

Native fish avoid parasite spillback from multiple exotic hosts: consequences of host density and parasite competency

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Received: 1 April 2012 / Accepted: 5 March 2013 / Published online: 17 March 2013
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Abstract Disease-mediated impacts of exotic species on their native counterparts are often ignored when parasite-free individuals are translocated. However, native parasites are frequently acquired by exotic species, thus providing a mechanism through which native host-parasite dynamics may be altered. In Argentina, multiple exotic salmonids are host to the native fish acanthocephalan parasite *Acanthocephalus tumescens*. Field evidence suggests that rainbow trout, *Oncorhynchus mykiss*, may be a major contributor to the native parasite's population. We used a combination of experimental infections (cystacanth—juvenile worm transmission from amphipod to fish; post-cyclic—adult worm transmission between definitive fish hosts) and dynamic population modelling to

determine the extent to which exotic salmonid hosts may alter *A. tumescens* infections in native freshwater fish. Experimental cystacanth infections demonstrated that although *A. tumescens* establishes equally well in native and exotic hosts, parasite growth and maturity is superior in exotic *O. mykiss*. Experimental post-cyclic infections also showed greater establishment success of *A. tumescens* in *O. mykiss*, though post-cyclic transmission did not result in greater parasite size or maturity. Dynamic population modelling, however, suggested that exotic salmonids may have a very limited influence on the *A. tumescens* population overall, due to the majority of *A. tumescens* individuals being maintained by more abundant native hosts. This research highlights the importance of considering both a host's relative density and its competency for parasites when evaluating whether exotic species can modify native host-parasite dynamics.

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Keywords Parasites · Acanthocephalan ·
Salmonids · Argentina · *Galaxias maculatus* ·
Oncorhynchus mykiss

Introduction

Whether through intentional release or accidental introduction, the deleterious impacts of exotic species on their native counterparts are well known (Sato et al. 2010), with many reviews predicting such impacts will

be a major driver of future biodiversity loss (e.g. Jenkins 2003; Kolar and Lodge 2001; Sala et al. 2000). The mechanisms underlying exotic species impacts have been a popular research focus for decades, with predation, competition and introduced diseases frequently cited (e.g. Miller 1989; Tompkins et al. 2003; Wiles et al. 2003). In the freshwater fish literature, for example, exotic salmonids are widely acknowledged to cause local declines and extinctions of native fish populations via predation and resource competition (Arismendi et al. 2009; Macchi et al. 2007; Townsend 2003). However, while exotic salmonids have been associated with epizootics of vertically and/or horizontally transmitted diseases (e.g. infectious hematopoietic necrosis virus-Japan, Nichol et al. 1995; bacterial kidney disease outbreak-Lake Michigan, USA, Holey et al. 1998), parasite mediated impacts have been largely discounted in situations where parasite-free eggs have been translocated (Clements 1988; Kennedy and Bush 1994; Poulin and Mouillot 2003), since the likelihood of introducing trophically transmitted parasites is limited. This may be an erroneous assumption since the parasite-free status of introduced salmonids does not preclude their influence on native fish populations via disease. Exotic salmonids have been shown to acquire native parasites after their introduction (Kelly et al. 2009a; Paterson et al. 2012; Poulin and Mouillot 2003). If exotic salmonids are competent hosts for such parasites, they may increase disease burdens in native hosts by acting as infection reservoirs from which parasites “spill back” (Daszak et al. 2000; Kelly et al. 2009b; Tompkins and Poulin 2006).

There is good field evidence that native host-parasite dynamics are being altered in Argentinean freshwater lakes into which multiple exotic salmonids have been introduced, including rainbow trout, *Oncorhynchus mykiss*. A recent population study of the native acanthocephalan parasite *Acanthocephalus tumescens* in native and exotic fish hosts in Lake Moreno indicated that approximately 20 % of parasite egg output (production) is generated by adult parasites present in this exotic host (Rauque et al. 2003). Additionally, Revenga et al. (2005) have shown that with increasing proximity to an *O. mykiss* fish farm in this lake, the native fish host *Galaxias maculatus* experience increased *A. tumescens* infection prevalence and intensity.

Acanthocephalus tumescens is a freshwater acanthocephalan that matures in the intestine of a definitive

fish host and releases its eggs into the water with fish faeces. Larval cystacanth stages develop in the amphipod intermediate host, *Hyaella patagonica*, after egg ingestion, with the lifecycle of *A. tumescens* completed following amphipod predation by the definitive host fish. Piscivorous fish may also acquire additional *A. tumescens* infections via post-cyclic transmission, whereby adult worms in definitive hosts are transmitted to other hosts via predation (Kennedy 1999; Nickol 1985), because the native host fish *G. maculatus* is consumed by the majority of other definitive hosts, as well as being a major diet component of some exotic salmonids (Macchi et al. 2007; Rauque et al. 2002; Rauque et al. 2003). This transmission pathway has been previously documented for *A. tumescens* in *O. mykiss* (Rauque et al. 2002), however the relative success of this pathway has not been compared between native and exotic fish hosts.

Here we investigate whether parasite spillback is indeed occurring in the Lake Moreno system, through a combination of experimental infections and dynamic population modelling. First, we assessed *A. tumescens* fitness in native and exotic fish through both transmission pathways—larval cystacanth infections from amphipods, and post-cyclic infections of adult worms from *G. maculatus*. Second, we examined the extent to which *A. tumescens* acquisition by exotic salmonids is predicted to alter native host-parasite dynamics. Finally, we identified the mechanisms likely to be responsible for observed patterns and discuss their implications for native host populations.

