

An Acad Bras Cienc (2023) 95(4): e20191316 DOI 10.1590/0001-3765202320191316

Anais da Academia Brasileira de Ciências | Annals of the Brazilian Academy of Sciences Printed ISSN 0001-3765 | Online ISSN 1678-2690 www.scielo.br/aabc | www.fb.com/aabcjournal

ECOSYSTEMS

Functional feeding groups of Chironomidae (Diptera: Nematocera) and their spatial variation in an intermittent hill stream (Ventana Stream, Buenos Aires, Argentina)

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Abstract: The feeding habits of Chironomidae in hill streams in the pampean region have not been described. In this study, we analyzed the gut contents of this insect family with an aim at establishing their diet in an intermittent stream in the Ventania-Hill system. We sampled three sites with different habitat characteristics (*i. e.*, altitude, substrate type, and current velocity). Of the total of nine taxa were recorded, the only one present at all sites was *Corynoneura* sp. 1. The food items found were detritus, diatoms, filamentous chlorophytes, euglenophytes, vascular plants, fungi, and animal remains. Most of the taxa could be classified as gathering collectors, with those having a higher proportion of detritus in the gut contents although the guts of *Pentaneura* nr. *cinerea*, *Cricotopus* sp. 1, and *Onconeura* analiae included high proportions of animal remains. No differences in the feeding habits were attributable to the location in the stream. This research contributes to our understanding of the trophic habits of Chironomidae in an intermittent hill stream system of South America.

Key words: Chironomidae, feeding strategy, gut contents, hill streams.

INTRODUCTION

The classification of benthic invertebrates in functional feeding groups (FFGs) based on what food is eaten and how that food is obtained has been an effective way to understand the trophic organization in river ecosystems (Allan & Castillo 2007). Gut-content analysis enables the reconstruction the diet of a particular species and therefore provides an inference of the trophic relationships among the members of a community. Moreover, feeding strategies reflect the adaptation of species to environmental conditions and may vary with the availability and quality of the resources, characteristics that are often affected by human activities (Statzner et al. 2001). The chironomids are an essential link in the aquatic food webs, connecting the basal resources (phytoplankton, benthic algae, and detritus) to the top consumers such as other invertebrates, birds, and benthic fish (Motta 1996, Henríquez de Oliveira et al. 2003). The Chironomidae is one of the most highly represented taxa in inland aquatic environments because of its abundance and diversity, with the immature stages being key elements in the ecology of almost all benthic environments (Paggi 2009).

According to Coffman & Ferrington (1996), the larvae can be predators (the Tanypodinae), gathering collectors and/or scrapers (the Orthocladiinae) and gathering collectors and/ or filtering collectors (the Chironominae); but information on this subject in South America is still scarce and fragmentary (Motta & Uieda 2004, Tomanova et al. 2006, Ramirez & Gutiérrez Fonseca 2014). Studies related to macroinvertebrate feeding and FFG assignments in South America were conducted by Nessimian & Sanseverino (1998), Nessimian et al. (1999), Callisto et al. (2001). Henríquez de Oliveira et al. (2003), Cummins et al. (2005) and Da Silva et al. (2008) for Brazil; Tomanova et al. (2006) for Bolivia; and Zilli et al. (2008), Príncipe et al. (2010), and Galizzi et al. (2012) for Argentina. Even though the interest in understanding the trophic relationships of inland-water invertebrates in our region has increased recently, most of the studies were based on Northern Hemisphere literature, mainly Merritt & Cummins (1996). In this regard, authors such as King et al. (1988) and Tomanova et al. (2006) noted that the transfer of information relating to the FFGs between continents (or between geographical regions within the same continent) requires caution.

Spatial differences over a lotic system can determine the distribution of Chironomidae species and the corresponding functional feeding groups (Príncipe et al. 2010, Zanotto-Arpellino et al. 2015). In order to improve our understanding of the trophic habits of the Chironomidae, we undertake a study in an intermittent stream of the Ventania-Hill system (Buenos Aires, Argentina) having spatial differences. The working hypothesis was that different types of habitat- characterized by different altitudes, substrates, and current velocity—could promote differences in the diet of the Chironomidae. The aims of the study were (1) to determine the diet of the most representative species of the Chironomidae from the Ventana Stream and assign the corresponding FFGs and (2) to test if differences existed in the diet of the species between different habitats.

