Effects of droughts on the larval digenean assemblage that parasitizes the snail *Biomphalaria peregrina* (Planorbidae): a 4-year study in a temporary pond from Argentina

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Abstract

Temporary ponds are ecologically valuable habitats and useful sites for studies of diversity, ecology, evolution, and climate change. Organisms inhabiting these environments have developed strategies to ensure their survival. However, little is known about the temporal dynamics and strategies of parasites in these habitats. A 4-year study was carried out in a temporary pond to analyze the larval digenean assemblage in *Biomphalaria peregrina*, a potential vector of *Schistosoma mansoni*, a zoonosis of global importance. This environment had intermittent and irregular hydroperiods, and the overall prevalence showed differences throughout the years. After drought seasons, eight out of a total of nine species of digeneans were observed, and almost half of the snails were parasitized. In addition, six of the nine species of digeneans showed some type of abbreviation of their life cycles. These results suggest that digeneans have certain degree of plasticity in their life cycles in response to environmental changes in this pond, and the abbreviation of the digenean life cycle could be regarded as a parasite strategy to resist prolonged periods of desiccation.

Keywords Trematoda · Drought resistance · Zoonotic vector · Abbreviated life cycles

Introduction

Human-induced climate change is recognized as a major threat to the survival of species and the integrity of ecosystems. Species diversity has strongly decreased, with a 58% decline in populations of vertebrates between 1970 and 2012, varying from 36 to 38% in terrestrial and marine ecosystems to 81% in freshwater habitats (WWF 2016). Parasites represent a considerable proportion of the total biodiversity with 15 phyla (Poulin 2014) and are probably the most threatened and under-protected organisms (Carlson et al. 2020).

They face a double threat; they are directly vulnerable to extinction and indirectly vulnerable through coextinction with hosts, especially in changing environments (Carlson et al. 2020). Temporary ponds are excellent *natural laboratories* to study adaptation processes and factors that regulate community composition, and can be considered as early indicators of climate change (Schwartz and Jenkins 2000). The habitat loss or degradation in these water bodies are the main causes of decline of species diversity, and the hydroperiod would not only influence the natural selection of organisms' adaptation to droughts but also determine the community structure (Schriever and Lytle 2016). Parasites and free-living organisms inhabiting these environments have developed strategies to ensure their survival such as life-cycle synchronization with flooding and desiccation periods, drought-resistant dormant stages, or migration to new water bodies (Williams 1997).

Typical digenean complex life cycles with three hosts include free-living infective stages (miracidia and cercariae) that are exposed to environmental fluctuations, which can affect their development and mobility, and the contact with the next host (Pietrock and Marcogliese 2003). In some species, however, evolution has taken a drastic approach, resulting in the typical three-host life cycle being truncated to two hosts or even

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to one host (Poulin and Cribb 2002). For instance, by adopting progenetic development (encystment as a metacercaria in the second intermediate host and developing precociously into an adult) (e.g., *Coitocaecum parvum*: Holton 1984), using the mollusk as the first and second intermediate host (e.g., *Microphallus simillimus*: Martorelli 1991) or developing the entire life cycle in a mollusk host (e.g., *Genarchella genarchella*: Martorelli 1989). These abbreviations of life cycles could be conditional life-history strategies in response to modifications of the trophic relationships between their hosts or of certain environmental conditions (Lagrue and Poulin 2009).

Planorbidae gastropods are one of the most abundant groups of invertebrates inhabiting temporary environments. Their pulmonary respiration along with a considerable genetic and phenotypic plasticity allows these mollusks to resist environmental fluctuations in their habitats (Gérard 2001). Particularly, *Biomphalaria* snails act as first and/or second intermediate host for several digenean species, some of them of health interest, like *Schistosoma mansoni*. Nonetheless, little is known about the effect of drought stress in its digenean assemblages, except for some studies limited to *S. mansoni* (for a review see Rubaba et al. 2016). To analyze the temporal dynamics of the larval digenean assemblage that parasitizes *Biomphalaria peregrina* in a temporary freshwater body, and to evaluate the response of these parasites to the environmental fluctuations caused by droughts, a 4-year study was conducted in a temporary pond located in Argentina.