Materials and methods

Study site

Lake Moreno (41°05'S, 71°32'W) is a small lake (10.6 km²) situated in Nahuel Huapi National Park, Rio Negro Province, Argentina. Its fish community is comprised of five native (*Diplomystes viedmensis*, *G. maculatus*, *Galaxias platei*, *Odontesthes hatcheri*, *Percichthys trucha*) and three exotic hosts (*O. mykiss*, *Salmo trutta*, *Salvelinus fontinalis*) of *A. tumescens* (Table 1). *Galaxias maculatus* is the most abundant native host, while *O. mykiss* is the most abundant exotic host, comprising approximately 99.99 and 0.005 % of the total fish community, respectively

Table 1 Definitive host parameter definitions and estimates used in the population model

| Parameter | Symbol | GM | GP | PT | DV | OH | OM | SF | ST | Units | Source |
|-------------------------------|------------|---------|----------|----------|----------|----------|----------|----------|----------|--|--|
| Density | N_i | 38.68 | 0.00054 | 0.00206 | 8.96e-06 | 6.14e-05 | 0.00180 | 0.00058 | 6.14e-05 | m ⁻² | Vigilano et al. (2009) |
| Natural host mortality | b_i | 0.00046 | 0.00030 | 0.00034 | 0.00036 | 0.00055 | 0.00039 | 0.00039 | 0.00039 | Fish ⁻¹ day ⁻¹ | Milano (1996); Vigilano et al. (2009); Bello(1995); Valiente et al. (2010); Winemiller and Rose (1992); Milano (2003) |
| Amphipod predation | C_i | 0.115 | 8.12 | 6.1 | 5 | 3.867 | 0.07 | 1.37 | 0 | Day ⁻¹ | P.J. Macchi, unpublished data; D. Milano, unpublished data; <i>Grupo de Evaluación y Manejo de Recursos Icticos</i> (GEMARI), unpublished data |
| <i>G. maculatus</i> predation | D_i | - | 2.80e-07 | 4.78e-06 | 0 | 5.82e-08 | 1.41e-04 | 1.53e-05 | 1.48e-06 | <i>G. maculatus</i> ⁻¹ host ⁻¹ day ⁻¹ | P.J. Macchi, unpublished data; D. Milano, unpublished data; GEMARI, unpublished data |
| Larval establishment | γ_i | 0.166 | 0.166 | 0.350 | 0.258 | 0.258 | 0.335 | 0.335 | 0.335 | Worm ⁻¹ | This study |
| Post-cyclic establishment | T_i | - | 0.025 | 0.009 | 0.017 | 0.017 | 0.256 | 0.256 | 0.256 | Worm ⁻¹ | This study |
| Parasite maturation | m_i | 0.022 | 0.022 | 0.022 | 0.022 | 0.022 | 0.027 | 0.027 | 0.027 | Worm ⁻¹ day ⁻¹ | This study |
| Parasite mortality | α_i | 0.0187 | 0.0187 | 0.0187 | 0.0187 | 0.0187 | 0.0187 | 0.0187 | 0.0187 | Worm ⁻¹ day ⁻¹ | Paterson et al. (2011) |

GM *Galaxias maculatus*; GP *Galaxias platei*; PT *Percichthys trucha*; DV *Diplomystes viedmensis*; OH *Odomesthes hatcheri*; OM *Oncorhynchus mykiss*; SF *Salvelinus fontinalis*; ST *Salmo trutta*

(hydro-acoustic/gill net surveys and survival/production estimates; Vigliano et al. 2009). The wild population of *O. mykiss* in Lake Moreno may also be supplemented by an unknown number of escaped fish from a cage farm (annual production 20–30,000 fish; M. Beveraggi, unpublished data). Although Rauque et al. (2003) detected no *A. tumescens* infection in native *O. hatcheri* ($n = 19$) or exotic *S. trutta* ($n = 1$) in Lake Moreno, field observations from other localities show that both species are hosts to *A. tumescens* (Semenas and Trejo 1997).

Infection experiments

Study organisms

Two native hosts, *G. platei* and *P. trucha*, in addition to the exotic *O. mykiss*, were selected for experimental infection. These species were assumed to be significant contributors to the *A. tumescens* population based on their relative densities, infection flow rates and parasite egg outputs quantified from field surveys (Rauque et al. 2003; Vigliano et al. 2009).

Infection experiments were carried out at the Centro de Salmonicultura, Universidad Nacional del Comahue, Bariloche, Río Negro Province, which provided *O. mykiss* (mean fork length: 189 mm) from commercially raised stock. *Galaxias maculatus* (mean fork length: 59 mm) were collected from Bahía Verde, Lake Mascaradi, Río Negro Province (41°17'S, 71°38'W) by seine-netting. *Perchictys trucha* (mean fork length: 358 mm) were collected from Laguna Blanca, Neuquen Province (39°03'S, 70°22'W) and *G. platei* (mean fork length: 153 mm) from Laguna Coyte, Chubut Province (42°25'S, 71°22'W) with gill nets. Both fish species were treated for fungal growth associated with capture (20 g NaCl L⁻¹ H₂O for 45 min × twice weekly × 3 weeks) and acclimatized in outdoor aquaria for 7 weeks prior to the experiment. Fish were maintained ad libitum on different diets because a common food consumed by all fish species was not available: *O. mykiss* and *P. trucha*—commercial fish pellets, *G. maculatus* and *G. platei*—*Tubifex* worms.

During acclimatisation, experimental fish were treated with an anthelmintic (Praziquantel 10 mg L⁻¹ × 3 h in a water bath). Anthelmintic efficacy was assessed by comparing parasite infections in sub-sets of five treated and five un-treated fish per species. Ten

G. maculatus collected from Lake Mascaradi were substituted for *G. platei* to test anthelmintic efficacy, as few *G. platei* were available for experimentation. Previous studies recorded moderate prevalence (59–75 %) and infection intensities (mean 7–14 worms fish⁻¹) in *G. maculatus* at this site (Rauque et al. 2002), so they were a suitable substitute to test anthelmintic efficacy. Treated and untreated fish were autopsied 48 h after anthelmintic exposure, with 80 % of untreated *G. maculatus* containing *A. tumescens* (mean infection intensity 4.25 worms fish⁻¹), while no intestinal parasites were recovered from treated fish, or from untreated *O. mykiss* and *P. trucha*.

