Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 990–998 doi: 10.1111/j.1365-2656.2011.01834.x

Introduced brown trout alter native acanthocephalan infections in native fish

Rachel A. Paterson[1]*, Colin R. Townsend[1], Robert Poulin[1] and Daniel M. Tompkins[2]

[1]*Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand; and* [2]*Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand*

Summary

1. Native parasite acquisition provides introduced species with the potential to modify native host–parasite dynamics by acting as parasite reservoirs (with the 'spillback' of infection increasing the parasite burdens of native hosts) or sinks (with the 'dilution' of infection decreasing the parasite burdens of native hosts) of infection.

2. In New Zealand, negative correlations between the presence of introduced brown trout (*Salmo trutta*) and native parasite burdens of the native roundhead galaxias (*Galaxias anomalus*) have been observed, suggesting that parasite dilution is occurring.

3. We used a multiple-scale approach combining field observations, experimental infections and dynamic population modelling to investigate whether native *Acanthocephalus galaxii* acquisition by brown trout alters host–parasite dynamics in native roundhead galaxias.

4. Field observations demonstrated higher infection intensity in introduced trout than in native galaxias, but only small, immature *A. galaxii* were present in trout. Experimental infections also demonstrated that *A. galaxii* does not mature in trout, although parasite establishment and initial growth were similar in the two hosts. Taken together, these results support the hypothesis that trout may serve as an infection sink for the native parasite.

5. However, dynamic population modelling predicts that *A. galaxii* infections in native galaxias should at most only be slightly reduced by dilution in the presence of trout. Rather, model exploration indicates parasite densities in galaxias are highly sensitive to galaxias predation on infected amphipods, and to relative abundances of galaxias and trout. Hence, trout presence may instead reduce parasite burdens in galaxias by either reducing galaxias density or by altering galaxias foraging behaviour.

Key-words: dilution effect, disease, galaxias, introduced species, New Zealand, parasite, salmonid

Introduction

Introduced species have the potential to modify native host–parasite dynamics through the acquisition of native parasites. Recent reviews have demonstrated that introduced animals may acquire about five native parasites on average, with some gaining more than 16 (Torchin *et al.* 2003; Kelly *et al.* 2009b). These reviews highlight that not only do a great variety of introduced species acquire native parasites, but also that the acquired parasites are highly diverse.

The frequency with which introduced species acquire native parasites has led to increasing attention to the ways they can modify native parasite dynamics. Parasite 'spillback' to a native host may result from the acquisition of native parasites by an introduced species, provided that it becomes a competent host that can act as a reservoir of infection (Daszak, Cunningham & Hyatt 2000; Tompkins & Poulin 2006; Kelly *et al.* 2009b). The spillback of parasites may act as an additional threat to native biodiversity via increased disease impacts on species already facing mounting pressures from other sources such as competition, predation, habitat loss, pollution and climate change. Recent studies have also documented how the acquisition of native parasites by introduced species may lead to parasite 'dilution', whereby native hosts experience lower parasite burdens in the presence of introduced hosts (Telfer *et al.* 2005; Kelly *et al.* 2009a; Thieltges *et al.* 2009). While reduced parasite burdens in native hosts may appear of less concern, alterations to processes that regulate population densities may have flow-on effects on native species dynamics, such as the modification of competitive advantage between conspecifics (Kopp & Jokela 2007), which could result in subsequent alterations to

*Correspondence author. E-mail: patra374@student.otago.ac.nz

community dynamics and ecosystem functioning. The frequency with which introduced species acquire native parasites and attain high population densities means there is much potential for either parasite spillback or dilution to occur.

Our current understanding of the potential impacts of introduced species on native host–parasite interactions relies largely on field-based observations of introduced populations, using a combination of parasite fitness parameters at individual (e.g. size, fecundity) and population scales (e.g. prevalence, infection intensity, abundance; Bush *et al.* 1997) to assess the competency of introduced species as native parasite hosts (Rauque, Viozzi & Semenas 2003). Such assessments have been made with or without sympatric native host populations (Galli *et al.* 2005), and occasionally native parasite dynamics have been surveyed within native-only host populations to provide baselines from which the effects of an introduced host are judged (Dubois, Marcogliese & Magnan 1996; Kelly *et al.* 2009a). However, native populations free from the effects of introduced species are not always available for such comparisons to be made.

While field-based observations are essential to ascertain which native parasites have been acquired by introduced species and to identify patterns, differences in parasite fitness parameters between native and introduced hosts may not provide a true reflection of a parasite's overall performance. Field observations can obscure differences in establishment success, survival/mortality, maturation, growth and relative fecundity. For example, poor host competency of an introduced host in terms of parasite establishment could be masked if this species was more likely to encounter infectious stages, resulting in similar levels of prevalence and/or infection intensity in native and introduced populations. Similarly, comparable numbers of mature parasites in native and introduced hosts might suggest equal compatibility for a native parasite in both hosts, but field observations of parasite maturity cannot take into account differing maturity rates between native and introduced hosts.

Recognizing the potential limitations of field observations, some researchers have used experimental infection trials to allow differences in parasite fitness between hosts to be verified under standard conditions (King, van Oosterhout & Cable 2009; Thieltges *et al.* 2009). However, even this approach fails to account for the dynamics of the whole host–parasite system in terms of relative abundances of host populations, infection encounter rates by intermediate hosts and potential host behavioural changes caused by the presence of an introduced species. For example, hosts that occur at high densities are more likely to influence parasite dynamics than less common hosts.

Here, we provide an in-depth assessment of parasite fitness in native and introduced hosts in a system previously identified as one in which the acquisition of native parasites by an introduced species results in the dilution of parasites in native hosts (Kelly *et al.* 2009a). We utilize a multiple-scale approach of field observations, experimental trials and dynamic population modelling to examine this complex system and identify mechanisms responsible for observed field patterns.