MATERIALS AND METHODS

Study area

The Ventania-Hill stream system is located between 37° 31' S; 62° 50' W and 38° 23' S; 61° 13' W, in the southwest of the Buenos Aires province, Argentina. This system extends for 170 km in a northwest-to-southeast direction and covers an area of approximately 4800 ha (Lizzi et al. 2007). The maximum altitude is 1.243 meters. The system contains an altitude gradient with increasing precipitation and decreasing temperature at higher levels (Pérez & Frangi 2000). The soils have developed from loess sediments that covered the slopes of the mountains with basement granite and rhyolites (Cappannini et al. 1971). This area possesses more than 400 native plant taxa, with several endemic species (Frangi & Barrera 1996). The streams of this system have high slope and flow velocity in their headwaters, with both parameters being reduced at the outlet (Frenguelli 1956, Ringuelet 1962).

The bottom substrate varies between gravel, a mixture of gravel and sand, or clay to silt-clay compacted in the potamon. Most of the streams of this system are temporary, forming pools or rocky pools that act as reservoirs of water when the streams are not flowing and are the most characteristic lentic habitats in the region remaining permanent throughout the year (Siri & Donato 2012).

For this study, the Ventana Stream located in the northwest slope of Sauce-Chico catchment was selected. Along this stream, three sampling sites were selected (Fig. 1): Site A (38° 03' 31.7" S; 62° 01' 11.8" W and located 574 m above sea level) and Site B (38° 03' 42.4" S; 62° 01'21.4" W and located 518 m above sea level) are pools without current velocity, connected by |hyporheic flow and characterized by the presence of a rocky bottom. Site C (38° 02' 53.1" S: 62° 07' 41.5" W and



Figure 1. Study sites. a: Site A, with the location exemplifying the rocky substratum; b: a typical pool in Site B; c: Site C, illustrating the components of the smaller-sized substratum. located 342 m above sea level) is characterized by a smaller-sized substratum (from boulder to silt) and a low current velocity (Siri & Donato 2012).

Chironomidae sampling

The material analyzed was obtained from a field trip carried out in May 2011, whose results were published in part in Donato et al. (2012), Siri et al. (2012), and Mauad et al. (2013). The specimens were collected with a D-Net of 270 cm² and a 200-µm mesh. Gut-content analysis and FFG determination

For each species and site, ten of the same instar larvae were analyzed. The gut dissection of each individual was conducted under a stereoscopic microscope to isolate the contents for transfer to 1.5-ml vials with rose-Bengal stain for 24 h. Distilled water was then added and the contents homogenized and mounted on microscope slides for observation under an optical microscope at a magnification of 400X. The scale bar of the microscope eyepiece was used as a transect. Photographs were taken of 15 random transects, where each food category was recorded at each sampling point after Reynaga & Rueda-Martín (2013). To quantify the food items, the area covered by each one relative to the total area occupied by the digestive content was recorded and expressed as the relative frequency (Winterbourn et al. 1984, Jaarsma et al. 1998, Albariño & Diaz Villanueva 2006).

The Chironomidae analyzed were assigned to the appropriate FFG on the basis of the classification proposed by Cummins (1973): shredders (feeding coarse particulate organic matter of size >1 mm), collector filterers (capturing fine particles between 0.45 µm and 1 mm from the water column), collector gatherers (removing fine particles within the bottom substrate), scrapers (scraping and consuming biofilm, algae and organic matter deposited on different substrates), and predators (eating other animals). If more than one food item was found in a particular specimen, the criteria used for assigning each group was determined by the dominant item (over 60% of the contents, according to Motta & Uieda, 2004).

