not coincident (Ballesteros et al., 2022). Other studies in the

Patagonian region (García & Añón Suárez, 2007; Medina et al., 2008) address the temporal changes of midge communities throughout the year and their life cycle characteristics, but biomass changes and production are not addressed. A recent paper reported the relationship with environmental conditions of the taxa “Genus 1 sp.2” (formally a subgenus of *Cricotopus*) (Ossa et al., 2018) as described in pupal stages in Prat et al. (2014). Several papers have been published on the glacial streams of Ecuador (Jacobsen et al., 2014a, b; Cauvy-Fraunié et al., 2015; Hamerlik et al., 2018). However, in some papers, despite its richness and abundance (e.g. Orthocladiinae may be up to 45% of the individuals in these studies), larvae are not identified at the genus level (except *Parochlus*, a member of the subfamily Podonominae). Including the Chironomidae at the genus level may considerably change the full species richness of such streams by more than 100%. Therefore, some conclusions about biodiversity and community composition may be incomplete.

The life cycle, population dynamics, and secondary production of Chironomidae in rivers were reviewed Tokeshi (1995a, b). Several papers show that midges can have very high productivity in some rivers (Stites & Benke, 1989), even in streams with low temperatures (Nolte & Hoffmann, 1992). Still, most papers on such topics were from temperate regions. In their revision of the life history of aquatic macroinvertebrates, Resh & Rosenberg (2010) concluded that most species' life cycles were virtually unknown, especially those of Diptera. Studies of the duration of larval development of chironomid laboratory experiments demonstrate a negative relationship between the temperature increase and the larval period's time (Menzie, 1981). The temperature-dependent growth rates of many taxa of larval midges were reported by Reynolds & Benke (2005), which conclude that “growth rates were a function of temperature at all taxonomic levels and fit 2nd-order polynomials with maximum growth rates (0.21-0.26 d/1) occurring near 20 °C”.

The relationships between Chironomids and temperature were also studied by Eggermont & Heiri (2012), which notes that some midge subfamilies are more common in cold water (Podonominae, Diamesinae, Orthocladiinae), dominating the upper part of the streams. The dominant subfamily at higher altitudes differs in different parts of the world: Diamesinae for the Palearctic region or central Africa and Podonominae for the high latitudes of the Southern Hemisphere (Eggermont

& Heiri, 2012). In the Andes, Eggermont & Heiri (2012) indicated that more data is needed for the moment, but this is because their work is focused on lakes, and in the summary of the Chironomid dominant taxa in the cold running waters of the Neotropics, Acosta & Prat (2010) concluded that Orthocladiinae dominates midge fauna. Still, some characteristics of Podonominae (e.g., *Podonomopsis illiesi*) are present and are distinctive species for high mountain tropical Andean streams. This and other genera of Gondwanan origin (e.g., *Barbadocladus*), common at low altitudes in Chile, are confined to the high altitudes in the tropical and subtropical zones (Prat et al., 2013).

In temperate running water streams, the cold-adapted midges can emerge during winter and early spring. At the same time, many other species of other subfamilies have the emergence restricted mainly to spring, summer, and autumn (Eggermont & Heiri, 2012). Studies on high altitude (Lencioni et al., 2007) or latitude (Gislasson & Gardarsson, 2010; Hannesdóttir et al., 2010) streams in the northern hemisphere have shown that many midges can live at low temperatures with life cycles usually one or two generations per year (Nolte & Hoffmann, 1992), which report for some species of *Diamesa* short life cycles and high secondary production. The situation in tropical areas at high altitudes, where the temperature is constant but low, has not been studied for most freshwater invertebrates. What should be expected for midges in the high-altitude Andean tropical streams? One hypothesis would be long generation times due to lower temperatures or, alternatively, short cycles due to preadaptation to low water temperatures of the species present in the stream. We know from a previous study (Ríos-Touma et al., 2012) that Chironomidae was the dominant group in the benthos in a stream located at 3300 m.a.s.l., with a temperature range of 6-7 °C. In emergence traps, no difference in the number of individuals of emergent taxa was found between months, suggesting a possible continuous emergence of midges at high altitudes of tropical streams (Prat et al., 2018a).

Other factors may influence such developmental time (e.g., food availability, environmental conditions, larval size) (Tokeshi, 1995b; Jacobsen et al., 2008), and as a result, the direct relationship between temperature and larval growth may not be as simple as formulated by Reynolds & Benke (2005). In tropical high-altitude streams, flow change is the most striking factor in understanding the dynamics and composition

of aquatic macroinvertebrates. Ríos-Touma et al. (2011) demonstrated that during the dry season, flow stability is higher, which increases the species richness, density, and diversity of macroinvertebrate assemblages. Cauvy-Fraunié et al. (2015) concluded in a similar way by looking at the differences in community composition due to changes in water level produced below a glacier stream in Ecuador at 4100 m.a.s.l. No data exist on the population dynamics, life cycles, and secondary production on midges at high altitudes at tropical streams.

Our main objective in this paper is to study the composition and population dynamics of a community of Chironomidae from Saltana River in Ecuador, located close to the equator at 3848 m.a.s.l. With this data, we will try to understand the midge community assemblage over time, as well as their population dynamics and biomass changes along the year. We hypothesised that the Chironomidae will have a constant but low growth rate, with continuous emergence and recruitment because of the relatively constant temperature.