Materials and methods

STUDY SYSTEM

In New Zealand, the introduced brown trout (*Salmo trutta* L.) is a dominant freshwater fish considered responsible for the decline and local extinction of native fish species (Townsend 2003). Since its introduction as parasite-free eggs in 1867 (MacCrimmon & Marshall 1968), more than 10 native parasite species have been acquired by brown trout, including the generalist freshwater acanthocephalan *Acanthocephalus galaxii* Hine (Hine, Jones & Diggles 2000). In the Otago province of the South Island of New Zealand, this acanthocephalan has been reported from sympatric stream populations of native roundhead galaxias (*Galaxias anomalus* Stokell) and brown trout (Kelly *et al.* 2009a). The parasite matures in the intestine of the definitive fish host and releases eggs into the water column via fish faeces. Larval cystacanth stages develop in the intermediate amphipod host *Paracalliope fluviatilis* Thomson after egg ingestion, with the life cycle of *A. galaxii* completed following predation of infected amphipods by the definitive host (Hine 1977). Brown trout are a major predator of galaxiids (Crowl, Townsend & McIntosh 1992; Townsend 1996) and thus may acquire additional *A. galaxii* infections via postcyclic transmission when roundhead galaxias are eaten. This additional transmission route has been reported in many acanthocephalan species, including native acanthocephalans transmitted from native galaxias to introduced trout in Argentina (Rauque, Semenas & Viozzi 2002), but has not been experimentally demonstrated for *A. galaxii*. Preliminary field observations suggest that *A. galaxii* attains equal or higher prevalence and infection intensity in brown trout (Kelly *et al.* 2009a), indicating the potential for modification of parasite–host dynamics by this introduced host.

FIELD SURVEYS

Field surveys were conducted to determine the prevalence (the percentage of infected hosts) and infection intensity (the number of worms per host; *sensu* Bush *et al.* 1997) of *A. galaxii* in its definitive and intermediate host species, and the relative densities of these hosts at three sites previously identified by Kelly *et al.* (2009a) as 'sympatric' for roundhead galaxias and brown trout infected with *A. galaxii*: Swin Burn Q1 (22°96′90″E, 55°58′70″N), Swin Burn Q2 (22°98′30″E, 55°59′40″N) and Old Hut Creek (22°94′00″E, 55°68′73″N), all in the upper Taieri River catchment in Otago. Each site was visited on 4–5 occasions between June 2007 and August 2008 to monitor temporal changes in host and parasite populations. Fish densities at each site were assessed by single-pass electric fishing of the same reach (230–416 m^2) on each occasion. Random subsamples of roundhead galaxias ($n = 5–27$) and brown trout ($n = 1–16$) from each site were euthanized, measured for fork length (FL) to the nearest 1 mm and preserved in 10% buffered formalin. In the laboratory, the alimentary canal from oesophagus to anus of each fish was removed and split longitudinally. The abundance of acanthocephalans was noted, and the length (μm) and sex of each worm were recorded. In addition, for female worms, developmental status (F1 – immature with ovarian balls only, F2 – maturing eggs, F3 – fully mature eggs) and proportion of mature eggs in a subsample of 50 eggs were also recorded. The number of *P. fluviatilis* and prey fish present in fish stomachs was also enumerated, to assess the relative importance of cystacanth and postcyclic infection pathways.

The prevalence of infection in the intermediate amphipod host *P. fluviatilis* was measured on each site visit from a 3–5-min kick sample spread diagonally across the stream to sample all microhabitats. Amphipods were preserved in 10% formalin and up to 1000 amphipods from each sample were examined for the presence of cystacanths.

INFECTION EXPERIMENT

An infection experiment was conducted to determine the fitness of *A. galaxii* worms in both definitive hosts, from which relative rates of parasite establishment, maturation and mortality could be estimated. Brown trout (131–191 mm) and roundhead galaxias (60–75 mm) were collected by electric fishing from the Cap Burn (22°95′56″E, 55°46′22″N) and a tributary of the Kye Burn (22°93′23″E, 55°63′67″N), and acclimatized in the University of Otago's controlled climate facilities (13-h day/11-h night period, 10°C, 15% daily water change, fed *ad libitum* with commercial pellets) for 6 months prior to experimentation. All experimental fish were treated with the anthelmintic Tetramisole HCl (10 mg L^{-1} 48 h × 2 repeat) at the beginning of the acclimatization period to remove any naturally acquired parasites prior to artificial infection. Infection status prior to the experiment was investigated by autopsy of five-treated and five-untreated fish per species, during which no intestinal parasites were found in treated or untreated fish. Six experimental fish of each species were randomly assigned to two infection time-periods (2 or 6 weeks). During the 48 h prior to experimental infection, each fish was measured (FL) and placed without food into an individual tank (tank size: 15 L – roundhead galaxias, 30 L – brown trout).

Intermediate infective stages of *A. galaxii* were obtained by collecting naturally infected *P. fluviatilis* amphipods by handnet from the Swin Burn (22°98′30″E, 55°59′40″N). Infection status was determined under a dissection microscope. A subsample of 15 amphipods identified as infected was autopsied to assess observer error in correctly identifying the presence of *A. galaxii*, with single infections of *A. galaxii* correctly identified in all amphipods. Ten live infected *A. galaxii* amphipods were placed into each tank. The number of amphipods consumed by each fish was monitored by checking for uneaten individuals 24- and 48-h postexposure. All unconsumed amphipods were removed at 48-h postexposure, and fish resumed their diet of *ad libitum* commercial fish pellets. At the completion of each infection period (2 or 6 weeks), fish were euthanized and immediately examined for parasites prior to fixing all acanthocephalans in 10% buffered formalin. Worm measurements were made as in the field survey.

STATISTICAL ANALYSES

Statistical analyses of field survey and experimental infection data were conducted using SPSS Statistic 15.0 (SPSS 2006). Parametric tests were used for all analyses, for which data were transformed when necessary to meet the normality assumptions of analysis of variance (ANOVA).

