



Trematodes and nematodes parasitizing the benthic insect community of an Andean Patagonian stream, with emphasis on plagiurchiid metacercariae

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Abstract. In freshwater systems, parasitological studies have mainly been carried out on vertebrates and molluscs, but little is known about parasites of aquatic insects. We describe the trematodes and nematodes parasitizing the benthic insects of an Andean Patagonian stream and the presence of parasites in the terrestrial adult stages. Members of 3 of 20 insect taxa were found to be parasitized by larval nematodes, and members of six taxa harbored metacercariae of digeneans. In benthic samples, chironomids, simuliids (Order Diptera), and baetids (Order Ephemeroptera) harbored mermithid larvae (Nematoda). The stonefly *Antarctoperla michaelsoni* (Order Plecoptera), the caddisfly *Smicridea annulicornis* (Order Trichoptera), a watersnipe fly (Order Diptera: Athericidae), and three species of leptophlebiid mayflies (Order Ephemeroptera) were parasitized by encysted plagiurchiid metacercariae (Order Plagiurchiida). Most metacercariae were found in the three species of mayflies with prevalences ranging 15–63% and mean intensities ranging 1.2–4.9. Prevalence declined from summer to early winter, probably because of the emergence of infected nymphs and the recruitment of uninfected new cohorts. The imagos had live metacercariae with higher prevalences and intensities of infection than nymphs. We suggest that these plagiurchiids have an allogenic life cycle, involving a terrestrial definitive host.

Additional key words: Allogenic cycle, leptophlebiid mayflies, mermithids, Patagonia

Parasitological studies are important in providing information about trophic interactions because many parasites possess complex life cycles that require multiple hosts at different trophic levels, and transmission often depends on predator–prey relationships (Valtonen et al. 2010). Adding trophic interaction-dependent parasites into food webs increases the complexity and stability of such networks (Huxham et al. 1995). In addition to the ecological relevance of host–parasite interactions, it has recently been reported that parasite biomass can exceed host biomass in some ecosystems (Kuris et al. 2008). However, no trophic studies on lotic systems have ever explicitly included parasites (Hernandez & Suhkdeo 2008).

In freshwater systems, parasitological studies have mainly been carried out on vertebrates and molluscs, but little is known about parasites from aqua-

tic insects. Some studies have reported infection by diverse parasites (Hirasawa & Urabe 2003; Hirasawa & Yuma 2003; Amato & Amato 2006), while others have explored behavioral aspects of both parasites (Snyder & Janovy 1996) and hosts (Vance & Peckarsky 1997) or more applied issues, such as the use of entomopathogenic nematodes against harmful insects (Camino & Maiztegui 2002; Camino & de Villalobos 2002). Most research has been centered on systems with single host and parasite species. In contrast, only a handful of studies (for example, those of González Lanza et al. [1986] and Manzanera Manzanera & Alvarez Pellitero [1987]) have been carried out on aquatic invertebrate communities and all their macroparasites. These authors studied the trematodes and nematodes associated with benthic macroinvertebrate communities in Spanish rivers, recording seasonal abundance, richness and diversity of plagiurchiid, strigeid, echinostomatid, and allocreadiid digeneans, and mermithid and rhabdochonid nematodes.

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In fluvial systems, benthic invertebrates play a substantial role in energy and matter fluxes, linking the base of food webs with upper trophic levels as they feed on autochthonous and allochthonous organic matter (primary producers and organic debris) and are consumed by vertebrates (Winterbourn & Townsend 1998). In Andean Patagonia, several studies have analyzed the assemblages of benthic invertebrates in streams and rivers. Many of them were focused on community structure and species distribution at different spatial scales (Albariño 1997; Miserendino 2001; Velásquez & Miserendino 2003), whereas others covered trophic interactions among aquatic insects, their resources and predators (Albariño & Balseiro 2002; Díaz Villanueva et al. 2004; Buria et al. 2010).

Plagiorchiids exhibit a typical digenetic life cycle that involves the following stages: an egg from which hatches a free living larva called a miracidium, which penetrates the body of the first intermediate host (usually a snail) and develops into a sporocyst. Sporocysts produce, via asexual reproduction, crawling xiphidiocercariae (stylet-bearing cercaria), which penetrate the bodies of aquatic insects, the second intermediate hosts, and become metacercariae. Finally, the swimming (or flying) insect is eaten by the vertebrate definitive host where the parasite matures and, after sexual reproduction, lays eggs (Roberts & Janovy 2005).

