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Trophic analysis of two species of *Atopsyche* (Trichoptera: Hydrobiosidae)

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A R T I C L E   I N F O

A B S T R A C T

To compare the trophic niche of coexisting larvae of *Atopsyche yunguensis* and *Atopsyche spinosa* we analysed their gut contents and found little niche overlap: *A. yunguensis* fed primarily on Trichoptera and amorphous matter, whereas *A. spinosa* fed on Diptera. *A. spinosa* showed both a spatial range and a niche breadth larger than those of *A. yunguensis*. Behavioural observations on *A. spinosa* may emphasize the use of chelate anterior legs for securing preys. Both species have been included into the predator–clingers functional group.

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Introduction

Trichoptera larvae are important participants in energy flow and nutrient dynamics in the aquatic environment. They display a wide diversity of trophic adaptations and exploit a great variety of aquatic microhabitats (Flint et al. 1999). Mendez and Resh (2007) surveyed literature on trichopteran life history and found that behavioural aspects are frequently understudied. In the Neotropical Region, the knowledge about ecology, behaviour or life history of caddisfly larvae is largely incomplete (Posada-García and Roldán-Pérez 2003). Available literature on this topic is mainly based on feeding habits (Albariño and Valverde 1998; Díaz Villanueva and Trochine 2005; Cummins et al. 2005; Rincón and Martínez 2006; Tomanova et al. 2006).

Mendez and Resh (2007) also detected that most English-language studies were conducted on families Hydropsychidae (24%) and Limnephilidae (20%), and mainly originated from North America (49%) and Europe (33%). To fill this gap of information, we focus on feeding habits of two sympatric *Atopsyche* species: *Atopsyche spinosa* Navás (1930) and *Atopsyche yunguensis* Rueda Martín (2006). *Atopsyche* is present in the Neotropical Region, except in the Chilean subregion (Flint et al. 1999), and represents the richest genus of Hydrobiosidae. General aspects of feeding behaviour have been described by Wiggins (2004). *Atopsyche* larvae are campodeiform and seem to fill the free-living predator niche in all instars (Wiggins 2004), although other authors found vestiges of microphytes and sediments particles in their guts (Tomanova et al. 2006). The anterior legs are chelate and probably are used for securing preys (Hinton 1950), but this behaviour has not been already empirically tested.

The overall scope of this paper is to analyse the trophic niche of two species with similar ecological requirements. Many species of invertebrates that share seemingly similar resource requirements live in sympatry (Keiper and Foote 2000). However, close scrutiny of invertebrate life histories has shown that niche partitioning frequently occurs, thus explaining the coexistence (Price 1997). This may include segregation by diet or feeding strategies (Harding 1997). The trophic niche is the relation between each species and its food (Holt 1993). A complete study of food niche should consider three different aspects: (1) where the food was obtained, (2) type of ingested material, and (3) feeding behaviour. The functional-feeding-groups refer to the feeding way and food type, whereas the habitat-trait include information about the food location (Merritt and Cummins 1996). The combination of functional-feeding-groups and habitat-trait have been used to define the Functional Groups (Heino 2005) to account for the functional roles of macroinvertebrates in stream ecosystems.

Life history studies are important in recent applications for community ecology (Mendez and Resh 2007). The species traits approach (Townsend and Hildrew 1994; Dolédec et al. 2000; Statzner et al. 2001) represents a clear example of this orientation. The species traits analysis may extract patterns of community structure, using both biological and ecological information about taxa. The great majority of studies on species traits derived from

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Europe where knowledge on aquatic fauna is more advanced (e.g., Tachet et al. 1994; Usseglio-Polatera et al. 2000). In the Neotropical Region, analogous research is difficult to carry out because of its entomofauna is poorly known. The asset of the present paper is to contribute to this knowledge, facilitating thus the implementation of methodologies that require biological data.

Material and methods

Gut content and morphometric measurements

A. spinosa and *A. yunguensis* (Fig. 1) are associated to small waterfalls in turbulent and well-oxygenated streams from the Andean Subtropical Mountain Forest. The range of *A. yunguensis*, northern Argentina and southern Bolivia, is embedded into the range of *A. spinosa* extended from Tucumán, in Argentina, to southern Bolivia (Fig. 2). Larvae of these two species were collected with a Surber sampler (900 cm^2 sampling area and 300 μm mesh size) and fixed with 75% ethyl alcohol. Thirty specimens of each species were picked out from samples of three different sites (Table 1). Morphometric measurements were considered for discounting a bias in dietary profiles due to instar stages. The head width and body length were compared through a *t*-test (INFOSTAT 2004).

