ARTICULO

Infection dynamics of *Posthodiplostomum* sp. (Digenea: Diplostomidae) in first and second intermediate hosts from an Andean Patagonian lake (Argentina)

Dinámica de la infección de *Posthodiplostomum* sp. (Digenea: Diplostomidae) en el primer y segundo hospedador intermediario de un lago Andino Patagónico (Argentina)

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ABSTRACT: In Argentinean Patagonia, a species of the genus *Posthodiplostomum* has been reported infecting populations of the snail *Anisancylus obliquus* and the galaxiid fish *Galaxias maculatus* (small puyen), meanwhile adults would develop in piscivorous birds. The aim of the present work was to describe the seasonal dynamics of this parasite in the intermediate hosts inhabiting a small, shallow Patagonian Andean lake. Samples of snails and fish from Patagua Lake (40° 46' S - 71° 36' W) were collected monthly from October 2010 to March 2011. The larval infection of *Posthodiplostomum* sp. increases in spring. Snails were infected from November to January, with the highest prevalence in December (8.2%), decreasing in January (3.1%). In fish, prevalence ranged between 70% (November) and 100% (December to March). The highest infection values were recorded in larger fish, while the small fish with sizes less than 40 mm exhibited low infection levels. So, we can infer that the life cycle of *Posthodiplostomum* sp. in Patagonia shows a seasonal pattern, with larval development during spring, when cercariae emerge from larger snails, resulting in a higher prevalence of fish in the littoral.

Keywords: Digenea, *Galaxias maculatus*, *Anisancylus obliquus*, infection dynamics, Argentinean Patagonia.

RESUMEN: En la Patagonia argentina se ha registrado una especie del género *Posthodiplostomum* que infecta a poblaciones del caracol *Anisancylus obliquus* y del pez de agua dulce, *Galaxias maculatus* (puyen chico), mientras que los adultos se desarrollarían en aves ictiófagas. El objetivo del presente trabajo fue describir la dinámica de infección de este parásito durante la primavera y el verano en sus hospedadores intermediarios en un lago somero de la región Andino Patagónica. Se recolectaron muestras mensuales de caracoles y de puyenes en la laguna Patagua (40° 46' S - 71° 36' O) desde octubre de 2010 a marzo de 2011 (primavera-verano). La infección de *Posthodiplostomum* sp. por estadios larvales aumentó en la primavera. Los caracoles estuvieron infectados desde noviembre a enero, con los mayores valores de prevalencia en diciembre (8,2%), decreciendo en enero (3,1%). En los peces, la prevalencia varió entre el 70% (noviembre) y 100% (diciembre a marzo). Los mayores valores de infección se registraron en los peces grandes mientras que los peces pequeños, inferiores a 40 mm, mostraron niveles muy bajos de infección. Por lo tanto, se puede inferir que el ciclo de vida de *Posthodiplostomum* sp. en la Patagonia muestra un patrón estacional, con desarrollo de las larvas durante la primavera, cuando las cercarias emergen de los caracoles más grandes, alcanzando una mayor prevalencia en los peces del litoral.

Palabras clave: Digenea, *Galaxias maculatus*, *Anisancylus obliquus*, dinámica de infección, Patagonia argentina.

INTRODUCTION

The species of *Posthodiplostomum* (Digenea: Diplostomidae) are worldwide distributed, and their life cycle includes pulmonate snails as first intermediate hosts, freshwater fish as second intermediate host, and ichthyophagous birds like herons, gulls, cormorants or grebes as definitive hosts (Niewiadomska, 2002). The cercariae emerge from the snails and infect the fish, developing into metacerariae, which remains en-