Diversity measurements and statistical analysis

The diets of the species between sites were compared by a one-way ANOVA. The analyses were made by comparing the relative frequency of each food item consumed.

The total richness, Shannon's diversity index and Pielou's evenness index of the food items were calculated for each site from the food item indexes of the species present at each site. Differences between sites for these descriptors were tested by a one-way ANOVA after an averaging of all the species found. Before the analyses, the data was $log_{10}(X+1)$ transformed to satisfy the assumptions of the ANOVA.

A nonmetric multidimensional-scaling (NMDS) analysis by means of the Bray-Curtis similarity index was applied to categorize the species according to the food items consumed. A similarity-percentage (SIMPER) analysis was carried out to determine which item contributed the most to the dissimilarity and then an analysis of similarities (ANOSIM) was applied to evaluate if those differences were significant. All these methods were computed with the program Past 3.0 (Hammer et al. 2001).

RESULTS

During the present study a total of 9 chironomid species were collected—one at Site A, six at Site B, and five at Site C, with *Corynoneura* sp. 1 being the only species shared among the three sites (Table I).

Site	Subfamily	Species		
А	Orthocladinae	Corynoneura sp1		
	Podonominae	Podonomus gr decarthrus		
		Podonomus albinervis		
В	Orthocladinae	Corynoneura sp1		
		Onconeura analiae		
		Cricotopus sp1		
	Tanypodinae	Pentaneura nr cinerea		
	Chironominae	Dicrotendipes alsinensis		
		Rheotanytarsus sp1		
С	Orthocladinae	Corynoneura sp1		
		Onconeura analiae		
	Tanypodinae	Labrundinia pilosella		

Table I. List of chironomid species per sampling sites.

Analysis of the gut composition and FFG determination

The digestive contents removed from the dissected guts were classified according to the following food categories: particulate organic matter (detritus), diatoms, filamentous chlorophytes, euglenophytes, vascular plants, animal remains, and fungi. The number of food items varied between two and six for the different species, with detritus being always present. In addition to these food categories, ingested mineral material was found in the guts.

Figure 2a summarizes the food items consumed by those species present at least two sites. *Corynoneura* sp. 1 was present at all the sites, with detritus being the main item in the gut contents. The second main item was the fungi, representing almost 30% of the total content. In this species the animal remains, represented by small insect appendage fragments with lengths of 10 to 100 μ m, were observed at Site B. A oneway ANOVA indicated no significant differences between the diets for *Corynoneura* sp. 1 among the three sites (p > 0.05) for all the food items

found. The species Onconeura analiae was found at sites B and C, where different food items were recorded. At Site B, detritus and fungi were the only food items found, while at Site C animal remains predominated; followed by detritus, fungi, and a low proportion of diatoms. A oneway ANOVA, however, did not detect significant differences in the relative frequencies of the various food items consumed between the sites (p > 0.05). Figure 2b depicts the proportions of the food items registered in the gut of those species registered in only one sampling site. The species present at Site B consumed detritus as the main food item. In both Podonomus species, vegetal remains and a small proportion of fungi were also found, while diatoms and a low proportion of Euglenophyta were present in the diet of P. gr. decarthrus but not P. albinervis. Pentaneura nr. cinerea and Cricotopus sp. 1 consumed a high proportion of animal remains, representing respectively about 40% and 30% of the total gut contents. At Site C, detritus was the dominant item for almost all the taxa recorded. In Dicrotendipes alsinensis, fungi were the second most consumed item, though euglenophytes and animal remains were also recorded. Similarly, in the gut content of *Rheotanytarsus* sp. 1, the second item was fungi, followed by filamentous chlorophytes and animal remains. Labrundinia pilosella consumed similar proportions of fungi and animal remains together with detritus, the latter being the principal item.

According to the relative proportion of the items consumed, most of the species analyzed were gathering collectors, except for *O. analiae* at Site C and *P.* nr. *cinerea* and *Cricotopus* sp. 1 at Site B, which consumed a high proportion—though lower than 60%—of animal remains. For that reason, assignment of those two species to a single FFG was not possible.