The diet was analysed by removing the foregut and midgut content using ventral dissection of thorax (Peckarsky 1996). The description and identification of ingested items were made under a microscope (200 ×). The gut content of each specimen was mounted with glycerine in a customized slide with a central squared receptacle of uniform depth. The receptacle (20 mm × 20 mm) was divided into 625 equal-sized grid cells (0.64 mm^2), from which 15 were randomly selected. At each cell, the point intercept method was employed for surveying diet composition. The scale bar of the microscope eyepiece was used as a transect. Ten points were identified along the transect, with a constant interval between them. Food categories were recorded at each point and their percentage cover estimated.

In order to evaluate the influence of local variability, specific dietary assemblages were compared among sites. As no single site was large enough to permit parametric tests (Siegel and Castellan 1988), comparisons were made using the non-parametric Kruskal–Wallis one-way analysis of variance. Pairwise comparisons of dietary components between species were performed through the Mann–Whitney *U*-test. The totality of non-parametric ana-

lyses was addressed via stats package of R-software (Ihaka and Gentleman 1996).

The search of a global pattern in diet data were made through a %PCA (de Crespin de Billy et al. 2000), a multivariate analysis designed for diet composition data established at the level of the individuals, including thus the intra-individual diet variations. The first %PCA plane is used for representation purposes. Each prey item is linked to the population centroid by an arrow whose length is proportional to the relative abundance of this prey item. Computations and graphical displays were performed with ADE-4 (Thioulouse et al. 1997) and R-softwares (Ihaka and Gentleman 1996).

Breadth and overlap niche analysis

For each species, the amplitude of niche was estimated with Levins (1968) index: $B = 1/\sum p_i^2$, where p_i = relative frequency of food item i across sites. This index ranges from 1 to n, n being the number of food items considered. As the number of food items can vary between species, a standardized measure of niche amplitude was used (Colwell and Futuyma 1971; Jaksic 2001): $B_{st} = (B_{obs} - B_{min})/(B_{max} - B_{min})$, where B_{st} = standarized amplitude of niche; B_{obs} = Levins' index; $B_{min} = 1$ (minimum available amplitude of niche); $B_{max} = n$ (maximum available amplitude of niche). This index varies from 0 to 1, and permits a comparison between the two species (Jaksic 2001).

The niche overlap was estimated with Schoener's (1970) method: $Ps = 1 - 1/2\sum|p_{ij} - q_{ik}|$, where p_{ij} and q_{ik} represent the fraction of food item i that is used by species j and k, respectively, with regard to the total of food items. This measure of overlap range from 0, no food item used in common, to 1, complete overlap (Jaksic 2001).

Behavioural observations

Our laboratory (Tucumán, Argentina) is near to streams inhabited by *A. spinosa*. This leads us to firstly collect fixed specimens until skills on dissections had been tuned. Here, gut content inspections revealed that *A. spinosa* fed on larvae of Simuliidae (Diptera) and *Smicridea* sp. (Trichoptera: Hydropsychidae). Next, 10 living specimens of *A. spinosa*, in addition to their detected preys, were selected to carry out behavioural observations, mainly oriented to elucidate the link between the chelate anterior legs and the feeding behaviour. Living specimens were individually placed in rearing containers with lateral nets for water flow. An aquarium, equipped with a water pump, simulated the turbulence of the natural habitat (Fig. 3). After 1 day of starvation, specimens were deposited on a Petri dish under a magnifying glass. As preys were supplied, feeding behaviour was evaluated *in vivo*.

Results

Gut content and morphometric measurement

A. spinosa and *A. yunguensis* have an average body length of 1.33 ± 0.09 and 1.34 ± 0.03 cm, respectively, and an average head width of 0.89 ± 0.03 and 0.88 ± 0.04 mm, respectively. Measurements conform significantly to normal distribution. No significant difference in body length and head width were detected (*t*-test: $P > 0.05$). All larvae here studied corresponded to the fifth instar.