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Figure 1. Hosts and larval stages of *Posthodiplostomum* sp. from Patagua Lake. A) *Anisancylus obliquus*, B) *Galaxias maculatus*, C) Sporocyst, D) Cercaria, E) Metacercaria

cysted in the abdominal cavity until the fish is preyed by an ichthyophagous bird. In Patagonia, a species of this genus has been reported (Ritossa *et al*., 2013) infecting populations of the snail *Anisancylus obliquus* and the galaxiid fish *Galaxias maculatus* (Fig. 1). Infected snails were previously found in Patagua Lake, showing a prevalence value of 3.5 % (Ritossa *et al.*, 2013), while in the galaxiid fish, metacercariae have been widely reported, with prevalence around 100% and high mean intensity values (Viozzi *et al*., 2009). In systems formed by digenean-snail-fish from temperate environments, water temperature affects larval development within these ectothermic hosts (Esch and Fernández, 1993). So, the annual changes in parasite populations are correlated with seasonal changes in temperature and photoperiod (Esch and Fernández, 1993). In Patagonia, no infection dynamics studies have been performed considering natural populations of *Posthodiplostomum* species in the first and second intermediate hosts.

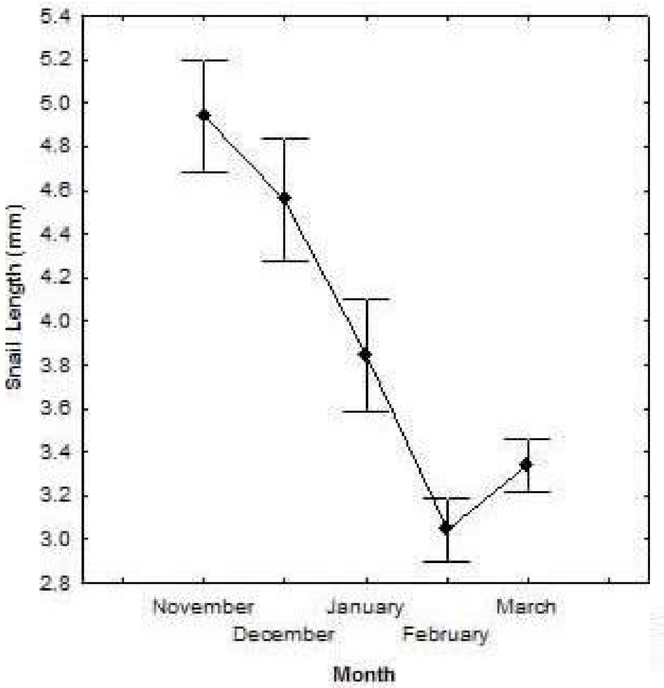

Figure 2. Length of the snail *Anisancylus obliquus* along sampling months.

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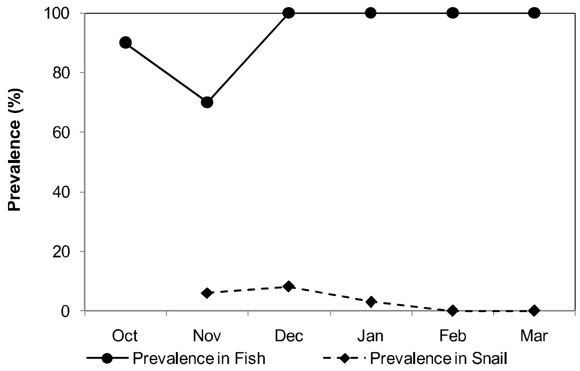

Figure 3. Prevalence of *Posthodiplostomum* sp. in *Anisancylus obliquus* and in *Galaxias maculatus* along sampling months.