POPULATION MODEL

A population model was constructed using MODEL MAKER 4.0 (Cherwell 2000) to dynamically simulate the influence of brown trout presence on *A. galaxii* in its definitive hosts.

Model formulation

The life cycle of *A. galaxii* was modelled using a series of linked differential equations that simulate (on a daily basis, scaled to 1 m^2) the populations of uninfected (A_{NP}) and infected (A_P) amphipods, the populations of immature and mature *A. galaxii* worms in roundhead galaxias (I_G, W_G) and trout (I_T, W_T), and the number of *A. galaxii* eggs in the environment (E), in discrete time steps:

$$\frac{dA_{NP}}{dt} = (\lambda_A S + \sigma e^{-x(A_{NP}+A_P)} - 1 - C_T T - C_G G - vE)A_{NP} \quad \text{eqn 1a}$$

$$\frac{dA_P}{dt} = vEA_{NP} + \Big((\sigma e^{-x(A_{NP}+A_P)} - 1)X + (C_T T + C_G G)Y\Big)A_P \quad \text{eqn 1b}$$

$$\frac{dI_G}{dt} = C_G G Y_\gamma A_P - (m_G + a_G + b_G + DT)I_G \quad \text{eqn 2a}$$

$$\frac{dI_T}{dt} = \gamma T(C_T Y A_P + DI_G) - (m_T + a_T + b_T)I_T \quad \text{eqn 2b}$$

$$\frac{dW_G}{dt} = m_G I_G - (a_G + b_G + DT)W_G \quad \text{eqn 3a}$$

$$\frac{dW_T}{dt} = m_T I_T + \gamma DTW_G - (a_T + b_T)W_T \quad \text{eqn 3b}$$

$$\frac{dE}{dt} = (W_G + W_T)\lambda_W - (\varepsilon + vA_{NP})E \quad \text{eqn 4}$$

The amphipod population was dynamically modelled to reflect changing amphipod densities throughout the year while fish densities were held constant (T and G for trout and galaxias, respectively) because field surveys indicate the latter remain relatively constant throughout the year, and there is no evidence of parasite impact on fitness (Kelly *et al.* 2009a).

The population of uninfected amphipods A_{NP} (eqn 1a) increases as a function of amphipod fecundity (λ_A) (toggled by S, a logic switch denoting the breeding season) and decreases as a function of natural mortality ($\sigma - 1$, where σ is survival) influenced by density dependence (x), predation by trout (C_T) and galaxias (C_G), and infection (ν).

The population of infected amphipods A_P (eqn 1b) increases as a function of infection (v), and is modified by a combination of natural mortality ($\sigma - 1$) modified by density dependence (x) and infection (X), and the predation of infected amphipods by trout (C_T) and galaxias (C_G), also modified by infection (Y). The parameter Y acknowledges that the presence of the parasite can be expected to increase the likelihood that an amphipod will be eaten. If the rate at which uninfected amphipods ingest acanthocephalan eggs exceeds the number of uninfected amphipods, all amphipods are considered to be infected.

The population of immature worms in galaxias I_G (eqn 2a) increases with the predation of infected amphipods ($C_G Y$), modified by establishment success (γ). The number of immature worms decreases with worm maturation (m_G), parasite mortality (α_G), natural host mortality (b_G) and postcyclic transmission of worms from galaxias to trout (D). The population of immature worms in trout I_T (eqn 2b) increases with the predation of infected amphipods (C_TY) and postcyclic transmission (D), both modified by establishment success (γ), and decreases with worm maturation (m_T), worm mortality (α_T) and natural host mortality (b_T).

The population of mature worms in galaxias W_G (eqn 3a) increases as a function of worm maturation (m_G) and decreases with parasite mortality (α_G), natural host mortality (b_G) and postcyclic transmission (D). The population of mature worms in trout W_T (eqn 3b) increases as a function of worm maturation (m_T), the establishment (γ) of postcyclically transmitted worms from galaxias to trout (D), and decreases because of the effects of parasite mortality (α_T) and natural host mortality (b_T). A density dependence parameter influencing worm survival was not incorporated into immature or mature worm equations, as very low field infection intensities of *A. galaxii* were observed in the species modelled in contrast to burdens recorded from other galaxias hosts in New Zealand (cf. *Galaxias maculatus* mean infection intensity 127 per fish; Hine 1977).

The number of *A. galaxii* eggs in the environment E (eqn 4) increases as a function of the number of eggs produced (λ_W) from mature worms in both galaxias (W_G) and trout (W_T), and decreases with natural mortality (ε) and the ingestion of eggs by amphipods (v).

Model parameterization

Parameter estimates were obtained, where possible, from the field surveys and experimental infections reported here, and from the published literature and unpublished data (see Tables 1 and 2). Host densities (G, T) were calculated as the average number of fish per m^2 at Swin Burn Q1 and Q2 combined (Old Hut Creek was not included in the parameterization of the model as only a single *A. galaxii* infection was recorded there). The daily mortality rate of brown trout was based on a maximum life span of 5–6 years for nonmigratory brown trout (Huryn 1996), whereas the mortality rate of roundhead galaxias was estimated from a closely related species, *Galaxias paucispondylus* (Bonnett 1990).

Mean amphipod density was estimated as 250 amphipods per m^2 (Weller 2003), with natural survival estimated from the maximum life span of 1 year (F. Wilhelm, unpublished). The daily fecundity rate of 0·058 new individuals per amphipod during the breeding season (September to March, austral spring to end of austral summer) was estimated from a maximum of 3·5 broods of five eggs per female and a 0·5 sex ratio (F. Wilhelm, unpublished). However, as a proportion of females are known to breed year round (Towns 1981), breeding from April to August (austral autumn and winter) was set at 20% of the maximum.