The life cycle of mermithid nematodes, on the other hand, involves four larval stages: the first larval (L_1) molt occurs within the egg (which is laid in the host's environment), and the escaping larva is an L_2 , which makes contact with the potential host (a terrestrial or aquatic insect) and penetrates it through the cuticle with the aid of the anteriorly situated stylet. The second molt occurs in the hemocoel of the host, resulting in an L_3 larva. After a parasitic existence of 10 days to several months, the L_3 is ready to leave the host, and finally after a period of maturation in the external environment, the final two molts occur, and the adult stage is attained (Cheng 1986).

Although parasitism in non-insect aquatic animals is well documented in Patagonia (e.g., Viozzi et al. 2009), parasitic relationships involving benthic insects remain unknown. Our general aim was to describe the community of trematodes and nematodes parasitizing the benthic insects of a Patagonian fluvial system. The specific objective was to investigate the infection of plagiorchiid trematodes through the study of host specificity, component population dynamics, and their presence in terrestrial stages of the aquatic insects.

Methods

Gutiérrez Stream ($41^{\circ}6'S$, $71^{\circ}25'W$) is located in the northwest of Andean Patagonia. It starts in Gutiérrez Lake and runs ~6 km before discharging into Nahuel Huapi Lake. Both lakes are of glacial origin and oligotrophic, and belong to the Atlantic watershed. The stream runs through suburban areas. Despite impacts related to urbanization and recreational uses, the ecological features and the macroinvertebrate community do not differ much from other non-urban streams in this region (Pedrozo et al. 1993).

Samples of benthic macroinvertebrates were taken monthly from January to June 2008 using a Surber sampler (area=0.0625 m², mesh size=200 μ m) in a 20-m long reach 3 km from the stream mouth. Temperatures ranged between 9.4 and 18°C, the stream had an average channel width and depth of 16 and 0.3 m, respectively, and mean flow was 2.9 m³ s⁻¹. The samples were taken at five points along a transverse section of the stream nearly 3 m from each other and starting at ~1 m from the shore. Erosional areas were chosen because of the high concentration of benthic invertebrates in these habitats. Each sample was placed in an individual container and carried to the laboratory, where they were fixed in 5% formalin until processing. Macroinvertebrates were separated into different size fractions with 500 and 1000 μ m sieves, and specimens of the larger fraction were counted and identified. Insects collected this way were stored in 70% ethanol until examination for parasites.

Using a stereomicroscope, we determined the stage of development of each insect specimen following Fernández & Domínguez (2001). Specimens of taxa which altogether contributed up to 95% of the community were examined from February, April, and June samples, whereas all leptophlebiid mayflies from the 6 months were examined because of previous data showing high prevalences and intensities of metacercariae in these insects. Specimens were measured (total length, from the head to the end of the abdomen), dissected, and examined with the microscope, and the number of metazoan parasites was recorded.

To study presence and viability of parasites in imagos, adult insects were collected using an emergence trap, which was rectangular (1.20×1.90 m, height=1.70 m) with a pyramidal-shaped net (mesh size=1000 μ m) and a container at the top. This net was set on the water surface of the stream, from February to April, when emergences are more frequent. The net was checked weekly. Some of the

imagos collected were dissected alive, while the rest were preserved in 70% ethanol until processing.

To explore variation in sizes of metacercariae, they were observed with a compound microscope, and the total diameter and the thickness of the cyst wall were measured with a calibrated ocular micrometer. We also recorded the presence of the stylet, which is often found as a remnant of the cercaria stage.

Data analysis

Prevalence, intensity, mean intensity, and abundance were obtained following Bush et al. (1997). Statistical differences between lengths of infected and uninfected specimens of the same species were tested using Mann–Whitney U tests. We also explored the relationships between infection values and shore proximity to see if values increased toward stream margins. Infection data were pooled for the three leptophlebiids from 6 months and intensity was plotted against a ranked distance from the shore (i.e., the closest sites at both shores ranked 1 and the farthest site, approximately at the center of the channel, ranked 3).

Results

Insect community and parasites

The benthic insect community was comprised of 20 identified taxa belonging to six different orders (Table 1). Collected insects had two different types of postembryonic development (hemi- and holometabolous), and in most cases, they were nymphs or larvae, although for some taxa pupae and adults were also collected. Except for beetles of the family Elmidae, all insects had life cycles involving terrestrial adults. Specimens of non-biting midges (Chironomidae) and black flies (Simuliidae) were only identified to the family level, despite there being more than one species present (indicated as “spp.”).