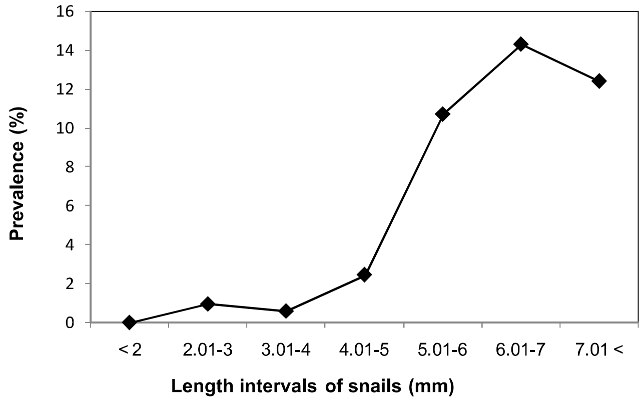

Figure 4. Variation of *Posthodiplostomum* sp. prevalence in different length classes of *Anisancylus obliquus*.

Anisancylus obliquus (Broderip and Sowerby) (Pulmonata) is a pateliform small snail, which lives in freshwater environments and measures between 2 and 6 mm long (Fernández, 1981; Rumi *et al.*, 2008). Specimens live attached to rocks or to the underside of aquatic vegetation, and feed on algae (Fernández, 1981). *Galaxias maculatus* (Jenyns) (Osmeriformes, Galaxiidae), called “small puyen”, is a small gregarious endemic fish, which inhabits lakes and rivers in Patagonia, and measures up to 80 mm long in some environments. This species has a wide distribution in the Southern Hemisphere (McDowall, 2006). In Northwestern Argentinean Patagonia, the populations do not migrate to the sea for spawning. From early spring to early summer the spawning occurs in the littoral and embryos and larvae coexist in the limnetic zone for about 6 months, and juveniles and adults are in the coast during summer and early autumn (Barriga *et al.*, 2002). This species is the main prey for native and introduced fish (Macchi *et al.*, 2007), and also for piscivorous birds (Rasmussen *et al.*, 1993; Alarcón *et al.*, 2012).

The aim of this study was to describe, during spring and summer, the infection dynamics of *Posthodiplostomum* sp. in a natural populations of the pulmonate snail *A. obliquus* and the galaxiid fish, *G. maculatus,* in a small Andean lake.

MATERIAL AND METHODS

This study was conducted in Patagua Lake (40° 46’ S-71° 36’ W), which is located in the Arrayanes National Park (Argentina). This lake has a surface of $1km^2$, with a maximum depth of 30 m, is surrounded by subantarctic forest dominated by *Nothofagus dombeyi*, and the shoreline of the lake is colonized by the reed, *Schoenoplectus californicus* (=*Scirpus californicus*). Water temperature was taken during the sampling period from October 2010 to March 2011. Snail samples were monthly collected by hand from the stem of *S. californicus* from November 2010 to March 2011. Fish samples were monthly collected from October 2010 to March 2011, using nets, from the littoral. Fish and snails were transported alive to the laboratory. Major

Table 1. Sample size, range, and mean length of Anisancylus obliquus and Galaxias maculatus along sampling months.

Months	Snail Length Range (mean±DS) (mm)	Sample Size	Fish Length Range (mean±DS) (mm)	Sample Size
October	-	-	37.1-74.1 (52.9 ± 8.4)	30
November	2.6-7.4 (4.9 ± 1.2)	82	32.6-76.3 (45.9 ± 11.4)	30
December	2.2-8.1 (4.5 ± 1.3)	85	36.7-71.5 (47.4 ± 7.7)	30
January	1.6-7.7 (3.8 ± 1.3)	95	37.7-64.2 (45.6 ± 5.1)	30
February	1.7-5.9 (3.1 ± 0.7)	100	43.3-58.7 (48.2 ± 4.2)	30
March	1.7-4.9 (3.3 ± 0.6)	100	42.1-60.2 (49.5 ± 4.3)	30

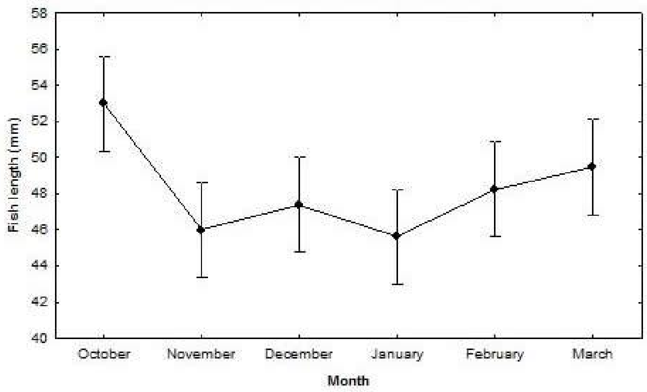

Figure 5. Length of the fish *Galaxias maculatus* along sampling months.