The probability of amphipods being consumed by each definitive host was calculated as the average number of amphipods in the host gut (with an assumed gut clearance time of 48 h; Tekinay, Guner & Davies 2003) relative to amphipod density (field survey). The potential for postcyclic transmission of parasites from galaxias to trout was calculated from the average number of roundhead galaxias present in the stomachs of brown trout in the field surveys.

Although acanthocephalans have been shown to markedly alter intermediate host behaviour (Baldauf *et al.* 2007), often increasing the likelihood that infected individuals will be eaten (Moore 1984; Lagrue *et al.* 2007), no information is available about how *A. galaxii* alters the risk of being eaten (Y) or mortality (X) of its amphipod host. Likewise, no information is available about amphipod density dependence (x) or parasite egg ingestion rate by amphipods (ν). These parameters were estimated by model optimization to the values

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

	Galaxias		Trout			
Parameter	Symbol	Value	Symbol	Value	Units	Source
Density	G	0·0763	T	0·0117	m^{-2}	This study
Predation of amphipods	C_G	0·00047	C_T	2e–05	amphipod per host per day	This study
Parasite establishment	γ	0·5078	γ	0·5078	per worm	This study
Parasite mortality	a_G	0·01869	a_T	0·0416	per worm per day	This study
Parasite maturation	m_G	0·006	m_T	0·000	per worm per day	This study
Natural host mortality	b_G	0·0007	b_T	0·0004	per host per day	Bonnett (1990), Huryn (1996)
Predation of galaxias	–	–	D	0·01	per galaxias per trout per day	This study

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

Parameter	Symbol	Value	Units	Source
Amphipod breeding rate	λ_A	0·058	per amphipod per day	F. Wilhelm, unpublished data
Amphipod natural mortality	σ	0·0027	per amphipod per day	F. Wilhelm, unpublished data
Parasite fecundity	λ_W	807·5	per worm per day	Crompton & Whitfield (1968)
Ingestion rate of eggs by amphipods	N	6e–06	per egg per amphipod per day	This study
Egg mortality	E	0·005	per egg per day	Crompton (1970)
Amphipod density dependence	x	0·0001	per amphipod per day	Model optimization
Parasite influence on amphipod mortality	X	26·68	per amphipod per day	Model optimization
Parasite influence on amphipod predation	Y	40·36	per amphipod per day	Model optimization

that result in predicted levels of prevalence and infection intensity, in both intermediate and definitive hosts, equivalent to those observed in the field (a mean population size of 250 m^{-2} for uninfected amphipods, a mean prevalence of infected amphipods of 0·1%, and a mean worm population size of 0·1 m^{-2} at equilibrium dynamics). Once an amphipod becomes infected with a single *A. galaxii*, we assumed it does not consume additional eggs. This assumption does not affect model dynamics as eggs are highly abundant in the environment, and prevalence of amphipod infection is low.

The establishment, maturation and mortality rates of *A. galaxii* in each definitive host were estimated from the infection experiment. Parasite establishment at day one and the daily mortality rate of *A. galaxii* in galaxias were estimated from the slope of the line calculated from the percentage of worms present at 2 and 6 weeks postinfection. No worms were present in trout at 6 weeks postinfection, so parasite establishment rate in trout was assumed to be the same as in galaxias, while parasite mortality rate was estimated from the decline to zero parasites at 6 weeks. No mature worms were present in trout from either the experimental infection or field survey; thus, the maturity rate in trout was set at 0.

The daily rate of parasite egg production was estimated from the acanthocephalan, *Polymorphus minutus* (1700 eggs per female per day; (Crompton & Whitfield 1968), divided by the overall parasite male:female ratio observed in the current study. Egg mortality was based on aquatic acanthocephalan eggs being known to survive a maximum of 6–9 months (Crompton 1970).

Model simulation

Although brown trout are known to have altered freshwater fish communities in New Zealand, resulting in the declining abundance and localized extinction of some *Galaxias* species (Townsend 2003), their influence on native host–parasite dynamics is largely unknown. Here, we use model simulations to examine the influence of brown trout on native parasite dynamics in roundhead galaxias by investigating varying ratios of fish community composition that represent (i) fish communities prior to trout introduction (galaxias scenario), (ii) trout presence in native communities (galaxias + trout scenario) and (iii) localized extinction of native fish (trout scenario). To understand how the presence of the exotic host might be influencing observed levels of infection in the native host, we use sensitivity analyses to test the validity of potential contrasting hypotheses in the galaxias + trout scenario: (i) brown trout out-compete roundhead galaxias for infected amphipods (varying C_T), (ii) brown trout prey on roundhead galaxias (varying D) and (iii) brown trout modify the behaviour of roundhead galaxias, resulting in altered consumption of infected amphipods (varying C_G).

Simulations were run varying the above parameters ± 100% around their estimated value in 10% increments, to investigate the influence of each parameter on the infection intensity of *A. galaxii* in roundhead galaxias. For each scenario, we monitored peak density of *A. galaxii* in the roundhead galaxias population (m^{-2}) after 3000 daily iterations.

Results

FIELD SURVEY

Roundhead galaxias was the most abundant definitive host in surveyed streams, with average densities of 0·05–0·20 fish per m^2 for roundhead galaxias and 0·005–0·07 fish per m^2 for brown trout. A total of 219 of 537 roundhead galaxias (39–91 mm) and 84 of 126 brown trout (63–189 mm) were examined for *A. galaxii*. At Old Hut Creek, 72 galaxias and 34 trout were examined, but only a single *A. galaxii* infection was recovered from one roundhead galaxias on a single occasion (in June 2007). This site was removed from further analysis of field survey observations.