Hyalella patagonica amphipods, naturally infected with *A. tumescens*, were collected by sweep netting from Bahía Verde, Lake Mascaradi. Acanthocephalan infection in amphipods was ascertained under a dissecting microscope.

Cystacanth infection

A larval infection experiment was conducted to determine the fitness of *A. tumescens* transmitted from cystacanths in infected amphipods to native (*P. trucha*, *G. platei*) and exotic (*O. mykiss*) hosts, from which relative rates of larval establishment, growth, adult fecundity and survival could be estimated. Six fish per species were randomly assigned to individual tanks and maintained without food for 48 h prior to experimental infection. Ten cystacanths were removed from infected amphipods under a dissecting microscope, and placed into a gelatine capsule (length 19.4 mm, diameter 6.9 mm). Using a pipette, each capsule was orally inserted into the stomach of an experimental fish previously anaesthetised in a Benzocaine solution (100 ppm). Fish were placed in a tank of freshwater and observed for 5 min post-recovery to ensure regurgitation did not occur. Fish were returned to their individual tanks and maintained for 4 weeks on their respective diets.

At the completion of the infection period, fish were euthanised and immediately examined for parasites by removing the alimentary canal from oesophagus to anus and splitting longitudinally. The abundance of acanthocephalans was noted prior to fixing worms in 2 % formalin. Length (μm) and sex of each worm were recorded. In addition, developmental status (F1-immature with ovarian balls only, F2-maturing eggs, F3-fully mature eggs) and the proportion of mature

eggs in a sub-sample of 50 eggs were also recorded for female worms.

Post-cyclic infection

A post-cyclic infection experiment was conducted to determine the fitness of post-cyclically transmitted *A. tumescens* from infected *G. maculatus* to native (*P. trucha*, *G. platei*) and exotic (*O. mykiss*) hosts, from which relative rates of post-cyclic establishment, growth and fecundity could be estimated. These experiments also examined whether post-cyclically transmitted worms in piscivorous hosts achieved greater size or maturity than in their original definitive host, *G. maculatus*. Six *P. trucha* and six *O. mykiss* were randomly selected for post-cyclic experiments, while only five *G. platei* were used due to the limited availability of specimens. All fish were maintained as for cystacanth infections prior to experimental infection.

Naturally infected *G. maculatus* were captured 1 day prior to experimental infections and transported live to the laboratory. Live adult *A. tumescens* were carefully removed from the intestine of freshly euthanised *G. maculatus* and placed into gelatine capsules (40 worms capsule⁻¹). Capsules were administered to anaesthetised fish, as for larval infections, with infected fish maintained in individual tanks for 4 weeks post-infection on their respective diets.

Sixty randomly selected *G. maculatus* were autopsied at both the beginning (source group) and end (control group) of the trial to assess natural parasite abundance, length and female maturity, for comparison to post-cyclically transmitted individuals. At the completion of the infection period, all fish were euthanised and immediately examined for parasites, with acanthocephalans preserved and measured as for cystacanth infections.

Statistical analyses

Statistical analyses of experimental infection data were conducted using SPSS Statistic 15.0 (SPSS 2006). With the exception of cystacanth infection establishment and male worm length data, analysis of variance (ANOVA) tests were used for all analyses, for which data were transformed when necessary to meet the normality assumptions of parametric tests. Cystacanth infection establishment and male worm length data could not be transformed to meet assumptions of

normality; therefore, non-parametric tests were used to assess differences in establishment (Kruskal–Wallis test) and male length (Mann–Whitney U test) between hosts. Male and female worm lengths were only compared between *O. mykiss* and *P. trucha* from the cystacanth infection experiment, because too few worms were present in *G. platei* for analysis. Post-cyclically transmitted male and female worms in *P. trucha* and male worms in *G. platei* were also excluded from length analysis due to insufficient worms.

Population model

A population model was constructed using Model Maker 4.0 (Cherwell 2000) to dynamically simulate the influence of three exotic salmonids on *A. tumescens* in its five native definitive hosts.

Model formulation

The lifecycle of *A. tumescens* was modelled using a series of linked differential equations, which simulated (on a daily basis, scaled to 1 m⁻²) the number of immature (I_{GM}) and mature (W_{GM}) worms in *G. maculatus*, the number of immature (I_i) and mature (W_i) *A. tumescens* worms in the i th predatory definitive host, and the number of eggs in the environment (E), in discrete time-steps. Model formulation follows previous acanthocephalan life-cycle models outlined by Dobson (1988) and Paterson et al. (2011).

$$\frac{dI_{GM}}{dt} = EAC_{GM}N_{GM}\gamma_{GM}e^{-\sigma W_{GM}} - (m_{GM} + \alpha_{GM} + b_{GM} + S_I)I_{GM} \quad (1a)$$

$$\frac{dW_{GM}}{dt} = m_{GM}I_{GM} - (\alpha_{GM} + b_{GM} + S_W)W_{GM} \quad (1b)$$

$$\frac{dI_i}{dt} = (EAC_i\gamma_i + D_iI_{GM}T_i)N_i e^{-\sigma W_i} - (m_i + \alpha_i + b_i)I_i \quad (2a)$$

$$\frac{dW_i}{dt} = m_iI_i + D_iW_{GM}N_iT_i - (\alpha_i + b_i)W_i \quad (2b)$$

$$\frac{dE}{dt} = (W_{GM} + P)\lambda - (\varepsilon + A)E \quad (3)$$

The number of immature worms in *G. maculatus* I_{GM} (Eq. 1a) increases with the number of eggs in the

