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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Migration as an escape from parasitism in New Zealand galaxiid fishes

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Abstract Parasite avoidance is increasingly considered to be a potential driving factor in animal migrations. In many marine and freshwater benthic fish, migration into a pelagic environment by developing larvae is a common life history trait that could reduce exposure to parasites during a critical window of developmental susceptibility. We tested this hypothesis on congeneric fish (family Galaxiidae, genus *Galaxias*) belonging to a closely related species complex sampled from coastal streams in southeastern New Zealand. Migratory *Galaxias* have larvae that migrate to pelagic marine environments, whereas the larvae of non-migratory species rear close to adult habitats with no pelagic larval phase. Both migratory and non-migratory fish are hosts to two species of skin-penetrating trematodes that cause spinal malformations and high mortality in young fish. Using generalized linear models within an Akaike information criterion and model averaging framework, we compared infection levels between migratory and non-migratory fish while taking into account body size and several other local factors likely to influence infection levels. For one trematode species, we found a significant effect of migration: for any given body length, migratory fish harboured fewer parasites than non-migratory fish. Also, no parasites of any kind were found in juvenile migratory fish sampled in spring shortly after their return to stream habitats. Our results demonstrate that migration spares juvenile fish from the debilitating parasites to which they would be exposed in adult stream habitats. Therefore, either the historical adoption of a migratory strategy in some *Galaxias* was an adaptation against parasitism, or it evolved for other reasons and now provides protection from infection as a coincidental side-effect.

Keywords Malformations · Metacercariae · Parasite-induced mortality · Pelagic larvae · Trematodes

Introduction

Animal migration, involving mass movements over large distances and often across inhospitable habitats, is one of the most spectacular behavioural phenomena (Dingle 1996; Dingle and Drake 2007). Biologists have made great strides toward identifying the ultimate causes of migrations in spite of the extensive variation, observed both among and within species, in the tendency to migrate and the scale of displacements. Most hypotheses typically invoke avoiding food scarcity, seeking physiologically optimal environments, avoiding predation during reproductive periods or avoiding high population density as causes of animal migration (e.g. Gross et al. 1988; Olsson et al. 2006; Taylor and Norris 2007; Boyle 2008). However, as recently pointed out (Altizer et al. 2011), parasitism and disease

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should not be ignored as potential driving forces behind migrations. Indeed, through their impact on host fitness, parasites exert strong selective pressures favouring the evolution of a range of life history traits that can reduce the risk of infection or mitigate its effects (e.g. Fredensborg and Poulin 2006; de Roij et al. 2011; Ohlberger et al. 2011).

Field studies reporting movement away from infection risk provide some supporting evidence that parasites could induce migratory behaviour (Folstad et al. 1991; Loehle 1995; Piersma 1997; Altizer et al. 2011). Nevertheless, a rigorous test of the 'parasitism begets migration' hypothesis has yet to be performed. Such a test would be challenging, however. Comparing parasitic infections between migratory and non-migratory animals almost inevitably involves comparing species, since intraspecific differences in migratory behaviour are often too small to allow any clear-cut distinction between the two strategies. The potential influence of other variables associated with different species or localities may therefore confound comparisons between migratory and non-migratory populations, and limit any inference from such contrasts.

Here, we take advantage of a set of closely related congeneric fish species (family Galaxiidae, genus *Galaxias*) that differ in their migratory tendencies and which occur in streams within the same area in the southeastern part of New Zealand's South Island. Galaxiids exhibit highly variable patterns of ontogenetic migration (McDowall 1988, 2008) and thus represent an ideal group in which to test the hypothesis that migration serves as an escape from parasites. Migratory galaxiid species have larvae that use a combination of preference for areas of strong current and passive drift to migrate downstream to either pelagic marine or lake environments, whereas the larvae of non-migratory species lack this behaviour and rear close to adult habitats, with no pelagic larval phase. Migration into a pelagic environment by developing larvae is a common life history trait of many marine and freshwater benthic fish species and is generally assumed to be related to dispersal or access to food (McDowall 1988; Lucas and Barras 2001; Levin 2006). We focus on the members of the New Zealand *vulgaris* species complex, which are closely related phylogenetically and consist of taxa that have only recently been recognized as separate species (Allibone and Wallis 1993; Waters et al. 2010): the migratory *Galaxias brevipinnis* and the non-migratory *G. depressiceps* and *G. gollumoides*. Although distinct genetically, these species are almost indistinguishable morphologically, providing a great opportunity for a contrast between migratory and non-migratory fish given that intraspecific comparisons are not possible.