2. Materials and Methods

2.1. Study site

Samples were taken in Saltana River (0°19'1.80" S, 78°13'8.8" W), a first-order pristine stream in the northeastern Andes of Ecuador. The "Ponce-Paluguillo Hydrological Production Reserve" protects the stream's drainage area. It is surrounded by mixed páramo vegetation consisting of *Calamagrostis intermedia* tussock grass mixed with shrubs such as *Baccharis* spp. and *Hypericum* spp. The creek, at 3848 m.a.s.l., is part of the headwaters of the Esmeraldas River basin that flows to the Pacific Ocean. We studied a 100 m reach of the creek. The mean stream width was 95 cm (40-140 cm). Coarse substrates (boulders, cobble, and gravel) dominate the creek substrate. During the study period (April 2009-November 2010), stream flow fluctuated between 33.1 and 469.54 L/s, with an annual mean of 130 L/s. Higher flows were found from June to August, whereas base flow conditions were found from September to March. Oxygen was close to saturation during the entire study period, while specific conductivity ranged from 63 to 70 $\mu\text{S}/\text{cm}$, pH ranged from 6.5 to 7.8, and water temperature ranged from 5.9 to 7.1 Celsius degrees.

2.2. Chironomidae sampling method

We sampled the river benthos monthly from April 2009 to June 2010, with two additional samples in September and November 2010. In each

survey, we took 12 random quantitative benthic samples (Hess sampler, 0.02 m², 250 microns mesh) and preserved them in 90% ethanol. The substrate was analysed visually in each sample and classified as Bedrock, Boulder, Cobbles, Gravel, Sand, and Silt. When two or more substrates were recorded, we selected the dominant species in each sample to explore the relationship between species and instars with the substrate. We used Kruskal-Wallis analysis of variance to explore the relationship between substrates and each species' instar. We use the head capsule length (HCL) to distinguish between different instars (McCauley, 1971).

The samples were cleaned and examined at the laboratory under a stereoscope at x10. All the animals were sorted out, and the larvae and pupae of Chironomidae were classified first into subfamilies and then into morphotypes using a morphotype key specific to Andean streams (Prat et al., 2018b). If there were few individuals of a morphotype, all animals were mounted in Euparal following Epler (2001). When a morphotype is abundant, up to 20 individuals were prepared in Euparal. All the individuals mounted in slides were examined in a Zeiss microscope with phase contrast and classified until genera or species groups using mainly the paper of Roback & Coffman (1983) and the key for the larvae of Chironomidae from High Andean rivers of Prat et al. (2011). The presence of pupae on samples allowed us to identify the genus and species group of larvae found using the key of Prat et al. (2014). We collected adults using three amphibious (1.1 3 × 1.1 3 × 1.1 m) emergence traps (model BD5740A; MegaView Science, Taiwan). These were placed immediately above the stream, covering the entire stream width from one side to the other for 24 h each month as described by Ríos-Touma et al. (2012). Adults were collected and preserved in 90% ethanol. Only part of this material has been studied (Prat et al., 2018a); therefore, the specific identity of many of our larvae still needs to be discovered, although barcoding and morphological analysis are ongoing.

2.3. Biomass estimations

We calculate the total biomass using the individual weight of the larvae of different instars multiplied by the density of each instar at each sample. Only for the species with densities higher than 5% of the total abundance (4 taxa) the individual biomass values were calculated by taking between 10 and 100 individuals that were dried out at 80 °C for 24 hours (no further weight

loss was detected after 24 hours). The other genera were by far less abundant, and their biomass was not estimated. Production is impossible to calculate using the usual direct methods (e.g., size-frequency methods) because we cannot differentiate generations or calculate the cohort production interval (CPI) value. Therefore, we were not able to calculate the production for these taxa.

3. Results

3.1. Taxa richness

We found up to 18 larval taxa in 14 different genera in the benthic samples (available on Ríos-Touma, 2024). The mean monthly richness is $9.6 (\pm 3.5)$ taxa, with a minimum value of 5 and a maximum value of 15. Two taxa are from the subfamily Podonominae (*Podonomus* and *Parochlus*) and two of the Diamesinae of the tribe Heptagyini (*Limaya* and *Paraheptagyia*). The richest subfamily is the Orthocladiinae, with 12 different genera and only two genera of the subfamily Chironominae. We have also collected 30 pupae or pupal exuviae in the benthic samples with seven taxa. The most frequent and abundant taxa captured as larvae and pupae were *Cricotopus* sp.3 (sensu Roback & Coffman, 1983), which comprises 68,72% of the individuals. Also present in all samples were the larvae and pupae of *Cricotopus* (*Oliveiriella*) *rieradevallae* (Prat et al., 2018a) (7.38% of individuals). Genus 1 sp.a (Orthocladiinae, sensu Ossa et al., 2018; Prat et al., 2018b) was the third most abundant taxa (6.7% of the individuals) but was absent in three sampling dates. The other genera had abundances lower than 5% and never in all sampling dates. We found a single pupa for *Paraheptagyia*, *Parametriocnemus*, and *Rheotanytarsus*. The analysis of pupae confirmed our genus larval identifications.

3.2. Population dynamics

We report the mean monthly densities of all Chironomidae in Saltana River for the study period in Ríos-Touma (2024). When available, the different instars are indicated. We have summarised the results in Table 1. In this table, apart from the most abundant taxa, we cluster the densities of the less abundant midges in three groups: 1) The Diamesinae of the tribe Heptagyini (*Limaya* and *Paraheptagyia*); 2) The rest of Orthocladiinae (*Cricotopus* sp. indet; *Limnophyes*, *Metriocnemus*, *Parakiefferiella*, *Parametriocnemus* and Genus near *Parametriocnemus*) and, 3) The Chironominae (*Stenochironomus* and *Tanytarsus*).

Total densities (Table 1; Ríos-Touma, 2024) fluctuate very much from one month to another following the changes of the most abundant species *Cricotopus* sp.3 (Figure 1), which comprises between 39% (June 2010) and 88,61% (November 2009) of the individuals. From February to May, the dominance of this species was the lowest. The second most abundant was another Orthocladiine, *Cricotopus* (*Oliveiriella*) *rieradevallae*, although it never represented more than 15% of the individuals. We do not observe any relevant changes in its densities over the year (Figure 1). Genus 1 was relatively abundant in April and September 2010 (Figure 1). Still, it was absent for several months and very scarce in 2009 (Table 1, Figure 1). On the other hand, we captured very few individuals of the two genera of Chironominae (*Stenochironomus* and *Tanytarsini*), and similar results for the two genera of Diamesinae (except in August 2009 when they made up 24% of the individuals). Finally, the genus *Podonomus* increased its abundance in the second year compared with the same period of the previous year (available in Ríos-Touma, 2024). However, densities are always low.