Infection prevalence did not differ significantly between sites or host species (GLM; $P > 0{\cdot}05$), with the percentage of fish infected ranging from 12·5% to 85% for roundhead galaxias and 0–100% for brown trout (Table 3). Infection intensities were highest in brown trout (natural log transformed: GLM species; $F_{1,93} = 4{\cdot}977$, $P = 0{\cdot}028$) but did not

Table 3. Seasonal prevalence, infection intensity and length *Acanthocephalus galaxii* in naturally infected roundhead galaxias and brown trout from sites Q1 and Q2 on the Swin Burn

Site	Host Species	Season	No. of hosts	Prevalence %	Infection intensity (mean ± SD)	Male length µm (mean ± SD)	Female length µm (mean ± SD)	No. of parasites
Q1	Roundhead galaxias	Jun 07	10	40	2·8 ± 1·5	1725 ± 527	4800 ± 566	11
		Oct 07	27	40·7	6·6 ± 6·3	2376 ± 1023	3002 ± 1844	72
		Mar 08	16	12·5	5	2600 ± 650	4350 ± 1222	10
		May 08	20	45	16·6 ± 19·7	1699 ± 563	2447 ± 963	149
		Aug 08	19	52·6	11·2 ± 16	2057 ± 393	3403 ± 1221	112
	Brown trout	Jun 07	0	–	–	–	–	–
		Oct 07	6	83·3	12·6 ± 14·6	1210 ± 323	1141 ± 266	63
		Mar 08	3	100	13·7 ± 16·8	1039 ± 239	1162 ± 232	41
		May 08	1	0	–	–	–	–
		Aug 08	0	–	–	–	–	–
Q2	Roundhead galaxias	Oct 07	20	80	11·2 ± 22·4	1851 ± 713	2520 ± 1374	179
		Mar 08	10	80	1·5 ± 0·5	2346 ± 940	2720 ± 952	12
		May 08	20	85	4·1 ± 3·8	2108 ± 716	3349 ± 1665	65
		Aug 08	5	60	5·7 ± 4·7	1642 ± 391	3255 ± 900	17
	Brown trout	Oct 07	14	85·7	10·8 ± 12·1	943 ± 193	967 ± 180	129
		Mar 08	4	75	6·3 ± 3·8	1378 ± 370	1295 ± 341	19
		May 08	2	50	27	1254 ± 192	1405 ± 208	27
		Aug 08	2	100	10	1478 ± 311	1475 ± 293	20

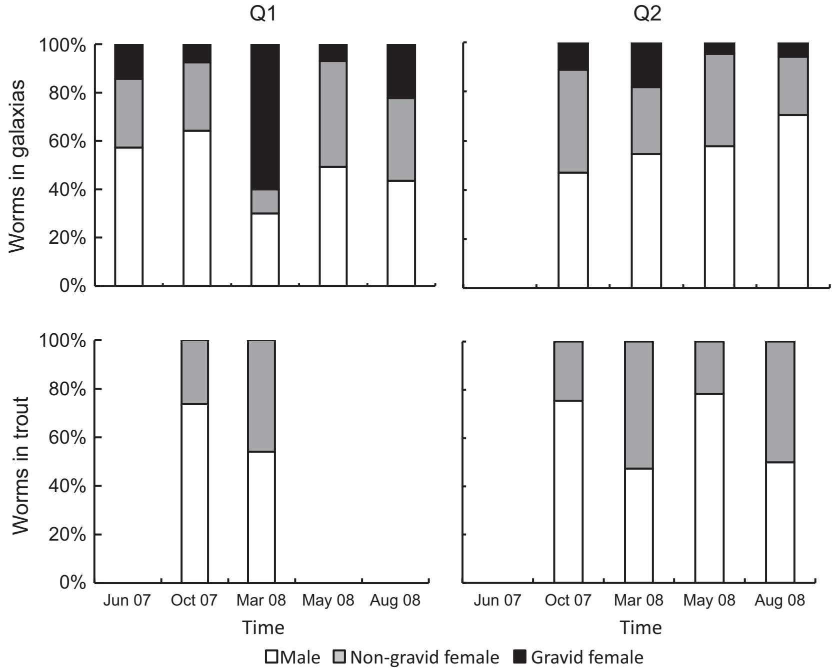

Fig. 1. Seasonal composition of *Acanthocephalus galaxii* sex and reproductive status in roundhead galaxias and brown trout at sites Q1 and Q2 on the Swin Burn. Gravid female worms with maturing eggs (F2) or fully mature shelled eggs (F3) were absent from brown trout throughout the study period.

differ between sites or seasons. Acanthocephalans were larger in roundhead galaxias than brown trout (GLM species; $F_{1,220} = 24{\cdot}803$, $P < 0{\cdot}001$), with female worms larger than male worms (GLM sex; $F_{1,220} = 5{\cdot}965$, $P = 0{\cdot}015$). All female worms recovered from brown trout were immature with ovarian balls present only, while on average 18·6% of female worms in roundhead galaxias contained developing eggs (F2) or fully mature shelled eggs (F3) (Fig. 1).

Examination of stomach contents showed that 71% of brown trout stomachs contained amphipods, with an average of 14·9 amphipods per fish, while 17% of roundhead galaxias stomachs contained amphipods, with an average of two amphipods per fish. Fourteen per cent of brown trout stomachs also contained roundhead galaxias, with between one and three galaxias present. Prevalence of infection in amphipods collected from kick samples was very low at all sites, with a maximum of 0·1% of amphipods infected.

INFECTION EXPERIMENT

Similar percentages of worms had established in each host species at 2 weeks postinfection, with an average of 38·6% of worms establishing in roundhead galaxias and 28·0% in brown trout (one-way ANOVA species; $P = 0{\cdot}465$; Fig. 2). The intensity of infection declined in both species between 2 and 6 weeks postinfection, with 19·2% of worms remaining in galaxias and no worms in trout (Fig. 2).

