FOLIA PARASITOLOGICA 50: 72–78, 2003

Component population study of *Acanthocephalus tumescens* (Acanthocephala) in fishes from Lake Moreno, Argentina

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Key words: *Acanthocephalus tumescens*, Patagonian freshwater fishes, host status, component population, suprapopulation

Abstract. Seasonal samples of all fish species from Lake Moreno were taken in order to determine the presence of paratenia, to evaluate the status of the hosts and to characterise the transmission of *Acanthocephalus tumescens* (von Linstow, 1896) at the component population level. Prevalence, mean abundance, mean intensity, numbers of gravid females, relative abundance of the different fish species, relative output of eggs and relative flow rates for each host species were computed. *Acanthocephalus tumescens* showed low host specificity, successfully parasitizing six out of eight fish species present in the lake. No paratenic infection was registered. If prevalence, mean abundance, and number of gravid females are considered, host species can be placed in a continuum from the most to least suitable as follows: *Galaxias platei* Steindachner, *Diplomystes viedmensis* (Mac Donagh), *Oncorhynchus mykiss* (Walbaum), *Salvelinus fontinalis* (Mitchill), *Percichthys trucha* (Cuvier et Valenciennes) and *Galaxias maculatus* (Jenyns). However, when parasite flow rates and egg output were calculated, including relative abundance of each fish species, the continuum was rearranged as follows: *P. trucha*, *O. mykiss*, *G. platei* / *G. maculatus*, *S. fontinalis* and *D. viedmensis*. The first four species would be the main contributors to the population of *A. tumescens* in this lake, *P. trucha* being the major one. Different regulatory and non-regulatory mechanisms are suggested.

Although the acanthocephalans with aquatic cycles can infect a wide range of fish hosts, in only a few of them can they establish themselves, reach the proper size, and attain sexual maturity (Crompton 1983, Kennedy 1993). For this reason, the host status should not be assigned only by the presence of the parasite (Hine and Kennedy 1974). Causes such as the food requirements of the parasite and diet and immune response of the host could determine this transmission pattern (Kennedy 1993). Different systems of classification have been worked out in order to establish the host status. Amin (1987) refers to principal, accessory and occasional host, and Holmes (1976, 1979) classifies them as required, suitable and unsuitable. These classification systems have been established using variables such as mean intensity and prevalence of infection, size and growth of parasites and maturity and proportion of gravid females. The proportion of gravid females is very important for the assessment of relative parasite flow rates through the different species of definitive hosts (Esch and Fernández 1993). The relative abundance of each fish host species, seldom considered, also contributes to a sharper evaluation of the relative flow of parasites at the component population level (Holmes et al. 1977). Particularly in this type of study, post-cyclic transmission and the presence of paratenic hosts should also be considered.

In Argentina research about host status for acanthocephalans has been carried out for *Pomphorhynchus patagonicus* Ortubay, Úbeda, Semenas et Kennedy, 1991 and *P. sphaericus* Gil de Pertierra, Spatz et Doma, 1996 (Úbeda et al. 1994, Gil de Pertierra et al. 1996). In Patagonia, Úbeda et al. (1994) found *Odontesthes hatcheri* (Eigenmann) as principal host, *Galaxias platei* Steindachner as secondary and *Oncorhynchus mykiss* (Walbaum) would act as a sink for *P. patagonicus*. Trejo (1994) also suggested the importance of the assemblage of fishes, feeding habits and environmental characteristics which vary among sites in order to assess the sustainability of *P. patagonicus.*

Acanthocephalus tumescens (von Linstow, 1896), the other acanthocephalan species in Patagonian freshwater systems has been found parasitizing the intestine of native fishes such as *Galaxias maculatus* Jenyns, *G. platei*, *Diplomystes viedmensis* (Mac Donagh), *Odontesthes hatcheri*, *Percichthys trucha* (Cuvier et Valenciennes) and *P. colhuapiensis* Mac Donagh and introduced species such as *Oncorhynchus mykiss*, *Salmo trutta* (Linnaeus), *S. salar* Linnaeus, *Salvelinus fontinalis* (Mitchill) and *Salvelinus namaycush* (Walbaum) (Torres et al. 1990, 1992, Ortubay et al. 1994, Semenas and Trejo 1997). The intermediate host is the amphipod *Hyalella patagonica* Ortmann, 1911 (Trejo et al. 2000).