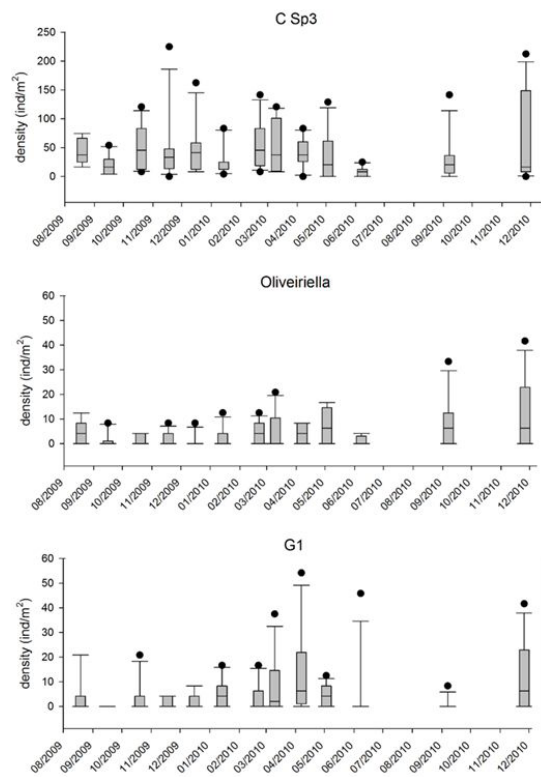


Figure 1. Changes along time of the densities (ind/m²) of four more abundant species of midges of Saltana River. C. sp.3 = *Cricotopus* sp.3; Oliveiriella = *Cricotopus* (*Oliveiriella*) *rieradevallae*; G1 = Genus 1.

Table 1. Date of collection and total density (ind/m²) of the Chironomidae taxa collected in the river Saltana (Ecuador).

Year	Date	Podo	Paro	Heptg	C. sp.3	Oliv	G1spa	Gnost	CricMR	Paraph	ROrtho	Chiro	Total	Sp rich
2009	1/IV	4.17	0	0	245.83	16.67	0	0	0	20.83	0	0	287.5	5
	1/V	4.17	4.17	0	887.5	87.5	0	0	0	12.5	4.17	4.17	1004.17	10
	1/VI	0	0	0	162.5	4.17	4.17	16.67	0	8.33	4.17	0	200	7
	19/VIII	0	0	21.43	507.14	71.43	42.86	0	7.14	42.86	7.14	0	700	9
	16/IX	0	0	0	191.67	12.5	0	3	0	8.33	4.17	0	219.67	6
	20/X	4.17	0	8.33	554.17	12.5	37.5	0	0	12.5	25	0	654.17	13
	18/XI	12.5	0	0	583.33	20.83	16.67	0	8.33	8.33	8.33	0	658.33	8
	16/XII	8.33	4.17	4.17	500	8.33	20.83	0	4.17	8.33	20.83	4.17	583.33	14
	14/I	16.67	0	8.33	316.67	41.67	50	12.5	37.5	16.67	12.5	4.17	516.67	15
	9/II	8.33	0	0	666.67	62.5	37.5	4.17	20.83	0	12.5	4.17	816.67	12
10/III	62.5	8.33	4.17	645.83	79.17	91.67	20.83	37.5	4.17	20.83	4.17	979.17	15	
7/IV	79.17	0	0	483.33	66.67	154.17	20.83	33.33	4.17	0	4.17	845.83	9	
3/V	75	0	4.55	490.91	86.36	54.55	18.18	13.64	4.55	4.55	0	752.27	11	
8/VI	41.67	0	0	100	33.33	54.17	25	0	0	0	0	254.17	5	
7/IX	173.61	0	0	416.67	138.89	225.69	33.33	0	0	0	0	988.19	5	
26/XI	4.17	0	4.17	750	137.5	8.33	83.33	0	91.67	0	4.17	1083.33	10	
Mean		30.9	1.04	3.45	468.89	55	49.88	14.87	10.15	15.2	7.76	1.82	658.97	9.63
St. D.		46.93	2.41	5.66	220.7	43.66	61.73	21.3	14.22	22.95	8.31	2.14	449.99	3.5
Total %		4.15	0.14	0.46	62.94	7.38	6.7	2	1.36	2.04	1.04	0.24		

Podo = *Podonomus*; **Paro** = *Parochlus*; **Heptg** = Diamesinac, Heptagyidae C. sp.3 = *Cricotopus* sp.3; **Oliv** = *Cricotopus (Oliveiella) niemdevallae*; **G1spa** = Genus 1 sp.a; **GNost**: Genus Nostroc; **CricMR** = *Cricotopus* MR; **Paraph** = *Paraphaenocladius*; **ROrtho** = Other Orthocladiinae; **Chiro** = Chironominae; **Sp rich** = Species Richness of each month. The complete list of taxa and their densities is available in Ríos-Touma (2024).

The only taxa that showed a strong relationship with the substrate were the III instar of Genus 1 ($X^2=13.50$; $p=0.009$), which showed a significant preference for cobbles and boulders. The IV instar of Genus 1 ($X^2=8.63$; $p=0.071$) and *Podonomus* ($X^2=9.26$; $p=0.055$) also showed a marginal significant preference for coarser substrates. The other taxa and instars did not show a larval presence and abundance relationship with different substrates.

