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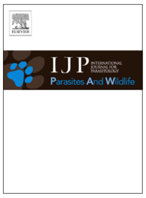

Relative competence of native and exotic fish hosts for two generalist native trematodes

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ABSTRACT

Exotic fish species frequently acquire native parasites despite the absence of closely related native hosts. They thus have the potential to affect native counterparts by altering native host–parasite dynamics. In New Zealand, exotic brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* have acquired two native trematodes (*Telogaster opisthorchis* and *Stegodexamene anguillae*) from their native definitive host (the longfin eel *Anguilla dieffenbachii*). We used a combination of field surveys and experimental infections to determine the relative competence of native and exotic fish hosts for these native parasites. Field observations indicated that the longfin eel was the superior host for both parasites, although differences between native and exotic hosts were less apparent for *S. anguillae*. Experimental infections indicated that both parasites had poorer establishment and survival in salmonids, although some worms matured and attained similar sizes to those in eels before dying. Overall, the field surveys and experimental infections indicate that these exotic salmonids are poor hosts of both native trematodes and their presence may decrease native parasite flow to native hosts.

Introduction

Whether through accidental introductions or intentional releases, many species attain distributions beyond their natural ranges and form novel interactions with native counterparts. Interactions mediated by predation and competition are frequently cited as detrimental outcomes of the presence of exotic species in novel habitats (e.g. Ricciardi et al., 1998; Wiles et al., 2003). Increasingly, however, exotic–native interactions mediated by disease are also recognised (e.g. Van Riper et al., 2002; Tompkins et al., 2003; LaDeau et al., 2007). Exotic salmonid fishes, for example, have long been known to influence native communities through novel predatory and competitive interactions (Crowl et al., 1992; Townsend, 2003), while the possibility of additional interactions mediated by disease have only recently been highlighted (Tompkins and Poulin, 2006; Kelly et al., 2009a).

Although salmonids are native to cold water environments of the Northern Hemisphere, global translocation for angling and aquaculture (Crawford and Muir, 2008) has resulted in the exchange of fish between regions where native salmonids already occur (e.g. rainbow trout *Oncorhynchus mykiss* native to North America's Pacific Coast introduced to the United Kingdom, and brown trout *Salmo trutta* native to Eurasia introduced to North America; MacCrimmon and Marshall, 1968; MacCrimmon, 1971) and the introduction of salmonids to regions where they were naturally absent (e.g. Australasia, South America). Salmonids introduced to the Southern Hemisphere have largely escaped salmonid-adapted diseases because the introduction of parasite-free ova or fry (Kennedy and Bush, 1994), and the use of multiple-stage translocations (e.g. New Zealand brown trout originated from fish introduced to Australia; MacCrimmon and Marshall, 1968), severely limited the likelihood of co-introducing diseases during translocations. However these fish have not escaped disease burdens entirely, with exotic salmonids acquiring generalist parasites from native fish communities (Dix, 1968; Ortubay et al., 1994) and, in some cases, attaining equal or greater parasite species richness than in their area of origin (Poulin and Mouillot, 2003).

The ease with which exotic salmonids acquire native parasites increases the potential for these fish to modify native host–parasite dynamics, either acting as competent parasite reservoirs that "spillback" infection to native hosts (see Daszak et al., 2000; Kelly et al., 2009b), or as incompetent parasite hosts that dilute disease burdens in native hosts (e.g. Telfer et al., 2005; Kopp and Jokela, 2007). While few studies have investigated the influence of exotic salmonids on native host–parasite dynamics, assessments of *Acan-*

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thocephalus tumescens in rainbow trout (Paterson et al., 2013) and *Acanthocephalus galaxii* in brown trout (Paterson et al., 2011) suggest that exotic salmonid competence for native parasites often differs from that of the native hosts.

In Lake Pearson, New Zealand, the co-existence of brown and rainbow trout presents an opportunity to compare the competence of two exotic salmonids for native fish parasites simultaneously. Although knowledge of native host–parasite dynamics in this lake was lacking prior to the current study, the native fish community was known to be comprised of multiple hosts of the native trematodes *Stegodexamene anguillae* MacFarlane, 1951 and *Telogaster opisthorchis* MacFarlane, 1945. These trematodes co-infect their definitive native eel hosts, *Anguilla* spp. (*S. anguillae* – upper intestine, *T. opisthorchis* – lower intestine; MacFarlane, 1945, 1951), and have been reported in exotic salmonids elsewhere in New Zealand (Dix, 1968; Hine et al., 2000; Kelly et al., 2009a). Both trematodes exhibit similar life cycles, with eggs released from adult worms reaching the water column with eel faeces, and the first intermediate host (the snail *Potamopyrgus antipodarum*) becoming infected by either ingesting eggs (for *T. opisthorchis*) or encountering free-living larvae that emerge from eggs (for *S. anguillae*). Second intermediate hosts, the native fish *Galaxias* spp. and *Gobiomorphus* spp., become infected by encountering cercarial infective stages released from snails that encyst as metacercariae in fish tissues. Eels acquire trematodes by consuming infected second intermediate hosts. Salmonids are known to prey on both *Galaxias* and *Gobiomorphus* in New Zealand lakes (e.g. McCarter, 1986; Rowe et al., 2002). Hence, they too frequently encounter trematode metacercarial cysts. Exotic salmonids may therefore modify native host–parasite dynamics by altering the abundance of second intermediate hosts through predation, in addition to altering disease burdens in both intermediate and definitive hosts.