environment (E), modified by a constant (A) that incorporates the egg ingestion rate by amphipods, the rate at which ingested eggs successfully develop to cystacanths in amphipods, any influence of infection on amphipod consumption by definitive hosts, and the loss of cystacanths due to amphipod mortality, and according to the consumption rate of amphipods (C_{GM}) by *G. maculatus* (N_{GM}). This is additionally modified by the rate at which cystacanths, acquired by the consumption of infected amphipods, successfully establish to become immature worms in this host (γ_{GM}), and density dependence (σ) acting on worm survival. The number of immature worms decreases with worm maturation (m_{GM}), the summed rate of post-cyclic transmission of immature worms from *G. maculatus* to all individuals of all predatory fish species (S_I), and natural mortality of both the parasite (α_{GM}) and its host (b_{GM}). Post-cyclic transmission of *A. tumescens* to predatory fish species was only included via *G. maculatus* consumption. Although other fish are occasionally consumed by both native and exotic predatory hosts, *G. maculatus* is the main prey species in Lake Moreno (Macchi et al. 1999).

The number of mature worms in *G. maculatus* W_{GM} (Eq. 1b) increases with worm maturation (m_{GM}) and decreases with the summed rate of post-cyclic transmission of mature worms from *G. maculatus* to all individuals of all predatory fish species (S_W), and the natural mortality of both the parasite (α_{GM}) and its host (b_{GM}).

The number of immature worms in the i th predatory fish host I_i (Eq. 2a) increases with the number of eggs in the environment (E), as for immature worms in *G. maculatus*, in addition to post-cyclically transmitted worms from *G. maculatus* to that predatory fish species (D_i). The number of immature worms decreases with worm maturation in that species (m_i) and the natural mortalities of both the parasite in that species (α_i) and its host (b_i).

The number of mature worms in the i th predatory fish host W_i (Eq. 2b) increases with worm maturation (m_i) and the establishment (T_i) of post-cyclically transmitted worms from *G. maculatus* to that predatory fish species (D_i). The number of mature worms decreases with the natural mortalities of both the parasite in that species (α_i) and its host (b_i).

The number of *A. tumescens* eggs in the environment E (Eq. 3) increases with egg production (λ) from the mature worms in both *G. maculatus* (W_{GM}) and in

all other fish hosts summed (P), and decreases with natural mortality (ε) and ingestion by amphipods (A).

Model parameterisation

Parameter estimates (daily values averaged over seasons) were obtained, where possible, from experimental infection trials (this study), the published literature and unpublished data (Tables 1, 2). Fish population densities were not dynamically modelled, with *Galaxias maculatus* density estimated from galaxias production and survival averaged over seasons (Vigliano et al. 2009), and the densities (N_i) for all other species estimated from gill-netting and hydroacoustic surveys (Vigliano et al. 2009). Daily mortality rates for each fish species were estimated from maximum known life spans in Lake Moreno (*O. mykiss* 7 years, *P. trucha* 8 years, *G. maculatus* 6 years, *O. hatcheri* 5 years; Bello 1995; Milano 1996; Vigliano et al. 2009) or the surrounding catchment (*S. trutta* 7 years, *G. platei* 9 years; Milano 2003; Valiente et al. 2010), with the lifespan of *S. fontinalis* assumed to be equivalent to other exotic salmonids. The maximum lifespan of *D. viedmensis* was estimated from the mean age for North American Siluriformes (7.6 years; Winemiller and Rose 1992).

Daily predation rates on amphipods and *G. maculatus* by each fish species were calculated as constant proportions consumed, based on the average number of each prey item in the stomach of each host species (P.J. Macchi, unpublished data; D. Milano, unpublished data), corrected for 48 h gut clearance duration (Tekinay et al. 2003).

Larval *A. tumescens* establishment rates in salmonids and galaxiids were estimated from experimental infections of *O. mykiss* and *G. platei*, respectively. Larval establishment in *D. viedmensis* and *O. hatcheri* were estimated from the mean establishment rate in experimentally infected native fish (*P. trucha* and *G. platei*). Parasite maturation in salmonids was estimated from *O. mykiss*, while maturation rates for native hosts were estimated from another acanthocephalan native to southern hemisphere galaxiids (*Acanthocephalus galaxii*; Paterson et al. 2011), because no *A. tumescens* had reached maturity in native fish by 4 weeks post-infection. Parasite mortalities in all hosts of *A. tumescens* were also estimated from mortality rates in *A. galaxii* native hosts, as *A. tumescens* mortality rates could not be calculated

Table 2 Intermediate host and parasite parameter definitions and estimates used in the population model

| Parameter | Symbol | Value | Units | Source |
|----------------------------------|---------------|-------------|--------------------------------------|-------------------------------|
| Parasite fecundity | λ | 807.5 | Worm ⁻¹ day ⁻¹ | Crompton and Whitfield (1968) |
| Egg mortality | ε | 0.005 | Egg ⁻¹ day ⁻¹ | Crompton (1970) |
| Worm density dependence survival | σ | 4.43492 | Worm ⁻¹ day ⁻¹ | Optimised |
| Amphipod constant | A | 9.99944e-06 | – | Optimised |

since the presence of parasites was only assessed on one occasion post-infection. Post-cyclic establishment rates were estimated from experimental infections as per larval establishment rates, while the mortality of post-cyclically transmitted parasites was assumed to be equal to that of larval transmitted worms. Post-cyclic maturation rates were calculated from the difference between the proportion of mature female worms in *G. maculatus* on Day 0 and in each host on Day 28.