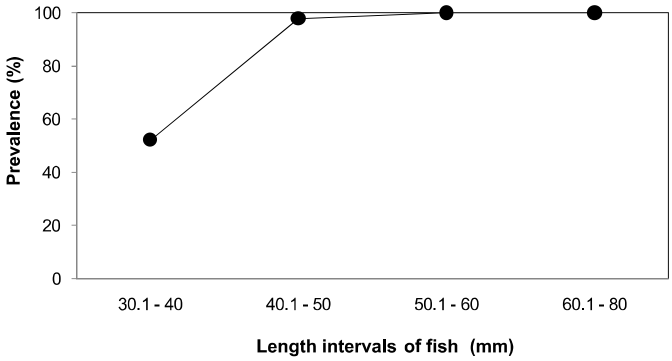

Figure 6. Variation of *Posthodiplostomum* sp. prevalence in different length classes of *Galaxias maculatus*.

diameter of snail shells and total length of fish were measured with a digital caliper (total length in mm, accuracy = 0.01 mm). Fish were also weighed with a digital balance (weight in gr, accuracy = 0.01 gr). Snails were isolated in individual containers with 20 ml of de-chlorinated tap water, and kept at room temperature to record the emergence of cercariae (patent infections). Subsequently, all the snails were dissected under a stereoscopic microscope to record infection site and the presence of sporocysts in those specimens which did not released cercariae (prepatent infections). Fish were examined under a stereoscopic microscope to record sex (female, male, undetermined), the site of infection, and the number of metacercariae. Prevalence (snail and fish), abundance and intensity of infection (fish) were calculated following Bush *et al.* (1997).

Statistical analysis

Snails

To characterize the length of the snails in the population along the sampling period, an ANOVA Test was performed. To evaluate the effects of potential determinants on overall infection levels of *Posthodiplostomum* sp. in snails, a Generalized Linear Model (GLM) was performed. The variation of prevalence in snails was analyzed using a binary measure of ''infection'' (no, yes) as the dependent variable, a binomial error term, and a logit link function; predictors were months, snail length, and their second order interactions. To analyze the monthly variation of prevalence in snails, a *Chi*^{2} Test was used.

Fish

To characterize the variation of the fish length in the population during the sampling period, an ANOVA Test was performed. To analyze the monthly variation of prevalence in fish, a *Chi*^{2} Test was used. As the distribution of abundances was aggregated (variance: mean ratio was 226.2), data were normalized using square root. To measure the effects of biotic and abiotic characteristics on parasite load, a GLM was performed assuming a normal structure of error and a log link function, with metacercariae abundance as dependent variable and months, fish length and weight, and their second order interactions as predictors. An ANOVA and Tukey HSD were performed as a *post-hoc* test. Associations between square root abundance and length and weight were examined using Pearson correlation coefficients. All tests were conducted in Statistica version 7, using a significance level of 0.05.