Considering the wide host range for *A. tumescens*, and the differences in size and feeding behaviour of its hosts, phenomena such as post-cyclic transmission, paratenia and different host status could be suspected. Post-cyclic transmission has been proven for *A. tumescens* (Rauque et al. 2002), so the aims of this study were to determine the presence of paratenia, to

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evaluate the status of the hosts for *A. tumescens* and to characterise the transmission of this acanthocephalan at the component population level in Lake Moreno.

MATERIALS AND METHODS

Study site and fish characteristics

Lake Moreno (41°04'S, 71°33'W) flows towards the Atlantic, is oligotrophic and is of glacial origin. This lake has a surface area of 10.3 km^2, is located at 764 m a.s.l. and has a maximum depth of 112 m. Native fish species such as *G. maculatus*, *G. platei*, *D. viedmensis*, *O. hatcheri* and *P. trucha* and introduced species such as *O. mykiss*, *S. trutta* and *S. fontinalis* are found in this lake.

Galaxias maculatus is the smallest fish in the lake, attaining 10 cm in length. It feeds on zooplanktonic and benthic organisms, swims in schools near the coast and is the major prey category for the other fishes (Macchi et al. 1999). *Galaxias platei* attains 35 cm in length and has a benthic habit; includes a wide range of prey in its diet, although *H. patagonica* is the most frequent (Úbeda et al. 1994). *Percichthys trucha* is the largest native fish, attaining 40 cm in length, and is mainly a benthic feeder, although it includes *G. maculatus* in its diet. It has a benthic habit and only its young specimens are preyed on by salmonids. *Odontesthes hatcheri* attains 20 cm in length and is mainly pelagic, omnivorous, feeding on zooplankton and zoobenthos and the largest specimens can be piscivorous (Macchi et al. 1999). Only young specimens are preyed on by salmonids. *Diplomystes viedmensis* attains 30 cm in length, feeding on insects and fishes. It has a benthic habit, being eaten exclusively by salmonids (Macchi et al. 1999). The salmonids are the largest fishes in the lake, are visual predators and potentially piscivorous when the availability of other prey is low (Macchi et al. 1999).

Data collection

Seasonal samples of all fish species in Lake Moreno were taken from November 1999 to August 2000. Specimens of *G. maculatus* were collected with net traps from the coast, transported to the laboratory and kept alive for up to 3 days until examined. The other fish species were captured using gillnets of various mesh sizes located in several places in the lake, from the coast to a depth of 50 m. These fishes were sacrificed and immediately brought to the laboratory. The intestines of all the fishes were removed and opened longitudinally in order to recover adult acanthocephalans and the other helminth species. The other abdominal organs were also checked in order to detect paratenic acanthocephalans. All the helminth parasites in the fish' intestines were counted. Also the content of stomachs was examined for food items. The relative CPUE (capture per unit effort) of all the sampled fishes (n = 1440) was used to evaluate the relative abundance of each host species from Lake Moreno. Although *G. maculatus* was captured with a different sampling method, its CPUE was also used.

Prevalence, mean abundance and mean intensity were calculated according to Bush et al. (1997). The sex of the acanthocephalans was recorded and the females were assigned to one of three categories: F1 immature with ovarian balls only, F2 with maturing eggs, and F3 with fully mature shelled eggs. The host status was analysed following Holmes (1979) and Amin (1987).

In order to study the relative flow rates of *A. tumescens* through each host species in Lake Moreno, mean abundance in a given host species was multiplied by the relative abundance of that host and then adjusted to a proportion of the total flow (sum of partial flows) of all host species (Holmes et al. 1977). The relative egg output from each host species was taken as the mean abundance of *A. tumescens* in a given host species multiplied by the percentage of F3 females in that host, multiplied by the relative abundance of that host in the lake, and then adjusted to a proportion of the total output (Holmes et al. 1977).

In order to detect potential interactions, a Spearman Rank Correlation Test (Conover 1980) was used to analyse the co-variation of *A. tumescens* abundance with the percentage of F3 females and with the abundance of the other parasite species. If negative co-variation between species was detected, correlation with intensity would be also tested.

RESULTS

Of the total number of fish captured, 882 specimens were analysed; numbers of each species and length fish range are shown in Table 1. *Acanthocephalus tumescens* infected six fish species belonging to four different families (Galaxiidae, Diplomystidae, Percichthyidae and Salmonidae). Only the specimens of *Odontesthes hatcheri* and *Salmo trutta* were not infected (Table 1).

All adult acanthocephalans recovered were normally attached in the intestine of fishes, and free larvae were found in the stomach of *Percichthys trucha*, *Galaxias platei* and *Salvelinus fontinalis*. No paratenic infection was found, since no acanthocephalans were recovered from the other abdominal organs.