3.3. Life history

We found adults of Chironomidae year-round using three emergence Malaise traps (Table 2). The mean number of adults per emergence trap was between 20.7 in November 2009 and 97.3 in April 2010 (Table 2). Emergencies increase from March to May (Table 2), with a minimum in June coincident with increased flow. Both males and females were present, including the adults of *Cricotopus (Oliveriella) rieradevallae* (Prat et al., 2018a). The number of adults found for other genera and species (e.g., Podonominae or the large *Parabeptagya*) was very low (one or two individuals).

Most of the larvae of *Cricotopus* sp.3 were in IV instar in all months (Table 3, Figure 2), except in July 2009 and July 2010 (higher flow months). Pupae and pupal exuviae of *Cricotopus* sp.3 were also present in all months, with a sex ratio of 3 females per male. This data already suggests a continuous emergence of adults and recruitment of larvae. There were large fluctuations in the abundance of larvae of *Cricotopus* sp.3, and a large variability of abundances between the 12 replicates (Figure 1).

The life cycle of *C. O. rieradevallae* is also difficult to disentangle from the relative

abundance of different larval instars (Figure 2). The larval abundances were different in 2009 than in 2010 (data available in Ríos-Touma 2024; Table 1). The presence of adults throughout the year (Table 2) and the fact that pupae have been found in many months suggest a continuous emergence throughout the year (Prat et al., 2018a).

In the case of Genus 1 sp.a., the densities of larvae between months and two years are very variable. The figure showing the importance of different instars (Figure 2) and the fact that the number of pupae found was low make the definition of the life cycle of this taxon compared with the two precedents even more speculative.

As explained previously, the number of individuals is very low for most of the other taxa, and little can be said about their life histories. For example, very small *Paraphaenocladus* larvae are present in most of the sampling dates but at very low density. *Podonomus* attained the highest density at the end of the study period, but no clear pattern emerged from data of larval instars (available in Ríos-Touma, 2024).

3.4. Biomass

We focused on the biomass changes of the three most abundant species. In the case of *Cricotopus* sp.3, the mean weight of larvae of the IV instar is 0.1579 mg, and those of instar III, 0.051 mg (Table 3). The mean annual biomass for this species was 55.91 mg/m² (instar IV accounts for 88% of total biomass). Biomass values are lower from June to August of both years, which matches the high flow season. For *Cricotopus (Oliveriella) rieradevallae*

Table 2. Adults found in the malaise traps in the Saltana river. The adults of *Cricotopus (Oliveriella) rieradevallae* and the mean total numbers are provided. Most of the other adults are *Cricotopus* spp.

Data	<i>C. (Oliveriella) rieradevallae</i>	Total Ind/trap
2/10/2009	3f	30
21/10/2009	1f	20
20/11/2009	0	20.7
17/12/2009	1m	30.3
14/1/2010	1m;7f	37.7
10/2/2010	1f	35.5
11/3/2010	9m;3f	63.7
8/4/2010	1m;13f	97.3
9/5/2010	4f	68.7
8/6/2010	0	1

F = female; m = male.

Table 3. Size and individual biomass of the four most abundant Chironomidae taxa in the river Saltana.

Taxa/instar	n	HCL	AFDW
<i>Cricotopus</i> sp.3			
IV	40	442 (366-467)	0.1579
III	30	275 (215-317)	0.0051
II	15	154 (104-120)	0.0006
<i>C. (Oliveriella) rieradevallae</i>			
IV	54	369 (281-441)	0.164
III	11	213 (187-234)	0.005
Genus 1			
IV	8	414 (353-360)	0.051
III	8	208 (240-307)	
<i>Paraphaenocladus</i>			
IV	31	147 (118-172)	0.013

n = individuals measured; HCL = Head capsule length (microns); AFDW = Ash free dry weight (mg). Genus 1 includes both Genus 1 sp. a and Genus 1 "Nostoc".

and Genus 1 sp. a, the mean annual biomass was 6.65 and 1.75 mg, respectively (Table 4).

4. Discussion

The macroinvertebrate richness of tropical high-altitude streams of the Andes is low (Jacobsen et al., 2008; Villamarín et al., 2020), including midges (Acosta & Prat, 2010). Saltana River, located at 3853 m.a.s.l, fits well into this model. From our results, the total midge species richness in the Saltana stream is 18 taxa with a mean monthly value of 9.6. In the high mountain rives in Europe (e.g., Lencioni & Rossaro, 2010), the mean richness of midges is nine taxa for glacial streams and 19 for non-glacial streams. The Saltana River has very low-temperature values throughout the year, similar to glacier streams. This can help explain the low species richness and relatively unpredictable rapid changes in flow or substrate instability. We found similar changes and a relationship between macroinvertebrate richness and flow and season in

another stream (Ríos-Touma et al., 2011). The high intensity of ultraviolet light may also be a factor that may explain the low richness of the fauna in high-altitude tropical streams, as has been found in the rivers of Perú (Loayza-Muro et al., 2013).

In high-altitude tropical rivers, usually, the Podonominae dominates in the glacial rivers (Kuhn et al., 2011), while Orthocladiinae is the most abundant midges in non-glacial rivers. Densities in Saltana stream ($698.37 + 449 \text{ ind/m}^2$) are lower than non-glacial rivers in the Alps ($1153 + 1333 \text{ ind/m}^2$) but higher than in glacial rivers of the Alps ($164 + 552 \text{ ind/m}^2$). And Orthocladiinae comprises up to 90% of midges present. The relatively low densities of Chironomidae in Saltana may be related to the low food availability in these streams. When food is available, densities and production in cold stenothermic rivers may arrive at high values (Gislsson & Gardarsson, 2010).