New Zealand's galaxiids are common hosts of trematode parasites whose larvae penetrate fish skin and encyst within muscle or liver tissue (Hine et al. 2000). Two trematodes are particularly widespread, *Telogaster opisthorchis* (Cryptogonimidae) and *Stegodexamene anguillae* (Lepocreadiidae), both of which have identical life cycles. They multiply asexually within the same first intermediate host, the snail *Potamopyrgus antipodarum*, from which free-swimming infective larvae emerge to seek fish second intermediate hosts, such as galaxiids, in which they encyst as metacercariae. The life cycle of both trematodes is completed when infected galaxiids are ingested by the parasites' definitive hosts, eels (*Anguilla* spp.). Both trematode species show no apparent host specificity and have been found in all *Galaxias* species investigated to date (Hine et al. 2000; Poulin, unpublished data). Previous research has indicated that *T. opisthorchis* has no measurable effect on adult galaxiids (Poulin 1993). In contrast, its impact on juvenile *Galaxias* is severe: when infecting fish in their first few weeks post-hatching (<20 mm TL), *T. opisthorchis* causes dramatic spinal malformations that lead to increased risk of mortality (Kelly et al. 2010). Therefore, at least one, and possibly both, of these common trematodes pose a threat to young galaxiids during the period of their ontogeny when some species migrate into pelagic environments.

We have tested the hypothesis that larval galaxiid migration into the pelagic environment removes larvae from parasite-rich benthic environments (where snails are a source of infective stages) during a vulnerable period of ontogenetic development. This hypothesis leads to the prediction that, all else being equal, i.e. taking into account environmental factors that may affect infection risk, fish with a migratory pelagic larval phase should have lower abundance of trematodes than related (and thus comparable) non-migratory fish. Thus, the main objective of our study was to use field surveys to assess whether patterns of infection differ between migratory and non-migratory galaxiids.

Materials and methods

Autumn fish sampling and parasite counts

Fish (*Galaxias brevipinnis*, *G. depressiceps* and *G. gollumoides*) were sampled from several small coastal or near-coastal streams along the southeast coast of New Zealand's South Island [Table 1; Electronic Supplementary Material (ESM) Fig. A1], over a few weeks during the austral autumn from mid-March to early May 2010. Larvae of migratory galaxiids, when present in any of the sampled streams, all go to the sea, and not to downstream lakes. Sampling was achieved by electrofishing in a 40- to 250-m reach, depending on the stream, for 15–25 min. All galaxiids caught were frozen for later identification to species followed by dissection in the laboratory. The presence of eels, *Anguilla* spp., was also recorded if any were observed at a site during sampling. Finally, three kick samples of benthic invertebrates were taken from each stream, at haphazardly chosen locations in riffles within the reach sampled for fish. For each kick-sample, all substrate types above a D-frame pole net were disturbed for 60 s along an upstream diagonal transect (see Kelly et al. 2009).

Specimens of two other *Galaxias* species, *G. maculatus* and *G. fasciatus*, were collected from some of the localities; however, because these do not belong to the *vulgaris* species complex and are therefore not closely-related to our three focal species (Allibone and Wallis 1993; Waters et al. 2010), they were excluded from the study. Prior to dissection, each fish of the three focal species was measured (total length); fish length was included as a predictor variable in our analyses (see below) as trematode metacercariae are known to accumulate in fish as a function of age/size (Poulin 2000). All metacercariae of both *Stegodexamene anguillae* and *Telogaster opisthorchis* were counted from all tissues of each fish. In addition, during dissection, the presence of other parasite species was also recorded, although these were relatively rare.