The thirteen taxa that altogether contributed up to 95% of the benthic insect community were examined for parasites. Nine of these taxa were infected by trematodes or nematodes. None of the infected specimens harbored more than one morphospecies of parasite (Table 2). The baetid mayfly *Andesiops peruvianus* (ULMER 1920) and some members of the Chironomidae and Simuliidae were parasitized with larvae of

Table 1. Postembryonic development, stages collected, and adult habitat of the insects sampled in this study. A, aquatic; HE, hemimetabolous; HO, holometabolous; T, terrestrial.

Taxon	Postembryonic development	Stage	Adult habitat
Odonata			
Anisoptera sp.	HE	nymphs	T
Ephemeroptera			
<i>Andesiops peruvianus</i> (ULMER 1920)	HE	nymphs	T
<i>Meridialaris chiloeensis</i> DEMOULIN 1955	HE	nymphs	T
<i>Nousia bella</i> PESCADOR & PETERS 1985	HE	nymphs	T
<i>Penaphlebia chilensis</i> EATON 1884	HE	nymphs	T
<i>Rhigotopus andinensis</i> PESCADOR & PETERS 1982	HE	nymphs	T
Plecoptera			
<i>Antarctoperla michaelsoni</i> (KLAPÁLEK 1904)	HE	nymphs	T
<i>Udamocercia arumifera</i> (AUBERT 1960)	HE	nymphs	T
Coleoptera			
<i>Austrelmis</i> sp.	HO	larvae & adults	A
Psephenidae sp.	HO	larvae	T
Diptera			
Athericidae sp.	HO	larvae	T
Chironomidae spp.	HO	larvae & pupae	T
Empididae sp.	HO	larvae	T
Simulidae spp.	HO	larvae & pupae	T
Tipulidae sp.	HO	larvae	T
Trichoptera			
Hydrobiosidae sp.	HO	larvae	T
<i>Metrichia</i> sp.	HO	larvae & pupae	T
<i>Oxyethira</i> sp.	HO	larvae & pupae	T
Leptoceridae sp.	HO	larvae	T
<i>Smicridea annulicornis</i> BLANCHARD IN GAY 1851	HO	larvae	T

Table 2. Prevalence (%) and mean intensities of infection of the examined insects with plagiorchiid trematodes or mermithid nematodes. “F-A-J” refers to the February, April, and June samples.

	Sampling date	Number of examined hosts	Plagiorchiid		Mermithids	
			Prevalence	Mean intensity (range)	Prevalence	Mean intensity (range)
Insecta						
Ephemeroptera						
Baetidae						
<i>Andesiops peruvianus</i>	F-A-J	90	-	-	6	1.0
Leptophlebiidae						
<i>Meridialaris chiloeensis</i>	Jan–Jun	556	15	1.4 (1–5)	-	-
<i>Nousia bella</i>	Jan–Jun	126	21	1.2 (1–4)	-	-
<i>Penaphlebia chilensis</i>	Jan–Jun	32	63	4.9 (1–22)	-	-
<i>Righthopus andinensis</i>	Jan–Jun	23	-	-	-	-
Plecoptera						
Gripopterygidae						
<i>Antarctoperla michaelsoni</i>	F-A-J	70	4	1.0	-	-
Coleoptera						
Elmidae						
<i>Austrelmis</i> sp.	F-A-J	90	-	-	-	-
Diptera						
Athericidae sp.	F-A-J	30	7	1.0	-	-
Chironomidae spp.	F-A-J	90	-	-	3	1.0
Empididae sp.	F-A-J	44	-	-	-	-
Simuliidae spp.	F-A-J	31	-	-	13	1.0
Trichoptera						
Hydropsychidae						
<i>Smicridea annulicornis</i>	F-A-J	90	1	1.0	-	-
Hydroptilidae						
<i>Oxyethira</i> sp.	F-A-J	70	-	-	-	-
Total		1272				

mermithid nematodes (Fig. 1A). Three species of leptophlebiid mayflies (*Meridialaris chiloeensis* DEMOULIN 1955, *Penaphlebia chilensis* EATON 1884 [Fig. 1B–D], and *Nousia bella* PESCADOR & PETERS 1985), the gripopterygid stonefly *Antarctoperla michaelsoni* (KLAPÁLEK 1904), the hydropsychid caddisfly *Smicridea annulicornis* BLANCHARD IN GAY 1851, and a watersnipe fly (Diptera, Athericidae) were recorded as second intermediate hosts for digenean metacercariae of the order Plagiorchiiida (Table 2). We assigned the metacercariae to the order Plagiorchiiida, because members of this group parasitize larval stages of aquatic insects and frequently retain the remnant of the stylet from the xiphidiocercariae (Schell 1985; Roberts & Janovy 2005).