The mean annual biomass (64.31 mg/m^2) is low, close to the lowest range of the values found in the

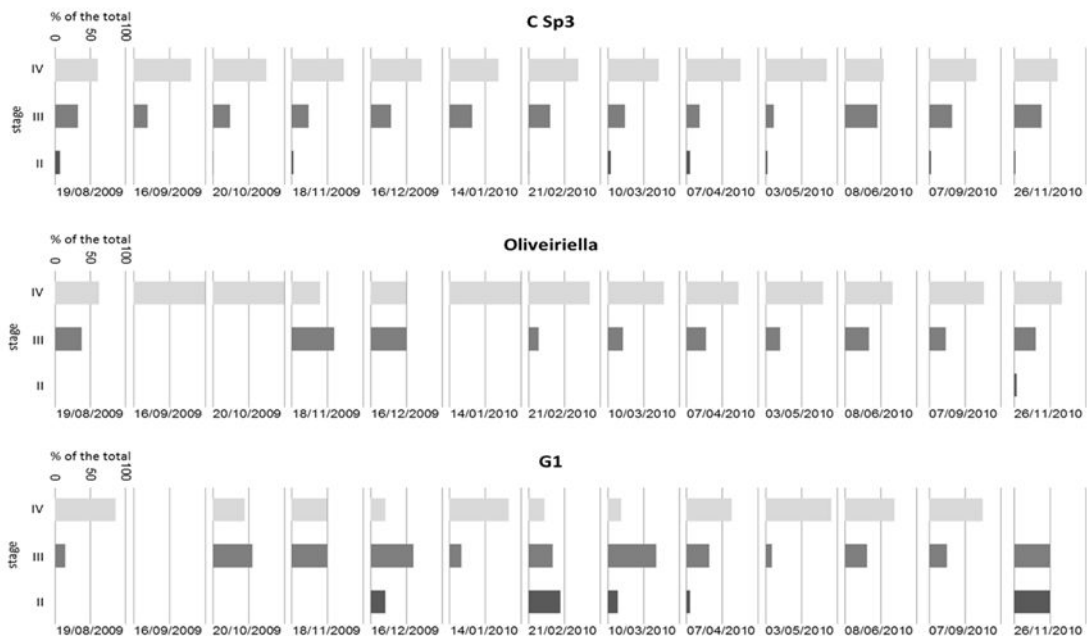


Figure 2. Changes in the percentage of different instars along time of the three most abundant taxa of Chironomidae in the river Saltana. C. sp.3 = *Cricotopus* sp.3.; Oliveiriella = *Cricotopus (Oliveiriella) rieradevallae*; G1 = Genus 1 sp.a.

Table 4. Summary of biomass values for the three more abundant Chironomid taxa.

Taxa	Mean density	Biomass mg	% IV instar
<i>Cricotopus</i> sp.3	468.89	55.91	88
<i>Cricotopus (Oliveiriella) rieradevallae</i>	47.53	6.65	91
Genus 1 sp.a.	49.88	1.75	86
Total	566.3	64.31	

Mean annual biomass in mg/m^2 .

literature (Figure 11.6 in Tokeshi, 1995b), and is a value very low for a *Cricotopus* species. We should consider that the size of the net of our Hess sampler (250 microns) probably allows the passing of many of the second and part of the third instars of most of the Chironomidae larvae of Saltana River (larval instar II has a head length of 154 microns; Table 3), another reason for not being able to calculate secondary production. Large fluctuations in the abundance of larvae of *Cricotopus* sp.3, and the large variability of abundances between the 12 replicates (Figure 1) also make the interpretation of this species' life cycle difficult.

The critical issue is if the life cycle of midges in Saltana is short (as in some species adapted to low temperatures, Nolte & Hoffmann, 1992) or long (as can be expected with temperatures of 6 °C). We know that the more abundant species are continuously emerging, and the IV instar larvae are always dominant in the stream even when densities diminish. In other cases, 1-year life cycles have been described, as in an Iceland river with similar temperatures year round (5.4 °C), in *Eukiefferiella claripennis* (Hannesdóttir et al., 2010), however in streams with temperatures from 9.7-21.3 °C the same species may be bivoltine or multivoltine. As the temperature in Andean streams may be variable along the day, we cannot discard that in Saltana River; we have multivoltine cycles (unfortunately, we cannot calculate the degrees-day for comparison with other studies).

Two interpretations may be provided of the dominance of the IV instar larvae and the presence of adults long year-round of the dominant species. The first one, and the more suitable compared with other studies, is the long life cycle of the individuals because of the low and constant temperatures throughout the year. The low food availability in these streams (no leaves decomposing, low algal biomass with the dominance of *Nostoc*) and the stress produced by continuous changes in river flow support this interpretation (Figure 1). This situation has been described for many high-latitude streams or lakes when semivoltine or even longer life cycles are the rule (Tokeshi, 1995a). The presence of adults most of the year may be due to the coexistence of several cohorts in the stream. According to this author, at 7 °C, the growth of larvae of Orthoclaadiinae is as low as 0.02 mg/mg per day (Figure 10.7 in Tokeshi, 1995a).

The alternative, less probable, would be a fast-growing cycle with several generations per year. This fast-growing cycle in cold waters has been described

for *Diamesa incallida* (Nolte & Hoffmann, 1992), that in waters with temperatures between 7.6 to 8 °C laid eggs continuously and produce eight to ten generations per year. The presence of adults throughout the year in Saltana Stream (Table 2) may also support this hypothesis. However, this hypothesis needs a constant supply of food to the stream through particulate or fine organic matter or a highly productive environment with plenty of algae in stones, which might not be the case in Saltana. However, small amounts of benthic algae have been recorded in rock substrates in this stream during different months (Vimos et al., 2015). The environmental characteristics of the site, with frequent disturbances due to the flow changes, do not seem to support the possibility of a highly productive with short life cycles of midge community, but this fact needs further studies.