Because the fish were sampled from different streams and because each stream yielded only one of our focal fish species, local habitat characteristics are likely to affect infection levels in combination with fish traits such as migratory status or body length. Therefore, we considered the following habitat variables (see Table 1), derived either from our field data or from the Water Resources Explorer NZ modelling database (New Zealand's National Institute of Water and Atmospheric Research Ltd; available at: http://wrenz.niwa.co.nz/webmodel/). First, the abundance of *Potamopyrgus antipodarum* snails was calculated as the average number from the three kick-samples taken in each stream. Since this snail is the first intermediate host of both trematode parasites considered here, its local density can be a determinant of infection risk (see Kelly et al. 2009). Second, the visible presence of eels at a site may indicate their relatively greater local abundance than at sites where they were not seen. Of course, their absence during sampling is no evidence of their total absence from a site, and this presence/absence variable is only a rough measure of the local abundance of the definitive host of both trematode species. Third, catch per unit effort (CPUE), adjusted for the area of stream sampled, was used as an estimate of local galaxiid density, because host density can influence parasite transmission and infection levels. We verified that using CUPE based on the duration of electrofishing—instead of the area of stream sampled—had no effect on the results of our statistical analyses, and hereafter use only area-adjusted catch per unit effort. Fourth, we also considered the mean annual water flow (m^3/s) in each reach of stream sampled, because the transmission of the parasites from snails to fish by microscopic free-swimming infective larvae is probably greatly influenced by water velocity. Finally, we also took into account both the elevation of the sampling sites above sea level and their upstream distance from the sea. Both these variables capture several biotic and abiotic characteristics of the sampled sites, from the general composition of their fauna to, more specifically, the probability that they have resident eels.

Spring sampling

In order to confirm that juveniles of the migratory *Galaxias brevipinnis* return to stream habitats free, or mostly free, of metacercariae of the two focal trematode species, juveniles were sampled by electrofishing in the austral spring from the three (out of the original 8) streams in which this species had been found. Sampling was carried out in early-to-mid October 2010, shortly after the young fish returned to stream habitats. Fish were frozen after capture and later identified to species level prior to dissection. All tissues were examined carefully for trematode metacercariae or any other parasites.

Table 1 Characteristics of the eight localities sampled for galaxiid fish

Site	Snail abundance[a]	Eel presence	CPUE	Mean annual water flow (m^3/s)	Elevation (m)	Distance from sea (km)
1	222.0 ± 28.0	No	0.10	0.081	357	68.7
2	533.3 ± 141.5	Yes	0.02	0.096	60	8.8
3	1,020.0 ± 271.5	Yes	0.43	0.130	413	41.1
4	817.7 ± 89.6	Yes	0.43	0.032	79	13.0
5	105.7 ± 33.7	No	0.16	0.047	93	28.5
6	273.3 ± 91.1	Yes	0.35	0.130	17	0.1
7	5.7 ± 3.3	Yes	0.07	0.023	258	43.0
8	31.0 ± 18.0	Yes	0.07	0.039	9	0.2

Locations of sampling sites are given in ESM Fig. A1

CPUE catch per unit effort, i.e. number of fish per square metre sampled, *SE* standard error

[a] Presented as the mean number of snails per sample

Statistical analyses

All statistical analyses described below apply strictly to fish sampled during the autumn, as those collected in spring proved to be uninfected (see "Results").

Migratory status and fish species are confounded variables and cannot both be included in the main analyses. Thus, we first tested whether there were differences in infection levels between the two non-migratory fish species, *Galaxias depressiceps* and *G. gollumoides*, to justify combining them and subsequently comparing migratory and non-migratory *Galaxias* independently of their species. Infection levels by *Stegodexamene anguillae* and *Telogaster opisthorchis* were assessed separately using generalized linear models (GLM), with fish species, body length, snail abundance, presence of eels, area-adjusted CPUE, flow, distance inland and elevation as main factors. Because of the aggregated distributions of parasites among their hosts, i.e. strongly right-skewed distributions of values for numbers of parasites per individual host, both response variables were fitted with a negative binomial error structure and a log-link function (see Wilson and Grenfell 1997). In both GLMs, only fish body length had an influence on infection levels [*S. anguillae*: estimate 0.625, standard error (SE) 0.058, $t = 10.76$, $df = 58$, $P < 0.001$; *T. opisthorchis*: estimate 0.701, SE = 0.077, $t = 9.15$, $df = 58$, $P < 0.001$], with the other predictors, including species identity, having no effect (all $P > 0.80$). Uncorrected infection levels were lower in *G. gollumoides* than in *G. depressiceps* (Table 2), but the analysis indicated that this was not significant when other factors were taken into account. Therefore, the two non-migratory *Galaxias* species were combined in the analyses that follow; it must be pointed out that only few non-migratory individuals belonged to *G. gollumoides* (7/58, 12%; Table 2).