Mermithid and plagiorchiid infection

Mermithids showed low prevalences (<15%) and the mean intensity was one in all samples (Table 2). The nematodes were always found in the abdominal cavities of their hosts, and sometimes found protruding out of the host body (Fig. 1A).

Plagiorchiid trematodes in non-leptophlebiid hosts showed low prevalences (1–7%) and mean intensities of one. In contrast, in the three species of leptophlebiids, the prevalences were higher (15–63%) as were the mean intensities (1.4–4.9) (Table 2). Metacercariae prevalences declined from summer to early winter in the three leptophlebiids (Fig. 2).

In two of these leptophlebiid species, we found that uninfected nymphs were shorter than infected ones (Fig. 3); these differences were significant only for *M. chiloeensis* and *N. bella* ($U=7567.50$; $N=556$; $p<0.0001$ and $U=505$; $N=126$; $p=0.0002$, respectively). Nymph size was related to individual developmental stage, with smaller nymphs having no or inconspicuous wing pads. Intensity of infestation was not related to shore proximity (Fig. 4).

We examined a total of 118 specimens of adult insects from February to April: 31 *M. chiloeensis*, eight *N. bella*, four *P. chilensis*, 30 *S. annulicornis*, and 45 Simuliidae. Except for the simuliids, at least some individuals of each taxon were infected with cysts, with prevalences ranging 30–90% (Table 3).

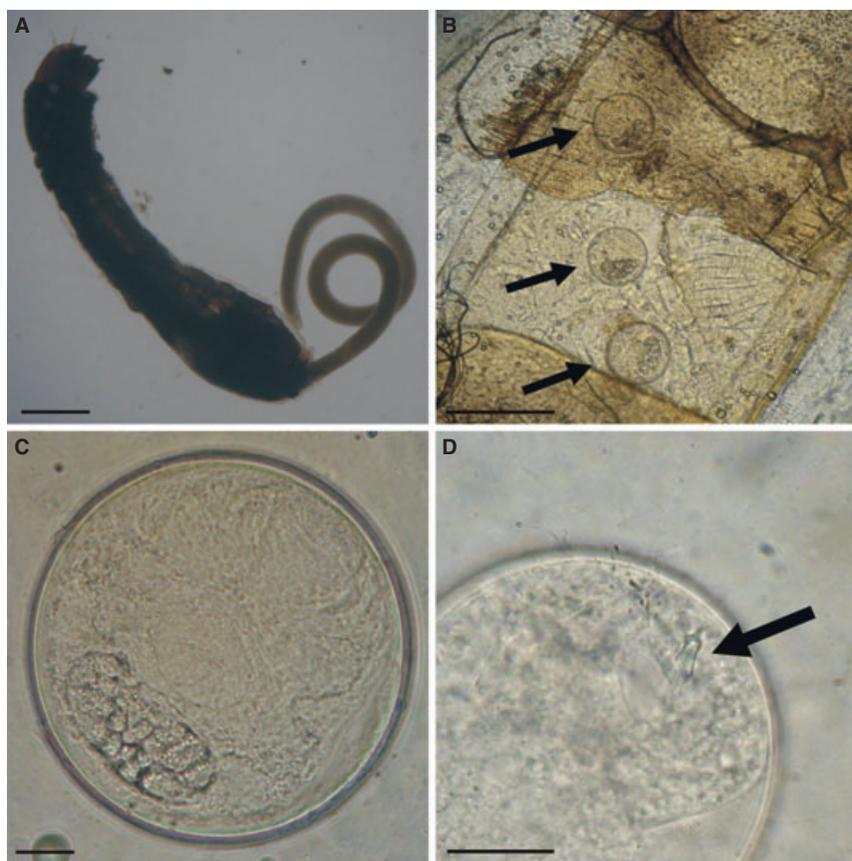


Fig. 1. **A.** A larva of a simuliid dipteran infected with a mermithid nematode (protruding from the host due to sample fixation). Scale bar=1 mm. **B.** Trematode metacercariae encysted in an individual of *Penaphebia chilensis*. Arrows indicate cysts. Scale bar=200 μ m. **C.** A plagiorchiid metacercaria. Scale bar=20 μ m. **D.** Detail of a metacercaria cyst. The arrow indicates the metacercaria stylet. Scale bar=20 μ m.