The prey items detected were categorized as following: (1) Oligochaeta, (2) Diptera (Chironomidae, Simuliidae and Psychodidae), (3) Trichoptera, (4) Ephemeroptera and (5) Amorphous
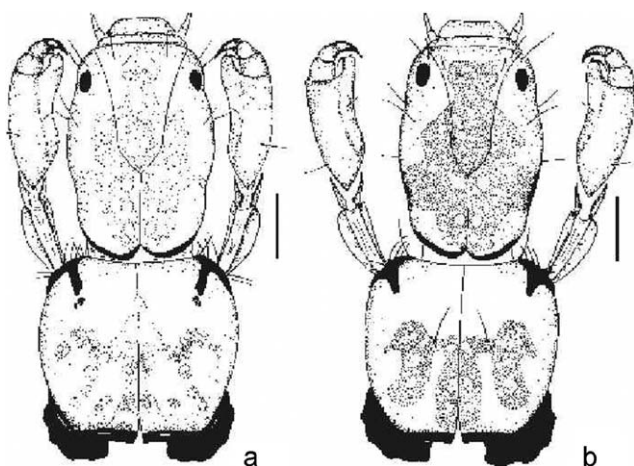

Fig. 1. Dorsal view of head, pronotum and anterior legs. (a) *Atopsyche spinosa*; (b) *Atopsyche yunguensis*. Scale bar: 0.5 mm.
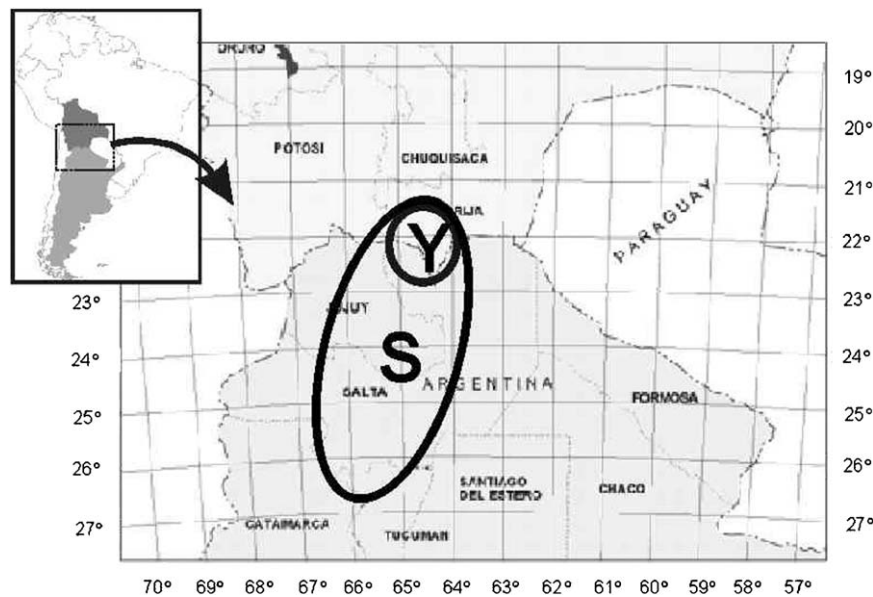
Fig. 2. Ranges of *Atopsyche spinosa* (S) and *Atopsyche yunguensis* (Y).

Table 1
Data of field collection

Sampling station	Geographical coordinates	Altitude (m)	Date (m/d/yr)	Number of selected specimens	
				Atopsyche yunguensis	*Atopsyche spinosa*
R. Orosa	22°12′9″S 64°37′36″W	1100	10/04/04	11	12
R. Huaico Grande	22°16′44″S 64°42′39″W	1645	11/11/04	10	9
R. Salinas	21°38′42″S 64°9′8″W	1160	10/05/04	9	9

The labels of sampling stations correspond to respective river (R.) name. Total selected specimens distributed among sampling stations in a balanced way.
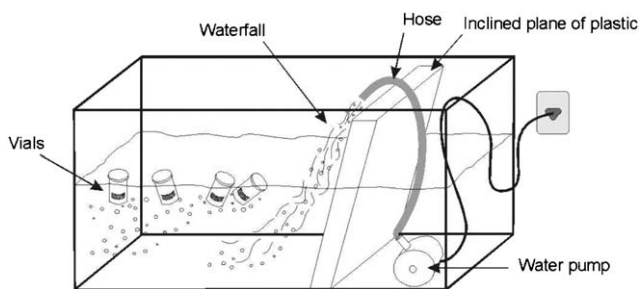

Fig. 3. Aquarium with water pump simulating a waterfall, the typical environment where *Atopsyche* larvae occur.