The native fishes, *Diplomystes viedmensis* and *G. platei* registered the highest values for prevalence, mean intensity and mean abundance (Table 1). Among the introduced species, *S. fontinalis* had the highest values for prevalence and *Oncorhynchus mykiss*, the highest values for mean intensity and mean abundance (Table 1). *Galaxias maculatus* had the highest values for F3 females among native fishes and *S. fontinalis* and *O. mykiss* among introduced ones (Table 1).

Major items found in the stomachs of all fishes were crustaceans such as *Hyalella patagonica*, insects, gastropods, annelids and *G. maculatus* as the only species of fish. *Hyalella patagonica* and *G. maculatus* are the only registered sources of *A. tumescens* infection, so the percentages of fishes containing them in the gut content are indicated in Table 2. The six host fish species fed on *H. patagonica* but only four fed on *G. maculatus*. A high percentage of *G. platei* fed on *H. patagonica* but *S. fontinalis*, *O. mykiss* and *P. trucha* showed the major percentages for *G. maculatus*. Also *O. hatcheri* and *S. trutta* fed on *G. maculatus*, but only the former fed on *H. patagonica*, too (Table 2).

Table 1. Number and length range of examined fish, prevalence, number of parasites, mean intensity, mean abundance, and percentage of F3 females from each fish species for *Acanthocephalus tumescens* in Lake Moreno.

	Host (No. examined fish)	Length range of fish (cm)	Prevalence (%)	No. parasites	Mean intensity ± SD	Mean abundance ± SD	Percentage of F3 females
Percichthyidae	*P. trucha (157)*	9.5–43	34.7	534	10.3 ± 14.9	3.4 ± 9.8	6.9
Galaxiidae	*G. platei (36)*	10.5–26.5	52.8	289	15.2 ± 17.0	8 ± 14.4	11.4
	G. maculatus (568)	3–9.7	1.8	22	2.2 ± 1.8	0.04 ± 0.4	25
Salmonidae	*O. mykiss* (63)	10–52	33.0	182	8.7 ± 10.0	2.9 ± 7.1	17.7
	S. fontinalis (33)	11–39.5	48.5	58	3.6 ± 3.7	1.8 ± 3.1	16.1
	S. trutta (1)	66	0	0	0	0	0
Diplomystidae	*D. viedmensis* (9)	14.3–19.5	55.5	134	26.8 ± 37.0	14.9 ± 29.3	6.2
Atherinidae	*O. hatcheri* (15)	28–36	0	0	0	0	0

Table 2. Percentage of each fish species containing *Galaxias maculatus* or *Hyalella patagonica* in the gut content.

Host	Percentage containing *G. maculatus*	Percentage containing *H. patagonica*
Percichthys trucha	30	33.7
Galaxias platei	8.6	74.3
Galaxias maculatus	–	2.2
Oncorhynchus mykiss	41.3	22.2
Salvelinus fontinalis	51.5	33.3
Salmo trutta	100	0
Diplomystes viedmensis	0	44
Odontesthes hatcheri	6.7	6.7

Table 3. Relative abundance of fish host and flow rates and output of *Acanthocephalus tumescens* eggs for each fish host in Lake Moreno.

Host	Relative abundance (%)*	Flow rates (%)	Egg output (%)
Percichthys trucha	12.2	71.7	51.1
Galaxias platei	0.6	8.3	9.8
Galaxias maculatus	83.8	5.8	15
Oncorhynchus mykiss	2.1	10.5	19.3
Salvelinus fontinalis	0.8	2.4	4
Diplomystes viedmensis	0.05	1.2	0.8

* data by Pablo Vigliano and Patricio Macchi, pers. comm.

Table 4. Mean abundance ± SD for each parasite species recovered from the intestine of the fish hosts of *Acanthocephalus tumescens* in Lake Moreno.