The midge community in the Saltana River has low biodiversity compared with temperate non-glacial streams (e.g., the Alps) but is similar to glacial streams worldwide. However, molecular studies could increase the number of species due to cryptic diversity, as seen for other taxa in the Neotropical mountains (Gill et al., 2016). The low biomass found makes the Saltana River akin to glacial rivers. Suppose we accept that the different species' life cycle may not be short due to temperature. In that case, we should expect univoltine, bivoltine, or multi-year life cycles and, as a result, very low secondary production values. No trout were found in this stream, so the possible effects of fish predation on the density of some macroinvertebrates should not be expected. However, in other Andean streams, the presence of trout does not change much the relative abundance of the Orthoclaadiinae (Vimos et al., 2015). Therefore, fish predation does not seem to be relevant in Saltana River. More studies are necessary to understand better the life cycles and variation of biomass and production of midges in high-altitude tropical Andean streams.

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Data availability

All research data analyzed in the research is available in the Dataverse of ALB in SciELO Data. It can be accessed in <https://doi.org/10.48331/scielodata.BYED2K>.

References

- Acosta, R., & Prat, N., 2010. Chironomid assemblages in high altitude streams of the Andean region of Peru. *Fundam. Appl. Limnol.* 177(1), 57-79. <http://doi.org/10.1127/1863-9135/2010/0177-0057>.
- Ballesteros, I., Bravo-Castro, M., Villamarín-Cortez, S., Jijón, G., Prat, N., Ríos-Touma, B., & Villamarín, C., 2022. Genetic variability of *Polypedilum* (Diptera: Chironomidae) from Southwest Ecuador. *Insects* 13(4), 382. <http://doi.org/10.3390/insects13040382>.
- Cauvy-Fraunié, S., Andino, P., Espinosa, R., Jacobsen, D., & Dangles, O., 2015. Temporal scaling of high flow effects on benthic fauna: insights from equatorial glacier-fed streams. *Limnol. Oceanogr.* 60(5), 1836-1847. <http://doi.org/10.1002/lno.10137>.
- Cranston, P., & Krosch, M., 2011. *Barbadocladius* Cranston & Krosch, a New genus of Orthoclaadiinae (Diptera: Chironomidae) from South America. *Neotrop. Entomol.* 40(5), 560-567. PMID:22068942.
- Cranston, P., & Krosch, M., 2015. Evidence from molecules and morphology expands *Podonomopsis* Brundin (Diptera: Chironomidae: Podonominae) to include “genus Chile”. *Invertebr. Syst.* 29(6), 610-627. <http://doi.org/10.1071/IS15018>.
- Eggermont, H., & Heiri, O., 2012. The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. *Biol. Rev. Camb. Philos. Soc.* 87(2), 430-456. PMID:22032243. <http://doi.org/10.1111/j.1469-185X.2011.00206.x>.
- Epler, J., 2001. Identification manual for the larval Chironomidae (Diptera) of North and South Carolina: a guide to the taxonomy of the midges of the southeastern United States, including Florida. Raleigh: North Carolina Department of Environment and Natural Resources, Special Publication, no. SJ2001-SP13.
- García, P., & Añón Suárez, D., 2007. Community structure and phenology of chironomids (Insecta: Chironomidae) in a Patagonian Andean stream. *Limnologica* 37(1), 109-117. <http://doi.org/10.1016/j.limno.2006.09.005>.
- Gill, B.A., Kondratieff, B.C., Casner, K.L., Encalada, A.C., Flecker, A.S., Gannon, D.G., Ghalambor, C.K., Guayasamin, J.M., Poff, N.L., Simmons, M.P., Thomas, S.A., Zamudio, K.R., & Funk, W.C., 2016. Cryptic species diversity reveals biogeographic support for the ‘mountain passes are higher in the tropics’ hypothesis. *Proc. R. Soc. Lond. B Biol. Sci.* 283(1832), 20160553. <http://doi.org/10.1098/rspb.2016.0553>.
- Gíslason, G.M., & Gardarsson, A., 2010. The production of Chironomidae and Blackflies in a subarctic river. In: Ferrington, L.C., ed. *Proceedings of the XV International symposium on Chironomidae*. Minneapolis: University of Minnesota, 45-54.
- González-Trujillo, J.D., Petsch, D.K., Córdoba-Ariza, G., Rincón-Palau, K., Donato-Rondon, J.C., Castro-Rebolledo, M.I., & Sabater, S., 2019. Upstream refugia and dispersal ability may override benthic-community responses to high-Andean streams deforestation. *Biodivers. Conserv.* 28(6), 1513-1531. <http://doi.org/10.1007/s10531-019-01739-2>.
- Hamada, N., Thorp, J.H., & Rogers, C., 2018. *Keys to Neotropical Hexapoda: Thorp and Covich's freshwater invertebrates*. Boston: Academic Press, vol. 3.
- Hamerlik, L., Silva, F.L., & Jacobsen, D., 2018. Chironomidae (Insecta: Diptera) of Ecuadorian high altitude streams: a survey and illustrated key. *Fla. Entomol.* 101(4), 663. <http://doi.org/10.1653/024.101.0404>.
- Hannesdóttir, E.R., Gíslason, G.M., & Ólafsson, J.S., 2010. Life cycles of *Eukiefferiella claripennis* (Lundbeck 1898) and *Eukiefferiella minor* (Edwards 1929) (Diptera: Chironomidae) in spring-fed streams of different temperatures with reference to climate change. *Fauna Norv.* 31, 35-46. <http://doi.org/10.5324/fn.v31i0.1367>.
- Jackson, J., & Sweeney, B., 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. *J. N. Am. Benthol. Soc.* 14(1), 115-130. <http://doi.org/10.2307/1467728>.
- Jacobsen, D., 2008. Tropical high-altitude streams. In: Dudgeon, D., ed. *Tropical stream ecology*. London: Academic Press, 219-256. <http://doi.org/10.1016/B978-012088449-0.50010-8>.
- Jacobsen, D., Andino, P., Calvez, R., Cauvy-Fraunié, S., Espinosa, R., & Dangles, O., 2014a. Temporal variability in discharge and benthic macroinvertebrate assemblages in a tropical glacier-fed stream. *Freshw. Sci.* 33(1), 32-45. <http://doi.org/10.1086/674745>.