Matter. Prey fragments recognizable as such, but not identified in their taxonomic origin, were characterized as Indeterminate Material.

The percentages of the different food items are unequally distributed along the two dietary profiles (Table 2). On the whole, *A. spinosa* appeared to be limited to eating Diptera ($>50\%$). In contrast, Trichoptera in addition to Amorphous Matter were the dominant food items ($>80\%$) in *A. yunguensis.* For such food items, significant differences between species were detected through *U*-test (test values in the tail of Table 2). Comparisons among sites do not reveal significant differences via Kruskal–Wallis test, suggesting stability of diet profile across the landscape.

The %PCA is concordant with results predicated on the first statistical analysis. According to the eigenvalues (Fig. 4a), the first two axes of %PCA were sufficient to capture the main structure of data. Individual gut contents are ordered along the first axis, and segregated as a function of the species considered. Similarly, the 95% confidence ellipses yield a segregation of the individuals into discernible groups, reflecting thus differences in diet preference. Trichoptera and Amorphous Matter were the dominant food items for *A. yunguensis*, while Chironomidae and Simuliidae, and to a lesser extent Ephemeroptera, prevailed in *A. spinosa* diet. Food items representing $<2\%$ of the total gut contents were omitted (Psychodidae and Oligochaeta).

Niche breadth and overlap analysis

The calculated breadths of the niche were $B = 4.59$ and $B_{st} = 0.60$ for *A. spinosa*, while those of *A. yunguensis* were $B = 2.47$ and $B_{st} = 0.24$. Food-niche overlap was small as revealed by Schoener's index: $Ps = 0.356$.

Behavioural observations

Once specimens of *A. spinosa* were deposited on the Petri dish, they showed a short period of "freezing" followed by an active

Table 2
Diet component percentages across sampling points and pooled by species

Species	Sampling point	Specimens dissected	% Oligochaeta	% Chironomidae	% Simuliidae	% Trichoptera	% Ephemeroptera	% Indeterminate	% Amorphous Matter	% Psychodidae
Atopsyche yunguensis	Orosa	11 (2)	0.00	0.00	1.05	30.87	1.78	3.36	62.93	0.00
	Huaico Grande	10 (1)	0.00	3.55	0.31	22.84	12.81	3.24	52.47	4.78
	Salinas	9 (2)	0.00	1.12	0.75	50.93	0.56	0.00	46.64	0.00
	Pooled data		0.00	1.72	0.67	34.16	5.62	2.25	53.75	1.84
	KW-test (n = 25, df = 2)		–	KW = 3.453, P ≈ 0.178	KW = 0.575, P ≈ 0.750	KW = 4.787, P ≈ 0.091	KW = 5.239, P ≈ 0.073	KW = 0.815, P ≈ 0.665	KW = 4.561, P ≈ 0.102	KW = 1.778, P ≈ 0.411
Atopsyche spinosa	Orosa	12 (2)	0.00	29.79	43.07	11.50	5.01	0.00	10.62	0.00
	Huaico Grande	9 (3)	4.18	23.79	19.61	2.89	13.50	13.83	22.19	0.00
	Salinas	9	0.00	32.05	32.94	2.67	8.61	10.98	12.76	0.00
	Pooled data		1.28	27.83	31.27	9.54	7.67	7.87	14.55	–
	KW-test (n = 25, df = 2)		KW = 3.167, P ≈ 0.205	KW = 2.172, P ≈ 0.338	KW = 0.284, P ≈ 0.868	KW = 1.202, P ≈ 0.548	KW = 1.464, P ≈ 0.480	KW = 3.333, P ≈ 0.189	KW = 2.920, P ≈ 0.232	–
	Mann–Whitney U-test (n₁ = n₂ = 25)		U = 325, P ≈ 0.337	U = 503, P ≈ 3.98E−05*	U = 480, P ≈ 2.05E−04*	U = 152, P ≈ 5.62E−04*	U = 308, P ≈ 0.920	U = 335.5, P ≈ 0.439	U = 45, P ≈ 2.14E−07*	U = 300, P ≈ 0.337

In parentheses, number of dissected specimens with empty gut contents discarded of comparative analysis. Kruskal–Wallis test lines evaluate differences among sampling points. Mann–Whitney U-test line shows pairwise comparisons between species.