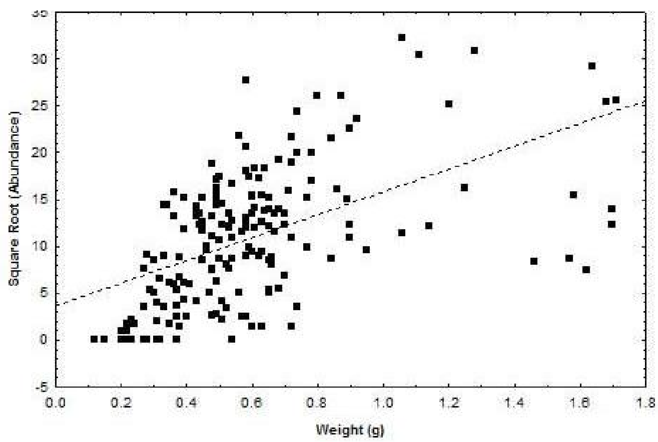

Figure 7. Abundance of *Posthodiplostomum* sp. metacercariae in *Galaxias maculatus* along sampling months.

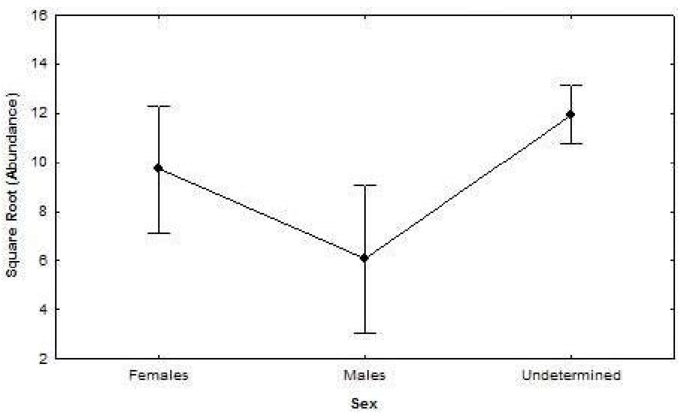

Figure 8. Abundance of *Posthodiplostomum* sp. metacercariae in *Galaxias maculatus* among sexes.

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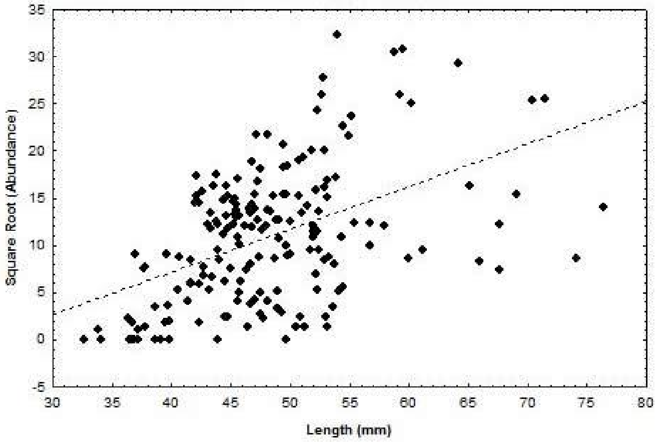

Figure 9. Abundance of *Posthodiplostomum* sp. metacercariae in *Galaxias maculatus* along host length range.

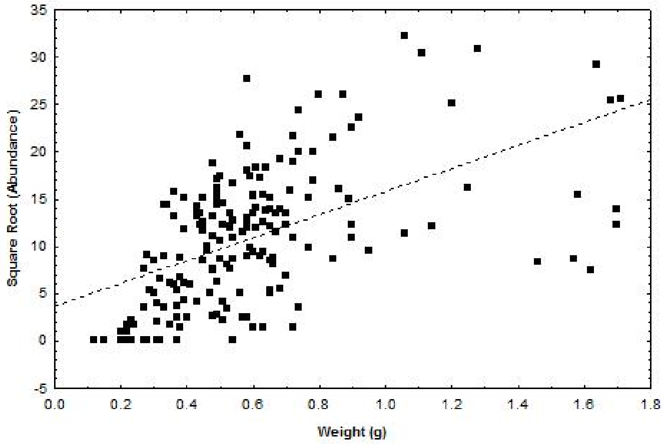

Figure 10. Abundance of *Posthodiplostomum* sp. metacercariae in *Galaxias maculatus* along host weight range.