Materials and methods

The temporary pond (37° 40′ S–57° 20′ W) is located in a large wetland area belonging to the Mar Chiquita Coastal Lagoon Basin (Argentina), a biosphere reserve under the UNESCO Man and Biosphere Program since 1996. The pond is located 2100 m from the lagoon and 500 m from the coastline. It has intermittent and irregular hydroperiods and is isolated from other water bodies (streams, ponds, lagoons, or the sea).

Specimens of *B. peregrina* were collected in one sampling trip per season, from summer 2013 to spring 2016. During the hydroperiods, one sampling trip per season was made, and 15 replicates were taken. Nevertheless, every time the pond dried up, the trips were repeated every month until the beginning of a new hydroperiod. Snails were collected with the aid of sieves (0.1 mm × 0.1 mm) and placed into 1.5 L plastic containers for transportation. The seasonal relative abundance of *B. peregrina* was estimated according to a standardized search effort (number of snails caught per hour) due to the turbidity of the pond, which made it impossible to see the substratum or collect all the snails in a given area. Water temperature and depth were measured on every sampling trip. In the laboratory, the shell diameter of each *B. peregrina* was measured to the nearest 0.05 mm. Randomly selected snails were isolated

individually and exposed to a 100-watt incandescent bulb for 48 h to stimulate the shedding of cercariae. Finally, all gastropods were dissected under a stereo microscope to detect the presence of sporocysts, rediae, developing cercariae, and metacercariae. Emerged cercariae were studied alive, under a light microscope, and identified according to Yamaguti (1975), Ostrowski de Núñez (1972, 1977, 1992), Morris (1976), Schell (1985), Ostrowski de Núñez et al. (1990, 1991, 1997), Martorelli (1991), Fernández et al. (2013), and Martorelli et al. (2013).

Two indices were used to analyze and compare the temporal dynamics of the community of larval digeneans in *B. peregrina*: seasonal prevalence by species (number of snails parasitized by that species/number of collected snails × 100) and seasonal overall prevalence (number of parasitized snails/number of collected snails × 100).

The differences in community structure between seasons were checked with a permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis similarity index, using the function *adonis* from the *vegan* package for R (Oksanen et al. 2016). Since permutational analysis of variance is sensitive to differences in multivariate dispersion between groups (sensu homogeneity of variances), the same models were tested for differences in dispersion using multivariate homogeneity of group dispersions PERMDISP.

Generalized linear models (GLMs) were used to explore differences between seasonal overall prevalence in the temporary pond (response variable). A mixed compound Poisson-gamma within the Tweedie family of distributions was specified, which had a positive mass at zero and was otherwise continuous. Tweedie GLM can be fitted in R using the usual glm function after loading the statmod package. The *Tweedie index parameter* (ξ) determining the distribution was specified as 1.18 using the function tweedie.profile in the package tweedie (Dunn and Smyth 2018). A total of five variables were considered for model selection in GLM: four continuous and explanatory variables: snail size, snail relative abundance, water temperature, and water depth; and one variable category: season. Model selection in GLM involved the stepwise backward selection procedure, starting with all four exploratory variables, and removing the water depth variable in the final model as it was not significant. Post hoc comparisons were made between the 2014 seasons (water was present during the entire year) and between the same seasons in different years.

Results and discussion

An alternation of dry and wet periods was observed in three of the 4 years assessed (2013, 2015, and 2016) in the temporary pond. The drought period spanned autumn and winter in 2013; summer, autumn, and winter in 2015; and summer in 2016. By contrast, there were no droughts in 2014. During the

study, 6300 individuals of *B. peregrina* were examined, and nine species of digeneans belonging to seven families were recorded (Table 1). These larval stages were previously described and characterized by Martorelli (1991), Etchegoin and Martorelli (1998), Parietti (2018), and Parietti et al. (2015).

Seasons and host length were significantly related to the structure of digenean assemblages in the whole sample (PERMANOVA, season: $F = 7.2$; P(perm) < 0.01; Mollusk size: $F = 6.6$; P(perm) < 0.01). Pairwise comparisons showed significant differences between all the seasons in 2014 (P(perm) < 0.01), and the comparison of the same seasons in different years generated mixed results: summers 2013–2014 were different, but autumns (2014–2016) and winters (2014–2016) were similar to each other. Finally, springs with previous drought (2013 and 2015) were different between them and from springs without previous drought (2014 and 2016). These differences can be partly attributed to differences in the dispersion of parasite communities throughout the seasons (PERMIDISP: $F = 2.9$; P(perm) = 0.02).