$* \ P \leqslant 0.01.$

search of their prey items. Next, they secured prey items through the combined action of the chelate anterior legs and the hook-like anal prolegs. Lastly, two ingestion ways were detected: (1) prey items smaller than predators (blackflies) were engulfed; (2) prey items with similar size to predators (*Smicridea* sp.) were cut into pieces.

Discussion

Theoretically, the coexistence of congeners requires that there must be some minimum ecological difference between the two species (May and MacArthur 1972). This coexistence would seem possible by feeding strategies minimizing niche overlap. Particularly, gut analyses of *A. spinosa* and *A. yunguensis* showed a difference in alimentary preference, in spite of the morphological similarities between species. The %PCA summarizes the segregation of trophic niche in highlighting the inner structure of diet data. Scarce observations that deviate from general pattern do not modify the overall dissociation between diets. The intra-specific coherence operates simultaneously with an inter-specific differentiation. In this manner, the conclusions about diet differentiation at species level are validated. As dissected specimens inhabited the same location (syntopic specimens *sensu* Rivas 1964), the difference in diet cannot be attributed to availability of food items at the scale of environment covered by a Surber sampler.

An exclusive predator habit was observed without any vegetable vestiges in the gut content, unlike a previous report (Tomanova et al. 2006) where microphytes and sediment particles were recorded at low quantities. These last findings may be attributed to the following causes: (a) accidental ingestion (vegetable vestiges may occur in the preys' gut), (b) geographical differences in feeding habit, (c) different species of *Atopsyche* that those considered here, (d) different instars (there may be a shift in diet during development), and (e) seasonality. There are antecedents making viable possibility *c*, like trichopterans *Brachycentrus* and *Rhyacophila* of which most species are predatory, although some are omnivorous or herbivorous (Irons 1988). The source of amorphous matter must be clarified in future studies, but we suggest advanced stages in the animal food digestion. Furthermore, amorphous matter was also detected in specimens submitted to behavioural observations. Martin and Mackay (1982) found unrecognizable organic matter in *Rhyacophila fuscula* and suggested that this is a result of feeding behaviour. The larvae of this species take the softer tissue and leave the chitinous exoskeleton. On the other hand, the use of the stain Phloxine B in gut analysis of *Rhyacophila* showed that much of the unidentifiable material was of animal origin (Irons 1988).

The standardized niche amplitudes differ between species. *A. yunguensis* shows a niche narrower than *A. spinosa*. The niche breadth is here related with distributional aspects, because the widespread species (*A. spinosa*) holds the niche more expanded. The positive relation between range size and breadth niche is connected with the conceptual core of Brown's hypothesis (Brown 1984, 1995; Brown et al. 1996). The essence of this hypothesis is that species capable to exploit a wide range of resources (whether resources are habitats, food sources or other variables) are likely to have larger range sizes (Briers 2003).