	P. trucha	*G. platei*	*G. maculatus*	*O. mykiss*	*S. fontinalis*	*D. viedmensis*
Austrocreadium sp.	0.012 ± 0.2	0	0	0	0	0
Polylekithum percai *	1.6 ± 5.9	0	0	0	0	0
Acanthostomoides apophalliformis	225.2 ± 432.5	0.1 ± 0.3	0	0.4 ± 2.1	3.3 ± 13.8	0.2 ± 0.4
Nippotaenia sp.	0.012 ± 0.1	0.5 ± 1.3	0.8 ± 3.0	0.3 ± 1.9	0.3 ± 1.6	0
Camallanus corderoi	28.8 ± 45.5	0.1 ± 0.2	0.3 ± 2.1	0.8 ± 2.4	5.3 ± 11.1	0
Nomimoscolex semenasae **	0	0	0	0	0	2.8 ± 3.3
Hysterothylacium patagonense ***	4.6 ± 19.9	0.4 ± 1.1	0	0.4 ± 1.0	4.1 ± 12.4	3.1 ± 5.1

* *P. percai* Ostrowski de Núñez, Brugui et Viozzi, 2000; ** *N. semenasae* Gil de Pertierra, 2002; *** *H. patagonense* Moravec, Urawa et Coria, 1997

Data of relative abundance of each fish species, flow rates of parasites and output of eggs are shown in Table 3. *Percichthys trucha*, *O. mykiss* and *G. maculatus* had the major values for egg output and *P. trucha*, *O. mykiss* and *G. platei* for parasite transmission.

When co-variation between intensity of *A. tumescens* and percentage of F3 females was analysed, *P. trucha* (rS = 0.429; n = 52; P < 0.05), *G. maculatus* (rS = 0.719; n = 10; P < 0.05) and *O. mykiss* (rS = 0.546; n = 22; P < 0.05) had a positive one and the other fish species showed no co-variation.

The mean abundance of the other intestinal parasite species recorded for the six fish hosts are shown in Table 4. Only the digenean *Acanthostomoides apophalliformis* Szidat, 1956 and the nematode *Camallanus corderoi* Torres, Teuber et Miranda, 1990 in *P. trucha* were abundant enough to be used for test correlations. The abundance of *A. apophalliformis* co-varied positively with the percentage of F3 females (rS = 0.138; n = 157; P < 0.05) and with the abundance of *A. tumescens* (rS = –0.254; n = 157; P < 0.05). The abundance of *C. corderoi* did not co-vary with the percentage of F3 females (rS = –0.02; n = 157; P > 0.05) and negatively co-varied with the abundance of *A. tumescens* (rS = –0.15; n = 157; P < 0.05). However, when correlation tests between intensities of *C. corderoi* and *A. tumescens* were performed no co-variation was found (rS = –0.126; n = 44; P > 0.05).

DISCUSSION

Nickol (1985), reviewing acanthocephalan infections, did not find paratenic hosts for species of *Acanthocephalus*. In agreement with this, no paratenic infections of *Acanthocephalus tumescens* were found in Lake Moreno. The free larvae found in the stomach of the fishes would come from recently ingested amphipods. Post-cyclic transmission of *A. tumescens* from *Galaxias maculatus* to other fishes could be suspected, as the former is the major prey category for the other Patagonian freshwater fishes (Macchi et al. 1999). Until now this kind of transmission has only been proven for *Oncorhynchus mykiss* (Rauque et al. 2002).

Maturity of females, prevalence, mean abundance and mean intensity of infection and growth of acanthocephalans are used to evaluate the host status (Holmes 1979, Amin 1987). Characteristics of parasitic population can be precisely established when these variables have extreme values, however, the intermediate cases are difficult to classify. Holmes (1979) also suggested a continuum of hosts from which the parasites never become established to those in which the parasites develop best. Considering the low specificity of *A. tumescens* which successfully parasitizes six out of eight fish species, such a continuum seems to be more appropriate in describing the status of hosts in Lake Moreno. A potential energy wastage due to the loss of cystacanths seems to be diminished in *A. tumescens* because almost all the fish species were parasitized, having considerable percentages of gravid females. Therefore, in Lake Moreno all the hosts could contribute to the overall reproduction activity of the parasite.

Ortubay et al. (1994) cited *Odontesthes hatcheri* and *Salmo trutta* parasitized by *A. tumescens* in Patagonian lakes, but no infection was registered in Lake Moreno. *Salmo trutta* is highly piscivorous, preying on *G. maculatus* (Macchi et al. 1999), however, no infection was recorded probably due to its small sample size. One *O. hatcheri* out of 15 had *Hyalella patagonica* or *G. maculatus* in stomach, so its pelagic feeding habit (Macchi et al. 1999) would reduce exposure to infection. Additional studies are required to confirm the status of these fish species in Lake Moreno.