Male *A. galaxii* were larger in brown trout than in roundhead galaxias at 2 weeks postinfection (one-way ANOVA male; $F_{1,14} = 5{\cdot}948$, $P = 0{\cdot}030$), while female worms were of similar length ($P = 0{\cdot}136$, Table 4). Worm size increased between 2 and 6 weeks postinfection, with average male and female lengths in galaxias at 6 weeks postinfection greater than in trout at 2 weeks postinfection. No gravid female worms were present in either host species at 2 weeks postinfection, while one of four female worms present in galaxias at 6 weeks postinfection was gravid.

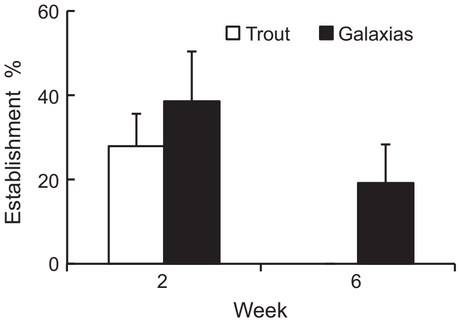

Fig. 2. Establishment (2 weeks) and survival (6 weeks) of *Acanthocephalus galaxii* in experimentally infected roundhead galaxias and brown trout. Establishment success did not differ between hosts ($P > 0{\cdot}05$).

POPULATION MODEL

Model simulations of varying fish community composition indicated that a minimum proportion of 70% galaxias in the total fish community is the threshold for the survival of *A. galaxii*, below which the native parasite rapidly goes extinct (Fig. 3). At the current field densities of the total fish community (0·088 individuals per m^2), densities of *A. galaxii* infection in galaxias are predicted to be only slightly lower than would be expected if trout were absent from the system, as the ability of trout to act as an infection sink is weakened by the low relative density of this introduced host.

Changing the rate of predation by brown trout on either amphipods or roundhead galaxias had little influence on the

Table 4. Prevalence, infection intensity, length and reproductive status *Acanthocephalus galaxii* in experimentally infected roundhead galaxias and brown trout. Gravid females represent females with maturing eggs (F2) and fully mature shelled eggs (F3)

Host	Week	No. of hosts	Prevalence %	Infection intensity (mean ± SD)	Parasite sex	Length µm (mean ± SD)	No. of parasites	Gravid females %
Roundhead galaxias	2	6	100	3·3 ± 2·5	M	1806 ± 84	8	0
					F1	2097 ± 108	12	
					M:F ratio	1:1·6		
	6	6	50	2·3 ± 1·5	M	2191 ± 141	3	25
					F1	2783 ± 65	3	
					F2	2425	1	
					M:F ratio	1:1·3		
Brown trout	2	6	100	2·6 ± 1·9	M	2128 ± 103	7	0
					F1	2338 ± 103	9	
					M:F ratio	1:1·3		
	6	6	0	0	–	–	–	–

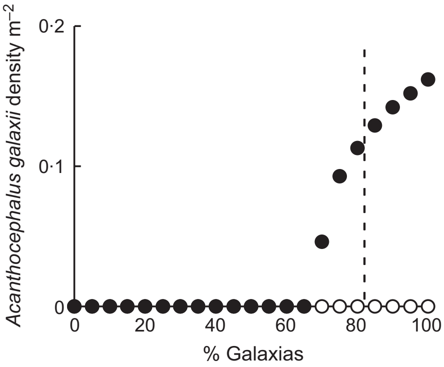

Fig. 3. Density of *Acanthocephalus galaxii* infections in roundhead galaxias (filled circle) and brown trout (open circle) in relation to percentage of galaxias in the combined total fish population (0·088 fish per m^2) predicted from model simulations. The dashed line represents the current percentage of galaxias in the total fish population as recorded in the field survey.

density of *A. galaxii* in the modelled roundhead galaxias population (Fig. 4a,c). In contrast, *A. galaxii* densities in roundhead galaxias were highly sensitive to changes in the rate of predation on amphipods by this fish (Fig. 4b), with predation rates below 0·004 per amphipod per host per day (−20%) resulting in extinction of the parasite.

Discussion

We used a combination of field observations, experimental infections and dynamic population modelling to examine the influence of an introduced species on a native host–parasite system. Our field observations indicated that although the prevalence and infection intensity of *A. galaxii* were similar in introduced trout and native galaxias, the native parasite attained smaller sizes and failed to mature in the introduced host. Our experimental infection results showed trout to be similar to galaxias in its competence as a host in terms of parasite establishment and initial growth, but trout was found to be unsuitable for maintaining *A. galaxii* populations, as worms did not reach maturity. Hence, the field and experimental results suggested that trout were likely to act as an infection sink because of poor host competency. However, the population model indicated that the influence of this mechanism on the dynamics of *A. galaxii* in its native host

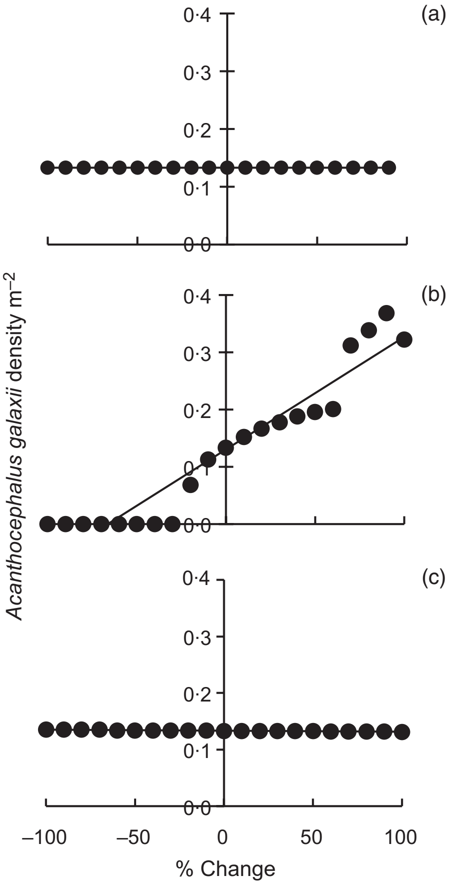

Fig. 4. Simulating the effect on the density of *Acanthocephalus galaxii* infections in roundhead galaxias of altering (a) trout predation on amphipods C_T, (b) galaxias predation on amphipods C_G and (c) trout predation on galaxias (D). Each estimate was modified ± 100% of current estimates in 10% increments.

would be limited because of only a small proportion of the total fish community being comprised of trout. In contrast, our model suggested that trout presence may have more substantial consequences for the native parasite population by altering amphipod consumption by roundhead galaxias, with such consequences being greater at higher trout densities.