The physical parameters assessed in every season (water temperature and depth) and the mollusk relative abundance and size are detailed in Table 2. Significant effects of water temperature and host biotic characteristics on the seasonal overall prevalence values were detected, and a season effect was observed ($P < 0.001$, for all cases; Fig. 1). During 2014, the only year without drought, spring showed the lowest prevalence value and differed significantly from summer and autumn of the same year ($P < 0.05$, in all cases). Meanwhile, the other seasons in 2014 showed no differences between them ($P > 0.05$, for all cases). When seasons from different years were compared, winters showed differences between them (2014–2015; $P < 0.05$), but summers (2013–2014) and autumns (2014–2016) had no differences between years ($P > 0.05$, in both cases). It is a remarkable result that post-drought springs (2013 and 2015) evinced higher prevalence than regular springs (2014 and 2016) ($P < 0.05$, in all cases), and spring 2015 showed the highest overall prevalence values for the whole 4-year study ($P < 0.05$, for all cases). In addition, six

out of nine digenean species (67%) were registered in spring 2013 (after two drought seasons), and eight (89%) in spring 2015 (after three drought seasons).

Biotic and abiotic factors affected, directly and indirectly, the temporal dynamics of these parasites. However, these factors form a complex set of interactions; thus, it is not always easy to identify the influence of each one on the species composition and dynamics of these assemblages. Nevertheless, the quick increase in species richness and seasonal overall prevalence in the post-drought seasons suggest that drought is an important structuring factor of this assemblage in *B. peregrina*. Moreover, these digenean species seem to have certain degree of plasticity in their life cycles in response to the environmental change in this pond and effectively resisted droughts. Digeneans present several strategies to resist drought periods in this type of environment and to allow the establishment and development in temporary water bodies (O'Dwyer and Poulin 2015). Six of the nine species (67%) that parasitize *B. peregrina* showed some type of abbreviation of their life cycles. Two were found in the metacercaria stage in the digestive gland of the mollusk (Metacercaria Strigeidae gen. sp. 1 and Metacercaria Echinostomatidae gen. sp. 1), and two showed cercariae encystment within the sporocyst (*Microphallus simillimus* and Furcocercaria gen. sp. 1). The metacercaria stage remains inside the mollusk host during the aestivation phase, sheltered in humid microhabitats, waiting for the water to reappear in the temporary pond. At the end of this phase, the parasite continues its life cycle in the definitive host giving rise to the adult stage. Another transmission pattern in the two-host life cycles occurs in Notocotylidae sp. 1. The cercariae are expelled from the snail host and encyst upon aquatic plants, shells, and other objects. Definitive hosts can get infected by feeding on plants that carry the metacercariae (Galaktionov and Dobrovolskij 2003). This species was recorded for all post-drought periods, suggesting that the permanence of metacercariae in the environment contributes to the reestablishment of the life cycle of this species. Additionally, Schistosomatidae gen. sp. 1 has an abbreviated life cycle, which

Table 1 Detailed list of species or morphological types of larval digeneans that parasitize *Biomphalaria peregrina* in the temporary pond throughout the 4-year study (2013–2016)

| Family	Species/morphological type	Ref.	Definitive host
Notocotylidae	Notocotylidae sp. 1	1	Birds and mammals
Echinostomatidae	Echinocercaria gen. sp. 1	3	Birds, mammals and fish
	Metacercaria Echinostomatidae gen. sp. 1	2	Birds, mammals and fish
	Cercaria magnacauda gen. sp. 1	2	Birds, mammals and fish
Reniferidae	Xiphidiocercaria gen. sp. 1	3	Reptiles
Microphallidae	*Microphallus simillimus*	4	Birds and mammals
Strigeidae or Diplostomidae	Furcocercaria gen. sp. 1	2	Birds and mammals
Strigeidae	Metacercaria Strigeidae gen. sp. 1	3	Birds
Schistosomatidae	Cercaria Schistosomatidae gen. sp. 1	2	Birds and mammals