Our results are in agreement with Wiggins (2004), who after dissecting three specimens, concluded that *Atopsyche* larvae were carnivorous. Hinton (1950) proposed that the chelate anterior legs were used for securing preys. Our behavioural observations have corroborated this suggestion. The analysed species must be included into the functional-feeding-group of predators. The ingested items are mainly represented by soft bodied benthic invertebrates. This
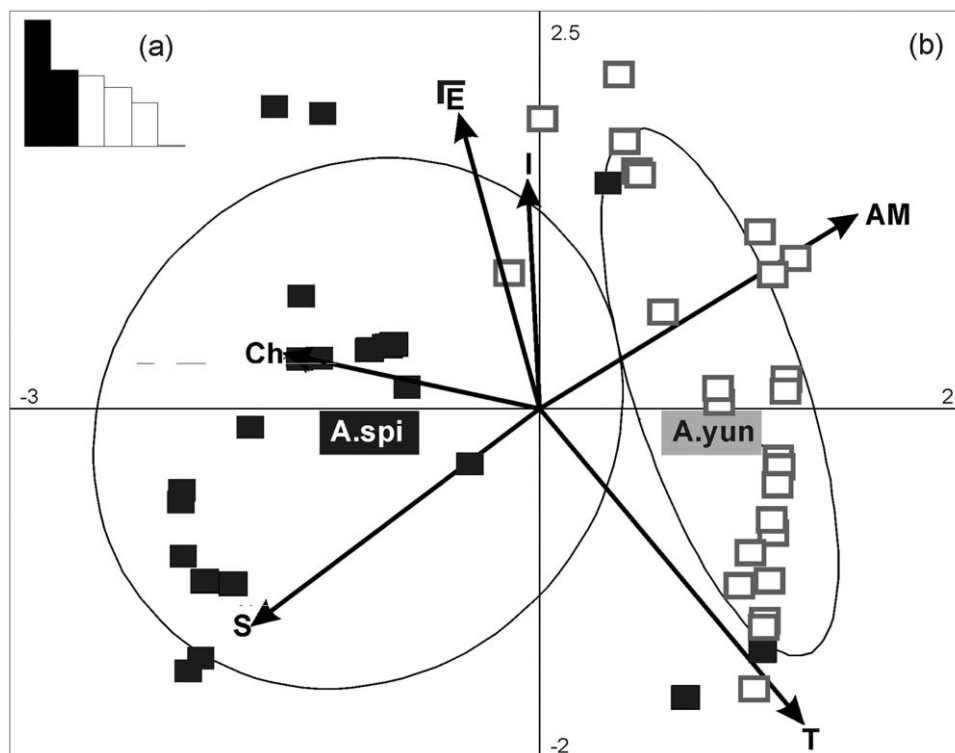
Fig. 4. Biplot of alimentary items and *Atopsyche* species obtained from a %PCA. (a) Histogram of eigenvalues (the first two values are in solid bars, 33.51% and 20.37% of the total variation, respectively). (b) Distribution of individual gut contents (squares) on the first factorial plane according to their prey items (arrows). *A. spinosa*: closed squares; *A. yunguensis*: empty squares. 95% confidence ellipses group together co-specific individuals. Ch = Chironomidae, E = Ephemeroptera, S = Simuliidae, T = Trichoptera, AM = Amorphous Matter, I = Indeterminate material. For difference between AM and I see text.

information, in addition to data on the habitat where species occur (i.e., the habitat-trait), may define their Functional Group (Heino 2005). *A. spinosa* belongs to the Functional Group of predator–clingers because (1) it attacks other animals and engulf preys or cut them into pieces and (2) it shows adaptations for the attachment on benthic substrate of riffles. In considering the gut content and the morphology resemblance to *A. spinosa*, *A. yunguensis* seems also to fulfill the charcteristics of predator–clingers.

Acknowledgements

References

Albariño, R.J., Valverde, A., 1998. Hábito alimenticio del estado larval de *Parasericostoma cristatum* (Trichoptera: Sericostomatidae). Rev. Soc. Entomol. Argent. 57, 131–135.

Briers, R.A., 2003. Range size and environmental calcium requirements of British freshwater gastropods. Global Ecol. Biogeogr. 12, 47–51.

Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279.

Brown, J.H., 1995. Macroecology. University of Chicago Press, London.

Brown, J.H., Stevens, G.C., Kaufman, D.M., 1996. The geographic range: size, shape, boundaries and internal structure. Ann. Rev. Ecol. System 27, 597–623.

Colwell, R.K., Futuyma, D.J., 1971. On the measurement of niche breadth and overlap. Ecology 52, 567–576.

Cummins, K.W., Merrit, R.W., Andrade, P.C.N., 2005. The use of invertebrates functional group to characterize ecosystem attributes in selected stream and rivers in south Brazil. Stud. Neotrop. Fauna Environ. 40, 69–89.

De Crespin de Billy, V., Dolédec, S., Chessel, D., 2000. Biplot presentation of diet composition data: an alternative for fish stomach contents analysis. J. Fish Biol. 56, 961–973.

Díaz Villanueva, V., Trochine, C., 2005. The role of microorganisms in the diet of *Verger cf. limnophilus* (Trichoptera: Limnephilidae) larvae in a Patagonian Andean temporary pond. Wetlands 25, 473–479.

Dolédec, S., Olivier, J.M., Statzner, B., 2000. Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities effects of taxonomic and spatial resolution. Arch. Hydrobiol. 148, 25–43.

Flint, O.S., Holzenthal, R., Harris, S.C., 1999. Nomenclatural and systematic changes in the Neotropical Caddisflies (Insecta: Trichoptera). Insecta Mundi 13, 73–84.

Harding, J.S., 1997. Strategies for coexistence in two species of New Zealand Hydropsychidae (Trichoptera). Hydrobiologia 350, 25–33.