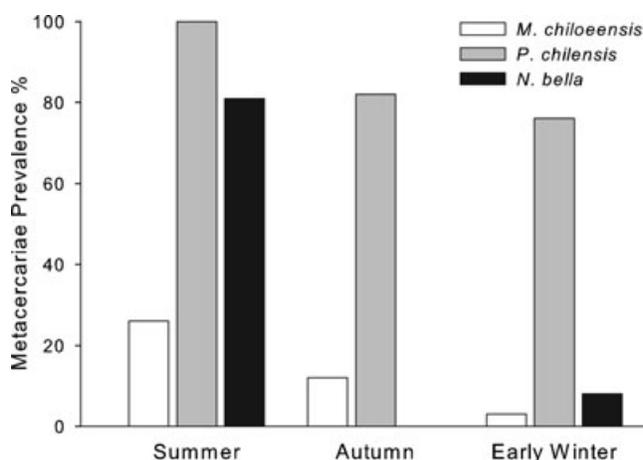


Fig. 2. Temporal variation in prevalence of infection by metacercariae in three species of leptophlebiid mayflies, *Meridialaris chiloensis*, *Nousia bella*, and *Penaphebia chilensis*.

Imagos of *P. chilensis* showed the highest mean intensity (22.3), whereas the lowest mean intensity

(1.6) was recorded for the caddisfly *S. annulicornis* (Table 3). All the imagos that were caught alive with the emergence trap (six *M. chiloensis*, two *P. chilensis*, two *N. bella*, and two *S. annulicornis*) were found to be infected with metacercariae that showed active movements inside their cysts.

Plagiorchiid metacercaria cysts were spherical in shape and translucent (Fig. 1C). Through the cyst wall in live specimens, we observed the body of the worm covered with spines, the oral and ventral sucker, the excretory bladder, and the stylet in some specimens (Fig. 1D). Cysts recovered from the three species of leptophlebiid hosts were similar in mean diameter (*M. chiloensis* 92 \pm 13 μ m [nymphs; mean \pm standard deviation] and 93 \pm 16 μ m [adults]; *N. bella* 96 \pm 17 μ m [nymphs] and 98 \pm 16 μ m [adults]; *P. chilensis* 100 \pm 14 μ m [nymphs]). In cysts recovered from leptophlebiid imagos, the thickness of the cyst wall ranged 4–6 μ m. The mean diameters of metacercariae recovered from nymphs of the stonefly *A. michaelsoni* and from adult caddisflies were 115 and