Following the criteria used by Amin (1987), all the hosts in Lake Moreno except *G. maculatus*, would be principal ones, and could be arranged in a decreasing suitability rank, considering the percentage of F3 females, prevalence and mean intensity as follows: *Galaxias platei*, *Diplomystes viedmensis*, *O. mykiss*, *Salvelinus fontinalis*, *Percichthys trucha* and *G. maculatus*. Although prevalence, mean intensity and reproductive potential of parasites are relevant indicators of the primary hosts, when a parasite species has low specificity, and the host species do not show great differences in those parameters, the analysis of the relative flow rates of the parasites through each host population is important (Holmes et al. 1977). If a decreasing continuum of parasite flow rates and egg output is considered, the suitability rank of host species could be arranged as follows: *P. trucha*, *O. mykiss*, *G. platei* / *G. maculatus*, *S. fontinalis*, and *D. viedmensis*. The position of *G. platei* and *G. maculatus* varied if transmission rates or output of eggs are considered. This continuum seems to be more appropriate in our study than the previous one because of the low specificity of *A. tumescens* and its ability to successfully establish itself in almost all fish species in this lake. In our host-parasite system, *G. maculatus* seems to be an unsuitable host due to the low values of prevalence and mean intensity, however its high percentage of F3 females and relative abundance make it one of the main contributor to sustain *A. tumescens* population in Lake Moreno. An abundant fish species like *P. trucha* with intermediate values of prevalence and mean intensity would be more important to the population of the parasite than highly parasitized scarce species, like *D. viedmensis*. As Holmes (1979) pointed out, the structure of the host community has the potential to affect the population dynamics of the parasite species. Interspecific relationships between hosts, like prey-predator one, should also be considered, specially in our case where post-cyclic transmission is suspected for all the fish hosts. If flow rates of parasites, output of eggs and post-cyclic transmission are considered the overall flow of *A. tumescens* in Lake Moreno can be summarised as in Fig. 1.

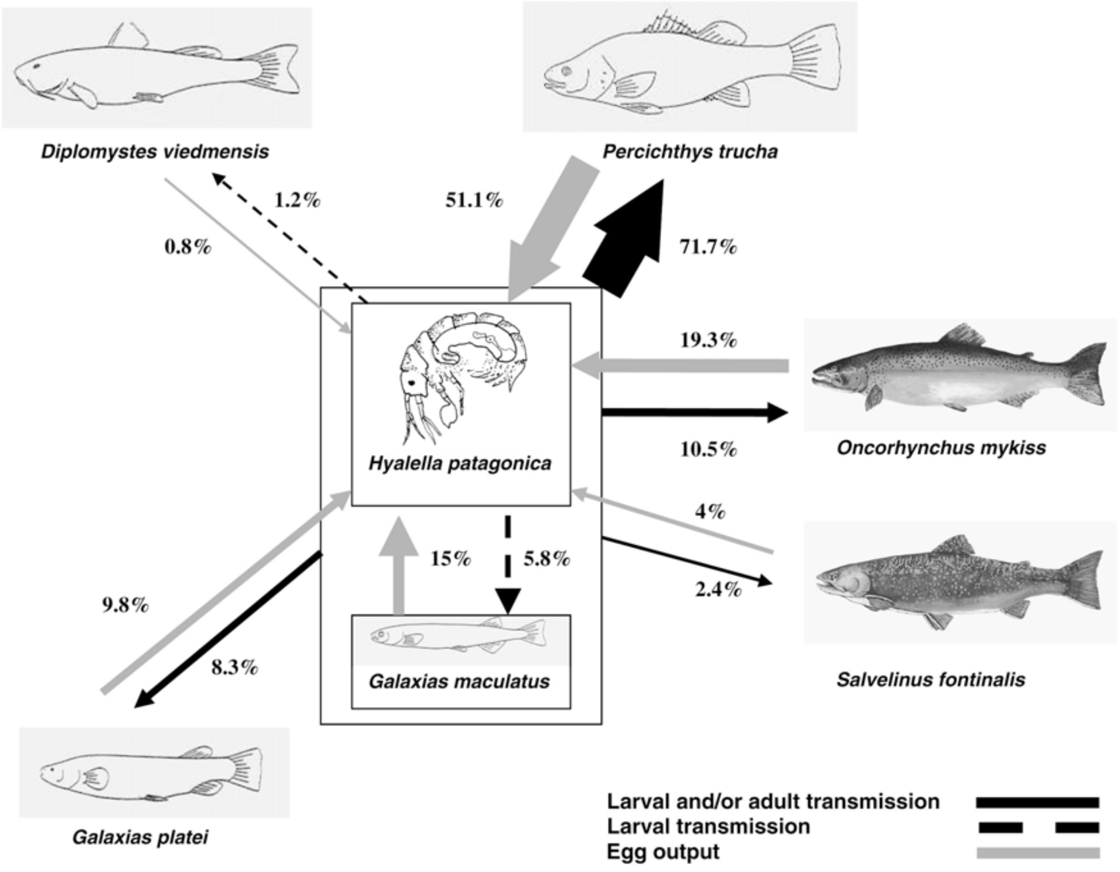

Fig. 1. Relative flow rates of *Acanthocephalus tumescens* in its hosts in Lake Moreno (the thickness of arrows indicates the relative values of parasite transmission and egg output).