Here we apply a three-pronged approach to (i) quantify the relative competence of native and exotic fish hosts for these two generalist native parasites and (ii) determine whether salmonid species differ in their influence on native host–parasite dynamics. First, we use field data to evaluate the relative acquisition of native trematodes by native and exotic hosts. Second, we use experimental infections to determine whether host competence for native parasites differs between exotic salmonids, and between native and exotic hosts. Third, we consider how the acquisition of native parasites by exotic salmonids may influence native host–parasite dynamics.

Materials and methods

Study site

Lake Pearson (24°10′520E, 57°87′570N) is a small, shallow lake (1.79 km^2, maximum depth 17 m) situated in the Waimakariri River Catchment, South Island, New Zealand. The fish community is comprised of four native fish species (longfin eel *Anguilla dieffenbachii*, common bully *Gobiomorphus cotidianus*, upland bully *Gobiomorphus breviceps* and koaro *Galaxias brevipinnis*), and four exotic salmonids (brown trout, rainbow trout, chinook salmon *Oncorhynchus tshawytscha* and lake trout *Salvelinus namaycush*), though the latter two salmonids are considered rare (Hutchison, 1981; Rowe and Graynoth, 2002).

Field surveys

Field surveys were conducted during April–May (Austral Autumn) and September 2008 (Austral Spring) to determine the prevalence (proportion of infected individuals) and infection intensity (number of parasites per infected host; Bush et al., 1997) of *T. opisthorchis* and *S. anguillae* in second intermediate and definitive fish hosts. Salmonids were sampled using sinking 25 m multi-panel gill nets (mesh sizes: 13, 25, 38, 56, 70 mm) set for 1–2 h during daylight hours, while longfin eels were sampled using unbaited fyke nets (wing length 450 cm, stretched mesh size 20 mm) set overnight. Koaro and bullies were sampled using unbaited minnow traps (height 25 cm, length 45 cm, stretched mesh size 5 mm) set overnight, with seine nets used to capture additional fish when minnow traps obtained fewer than 30 individuals/species/survey. The number of fish captured by each sampling technique was used to determine the relative abundance ratios of fish hosts, comparable only between species caught using the same sampling technique.

A random sub-sample of up to 30 fish per species per sampling period was euthanized (totals: 47 brown trout, 42 rainbow trout, 40 common bully, three upland bully, two koaro). Fork length (FL mm; salmonids) or total length (TL mm; native fish) were recorded for each fish prior to preserving the alimentary canal (oesophagus to anus) in 10% buffered formalin. Remaining body tissues of bullies and koaro were frozen for later examination for metacercarial cysts. Body tissues of salmonids were not examined for metacercarial cysts because previous field surveys showed brown trout had very low prevalence and infection intensity of metacercarial cysts, although sympatric native fish had moderate infections (Kelly et al., 2009a). Longfin eels were not examined for intestinal parasites and were instead released alive, as this native fish is of high conservation status in Lake Pearson. To provide a reference for trematode prevalence, infection intensity and maturity in native definitive hosts, nine longfin eels were collected from a nearby lake that supported the same fish species as Lake Pearson (Lake Sumner; 24°42′440E, 58°33′810N).

Trematodes in the alimentary canals of trout and eels were enumerated in the laboratory. The development status (non-gravid or gravid, based on the presence of eggs in utero) and worm size (calculated from the surface area of an ellipse = $\pi \times (L/2) \times (W/2)$, L = length in μm and W = width at widest point in μm) were determined for each worm. The number of eggs in the uterus and egg volume ($V = \pi \times L \times W^2/6$, where L = length and W = width) of a subsample of five eggs were measured for each gravid worm. Stomach contents of each definitive host were examined to estimate the number of koaro and bullies consumed.

The density of the snail *P. antipodarum* was estimated from 12 benthos samples (706 cm^2) collected from random locations within 5 m of the shore during April–May 2008 (n = 12), with samples preserved in 10% formalin prior to enumeration of snails.

Experimental infection

An infection experiment was conducted to evaluate rates of parasite establishment, fecundity and mortality for both trematode species in native and exotic definitive hosts. Brown trout (FL 107–148 mm) were collected by electric fishing from the Cap Burn (22°95′560E, 55°46′220N), Otago. Rainbow trout (FL 182–244 mm) were obtained from Otago Fish and Game's Macraes Hatchery, Otago. Wild-caught longfin eels (TL 460–550 mm) were sourced from New Zealand Eels Limited, Te Kauwhata, Waikato. All fish were acclimatised in separate 200 L tanks in the University of Otago's controlled climate facilities (13 h day/11 h night period, 10 °C, 15% daily water change) for 2 weeks prior to experimentation. A common food consumed by all fish species was not available so fish were maintained on different diets fed *ad libitum* (longfin eel and brown trout – blood worms; rainbow trout – commercial fish pellets).

Experimental fish were treated during acclimatisation with an anthelmintic, Praziquantel, in tablet form (25 mg – longfin eel;