Ref. 1, Etchegoin and Martorelli (1998); 2, Parietti (2018); 3, Parietti et al. (2015); 4, Martorelli (1991)

Table 2 Sample composition of *Biomphalaria peregrina* and environmental variables in the seasons analyzed throughout the 4-year study (mean (standard deviation)). *D.S.* dry season

Year	Season	Mollusk abundance (ind/h)	Mollusk size (mm)	Depth (cm)	Water temperature (°C)
2013	Summer	335.9 (149.5)	6.3 (1.4)	20.4 (5.3)	25.9 (1.2)
	Autumn	D. S.	D. S.	D. S.	D. S.
	Winter	D. S.	D. S.	D. S.	D. S.
	Spring	83.8 (16.2)	6.5 (2.1)	18.9 (4.2)	31.4 (4)
2014	Summer	198 (40.5)	6.7 (1.4)	12.7 (7.8)	29.3 (1.7)
	Autumn	328.1 (101.7)	7.5 (1.9)	19 (11.1)	17.8 (5.4)
	Winter	330 (93.8)	7.9 (1.9)	39 (6.6)	12.9 (6)
	Spring	483.2 (140.6)	8 (1.9)	25.4 (6.9)	23.3 (3.7)
2015	Summer	D. S.	D. S.	D. S.	D. S.
	Autumn	D. S.	D. S.	D. S.	D. S.
	Winter	D. S.	D. S.	D. S.	D. S.
	Spring	222 (56.9)	9.1 (2.2)	17.2 (1.7)	24.7 (0.9)
2016	Summer	D. S.	D. S.	D. S.	D. S.
	Autumn	312 (65.7)	4.5 (1)	27 (2.7)	6.2 (0.1)
	Winter	282.9 (76.2)	7.9 (1.2)	34.5 (4.4)	10.2 (1.1)
	Spring	450.3 (53.2)	5.1 (1.4)	20.7 (3.1)	20.2 (1.2)

eliminates the metacercaria stage, and the cercariae emerge from the snail and penetrate the skin of a vertebrate definitive host (Galaktionov and Dobrovolskij 2003). This allows to complete the life cycle quickly, avoiding periods of drought. Similar results were obtained by other authors for *B. peregrina* and *B. straminea* in temporary habitats from Argentina (Flores et al. 2010; Fernández et al. 2013). In these two studies, the 100% of the digenean species evidenced some type of abbreviation of their life cycles (three and five species respectively). Furthermore, the effect of desiccation could be to concentrate

the release of cercariae from the mollusks during periods of immersion; they would release more cercariae than those exposed to previous humid conditions (O'Dwyer and Poulin 2015). Badger and Oyerinde (1996) observed that cercaria development was delayed by prolonged desiccation of the aestivating-infected snails. These adaptations of the parasites to desiccation could explain the higher prevalence values observed after the droughts, particularly in spring 2013 and spring 2015, for example in Xiphidiocercaria gen. sp. 1, Cercaria Echinocercaria gen. sp. 1, Cercaria magnacauda gen. sp. 1,
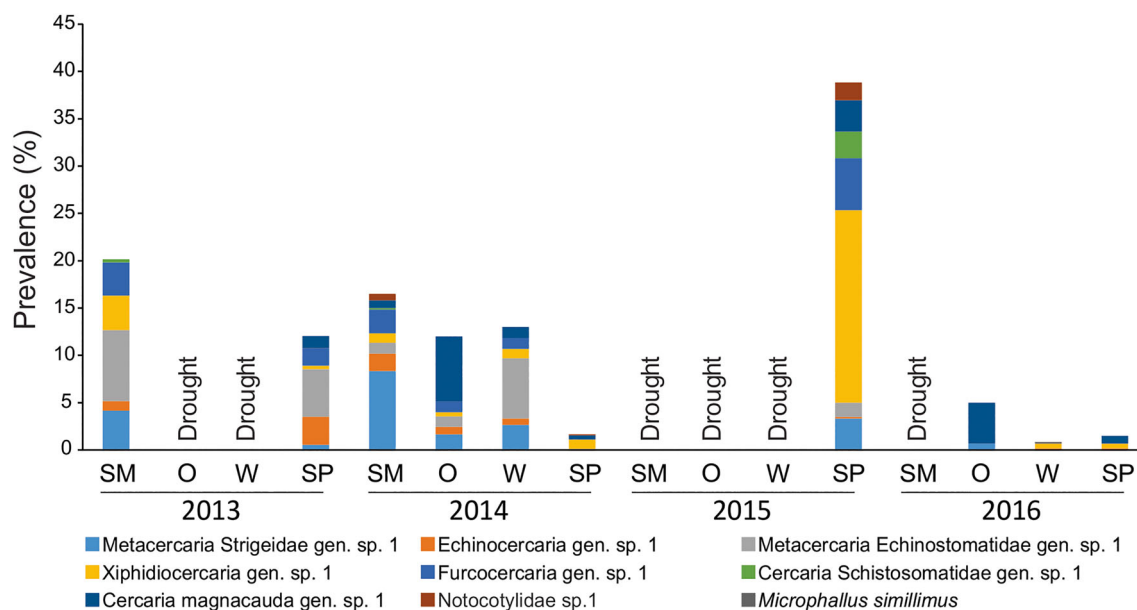
Fig. 1 Seasonal variation of the overall prevalence of larval digeneans that parasitize *Biomphalaria peregrina*, color bars indicate every species prevalence (data not transformed)