- Jacobsen, D., Cauvy-Fraunie, S., Andino, P., Espinosa, R., Cueva, D., & Dangles, O., 2014b. Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming. *Freshw. Biol.* 59(10), 2038-2050. <http://doi.org/10.1111/fwb.12405>.
- Jacobsen, D., Cressa, C., Mathooko, J., & Dudgeon, D., 2008. Macroinvertebrates: composition, life histories and production. In: Dudgeon, D., ed. *Tropical stream ecology*. London: Academic Press, 65-105. <http://doi.org/10.1016/B978-012088449-0.50006-6>.
- Krosch, M., & Cranston, P.S., 2013. Not drowning, (hand) waving? Molecular phylogenetics, biogeography and evolutionary tempo of the “Gondwanan” midge *Stictocladus* Edwards (Diptera: Chironomidae). *Mol. Phylogenet. Evol.* 68(3), 595-603. PMID:23608128. <http://doi.org/10.1016/j.ympev.2013.04.006>.
- Kuhn, J., Andino, P., Calvez, R., Espinosa, R., Hamerlik, L., Vie, S., Dangles, O., & Jacobsen, D., 2011. Spatial variability in macroinvertebrate assemblages along and among neighbouring equatorial glacier-fed streams. *Freshw. Biol.* 56(11), 2226-2244. <http://doi.org/10.1111/j.1365-2427.2011.02648.x>.
- Lencioni, V., & Rossaro, B., 2010. Chironomid assemblages in different alpine streams. In: Ferrington, L.C., ed. *Proceedings of the XV International symposium on Chironomidae*. Minneapolis: Chironomid Research Group, University of Minnesota, 95-102.
- Lencioni, V., Marziali, L., & Rossaro, B., 2007. I Ditteri Chironomidi morfologia, tassonomia, ecologia, fisiologia e zoogeografia. Trento: Museo Tridentino di Scienze Naturali.
- Loayza-Muro, R.A., Marticorena-Ruiz, J.K., Palomino, E.J., Merritt, C., Breeuwer, J.A.J., Kuperus, P., Kraak, M.H.S., & Admiraal, W., 2013. Ultraviolet-B-driven pigmentation and genetic diversity of benthic macroinvertebrates from high-altitude Andean streams. *Freshw. Biol.* 58(8), 1710-1719. <http://doi.org/10.1111/fwb.12161>.
- McCauley, V., 1971. Instar differentiation in larval Chironomidae (Diptera). *Can. Entomol.* 200(256), 179-200. <http://doi.org/10.4039/Ent106179-2>.
- Medina, A., Scheibler, E.E., & Paggi, A., 2008. Distribución de Chironomidae (Diptera) en dos sistemas fluviales ritrónicos (Andino-serrano) de Argentina. *Rev. Soc. Entomol. Argent.* 67(1-2), 69-79.
- Menzie, C.A., 1981. Production ecology of *Cricotopus sylvestris* (Fabricius) (Diptera: Chironomidae) in a shallow estuarine cove. *Limnol. Oceanogr.* 26(3), 467-481. <http://doi.org/10.4319/lo.1981.26.3.0467>.
- Nolte, U., & Hoffmann, T., 1992. Fast life in cold water: *Diamesa incallida* (Chironomidae). *Ecography* 15(1), 25-30. <http://doi.org/10.1111/j.1600-0587.1992.tb00004.x>.
- Ossa, P., Prat, N., Castaño, G., Ospina, E., Rodriguez, G., & Rivera Páez, F., 2018. Genus 1 sp. 2 (Diptera: Chironomidae): the potential use of its larvae as bioindicators. *EAES J.* 4(3), 1-10. <http://doi.org/10.31031/EAES.2018.04.000589>.
- Prat, N., Rieradevall, M., Acosta, R., & Villamarín, C., 2011. Guía para el reconocimiento de las larvas de Chironomidae (Diptera) de los ríos Altoandinos de Ecuador y Perú: clave para la determinación de los géneros. Barcelona: Grupo de Investigación F.E.M., Departamento de Ecología, Universidad de Barcelona, 78.
- Prat, N., Ribera, C., Rieradevall, M., Villamarín, C., & Acosta, R., 2013. Distribution, abundance and molecular analysis of genus *Barbadocladius* Cranston & Krosch (Diptera, Chironomidae) in tropical, high altitude Andean streams and rivers. *Neotrop. Entomol.* 42(6), 607-617. PMID:27193279. <http://doi.org/10.1007/s13744-013-0161-1>.
- Prat, N., González-Trujillo, J.D., & Ospina-Torres, R., 2014. Clave para la determinación de exuvias pupales de los quironómidos (Diptera: Chironomidae) de ríos altoandinos tropicales. *Rev. Biol. Trop.* 62(4), 1385-1406. PMID:25720175. <http://doi.org/10.15517/rbt.v62i4.9844>.
- Prat, N., Paggi, A., Ribera, C., Acosta, R., Ríos-Touma, B., Villamarín, C., Rivera, F., Ossa, P., & Rieradevall, M., 2018a. The *Cricotopus* (*Oliveiriella*) (Diptera: Chironomidae) of the high altitude andean streams, with description of a new species, *C. (O.) rieradevallae*. *Neotrop. Entomol.* 47(2), 256-270. PMID:28905263. <http://doi.org/10.1007/s13744-017-0548-5>.
- Prat, N., Rieradevall, M., Acosta, R., Villamarín, C., & Rieradevall, M., 2018b. Guía para el reconocimiento de las larvas de Chironomidae (Diptera) de los ríos Altoandinos de Ecuador y Perú: clave para la determinación de los principales morfotipos larvarios. Barcelona: Grupo de Investigación F.E.M., Departamento de Ecología, Universidad de Barcelona.
- Ramírez, A., & Pringle, C.M., 1998. Structure and production of a benthic insect assemblage in a neotropical stream. *J. N. Am. Benthol. Soc.* 17(4), 443-463. <http://doi.org/10.2307/1468365>.
- Resh, V.H., & Rosenberg, D.M., 2010. Recent trends in life-history research on benthic macroinvertebrates. *J. N. Am. Benthol. Soc.* 29(1), 207-219. <http://doi.org/10.1899/08-082.1>.
- Reynolds, S., & Benke, A., 2005. Temperature-dependent growth rates of larval midges (Diptera: Chironomidae) from a southeastern U.S. stream. *Hydrobiologia* 544(1), 69-75. <http://doi.org/10.1007/s10750-004-8334-x>.
- Ríos-Touma, B., 2024. Data for: Composition, life-history, and population dynamics of the Chironomidae from a tropical high-altitude stream