FIELD OBSERVATIONS

Field observations are often the first source of information used to determine the influence of introduced species on host/parasite dynamics. For example, Telfer *et al.* (2005) used field surveys to determine the influence of the introduced bank vole (*Myodes glareolus*) on *Bartonella* sp. infections in native wood mice (*Apodemus sylvaticus*), concluding that infection prevalence in wood mice decreased with increasing bank vole density. Moreover, Rauque, Viozzi & Semenas (2003) used the results of field surveys to demonstrate that parasites in the introduced rainbow trout (*Oncorhynchus mykiss*) contributed 20% of total egg output by the native acanthocephalan parasite *Acanthocephalus tumescens*. Field observations may provide useful insights into the potential impacts of introduced species on native parasite–host dynamics. However, as demonstrated by our study, assessment of parasite maturation is needed in addition to observations of infection prevalence and intensity to determine the impact of an introduced species.

INFECTION EXPERIMENT

Our experimental infections generally supported the field-based conclusions that trout are inferior hosts of *A. galaxii*, yet interestingly *A. galaxii* initially experienced similar establishment success and equivalent or greater growth in this host. Although worms in galaxias were relatively slower growing, in the long term they attained larger sizes than in trout. Most importantly, *A. galaxii* worms failed to reach maturity in brown trout; thus, the introduced host was unsuccessful at supporting this stage of the parasite's life cycle.

POPULATION MODEL

The population model revealed that the density of *A. galaxii* in roundhead galaxias may only be slightly reduced as a result of parasite dilution by trout. In sensitivity analyses, modifying either the rate at which trout feed on roundhead galaxias or on amphipods caused little change to the native parasite's density in its native roundhead galaxias host. However, decreasing the rate of amphipod predation by roundhead galaxias markedly decreased the parasite's adult population. The model also revealed that parasite burdens were highly sensitive to relative host abundances. Hence, a correlation between increasing trout presence and decreasing native parasitism of roundhead galaxias, as observed for the parasite *Deretrema philippae* by Kelly *et al.* (2009a), may just as likely be caused by trout reducing galaxias density or altering their foraging behaviour, rather than trout serving as an infection sink. This conclusion is supported both by demonstrations that trout predate galaxias (Crowl, Townsend & McIntosh 1992; Townsend 2003) and experimental studies of habitat use by native galaxiids in the presence of brown trout (McIntosh, Townsend & Crowl 1992), which showed that trout out-compete *Galaxias* spp. in streams, forcing them to forage in areas with lower invertebrate drift.

Native parasite loss through dilution or via other mechanisms, such as altered predation on intermediate hosts by native species, is a largely unrecognized consequence of the invasion of introduced species. Most commonly, invasion biology research has focused on the impacts of introduced species on native conspecifics via predation and/or competition and through the introduction of novel parasites. However, as native parasites play major roles in the structuring of native communities, neglecting the potential for native parasite loss subsequent to the arrival of exotic species overlooks a potentially important consequence of invasions.

LIMITATIONS AND STRENGTHS OF DYNAMIC POPULATION MODELS

We acknowledge that the strength of population simulation models in depicting 'real-world' dynamics is only as good as the data used to parameterize them. In the present study, we utilized field information from multiple sites and seasons, experimental infections and published literature to generate the majority of parameter estimates. However, we were unable to draw on these sources to estimate the amphipod's mortality and predation risk, although the dynamic model suggested that *A. galaxii* infections are strongly influenced by both parameters. Manipulation of intermediate host behaviour to enhance transmission success via predation is a common strategy of parasites that utilize hosts at different trophic levels and is frequently adopted by acanthocephalans (Moore 1984; Poulin 1995). Acanthocephalan infections in amphipods have also been reported to alter host immune responses to bacterial infections, potentially increasing intermediate host mortality (Cornet *et al.* 2009). Experimental studies are required to fully quantify the mechanism and degree to which *A. galaxii* infection alters the mortality and predation risk of amphipods, and to identify whether behavioural responses of infected amphipods to predator presence differ between native and exotic fish.

Acknowledgements

We thank D. Kelly, M. Green and A. Lal for field and laboratory assistance, and F. Wilhelm for *P. fluviatilis* life-history information. We are also grateful to R. Scott and D. Crutchley for site access. Permission was obtained from the Department of Conservation, NZ Fish and Game and the University of Otago Animal Ethics Committee (ET 16/7). Funding for this research was provided by the Royal Society of New Zealand Marsden Fund.

References

Baldauf, S.A., Thunken, T., Frommen, J.G., Bakker, T.C.M., Heupel, O. & Kullmann, H. (2007) Infection with an acanthocephalan manipulates an amphipod's reaction to a fish predator's odours. *International Journal for Parasitology*, **37**, 61–65.

Bonnett, M.L. (1990) Age and growth of alpine galaxias (*Galaxias paucispondylus* Stokell) and longjawed galaxias (*Galaxias prognathus* Stokell) in the Rangitata River, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **24**, 151–158.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology*, **83**, 575–583.

Cherwell (2000) *ModelMaker User Manual*. Cherwell Scientific Limited, Oxford.