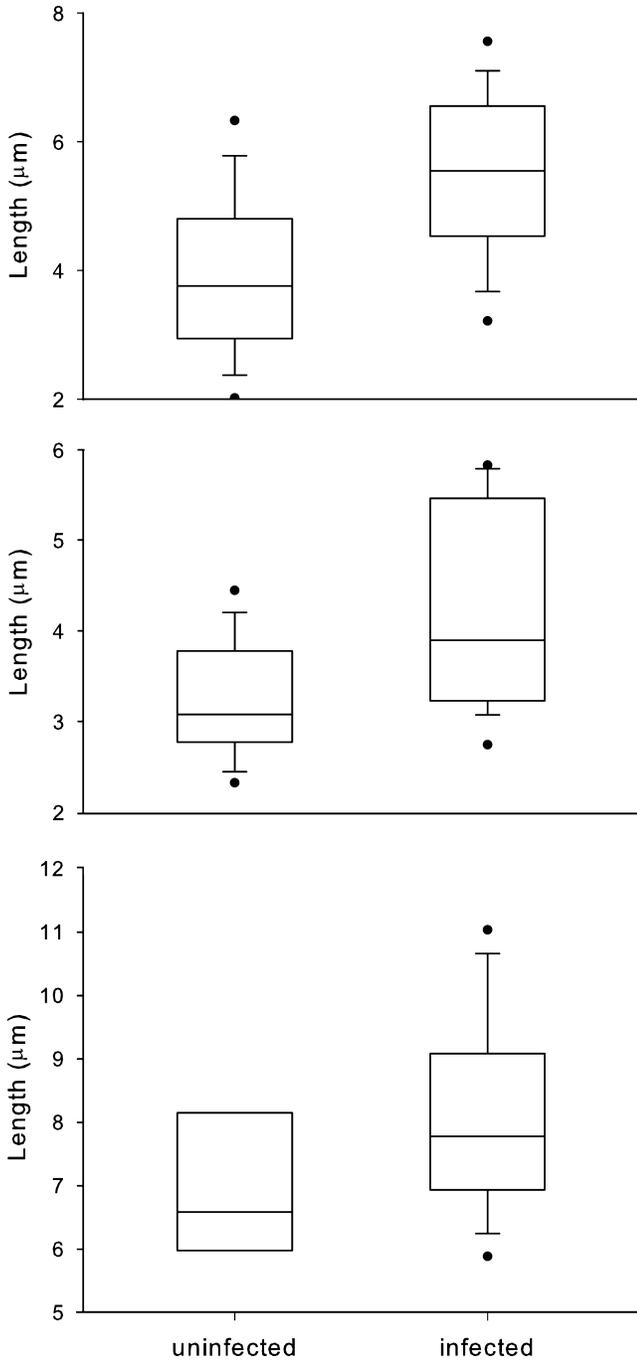


Fig. 3. Distribution of body lengths of three species of leptophlebiid mayflies infected or uninfected by plagiorchid trematodes. **A.** *Meridialaris chiloeensis*. **B.** *Nousia bella*. **C.** *Penaphlebia chilensis*. Boxes represent median and 25th and 75th percentiles, whiskers 10th and 90th percentiles, and black dots the mean of outlier values.

117 µm, respectively. The cysts recovered from watersnipe flies were similar in appearance, but were twice the diameter and thickness of all the other cysts (Fig. 5).

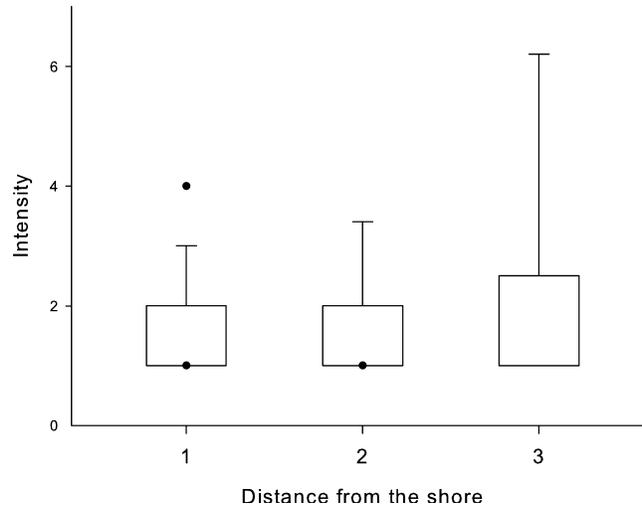


Fig. 4. Distribution of intensities of metacercarial infection in leptophlebiid mayflies found at three distances from the shore (1, closest to shore; 2, medium distance from the shore; and 3, furthest from the shore, approximately in the center of the channel).

Table 3. Prevalence (%) and mean intensities of infection of adult insects by plagiorchid metacercariae.

Species	Number of examined hosts	Prevalence	Mean intensity (range)
<i>Meridialaris chiloeensis</i>	31	90	3.9 (1–12)
<i>Penaphlebia chilensis</i>	4	75	22.3 (1–36)
<i>Nousia bella</i>	8	75	3.2 (1–5)
<i>Smicridea annulicornis</i>	30	30	1.6 (1–4)
Simuliidae spp.	45	-	-

Discussion

Insect community and parasites

The aquatic insect community of the studied section of Gutiérrez Stream consisted mostly of larval and nymphal stages of mayflies, stoneflies, beetles, non-biting midges, black flies, and caddisflies, as previously recorded for other streams and rivers in the region (Wais 1987; Miserendino 2001).