Schistosomatidae gen. sp. 1, and Furcocercaria gen. sp. 1. The release of cercariae should be synchronized with the presence of the definitive host in the environment. Xiphidiocercaria gen. sp. 1 uses amphibians as second intermediate host, and reptiles as definitive host (Santoro et al. 2011). Some of these organisms that frequent grasslands and humid zones near the shores of ponds make a stable source of hosts for this parasite, allowing for the reestablishment of its life cycle during the hydroperiods. In the area, Vega (2001) reported 10 species of amphibians and 17 of reptiles. Echinocercaria gen. sp. 1 and Cercaria magnacauda gen. sp. 1 presented typical life cycle of Echinostomatidae and low prevalence values, using fish as second intermediate host (Schell 1985). The changeable environmental conditions of the pond and the absence of connections with other water bodies limit the presence of juvenile and adult fish. The presence of digenean in the post-drought periods can be explained by the return of birds to the pond (main definitive host). An important increase of migratory birds can be observed during spring and summer in Mar Chiquita Coastal Lagoon (Ferrero 2001). Due to the proximity between the pond and the lagoon, migratory birds, together with local breeding species of shorebirds, can use the pond as a resting and feeding area, contributing to increase the influx of digenean-infective stages.

The external environment exerts strong effects on the life-history of internal parasites, and induces changes in the strategies adopted by these parasites (Poulin and Cribb 2002). Particularly, in ephemeral or temporary habitats, life cycle abbreviations would be selected because under such conditions intermediate hosts can become limited to marginal pools where no definitive hosts are available for the completion of the life cycle (Holton 1984). Parasites may have the ability to perceive a diversity of signals from environmental parameters that could affect their future fitness (Thomas et al. 2002) and to strategically respond to a diversity of signals coming from their host environment (Combes et al. 2002). The analysis of parasite assemblage in environments exposed to environmental stressors (e.g., droughts) contributes to the knowledge of the effects of climate warming on parasites. Here, we found a clear parasite strategy to counteract the effect of this stress, those flexible transmission, and developmental pathways necessary to adjust to environmental changes. Additionally, we provide valuable information for the implementation of diversity conservation policies in parasite species in this temporary habitat.