Parasite population studies usually show a delicate equilibrium between reproductive and transmission efficiencies in the dynamics of life cycles considering, the same parasite species in a lake can be regulated in different ways depending on the host species and assemblages of them (Holmes et al. 1977, Aho and Kennedy 1987). Three ways in which the parasitic populations can be affected have been addressed (Bradley 1974, Holmes et al. 1977, Kennedy 1985): by transmission without regulation or by regulation at the level of the host population or at the level of the parasite's infrapopulation. Although several acanthocephalan-host interactions have been analysed, the regulatory mechanisms have been little considered because most studies have only examined one host species (Kennedy 1985).

Acanthocephalus tumescens does not provoke a strong tissue reaction in the host and encapsulation does not take place (Rauque et al. 2002), besides, in Lake Moreno high levels of infection were not registered. The establishment and the fecundity of females would not be affected by the presence of specimens of the same or different species, as the only negative correlation detected (between the abundance of *A. tumescens* and the abundance of *Camallanus corderoi*) has a low association value (rS = –0.15), suggesting that neither regulation through mortality at the level of the host population nor intra- or interspecific interactions at the level of the parasite's infrapopulation take place.

Although a high percentage of females reached maturity in *G. maculatus*, *O. mykiss* and *S. fontinalis* (Table 2), the low values of prevalence and mean intensity and the low preference for *H. patagonica* suggest feeding habits would affect the populations of *A. tumescens* in them. Holmes et al. (1977) found this type of regulation in *Metechinorhynchus salmonis* parasitizing *Coregonus artedii*. In *D. viedmensis* and *G. platei*, the transmission from the intermediate host could not be the limiting factor of infection because fish of these species fed mainly on amphipods (Table 2) and besides, they had the highest values of prevalence and mean intensity, although *D. viedmensis* had the lowest percentages of F3 females (Table 1). Holmes et al. (1977) have also found this type of regulation in *M. salmonis* parasitizing *Salvelinus namaycush*.

Holmes et al. (1977) found that only four of ten host species were important in maintaining the cycle of *M. salmonis*. In our study, four of six host species (*P. trucha*, *O. mykiss* and *G. platei* / *G. maculatus*) showed high values of relative parasite flow rates and egg output, but like the whitefish for *M. salmonis* in Cold Lake (Holmes et al. 1977), *P. trucha* was the main contributor for the suprapopulations of *A. tumescens* in Lake Moreno.

Five salmonid species were introduced into Patagonia at the beginning of the 20th century (Navas 1987), and three of them inhabit Lake Moreno. Although there are no data on the relative abundance of native species before the introductions, *D. viedmensis* seems to be the most affected, being the least abundant today, probably due to predation by salmonids (Macchi et al. 1999). *Acanthocephalus tumescens* has been cited in Patagonia before the introduction of salmonids (von Linstow 1896) so, if *D. viedmensis* was more abundant, perhaps it played a more important role then than today in the sustaining of the *A. tumescens* suprapopulation. The low specificity and its capacity for post-cyclic transmission (Rauque et al. 2002) made *A. tumescens* a better coloniser than *Pomphorhynchus patagonicus* in Patagonian freshwater lakes. This ability and the introduction of exotic salmonid fishes allowed for the enlargement of the host range, so *O. mykiss* now harbours a large proportion of the adult component population of *A. tumescens*. The introduction of exotic salmonids seems to be less important for *P. patagonicus* since *O. mykiss* acts as a sink for this acanthocephalan species (Trejo 1994, Úbeda et al. 1994).

Acknowledgements. We are very grateful to Edward and Audrey Shaw for English revision of the manuscript. Samples were done under permission of local Government authorities. Financial support was provided by the Universidad del Comahue B-092 and Agencia Nacional de Promoción Científica y Tecnológica 01-402-3067.

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Received 6 February 2002 Accepted 30 July 2002