Cornet, S., Franceschi, N., Bauer, A., Rigaud, T. & Moret, Y. (2009) Immune depression induced by acanthocephalan parasites in their intermediate crustacean host: consequences for the risk of super-infection and links with host behavioural manipulation. *International Journal for Parasitology*, **39**, 221–229.

Crompton, D.W. (1970) *An ecological Approach to Acanthocephalan Physiology*. University Press, Cambridge.

Crompton, D.W. & Whitfield, P.J. (1968) Course of infection and egg production of *Polymorphus minutus* (Acanthocephala) in domestic ducks. *Parasitology*, **58**, 231–246.

Crowl, T.A., Townsend, C.R. & McIntosh, A.R. (1992) The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Reviews in Fish Biology and Fisheries*, **2**, 217–241.

Daszak, P., Cunningham, A.A. & Hyatt, A.N. (2000) Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science*, **287**, 443–449.

Dubois, N., Marcogliese, D.J. & Magnan, P. (1996) Effects of the introduction of white sucker, *Catostomus commersoni*, on the parasite fauna of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Zoology – Revue Canadienne De Zoologie*, **74**, 1304–1312.

Galli, P., Stefani, F., Benzoni, F. & Zullini, A. (2005) Introduction of alien host-parasite complexes in a natural environment and the symbiota concept. *Hydrobiologia*, **548**, 293–299.

Hine, P.M. (1977) *Acanthocephalus galaxii* n.sp. parasitic in *Galaxias maculatus* (Jenyns, 1842) in Waimeha Stream, New-Zealand. *Journal of the Royal Society of New Zealand*, **7**, 51–57.

Hine, P.M., Jones, J.B. & Diggles, B.K. (2000) *A checklist of the parasites of New Zealand fishes, including previously unpublished records*. National Institute of Water and Atmospheric Research, Wellington.

Huryn, A.D. (1996) An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography*, **41**, 243–252.

Kelly, D.W., Paterson, R.A., Townsend, C.R., Poulin, R. & Tompkins, D.M. (2009a) Has the introduction of brown trout altered disease patterns in native New Zealand fish? *Freshwater Biology*, **54**, 1805–1818.

Kelly, D.W., Paterson, R.A., Townsend, C.R., Poulin, R. & Tompkins, D.M. (2009b) Parasite spillback: a neglected concept in invasion ecology? *Ecology*, **90**, 2047–2056.

King, T.A., van Oosterhout, C. & Cable, J. (2009) Experimental infections with the tropical monogenean, *Gyrodactylus bullatarudis*: potential invader or experimental fluke? *Parasitology International*, **58**, 249–254.

Kopp, K. & Jokela, J. (2007) Resistant invaders can convey benefits to native species. *Oikos*, **116**, 295–301.

Lagrue, C., Kaldonski, N., Perrot-Minnot, M.J., Motreuil, B. & Bollache, L. (2007) Modification of hosts' behavior by a parasite: field evidence for adaptive manipulation. *Ecology*, **88**, 2839–2847.

MacCrimmon, H. & Marshall, T.L. (1968) World distribution of brown trout *Salmo trutta*. *Journal of the Fisheries Research Board of Canada*, **25**, 2527–2548.

McIntosh, A.R., Townsend, C.R. & Crowl, T.A. (1992) Competition for space between introduced brown trout (*Salmo trutta* L.) and a native galaxiid (*Galaxias vulgaris* Stokell) in a New Zealand stream. *Journal of Fish Biology*, **41**, 63–81.

Moore, J. (1984) Altered behavioral responses in intermediate hosts – an acanthocephalan parasite strategy. *American Naturalist*, **123**, 572–577.

Poulin, R. (1995) "Adaptive" changes in the behaviour of parasitized animals: a critical review. *International Journal for Parasitology*, **25**, 1371–1383.

Rauque, C.A., Semenas, L.G. & Viozzi, G.P. (2002) Post-cyclic transmission in *Acanthocephalus tumescens* (Acanthocephala: Echinorhynchidae). *Folia Parasitologica*, **49**, 127–130.

Rauque, C.A., Viozzi, G.P. & Semenas, L.G. (2003) Component population study of *Acanthocephalus tumescens* (Acanthocephala) in fishes from Lake Moreno, Argentina. *Folia Parasitologica*, **50**, 72–78.

SPSS (2006) *SPSS for Windows Version 15.0.0*. SPSS, Inc., Chicago.

Tekinay, A.A., Guner, Y. & Davies, S.J. (2003) Influence of dietary energy level on stomach emptying and appetite revival rates in rainbow trout, *Oncorhynchus mykiss*. *Turkish Journal of Veterinary and Animal Sciences*, **27**, 1077–1084.

Telfer, S., Bown, K.J., Sekules, R., Begon, M., Hayden, T. & Birtles, R. (2005) Disruption of a host-parasite system following the introduction of an exotic host species. *Parasitology*, **130**, 661–668.

Thieltges, D.W., Reise, K., Prinz, K. & Jensen, K.T. (2009) Invaders interfere with native parasite-host interactions. *Biological Invasions*, **11**, 1421–1429.

Tompkins, D.M. & Poulin, R. (2006) Parasites and biological invasions. *Biological Invasions in New Zealand* (eds R.B. Allen & W.G. Lee). pp. 67–86, Springer, Berlin, Heidelberg.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J. & Kuris, A.M. (2003) Introduced species and their missing parasites. *Nature*, **421**, 628–630.

Towns, D.R. (1981) Life histories of benthic invertebrates in a kauri forest stream in northern New Zealand. *Australian Journal of Marine and Freshwater Research*, **32**, 191–211.

Townsend, C.R. (1996) Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation*, **78**, 13–22.

Townsend, C.R. (2003) Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology*, **17**, 38–47.

Weller, F. (2003) *Effects of increased fine sediment inputs due to different land use regimes on stream invertebrates*. MSc thesis. University of Munich.

Received 31 May 2010; accepted 22 February 2011
Handling Editor: Mike Boots