The daily rate of egg production of *A. tumescens* was unknown and was estimated from the acanthocephalan *Polymorphus minutus* (1,700 eggs per female per day; Crompton and Whitfield 1968), divided by the overall parasite male:female ratio of 0.41:0.59 (Rauque et al. 2006). Egg mortality was estimated from a maximum survival period of 6–9 months for aquatic acanthocephalan eggs (Crompton 1970).

Amphipod populations were not dynamically modelled because the density of *H. patagonica* in Lake Moreno, or other Patagonian lakes, was unavailable from the literature. The rate of egg ingestion, the establishment and development of eggs to cystacanths in amphipods and the loss of cystacanths due to amphipod mortality were also unknown. A constant (A) was used to represent the infection maintained by the amphipod population in Lake Moreno. Additionally, the influence of density dependence on worm survival (σ) was unknown for *A. tumescens*, but experimental studies on other acanthocephalan species suggest a negative relationship between worm abundance and survival (e.g. Brown 1986). Both A and σ were thus estimated by model optimisation (Marquardt method with ordinary least squared weightings) to the values that resulted in predicted levels of prevalence and infection intensity in definitive hosts that were equivalent to those observed in the field (a mean prevalence of 1.8 %, and a mean worm population size of 1.55 m⁻² in infected *G. maculatus* at

equilibrium dynamics). Furthermore, the model assumes no distribution of infection across amphipod and fish host populations.

Model simulation

We conducted model simulations to examine the influence of exotic salmonids on the dynamics of the native parasite *A. tumescens* in its native definitive hosts by investigating different fish community compositions representing (1) the fish community prior to exotic salmonid introduction (native only scenario), and (2) the current fish community with exotic salmonids present (native + exotic scenario). To determine the relative influence of each exotic salmonid on the modelled native host-parasite dynamics, we separately simulated fish communities comprised of all native fish species together with just one of the exotic salmonids (*O. mykiss* only, *S. fontinalis* only or *S. trutta* only). Additionally, because a field survey has suggested that the presence of an *O. mykiss* fish farm in Lake Moreno may increase the prevalence of *A. tumescens* infections in *G. maculatus* (Revenga et al. 2005), though the *A. tumescens* infection status in farmed *O. mykiss* themselves is unknown, we also simulated fish communities representing the current fish community with a fish farm present (native + exotic + fish farm scenario), and separately simulated the fish community comprised of all native fish species with wild and farmed *O. mykiss* (*O. mykiss* + fish farm).

Highly abundant host species often have the greatest influence on host-parasite dynamics (e.g. Mastitsky and Veres 2010). In Lake Moreno, *G. maculatus* is highly abundant in relation to all other fish species; therefore *G. maculatus* is likely to strongly influence the dynamics of *A. tumescens* infections. *Galaxias maculatus* is also a major prey item for exotic salmonids, comprising up to 37 % of prey consumed by *O. mykiss* in Lake Moreno (Vigliano et al. 2009). Thus, high abundances of *A. tumescens* infections in *O. mykiss* could be attributed to post-cyclic transmission from

native *G. maculatus*, and the high abundance of *G. maculatus* in Lake Moreno relative to other fish species. In light of this, we used sensitivity analyses to investigate whether *A. tumescens* infection in Lake Moreno is (1) maintained by *G. maculatus* (varying *G. maculatus* abundance) and (2) strongly influenced by post-cyclic infection from *G. maculatus* (varying post-cyclic transmission rates).

Results

Cystacanth infection

Acanthocephalus tumescens established equally well in *P. trucha* and *O. mykiss*, with fewer worms establishing in *G. platei* (Kruskal–Wallis $\chi = 5.839$, $P = 0.054$; Table 3). Worms of both sexes achieved greater length in *O. mykiss* than *P. trucha* (Mann–Whitney U test, males: $U = 13.00$, $P = 0.01$; one-way ANOVA, females: $F_{1,20} = 21.670$, $P < 0.001$). Seventy-five percent of female worms in *O. mykiss* were gravid at 4 weeks post-infection, containing either maturing eggs (F2 status) or fully mature shelled-eggs (F3 status). All female worms in *G. platei* and *P. trucha* were immature, containing ovarian balls only (F1 status).

Post-cyclic infection

Post-cyclically transmitted *A. tumescens* experienced greater establishment success in *O. mykiss* than in

native *G. platei* or *P. trucha* (log x + 1 transformed; one-way ANOVA: $F_{2,14} = 7.619$, $P = 0.006$; Tukey post hoc test; Table 4). Neither male nor female worms in post-cyclic hosts or control *G. maculatus* (Day 28) differed in length from the source *G. maculatus* (Day 0; one-way ANOVA, males: $P = 0.157$, females: $P = 0.360$). Female worms were consistently more abundant than males in all infection groups. The proportion of gravid female worms in *G. maculatus* declined during the 28 day infection period, with a similar proportion of gravid worms in the *O. mykiss* and *G. maculatus* control groups. All female worms recovered from *P. trucha* ($n = 1$) and *G. platei* ($n = 4$) were gravid.