We found larvae of mermithid nematodes in chironomids, simuliids, and mayflies, and metacercariae of plagiorchid trematodes in mayflies, stoneflies, caddisflies, and watersnipe flies. Even though parasite morphospecies richness was low (two), we

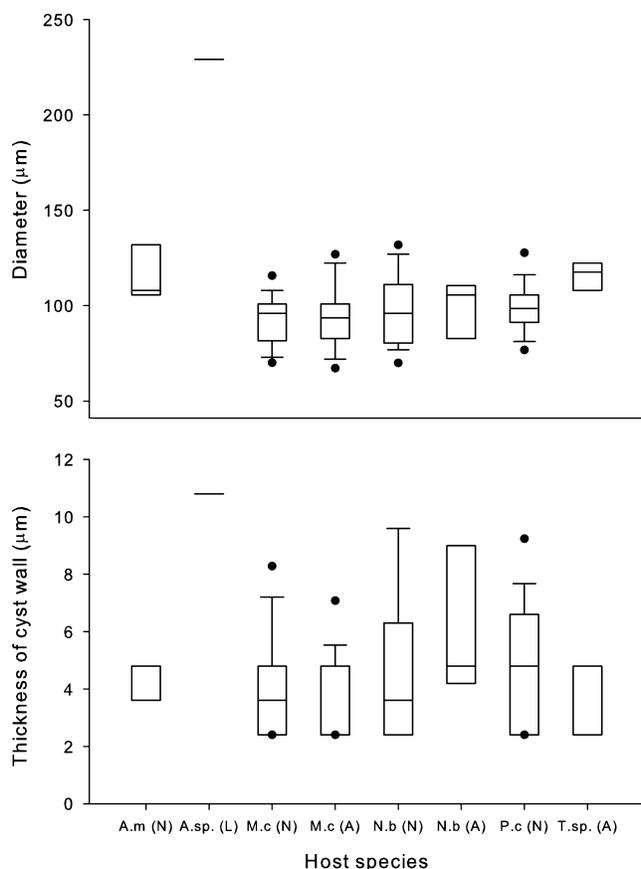


Fig. 5. Diameter and thickness of the cyst walls of meta-cercarial cysts in *Antarctoperla michaelsoni* (A.m.), Athericidae sp. (A. spp.), *Meridialaris chiloeensis* (M.c.), *Nousia bella* (N.b.), *Penaphlebia chilensis* (P.c.), and Trichoptera spp. (T. spp.). A, adults; L, larvae; N, nymphs. Boxes and whiskers plots as in Fig. 3. In A. spp., only the median value is shown, as only two cysts were found.

recorded more species acting as hosts for macroparasites than in similar studies where parasite morpho-species richness was higher (between 4 and 7) (González Lanza et al. 1986; Manzanera Manzanera & Alvarez Pellitero 1987). Mermithids were also found in non-biting mites with higher prevalences than in those studies. As all infracommunities were composed of one taxon of parasite, we could not observe interspecific interactions or associations.

Infection by plagiurchiid metacercariae

Plagiurchiid cercariae bear an anteriorly sclerotized stylet that is used to penetrate the cuticle of the second intermediate host. The basic morphology of the cysts found was not much different from other plagiurchiid metacercariae (Hong et al. 1999), and their localization in the hemocoel of the host body

has been noted in other members of this taxon (Hall 1960; Digiani 2002). The differences in the sizes of metacercariae found in the six host species suggest that metacercariae parasitizing watersnipe flies could belong to another species of plagiurchiid, as the diameter and thickness of the cyst walls were twice those of metacercariae found in leptophlebiid mayflies. Moreover, two types of virgulate, stylet-bearing cercariae were found in prosobranch snails (*Heleobia hatcheri* PILSBRY 1911) living in the same habitat (V. Flores, unpubl. data). To clarify this question, it is necessary to make laboratory infections in experimental definitive hosts with metacercariae from all intermediate hosts found in this study.

The morphological features of the metacercariae (spinous tegument, two suckers, paired caeca, intestinal bifurcation in forebody, two testes, among others), the virgulate-type cercariae found in snails at the study stream, and the intermediate hosts involved (prosobranch snails and mayflies) suggest that these digeneans belong to the family Lecithodendriidae (Superfamily Microphaloidea) (Schell 1985; Bray et al. 2008), whose adults usually parasitize bats.