Figure 2. Percentage of food items for each species at the sampling sites. a: comparison of the items composing the diet of *Corynoneura* sp. (left half) and of *Onconeura analiae* (right half) when present at different sites. b: comparison the dietary compositions of the additional species indicated below each bar present at only site B or C.

Site	Таха	S	D	H'	J'
А	Corynoneura sp1	2	0.9552	0.1092	0.1576
В	P. gr. decarthrus	6	0.3631	1.252	0.6989
В	P. albinervis	4	0.7194	0.5985	0.4317
В	Corynoneura sp1	4	0.3486	1.145	0.8256
В	O. analiae	3	0.5639	0.7782	0.7083
В	P. nr cinerea	4	0.4143	0.9599	0.6925
В	Cricotopus sp1	4	0.4243	0.986	0.7112
С	D. alsinensis	5	0.5872	0.8391	0.5214
С	Rheotanytarsus sp1	5	0.4889	0.9605	0.5968
С	Corynoneura sp1	2	0.5259	0.667	0.9623
С	L. pilosella	3	0.6592	0.6382	0.5809
С	O. analiae	4	0.3736	1.092	0.7875

Table II. Diversity measurements: S: Richness; D: dominance; H': Shannon´s diversity index; J': Pielou´s evenness index.

Diversity measurements and statistical analysis

Table II summarizes the diversity measurements of the food items at each study site. No significant differences were obtained with any of the indices tested for the taxa present at sites B and C based on the food items present (ANOVA, p > 0.05). Since Site A was represented by only *Corynoneura* sp. 1, that site was excluded from the ANOVA.

The NMDS revealed groupings of the species analyzed according to the predominant food items, regardless of the sites from where the species were recorded. As a result of this ordination analysis, two main groups were obtained (Fig. 3). One was composed of *P*. nr. *cinerea* (Site B), *Cricotopus* sp1 (Site B), and *O. analiae* (Site C), where animal remains were the dominant item. The other group comprised the remaining species, where the dominant item was detritus. Within this group, three subgroups were found, a unique species related to vegetal

remains (*P.* gr. *decarthrus* at Site B), a group consisting of species that consumed more than 70% detritus and less than 20% fungi, and a group ingesting less than 70% detritus and more than 20% fungi. The results of SIMPER analysis (Table III) indicated that animal remains were the item that most greatly contributed to the dissimilarity between groups (42.7%), at statistically significant differences (ANOSIM, R = 0.84; p = 0.004).

DISCUSSION

In the present study, we analyzed the diets of the larvae of different chironomid species from the Ventania-Hill system. Even though functional group designations are based partially on morphology, the mode of feeding within the Chironomidae exhibits considerable flexibility (Berg 1995). In our study, from the analysis of gut contents, we found that the number of food items for each species varied between two to six. These results agreed with

Item	Mean dissimilarity	% Contribution	Cummulative %
animal remains	17,71	42,66	42,66
detritus	12,94	31,18	73,84
fungi	4,462	10,75	84,59
Chlorophyta	3,771	9,085	93,67
vegetal remains	1,665	4,011	97,69
diatoms	0,7972	1,92	99,61
Euglenophyta	0,1634	0,3936	100

Table III. Results of the SIMPER analysis. In bold the item which more contributes to dissimilarity.

Figure 3. NMDS analysis performed by means of the Bray-Curtis similarity index. The abbreviations used are the same as those in Table I.