Population model

The population model successfully replicated the population of *A. tumescens* in the most abundant host, *G. maculatus*, but it slightly underestimated the infection in other less abundant host species. Model simulations of fish communities, with and without exotic salmonids, indicated that salmonid presence is predicted to have caused very minor increases in *A. tumescens* infection in native fish species (Fig. 1). *Salvelinus fontinalis* had a greater influence on *A. tumescens* infections than *O. mykiss*, whilst *S. trutta* maintained a very small proportion of the acanthocephalan population. The inclusion of the *O. mykiss* fish farm in model simulations increased the influence of this salmonid on infection levels, although overall

Table 3 Prevalence, establishment, length and reproductive status of *A. tumescens* in fishes experimentally infected with cystacanths. Gravid females represent worms with maturing eggs (F2) and fully mature shelled eggs (F3)

| Host | No. of fish | Prevalence (%) | Establishment (%) [mean \pm SE] | Parasite sex | Length (μm) [mean \pm SE] | No. of worms | Gravid females (%) [F2 + F3] |
|----------------------------|-------------|----------------|-----------------------------------|--------------|--|--------------|------------------------------|
| <i>Oncorhynchus mykiss</i> | 6 | 83.3 | 33.5 \pm 9.5 | M | 2,695 \pm 225 | 8 | 75 |
| | | | | F | 3,370 \pm 150 | 12 | |
| | | | | M:F ratio | 1:1.5 | | |
| <i>Percichthys trucha</i> | 6 | 100 | 35 \pm 5 | M | 1,913 \pm 18 | 11 | 0 |
| | | | | F | 2,414 \pm 20 | 9 | |
| | | | | M:F ratio | 1:0.8 | | |
| <i>Galaxias platei</i> | 6 | 16.6 | 8.3 \pm 8.3 | M | 2,386 | 1 | 0 |
| | | | | F | 2,300 | 1 | |
| | | | | M:F ratio | 1:1 | | |

Establishment refers to the presence of attached worms

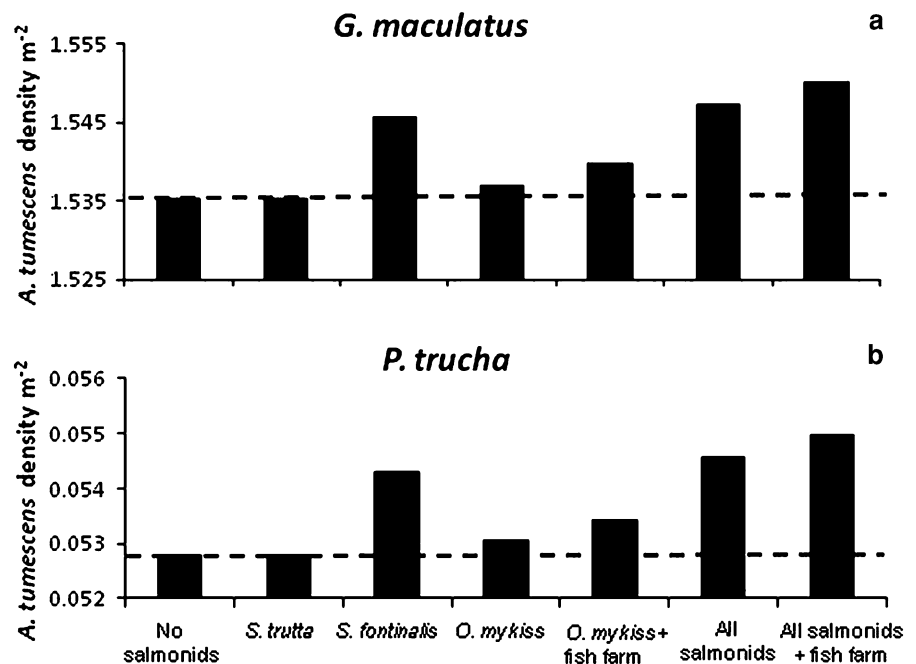
Table 4 Prevalence, establishment, length and reproductive status of *A. tumescens* in fishes experimentally infected with post-cyclically transmitted worms

| Host | Infection level | No. of fish | Prevalence (%) | Establishment (%) [mean ± SE] | Parasite sex | Length (µm) [mean ± SE] | No. of worms | Gravid females (%) [F2 + F3] |
|----------------------------|-----------------|-------------|----------------|-------------------------------|--------------|-------------------------|--------------|------------------------------|
| <i>Oncorhynchus mykiss</i> | 40 | 6 | 83.3 | 21.8 ± 5.7 | M | 2,969 ± 132 | 15 | 73.7 |
| | | | | | F | 4,289 ± 182 | 38 | |
| | | | | | M:F | 1:2.5 | | |
| <i>Percichthys trucha</i> | 40 | 6 | 16.6 | 0.9 ± 0.5 | M | 3,777 | 1 | 100 |
| | | | | | F | 5,339 | 1 | |
| | | | | | M:F | 1:1 | | |
| <i>Galaxias platei</i> | 40 | 5 | 40 | 2.5 ± 0.7 | M | 3,294 | 1 | 100 |
| | | | | | F | 4,700 ± 490 | 4 | |
| | | | | | M:F | 1:4 | | |
| <i>Galaxias maculatus</i> | Source group | 60 | 55 | – | M | 3,056 ± 110 | 33 | 81.3 |
| | | | | | F | 4,430 ± 91 | 73 | |
| | | | | | M:F | 1:2.1 | | |
| | Control group | 54 | 41.7* | – | M | 3,399 ± 104 | 55 | 73.5 |
| | | | | | F | 4,574 ± 83 | 109 | |
| | | | | | M:F | 1:2 | | |

Gravid females represent worms with maturing eggs (F2) or fully mature shelled eggs (F3)

Establishment refers to the presence of attached worms. *Prevalence calculated from first 30 *G. maculatus* autopsied

Fig. 1 Influence of salmonid presence on *A. tumescens* infections in native **a** *G. maculatus* and **b** *P. trucha*. Note Y-axis does not begin at 0 and scale differs for each species. Dashed line represents infection density in native host populations in absence of salmonids



increases in infection attributed to *O. mykiss* presence were still minor (Fig. 1).

Model exploration indicated that *G. maculatus* maintains the greatest proportion of the *A. tumescens*

population (1.54 worms m⁻²), with minor contributions made by all other fish species (<0.33 worms m⁻²; Table 5). Differences in the mean *A. tumescens* infection in all native hosts with and without salmonids

present, and at varying *G. maculatus* densities, indicated that native fish would experience on average only slight increases in infection with decreasing *G. maculatus* abundance (Fig. 2). Post-cyclic transmission had little effect on overall infection dynamics. Altering post-cyclic transmission rates had little influence on the density of worms in native and exotic fish, with the exception of *S. trutta*, which requires post-cyclic transmission to become infected (and then only at low intensity; Table 5).