RESULTS

The water temperature variation in the littoral of the lake was low during the sampling period; the lowest temperature was recorded in December (15° C) and the highest in February (19.5° C).

Snails

A total of 462 specimens of *A. obliquus* were analyzed, length ranged between 1.5 mm and 8 mm (mean: 3.9 ± 0.8) (Table 1), being most specimens (N= 284) within the size range of 3 to 4 mm. The length of snails varied among sampling months, showing significant differences (F=53.55, d.f.=4, N=454, P<0.0001),with a decrease in size along the sampling period, showing the spring samples (November and December) larger snails than the summer ones (January-March) (Fig. 2). *Posthodiplostomum* sp. was the only digenean species recorded in *A. obliquus* from Patagua Lake. Snails were infected from November to January (Fig. 3), with the highest prevalence in December (8.2%), decreasing in January (3.1%). All the infected snails from November (5/5) and December (7/7) had patent infections, while in January the 66% (2/3) released cercariae. No infected snails were found in February neither in March. In the analysis of prevalence of *A. obliquus*, both predictors (months and length) were significant, but not the second order interactions (Table 2). The Chi^2 Test showed significant differences in prevalence among the different sampling months (Chi^2=1481.4, d.f.=4, P<0.05; Fig. 3). The snails smaller than 2 mm were not infected, the lowest values of prevalence (0 to 2.5%) were recorded in snails smaller than 5 mm, and the highest values (10.2 to 14.2%) in snails larger than 5 mm (Fig. 4).

Table 2. Generalized linear model (GLM) for the prediction of *Anisancylus obliquus* prevalence related to months, snail length, and interaction between months and snail length (Significant differences are given in bold font).

Predictor	d.f.	Chi	Prob.
Intercept	1		
Month	4	**14.88**	**<0.01**
Length (mm)	1	**6.85**	**<0.01**
Month*Length	4	2.31	0.678

Fish

A total of 180 *G. maculatus* were analyzed, with a total length ranging between 33 and 76 mm (mean: 48 ± 3) (Table 1). Most studied fish (N=96) showed a size range of 40 to 50 mm. The fish length was significantly different among months, being the biggest fish those of October (F=4.086, d.f.=4, N=174, *P*=0.0001), showing an increase in the proportion of smaller fish from November to January (Table 1, Fig. 5). Fish smaller than 40 mm were not collected in February neither in March, when an increase of intermediate fish sizes were observed (Table 1, Fig. 4). The prevalence of *Posthodiplostomum* sp. metacercariae showed their lowest values (70% in November; 90% in October), and in the remaining months all fish were infected (Fig. 3), the Chi^2 Test showed significant differences in prevalence between months (Chi^2=750, d.f.=5, N=180, *P*<0.05). When the infection pattern was analyzed in relation to the length of *G. maculatus*, the lowest prevalence (52%) (Fig. 6) was recorded in fish between 31 and 40 mm, and the highest prevalence (100%) was observed in fish longer than 40 mm (Fig. 6).

The intensity of infection varied between 1 and 1,041 metacercariae, this value was recorded in a fish from January. Metacercariae abundance was significantly related with the 4 predictors (months, sex, total length and weight) (Table 3). The second order interactions were significant. Two groups of fish were observed, one represented by specimens captures in spring, including those from October, November and December and the other one represented by specimens from summer, including those from January, February and March (F=21.131, p=0.00001, d.f.=5, N= 174) (Table

Table 3. Generalized linear model (GLM) for the abundance of metacercaria infection in *Galaxias maculatus* related to months, and length, weight, and sex of fish, and the interaction between months and fish length (Significant differences are given in bold font).