the findings from previous studies (Nessimian et al. 1999, Henríquez de Oliveira et al. 2003), with most of Chironomidae not being restricted to a single food item. In the Ventana Stream detritus was the principal food source for most of the larvae analyzed. In agreement with Berg (1995), this nutritional resource usually represents between 50 to 70% of the total gut contents of those invertebrates. For this reason, many authors consider that most members of this family are detritivorous. Nonetheless, the diet is usually diversified, with fungi and diatoms and animal remains being frequently found in the gut contents of the Tanypodinae (Henríquez de Oliveira et al. 2003, Motta & Uieda 2004, Ocon et al. 2013). In our study, the higher richness of food items corresponds to P. gr. decarthrus (Podonominae). Few Chironomidae species exhibit nutritional selectivity, with most being generalists and opportunists (Berg, 1995). Accordingly, Woodward & Hildrew (2002) stated that feeding flexibility was an essential adaptation because that versatility reduced the overlap of niches and thus the inter- and intraspecific competition. Moreover, the availability of an item in the environment would appear to be more influential on the diet than the preference for a specific food (Butakka et al. 2016). Six of the nine species found in this work can be classified as gathering collectors because of prevalence of detritus (in the form of fine particulate organic matter) in the gut contents. This result agreed with the observations of Nessimian & Sanseverino (1998), Da Silva et al. (2008) and Saito and Fonseca Gessner (2014), who also classified most of the chironomid species as gathering collectors in other neotropical environments.

Several environmental features-such as current velocity, substrate, and organic matterare the most significant variables for explaining the influence of the availability and quality of

potential food resources on the distribution of functional feeding groups (Príncipe et al. 2010). Thus, Nessimian et al. (1999) suggested that changes in the feeding habits of chironomids are strongly based on the environmental conditions. The larvae of Corynoneura sp. 1 exhibited feeding flexibility, with differences in the dietary habits occurring among the three sampling sites. Despite the presence of animal remains in the gut contents of this species at one site, no significant differences were found with the other sites. The same occurred for O. analiae between sites B and C. As was noted above, animal remains have been associated with predator subfamily Tanypodinae (Berg 1995, Paggi 2009). In the present study, the guts of the two Tanypodinae species, P. nr. cinerea and L. pilosella, contained animal remains, but a higher proportion was found for O. analiae (Orthocladiinae) at Site C. Even though other species evidenced this item in their gut contents, but in lower proportions; the presence of animal remains does not necessarily signify a predatory habit when the proportions are lower than 60%. A possible explanation is that larvae feed on benthic organic matter that contains the remains of dead organisms that are included because of their nonselective food acquisition. The lower percentage of animal remains found in *L. pilosella* could be attributed to the early larval stages of the specimens studied. This finding was in agreement with the observations of Felten et al. (2008), who indicated that fooditem size and predatory behavior increased with body size. Nevertheless, Konstantinov (1961) pointed out that the incidence of predation by chironomids, especially Tanypodinae, can be substantially underestimated if the presence of animal material in the gut contents is used as the sole indicator of a carnivorous diet. This underestimation is primarily a result of the

ability of many tanypods to pierce their prey and withdraw body fluids.

The NMDS analysis indicated that Chironomidae species were grouped mainly by their affinity for a certain food item, instead of according to the sampling sites. Likewise, comparisons of the diversity measurements of food items between sites evidenced no significant differences, and no variation among the FFGs was observed.

From the results obtained, we can conclude that most of the species found corresponded to the gathering-collector FFG. The main food item was detritus, although the diets were generally varied. In contrast, no variation was observed in the FFGs among the sites surveyed. These results will contribute to our understanding of the feeding habits of Chironomidae in South-American streams, particularly in intermittent hill stream systems. Future comparative investigations involving these results and an analysis of the diet of Chironomidae larvae in other hill streams could be informative in further increasing our knowledge of this family.

Acknowledgments

This study was supported by PIP 0570 and 1010 CONICET, N 869 and N 914 UNLP. This is Scientific Contribution N° 1167 from the Instituto de Limnología Dr. Raúl A. Ringuelet (CONICET La Plata-UNLP). Dr. Donald F. Haggerty, a retired academic career investigator and native English speaker, edited the final version of the manuscript.

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How to cite

OCON C, SIRI A, ALTIERI P & DONATO M. 2023. Functional feeding groups of Chironomidae (Diptera: Nematocera) and their spatial variation in an intermittent hill stream (Ventana Stream, Buenos Aires, Argentina). An Acad Bras Cienc 95: e20191316. DOI 10.1590/0001-3765202320191316

Manuscript received on October 30, 2019; accepted for publication on July 7, 2020

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