Discussion

Experimental cystacanth infections demonstrated that *A. tumescens* in exotic *O. mykiss* had equal establishment success, and superior growth and attainment of maturity, compared to worms infecting native hosts. Post-cyclic infections demonstrated that *O. mykiss*

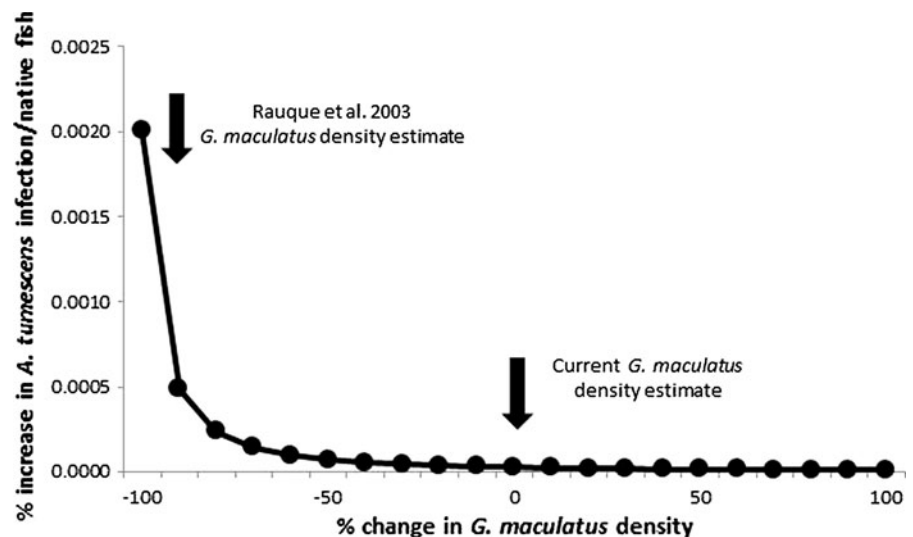
was also a competent host of *A. tumescens*, showing greater parasite establishment success than in native hosts. However, this transmission pathway was not linked to greater parasite growth or maturity, in either native or exotic post-cyclic hosts. Dynamic population modelling, incorporating data from experimental infections and previous field studies, revealed that of the three salmonids introduced to Lake Moreno, *S. fontinalis* is likely to make the greatest contribution to *A. tumescens* populations. However, the overall influence of exotic salmonids (including the *O. mykiss* fish farm) on *A. tumescens* infection in native hosts is predicted to be very limited. The model also indicated that *G. maculatus* maintains the majority of *A. tumescens* individuals in the system, with sensitivity analysis suggesting that changes in the rate of post-cyclic transmission of *A. tumescens* from infected *G. maculatus* have minimal influence on infection in other native and exotic hosts.

Table 5 Simulating the effects of altering post-cyclic transmission rates to exotic salmonids on *A. tumescens* infection densities (worms m⁻²) in native and exotic hosts

| Parameter changed | (%) of change | GP | PT | DV | OH | OM | SF | ST |
|-------------------------|---------------|----------|----------|----------|----------|----------|----------|----------|
| Post-cyclic consumption | 100 | 0.054549 | 0.330030 | 0.001598 | 0.008167 | 0.006801 | 0.039482 | 9.88e-10 |
| | 0 | 0.054549 | 0.330029 | 0.001598 | 0.008167 | 0.006800 | 0.039481 | 4.98e-10 |
| | -100 | 0.054549 | 0.330029 | 0.001598 | 0.008167 | 0.006798 | 0.039480 | 0 |

GP *Galaxias platei*, PT *Percichthys trucha*, DV *Diplomystes viedmensis*, OH *Odontesthes hatcheri*, OM *Oncorhynchus mykiss*, SF *Salvelinus fontinalis*, ST *Salmo trutta*

Fig. 2 Simulating the effect of altering *G. maculatus* abundance on *A. tumescens* infections in native fish. Values shown are outcomes of changes of $\pm 100\%$ in current estimates, in 10% increments



Although exotic host competency for native parasites is an important determinant of whether or not parasite spillback may occur (Kelly et al. 2009b), our study demonstrates that low relative density of exotic hosts diminishes the potential influence of exotic competency. This contrasts with situations involving pathogens with extremely high reproductive potentials such as bacteria or viruses (e.g. Hershberger et al. 2010a), which can potentially overcome limitations of low relative host densities. The high competency of *O. mykiss* for *A. tumescens* observed in infection experiments did not result in infection spillback to native fish in the model, because the low relative host density of salmonids weakened the potential for infection amplification. Minimal changes to native disease dynamics by exotic hosts occurring at low relative densities have also been reported for native *Ichthyophonus* sp. fungal infections acquired by American shad, *Alosa sapidissima*, a fish introduced to the Pacific coast of North America. Although American shad are highly susceptible to the disease, population densities of this exotic species have remained low until recent years (Hershberger et al. 2010b). American shad densities now exceed those of native salmonids, and the exotic species is considered responsible for the amplification of *Ichthyophonus* sp. infections, although this has yet to be linked to infection spillback in native fish (Hershberger et al. 2010b). Where spillback of infection has been suggested to occur, exotic species tend to occur in high abundances relative to native hosts. Such is the case in Lake Naroch, Belarus, where the exotic mollusc, *Dreissena polymorpha*, is very abundant in relation to native molluscs and is thought to have increased the abundance of metacercarial stages of the trematode *Echinoparyphium recurvatum* that infect waterfowl as a final host (Mastitsky and Veres 2010).