Predictor	d.f.	Chi	Prob.
Intercept	1		
Month	5	**86.1861**	**<0.01**
Sex	2	**16.9389**	**<0.01**
Length (mm)	1	**102.9203**	**<0.01**
Weight (g)	1	**6.2735**	**0.012**
Month*Length	5	5.3655	0.373

4). The abundance showed higher values in January, February and March (summer) (Fig. 7). Regarding sex, the undetermined specimens had the highest values, males the lowest, and females showed intermediate values (F=177, p=0.00121, d.f.=2, N=177; Fig. 8; Table 5). Metacercariae abundance increased significantly with total length (Pearson= 0.482; p<0.01, N=180), and weight (Pearson= 0.539; p<0.01, N=180) (Figs.9 and 10).

DISCUSSION

The diplostomids of temperate environments generally show a seasonal infection pattern in their intermediate hosts. For the second intermediate host, the infection dynamics is strongly influenced by temperature, showing high values of prevalence and abundance in spring and autumn (Flores and Semenas, 2002; Ondraĉková *et al.*, 2004). Besides, the metacercariae abundance increases with age and length of the fish, but often decreases in older fish due probably to mortality of specimens with high parasitic loads, which die during unfavorable periods as winter (Pennycuick, 1971 a, b).

The monthly variation observed in *A. obliquus* size (Fig. 2), suggests the following pattern of development and reproduction: the larger snails collected in November correspond to those born in summer (February 2010) that hibernated during the winter 2010. This snail cohort spawns during spring and dies during midsummer (January 2011), as it is indicated by the absence of larger specimens in February and March. The second cohort, correspond to small snails born in December 2010 and January 2011, which grow almost up 4.9 mm and hibernate during the following winter. The snail population dynamics of *A. obliquus* is similar to other freshwater limpets of temperate cold climates, like *Ferrisia* spp., whose eggs hatch a week after spawning, and grow up to 3 mm in a period of four to five weeks (Dillon and Herman, 2009). Martín and Díaz (2012) in a population dynamics study of the snail *Uncancylus concentricus* from Río de la Plata found that the longevity of the snails does not exceed one year, and the recruitment of juvenile snails occurs in spring and summer. In our study the snails also live one year, but the recruitment of juveniles seems to occur in late summer, probably related with the lower temperatures.

The patent infection of *Posthodiplostomum* sp. were observed in snails of the first cohort, while no infection was recorded in snails of the second cohort during February and March, because they were not infected yet. The high values of prevalence in December (8.2%) would be the result of exposure of hibernating snails to miracidia during early spring. *Posthodiplostomum cuticula* (v. Nordmann, 1832) releases cercariae after 52 days of miracidium penetration (Dönges, 1963), and has an optimum development at 10ºC, requiring between 4 to 8 weeks to release the maximum number of cercariae (Ondraĉková *et al.*, 2004). A similar developmental pattern can be assumed for miracidia of *Posthodiplostomum* sp. infecting *A. obliquus* in Patagua Lake. The infection dynamics of larval digeneans in freshwater pulmonate snails shows two different patterns: a) infected snails hibernate during winter, and release cercariae during the following spring; b) small uninfected snails hibernate and were infected with miracidia that hatch in spring from eggs that survived the winter in a dormant way (Goater *et al.*, 1989). According to the observed infection pattern of *Posthodiplostomum* sp. in *A. obliquus* and their population dynamics, this snail digenean system would belong to the second pattern. The second cohort showed no infections in February and March, they grow, and then hibernate during winter. Therefore, it can be assumed that the infection of overwintered *A. obliquus* occurs from early spring (September) when lakes reach a water temperature of 10 ºC. The source of these infec-

Table 4. Results of a *post hoc* test of Tukey HSD for abundance among sampling months (Significant differences are given in bold font).

Month	October	November	December	January	February	March
October						
November	0.505654					
December	0.902207	0.059781				
January	**0.000057**	**0.00002**	**0.003576**			
February	**0.00002**	**0.00002**	**0.000028**	0.755286		
March	**0.000021**	**0.00002**	**0.000127**	0.962949	0.995098	

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Table 5. Results of a *post hoc* test of Tukey HSD for abundance among sexes (Significant differences are given in bold font).