- (Saltana River, Ecuador). SciELO Data. <http://doi.org/10.48331/scielodata.BYED2K>.
- Ríos-Touma, B., Acosta, R., & Prat, N., 2014. The Andean Biotic Index (ABI): revised tolerance to pollution values for macroinvertebrate families and index performance evaluation. *Rev. Biol. Trop.* 62(Suppl.2), 249-273. PMID:25189082. <http://doi.org/10.15517/rbt.v62i0.15791>.
- Ríos-Touma, B., Encalada, A.C., & Prat, N., 2011. Macroinvertebrate assemblages of an Andean high-altitude tropical stream: the importance of season and flow. *Int. Rev. Hydrobiol.* 96(6), 667-685. <http://doi.org/10.1002/iroh.201111342>.
- Ríos-Touma, B., Encalada, A.C., & Prat, N., 2012. Oviposition of aquatic insects in a tropical high altitude stream. *Environ. Entomol.* 41(6), 1322-1331. PMID:23321079. <http://doi.org/10.1603/EN12037>.
- Roback, S., & Coffman, W., 1983. Results of the Catherwood Bolivian- Peruvian Altiplano Expedition Part II. Aquatic Diptera including Montane Diamesinae and Orthocladiinae (Chironomidae) from Venezuela. *Proc. Acad. Nat. Sci. Philadelphia* 135, 9-79.
- Rodríguez, G.N., Paggi, A.C., & Scheibler, E.E., 2020. Chironomidae assemblages at different altitudes in Northwest Argentina: the role of local factors. *An. Acad. Bras. Ciênc.* 91, 1-18. <http://doi.org/10.1590/0001-3765202020190953>.
- Rojas-Sandino, L.D., Reinoso-Flórez, G., & Vásquez-Ramos, J.M., 2018. Distribución espacial y temporal de dípteros acuáticos (Insecta: Diptera) en la cuenca del río Alvarado, Tolima, Colombia. *Biota Colomb.* 19(1), 70-91. <http://doi.org/10.21068/c2018.v19n01a05>.
- Silva, F.B., Pinho, L.C., Wiedenbrug, S., Dantas, G.P.S., Siri, A., Andersen, T., & Trivinho-Strixino, S., 2018. Chironomidae. In: Hamada, N., Thorp, J.H., & Rogers, D.C., eds. *Keys to Neotropical Hexapoda: Thorp's and Covich freshwater invertebrates*. Boston: Academic Press, 661-700, 4 ed.
- Stites, D.L., & Benke, A.C., 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for P : B ratios. *Limnol. Oceanogr.* 34(7), 1278-1289. <http://doi.org/10.4319/lo.1989.34.7.1278>.
- Tokeshi, M., 1995a. Life cycles and population dynamics. In: Armitage, P., Cranston P., & Pinder, L., eds. *The Chironomidae: biology and ecology of non-biting midges*. London: Chapman & Hall, 225-268. http://doi.org/10.1007/978-94-011-0715-0_10.
- Tokeshi, M., 1995b. Production ecology. In: Armitage, P., Cranston P., & Pinder, L., eds. *The Chironomidae: biology and ecology of non-biting midges*. London: Chapman & Hall, 269-295. http://doi.org/10.1007/978-94-011-0715-0_11.
- Torrejon, S.E., Pereyra, L., Vargas, N., & Molineri, C., 2022. Chironomidae (Diptera) diversity in extreme environments (Salar de Olaroz, Puna Desert, Argentina). *Ecol. Austral* 32(3), 1029-1038. <http://doi.org/10.25260/EA.22.32.3.0.1902>.
- Villamarín, C., 2012. Estructura y composición de las comunidades de macroinvertebrados acuáticos en ríos altoandinos del Ecuador y Perú: diseño de un sistema de medida de la calidad del agua con índices multimétricos. Barcelona: Universitat de Barcelona.
- Villamarín, C., Rieradevall, M., & Prat, N., 2020. Macroinvertebrate diversity patterns in tropical highland Andean rivers. *Limnetica* 39(2), 677-691. <http://doi.org/10.23818/limn.39.44>.
- Villamarín, C., Villamarín-Cortez, S., Salcido, D.M., Herrera-Madrid, M., & Ríos-Touma, B., 2021. Drivers of diversity and altitudinal distribution of chironomids (Diptera: Chironomidae) in the Ecuadorian Andes. *Rev. Biol. Trop.* 69(1), 113-126. <http://doi.org/10.15517/rbt.v69i1.40964>.
- Vimos, D.J., Encalada, A.C., Ríos-Touma, B., Suárez, E., & Prat, N., 2015. Effects of exotic trout on benthic communities in high-Andean tropical streams. *Freshw. Sci.* 34(2), 770-783. <http://doi.org/10.1086/681540>.

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