Our study demonstrates that taking into account the relative contribution of each transmission pathway to the flow of infection to a host is important when multiple pathways are available which differ in fitness benefits to a parasite. Different host species are not equally important to the overall dynamics of the parasite. While *A. tumescens* achieved greater components of fitness in salmonids when transmitted at the cystacanth stage, this transmission pathway was not the major source of parasites for salmonids. Instead, *A. tumescens* infections in salmonids were maintained by post-cyclic infection, a transmission pathway

shown to generate minimal fitness benefits to the parasite. Differences in parasite fitness between transmission pathways also provide an explanation for the model prediction that *S. fontinalis* may have a greater influence on *A. tumescens* infections than *O. mykiss*, as the former species acquires a greater proportion of parasites through cystacanth infections, while the latter obtains more parasites through post-cyclic transmission. The relative importance of each transmission pathway may also explain the minimal change in *A. tumescens* infections attributed to the presence of *S. trutta*, as this species not only occurred at low densities, but also relied on post-cyclic transmission to acquire infections. The relative contributions of multiple transmission pathways may be obscured when relying on field observations alone to provide indications about a parasite's fitness. Thus, utilising both experimental infections and population modelling is necessary, first to experimentally assess the relative parasite fitness associated with different transmission pathways and hosts, and second to dynamically model their influence on the parasite population.

Prior to salmonid introduction, little information was available about the composition and functioning of the Lake Moreno fish community (Macchi et al. 2007; Pascual et al. 2009). Population modelling provides an opportunity to reconstruct native host-parasite dynamics prior to the introduction of exotic species, and enables the evaluation of the relative importance of each host species to a parasite's population. Model simulations indicate that it is unlikely that exotic salmonids have negatively affected native fish communities in Lake Moreno by acting as competent reservoirs of native infection that spillback into native hosts. Declining populations of native species such as *D. viedmensis* and *O. hatcheri* are more likely explained by competition and predation by salmonids, rather than slight increases in *A. tumescens* infections driven by the exotic fish. This conclusion is also supported by diet surveys of native and exotic fish that show *D. viedmensis* only present in the guts of salmonids, and thus *D. viedmensis* may not have experienced predation pressure prior to the introduction of salmonids (Macchi et al. 1999).

Although previous field observations in Lake Moreno indicated that *A. tumescens* infections in *G. maculatus* may increase in prevalence and infection intensity with decreasing distance to the *O. mykiss* fish

farm (Revenga et al. 2005), and the presence of salmonid farms has been linked to increasing infection pressure to native fishes elsewhere (e.g. Krkosek et al. 2005), our modelling suggests that the fish farm in Lake Moreno causes little change to infection of native hosts overall. The increases in parasite infection observed by Revenga et al. (2005) may be localised around the fish farm due to high densities of *O. mykiss* in a relatively confined space, and indicate that if salmonid densities increased significantly, native fish might experience greater parasite burdens. As neither the parasite burdens in farmed *O. mykiss*, nor the density or infection status of amphipods in proximity to the fish farm, were reported by Revenga et al. (2005), we cannot speculate whether the relationship between parasite burdens and proximity to the farm is due to spillback of infection from exotic hosts, or increasing intermediate host density and enhanced transmission success.

Model limitations

Our ability to realistically model the dynamics of *A. tumescens* relies on assumptions about amphipod dynamics and fish densities that influence the conclusions derived from the population model. The lack of amphipod density information from the literature prevented the infection of amphipods being dynamically modelled. While we substituted the amphipod population for a constant to represent the infection in that population, which assumed that the proportion of infected amphipods is relatively constant throughout the year, we could not incorporate the natural fluctuations of infection observed by Rauque and Semenas (2007).

Recent advances in acoustic fisheries assessment have provided more accurate measurements of densities of larger fish species in Lake Moreno than in previous studies, while larval galaxiid abundance, production and survival studies have enabled densities of *G. maculatus* to be quantified (Vigliano et al. 2009). These density estimates, which we used in our modeling, suggest that the abundance of *G. maculatus* relative to other fish species in Lake Moreno is significantly greater than previously reported by Rauque et al. (2003). Our sensitivity analysis demonstrates that even if the density of this key species was over-estimated or under-estimated in the model, in relation to that for other fish, salmonids would still

only cause negligible increases of infection in native fish. This result however may not be the case if a highly virulent pathogen were involved. Likewise, although our model slightly underestimates the infection in the less abundant hosts, possibly due to greater infected amphipod or *G. maculatus* consumption rates than were estimated from previous studies, changes to the overall parasite dynamics are unlikely since the *A. tumescens* population is influenced by the most abundant parasite host.

In conclusion, this study suggests that although exotic salmonids are competent hosts of *A. tumescens*, their introduction to Lake Moreno is unlikely to have affected native fish populations through the amplification of infection. A low density of salmonids, relative to native fish, and the reliance of salmonids on post-cyclic transmission to obtain infection, weakens the potential spillback effects of enhanced parasite fitness in exotic hosts. It is likely that salmonids have had greater impacts on native fish communities through predation and competition, than via modified native host-parasite dynamics. Furthermore, the results of this study indicate that researchers must be cautious when assessing the influence of exotic species on native host-parasite dynamics based on field observations alone.

Acknowledgments We wish to thank L. Semenas, G. Viozzi, R. Vega (Laboratorio de Parasitología, Universidad Nacional del Comahue), M. Alonso, P. Di Giusto, O. Quatrin, M. Ugoccioni, V. Baez and the staff of Centro de Salmonicultura Bariloche for their assistance. Funding for this project was provided by a Marsden grant (Royal Society of New Zealand), Landcare Research, and the Elman Poole Travelling Fellowship (RAP). The manuscript was greatly improved by the comments of three anonymous reviewers.

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