Sex	Female	Male	Undetermined
Female			
Males	0.160318		
Undetermined	0.274762	**0.000924**	

tions are the miracidia that hatch from eggs that also overwinter in the environment, like occurs for eggs of the digenean *Halipegus occidualis* Stafford, 1905, which can be held at 4° C for 28 months, showing a similar hatchability as the newly laid (Goater *et al.*, 1989). After 4 to 8 weeks, by November-December, snails show patent infections, shedding the cercariae. Regarding the definitive hosts, the adult of other species such as *Posthodiplostomum nanum* Dubois, 1937 have been recorded in herons (Doma and Ostrowski, 1994). In the National Parks of Northern Patagonia the piscivorous birds better represented are *Phalacrocorax olivaceus*, *Podiceps major,* and *Larus dominicanus* (Frixione *et al.*, 2012; Pescador *et al.*, 2012) but there is no information about their ecology, movement and behavior during the year. The only data about parasites of these birds are for *L. dominicanus*, although no specimens of *Posthodiplostomum* were recorded (Kreiter and Semenas, 1997).

The size distribution of *G. maculatus* specimens, suggests the existence of a recruitment of juveniles in November (Fig. 5). The adult fish spawns in spring and the bigger specimens collected in late summer represent the post-spawning specimens which have no gonads. The development periods observed in *G. maculatus* in this study are consistent with those reported for this fish species in other lakes of the region (Barriga *et al.*, 2002).

Metacercariae of *Posthodiplostomum* sp. showed a prevalence value ranging between 70% (spring) to 100% (summer). The highest prevalence was recorded in largest fish. Small fish with sizes less than 40 mm exhibited low infection levels. This increment is explained as the result of the recruitment of metacercariae during December-January. The same pattern has been observed for other *Posthodiplostomum* species, e.g. *Posthodiplostomum nanum* Dubois, 1937 in *Cnesterondon decemmaculatus* (Jenyns) and *P. cuticola* in many cyprinid, anablepid and poecilid fishes (Doma and Ostrowski de Núñez, 1994; Zrnčic *et al.*, 2009). The abundance of *Posthodiplostomum* sp. in fish varied significantly between months, increasing in February. A slight decrease of abundance in March was observed, probably due to the lack of metacercariae recruitment in the summer, since no patent or prepatent infections were observed in the snails during these months. The lowest values of metacercaria infection were recorded in November, when the smallest fish were captured. The decrease of metacercariae infection in March could be explained by the death of larger fish, heavily infected. A similar pattern was recorded for different diplostomids, e.g. *Diplostomum gasterostei* Williams 1966 in *Gasterosteus aculeatus* Linnaeus, which begins to recruit metacercariae in spring through fall, showing an increase in summer and a decrease in winter, associated to mortality of those fish which could not survive the low temperatures (Pennycuick, 1971a).

In summary, we can infer that the life cycle of *Posthodiplostomum* sp. in Northwestern Patagonia shows a seasonal pattern, during spring the development of the larval stages of the parasite occurs, resulting in a higher prevalence in both intermediate hosts. The eggs hatch in the environment and miracidia infect the first intermediate host, the pulmonate snail *A. obliquus*, which recently emerged from hibernation. Snails belonging to the first cohort, release cercariae during the spring and die in late summer. The second snail cohort, which is not infected in late summer, will overwinter. *Galaxias maculatus* is the second intermediate host, inhabiting the littoral zone during late spring when they spawn and be infected by released cercariae. The cercariae penetrate and reach the abdominal cavity, developing fastly into metacercariae. Fish accumulate metacercariae increasing the abundance of infrapopulations until February.

This work is the first study in South America describing the infection dynamics of a *Posthodiplostomum* species in all their intermediate hosts.

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