Heino, J., 2005. Functional biodiversity of macroinvertebrates assemblage along major ecological gradients of boreal headwater streams. Freshwater Biol. 50, 1578–1587.

Hinton, H.E., 1950. A trichopterous larva with chelate front leg. Proc. R. Entomol. Soc. London 35, 55–64.

Holt, D.W., 1993. Trophic niche of nearctic short-eared owls. Wilson Bull. 105, 497–503.

Ihaka, R., Gentleman, R., 1996. R: a language for data analysis and graphics. J. Comput. Graph. Stat. 5, 299–314.

INFOSTAT, 2004. InfoStat versión 2004. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Irons III, J.G., 1988. Life history patterns and trophic ecology of Trichoptera in two Alaskan (USA) subartic streams. Can. J. Zool. 66, 1258–1265.

Jaksic, F., 2001. Ecología de Comunidades. Ediciones Universidad Católica de Chile, Santiago, Chile.

Keiper, J.B., Foote, B.A., 2000. Biology and larval feeding habits of coexisting Hydroptilidae (Trichoptera) from a small woodland stream in northeastern Ohio. Ann. Entomol. Soc. Am. 93, 225–234.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, NJ.

Martin, I.D., Mackay, R.J., 1982. Interpreting the diet of *Rhyacophila* larvae (Trichoptera) from gut analyses: an evaluation of techniques. Can. J. Zool. 60, 783–789.

May, R.M., MacArthur, R.H., 1972. Niche overlap as a function of environmental variability. Proc. Nat. Acad. Sci. USA 69, 1109–1113.

Mendez, P.K., Resh, V.H., 2007. What aspects of the life history of Trichoptera have been studied? In: Bueno-Soria, J., Barba-Álvarez, R., Armitage, B. (Eds.), Proceedings of the XIIth International Symposium on Trichoptera. The Caddis Press.

Merritt, R.W., Cummins, K.W., 1996. An Introduction to the Aquatic Insects of North America. Kendall/Hunt, Iowa.

Navás, L., 1930. Insectos de la Argentina. Rev. Soc. Entomol. Argent. 3, 125–132.

Peckarsky, B.L., 1996. Predator–prey interactions. In: Hauer, F.R., Lamberti, G.A. (Eds.), Methods in Stream Ecology. Academic Press, California, pp. 431–451.

Posada-García, J.A., Roldán-Pérez, G., 2003. Clave ilustrada y diversidad de las larvas de Trichoptera en el Nor-Occidente de Colombia. Caldasia 25, 169–192.

Price, P.W., 1997. Insect Ecology, third ed. Wiley, New York.

Rincón, J., Martínez, I., 2006. Food quality and feeding preference of *Phylloicus* sp. (Trichoptera: Calamoceratidae). J. N. Am. Benthol. Soc. 25, 209–215.

Rivas, L.R., 1964. A reinterpretation of the concepts "Sympatric" and "Allopatric" with proposal of the additional terms "Syntopic" and "Allotopic". Syst. Zool. 13, 42–43.

Rueda Martín, P.A., 2006. Associations, new records, and a new species of Atopsyche from Northwestern Argentina and Southern Bolivia (Trichoptera: Hydrobiosidae). Zootaxa 1367, 51–62.

Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51, 408–418.

Siegel, S., Castellan, N.J., 1988. Nonparametric Statistics for the Behavioral Sciences, second ed. McGraw-Hill Book Company, New York.

Statzner, B., Hildrew, A.G., Resh, V.H., 2001. Species traits and environmental constraints: entomological research and the history of ecological theory. Ann. Rev. Entomol. 46, 291–316.

Tachet, H., Usseglio-Polatera, P., Roux, C., 1994. Theoretical habitat templets, species traits, and species richness: Trichoptera in the Upper Rhône River and its floodplain. Freshwater Biol. 31, 397–415.

Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE-4: a multivariate analysis and graphical display software. Stat. Comput. 7, 45–83.

Tomanova, S., Goitia, E., Helešic, J., 2006. Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams. Hydrobiologia 556, 251–264.

Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biol. 31, 265–275.

Usseglio-Polatera, P., Bournaud, M., Richoux, P., Tachet, H., 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshwater Biol. 43, 175–205.

Wiggins, G.B., 2004. Caddisflies. The Underwater Architects. University of Toronto Press, Toronto.