Declarations

Conflict of interest The authors declare no competing interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Badger LI, Oyerinde JPO (1996) *Schistosoma mansoni*: effect of aestivation on the intra-molluscan stages and the survival rate of infected *Biomphalaria pfeifferi*. Ann Trop Med Parasitol 90(6):617–620. https://doi.org/10.1080/00034983.1996.11813091

Carlson CJ, Hopkins S, Bell KC, Doña J, Godfrey SS, Kwak ML, Lafferty KD, Moir ML, Speer KA, Strona G, Torchin M, Wood CL (2020) A global parasite conservation plan. Biol Conserv 250: 108596. https://doi.org/10.1016/j.biocon.2020.108596

Combes C, Bartoli P, Thèron A (2002) Trematode transmission strategies. In: Lewis EE, Campbell JF, Sukhdeo MVK (eds) The behavioural ecology of parasites. CAB Int, Wallingford, pp 1–12

Dunn PK, Smyth GK (2018) Generalized linear models with examples in R. Springer, New York

Etchegoin JA, Martorelli SR (1998) Nuevas cercarias en *Heleobia conexa* (Mollusca: Hydrobiidae) de la albufera Mar Chiquita. Neotropica 44:41–50

Fernández MV, Hamann MI, Ostrowski de Núñez M (2013) Larval trematodes of *Biomphalaria straminea* (Mollusca: Planorbidae) in a ricefield in Corrientes Province, Argentina. Rev Mex Biodiversidad 84:756–764

Ferrero L (2001) Avifauna de Mar Chiquita (Síntesis del trabajo de Mariano M. Martínez). In: Iribarne OO (ed.). Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas. Ed Martín, Mar del Plata, Argentina

Flores VR, Semenas LG, Veleizan AA (2010) Larval digenean community parasitizing the freshwater snail, *Biomphalaria peregrina* (Pulmonata: Planorbidae), from a temporary pond in Patagonia, Argentina. J Parasitol 96(3):652–656

Galaktionov KV, Dobrovolskij AA (2003) The biology and evolution of trematodes: an essay on the biology, morphology, life cycles, transmission, and evolution of digenetic trematodes. Kluwer Academic Pub, Dordrecht

Gérard C (2001) Consequences of a drought on freshwater gastropod and trematode communities. Hydrobiol 459:9–18

Holton AL (1984) A redescription of *Coitocaecum parvum* Crowcroft, 1945 (Digenea: Allocreadiidae) from crustacean and fish hosts in Canterbury. N Z J Zool 11:1–8

Lagrue C, Poulin R (2009) Life cycle abbreviation in trematode parasites and the developmental time hypothesis: is the clock ticking? J Evol Biol 22(8):1727–1738. https://doi.org/10.1111/j.1420-9101.2009.01787.x

Martorelli SR (1989) Estudios parasitológicos en biotopos lénticos de la República Argentina y desarrollo del ciclo biológico monoxeno de la metacercaria progenética de *Genarchella* travassos, 1928 (Digenea, Hemiuridae) parásita *Littoridina parchappei* (Mollusca, Hidrobiidae). Rev Museo Plata 14(157):109–117

Martorelli SR (1991) El ciclo biológico abreviado de *Microphallus simillimus* (Travasos, 1920), comb. N. (Digenea; Microphallidae). Parásito de *Heleobia conexa* (Mollusca, Hydrobiidae) y de *Himantopus melanurus* (Aves; Recurvirostridae) en Argentina. Iheringia 71:91–98

Martorelli SR, Alda MP, Marcotegui PS, La Sala LF, Montes MM (2013) Larval digeneans in *Biomphalaria* snails from the Salto Grande Dam in the Uruguay river. http://sedici.unlp.edu.ar/handle/10915/30501. Accessed 8 Mar 2021

Morris R (1976) Contribución al conocimiento del parasitismo de *Biomphalaria peregrina* (D'Orbigny) (Mollusca, Gastropoda). *Neotrópica* **22**:93–98

O'Dwyer K, Poulin R (2015) Taken to the limit. Is desiccation stress causing precocious encystment of trematode parasites in snails? Parasitol Int 64(6):632–637. https://doi.org/10.1016/j.parint.2015.09.001

Oksanen J, Blanchet FG, Friendly M et al (2016) Vegan: community ecology package. R package version 2.4-3. Vienna: R Foundation for Statistical Computing

Ostrowski de Núñez M (1972) Fauna de agua dulce de la República Argentina. I Anotaciones sobre furcocercarias. Neotropica 18:137–140

Ostrowski de Núñez M (1977) Fauna de agua dulce de la republica argentina. VIII. furcocercarias (trematoda) nuevas de moluscos de las familias planorbidae y ancylidae. Physis Sección B 37(93):117–125