Larval stages of trematodes are known to have low specificity for the second intermediate host, which relates directly with swimming and adherence abilities of cercariae (Snyder & Janovy 1996). In this study, we found meta-cercarial cysts in 6 of 20 taxa of stream insects, which were either hemimetabolous (leptophlebiid mayflies and stonefly *Antarctoperla michaelsoni*) or holometabolous (caddisflies and watersnipe flies). This variety in host life cycles is similar to that in several other studies in plagiurchiid digeneans, where aquatic stages of dragonflies, mayflies, stoneflies, water bugs, beetles, dipterans, and caddisflies have been recorded as hosts in the wild or as experimental hosts in the laboratory (Hall 1960; Snyder & Janovy 1996; Bolek & Janovy 2007). Despite such general plasticity, the highest prevalences and mean intensities of infection occurred in the three species of leptophlebiid mayflies. Nymphs of this family have dorso-ventrally flattened bodies and are highly adapted for crawling on rock surfaces and grazing on periphyton. In this study, these three species had similar population dynamics with increasing densities from late summer to winter. We suggest that the low prevalences and mean intensities in non-leptophlebiid hosts are a consequence of ecological features related to the multiple potential second intermediate host species, the snails acting as first intermediate hosts, and the microhabitat they share—that is, crawling xiphidion-cercariae are likely to be more successful at infecting crawling, highly mobile aquatic insects than

burrowing or swimming insects. In addition, the pupal stages of holometabolous insects could be an obstacle, first for the entrance of cercariae, and then for subsequent development within the insect.

Temporal variation in the prevalence and intensities of parasitic worm infection has been widely studied in fish with seasonal temperature cycles producing seasonal cycles of infection (Williams & Jones 1994). We observed prevalences and intensities declining from summer to early winter in the three analyzed leptophlebiid species during the 6 months sampled, with these patterns being clearest in *Meridialaris chiloeensis* and *Penaphlebia chilensis*. Such a phenomenon could correspond to the emergence of specimens as infected imagos and the hatching of new cohorts of insects. Members of new cohorts might not be large enough to act as hosts until the subsequent summer, and they also might not have sufficient exposure time to acquire infections. Schloesser (2005) found similar dynamics in the abundance of metacercariae of *Crepidostomum* spp. (Plagiorchiida, Allocreadiidae) parasitizing nymphs of *Hexagenia* spp. (Ephemeroptera, Ephemeridae) in North American rivers, reporting infection during summer and linking low abundances with small size and short exposure time. In studies of macroparasite communities carried out throughout the whole year in Spanish rivers, a bimodal seasonality of infection with nematodes and trematodes was recorded, associated with environmental temperatures and the host's life cycles (González Lanza et al. 1986; Manzanera Manzanera & Alvarez Pellitero 1987).

The host's body length, as an indicator of age, is one of the most important factors in driving variation of parasitic infrapopulations (Esch & Fernández 1993). In two species of leptophlebiid mayflies, we found significant differences between body sizes of infected and uninfected nymphs. The observed pattern seems to be related to the longer exposure of older nymphs to infective cercariae, although we cannot exclude the possibility that parasites are actively selecting larger hosts.

Parasite life cycles in aquatic environments can be divided into two types depending on the habitat of the definitive host. Allogenic cycles involve terrestrial definitive hosts, whereas autogenic cycles are those which have aquatic definitive hosts (Esch & Fernández 1993). Cycles involving aquatic insects as second intermediate hosts can be of either of these types, as they can be consumed by fish, amphibians, birds, and mammals (Gullan & Cranston 1994; Allan 1995). We found live plagiorchiids in fresh imagos with higher prevalences and mean intensities than in nymphs, which suggest the existence of a terrestrial definitive

host for these parasites, probably a bat. If correct, these would then be classified as allogenic life cycles.

Although it is widely known that parasites can strongly affect ecosystems, their importance is often underestimated. Kuris et al. (2008) quantified the biomass of free living and parasitic species in three estuaries of United States and found that parasite biomass exceeded that of top predators, and that the production of free-swimming trematode stages was higher than bird biomass. An approximate quantification of metacercariae density per stream area can be performed for the section of the stream that we studied, resulting in estimated densities of 460 metacercariae m^{-2} in late summer, and 80 metacercariae m^{-2} in early winter. If we extrapolate these values to an area of 100 lineal meters of stream (with 16 m of average width), 120,000–730,000 metacercariae might be found in this reach. It is noteworthy that this estimate does not consider environmental heterogeneity or the clustered distribution of organisms. Even though biomass was not calculated, such rough estimates show the numerical relevance in terms of trophic interactions that a single species of parasite, or group of species of the same family, can have at the ecosystem level.

Acknowledgments. We thank Dr. Verónica Flores for her help in identifying the trematodes, and Drs. Liliana Semenas and Carlos Rauque and two anonymous reviewers for their suggestions on an earlier version of the manuscript. This work was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) PIP 112-200801-01702 and Universidad Nacional del Comahue UNCo B-137.

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