Ostrowski de Núñez M (1992) Trematoda. Familias Strigeidae, Diplostomidae, Clinostomidae, Schistosomatidae, Spirorchiidae y Bucephalidae. Fauna de agua dulce de la República Argentina 9(1):1–55

Ostrowski de Núñez M, Hamann MI, Rumi A (1990) Larval trematodes of *Schistosoma mansoni* transmitting snails, *Biomphalaria spp.*, in northeastern Argentina. Acta Parasitol Pol 35(2):85–96

Ostrowski de Núñez M, Hamann MI, Rumi A (1991) Population dynamics of planorbid snails from a lenitic biotope in northeastern Argentina. Larval trematodes of *Biomphalaria occidentalis* and analysis of their prevalence and seasonality. Acta Parasitol Pol 36(4):159–166

Ostrowski de Núñez M, Hamann MI, Rumi A (1997) Estudios de trematodes larvales en *Biomphalaria spp.* (Mollusca, Planorbidae) de la localidad de San Roque, provincia de Corrientes, Argentina. Physis Seccion B 126(127):7–15

Parietti M (2018) Ecología de las comunidades de digeneos larvales en hospedadores moluscos que habitan ambientes dulceacuícolas de la Provincia de Buenos Aires, Argentina. PhD Thesis. Universidad Nacional de Mar del Plata, Argentina

Parietti M, Merlo MJ, Etchegoin JA (2015) Larval digenean stages (Trematoda) that parasited *Biomphalaria peregrina*, D'Orbigny, 1835 (Mollusca, Planorbidae) in the Southeast of the Buenos Aires province (Argentina). Rev Arg Parasitol 3:10–17

Pietrock M, Marcogliese DJ (2003) Free-living endohelminth stages: at the mercy of environmental conditions. Trends Parasitol 19(7):293–299. https://doi.org/10.1016/S1471-4922(03)00117-X

Poulin R (2014) Parasite biodiversity revisited: frontiers and constraints. Int J Parasitol 44(9):581–589. https://doi.org/10.1016/j.ijpara.2014.02.003

Poulin R, Cribb TH (2002) Trematode life cycles: short is sweet? Trends Parasitol 18:176–183. https://doi.org/10.1016/S1471-4922(02)02262-6

Rubaba O, Chimbari MJ, Mukaratirwa S (2016) The role of snail aestivation in transmission of Schistosomiasis in changing climatic conditions. Afr J Aq Sci 41(2):143–150. https://doi.org/10.2989/16085914.2016.1145103

Santoro M, Tkach VV, Mattiucci S, Kinsella JM, Nascetti G (2011) *Renifer aniarum* (Digenea: Reniferidae), an introduced North American parasite in grass snakes *Natrix natrix* in Calabria, southern Italy. Dis Aquat Org 95:233–240. https://doi.org/10.3354/dao02365

Schell SC (1985) Trematodes of North America north of Mexico. Idaho Research Foundation

Schriever TA, Lytle DA (2016) Convergent diversity and trait composition in temporary streams and ponds. Ecosphere 7(5):e01350. https://doi.org/10.1002/ecs2.1350

Schwartz SS, Jenkins DG (2000) Temporary aquatic habitats: constraints and opportunities. Aquat Ecol 34(1):3–8

Thomas F, Brown SP, Sukhdeo M, Renaud F (2002) Understanding parasite strategies: a state-dependent approach? Trends Parasitol 18:387–390. https://doi.org/10.1016/S1471-4922(02)02339-5

Vega LE (2001) Herpetofauna: diversidad, ecología e historia natural. In: Iribarne OO (ed.). Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas. Ed Martín, Mar del Plata, Argentina, pp. 213-226

Williams DD (1997) Temporary ponds and their invertebrate communities. Aquat Conserv Mar Freshwat Ecosyst 7(2):105–117. https://doi.org/10.1002/(SICI)1099-0755(199706)7:2%3C105::AID-AQC222%3E3.0.CO;2-K

WWF (2016) Living Planet Report 2016. Risk and resilience in a new era. WWF, Gland

Yamaguti S (1975) A synoptical review of life histories of digenetic trematodes of vertebrates: with special reference to the morphology of their larval forms. Keigaku Publishing Co, Tokyo 590p