In the main analyses, the two response variables, i.e. infection levels by *S. anguillae* and *T. opisthorchis*, were assessed separately using GLM within an Akaike information criterion (AIC) and model averaging framework (Burnham and Anderson 2002). Again, both response variables were fitted with a negative binomial error structure and a log-link function. The main factors included were migratory status, body length, snail abundance, presence of eels, area-adjusted CPUE, flow, distance inland and elevation. No interactions were included in the global models, since we had no a priori reasons to expect any and because none became apparent in exploratory analyses.

Global models were fitted using the package MASS (Venables and Ripley 2002) in the program R (R Development Core Team 2009). The global model was then used to generate a set of all possible models, with functions from the R package MuMIn (Bartoñ 2009). Our aim was to assess the importance of each predictor variable, taking into account possible multicollinearity between predictors and thus considering all possible combinations of factors. Each model in the set was ranked by AIC_C, and model averaging using MuMIn was performed on all models within four small sample-size corrected AIC (AIC_C) of the best model. The predictor variables in the top models are reported with their relative importance weights, model-averaged parameter estimates, standard error (SE) and 95% confidence (CI) intervals. In all figures, the variables shown are uncorrected, i.e. they have not been adjusted for the influence of other predictors.

Results

Autumn samples

Overall, 92 fish were included in the study, including 58 non-migratory (51 *Galaxias depressiceps* and 7 *G. gollumoides*) and 34 migratory (*G. brevipinnis*) individuals (Table 2). Initially, a few fish (2 *G. depressiceps*, 5 *G. gollumoides* and

Table 2 Species of *Galaxias* fish sampled, their body length, and their infection levels by metacercariae of *Stegodexamene anguillae* and *Telogaster opisthorchis*, from eight localities

Site	Fish species	Number sampled	Total length[a] (cm)	Prevalence of *S. anguillae*[b]	Prevalence of *T. opisthorchis*[b]
1	*G. depressiceps*	13	5.69 (4.6–9.1)	100% (11–112)	100% (20–568)
2	*G. brevipinnis*	15	6.74 (4.3–15.2)	100% (14–179)	93% (2–330)
3	*G. depressiceps*	9	6.37 (4.8–9.2)	100% (18–500)	100% (20–547)
4	*G. depressiceps*	14	5.56 (3.9–8.4)	100% (11–197)	79% (2–37)
5	*G. depressiceps*	15	5.10 (3.8–6.8)	100% (3–171)	47% (2–14)
6	*G. brevipinnis*	8	5.91 (5.0–10.5)	88% (1–22)	38% (1–17)
7	*G. gollumoides*	7	4.34 (3.4–7.4)	43% (1–2)	0%
8	*G. brevipinnis*	11	9.49 (5.6–15.3)	73% (1–121)	0%

[a] Data are presented as the mean, with the range in parenthesis

[b] The range is given in parenthesis

Table 3 The top-ranked candidate models for each response variable, i.e. infection by *S. anguillae* and by *T. opisthorchis*

Response	Model[a]	Deviance	AIC_C	ΔAIC_C	AIC_W
S. anguillae	CPUE + eels + elevation + flow + length + migratory + snails	98.32	753.21	0.00	0.53
	CPUE + distance + eels + elevation + flow + length + migratory + snails	97.45	754.89	1.67	0.23
	CPUE + eels + elevation + length + snails	103.41	756.03	2.81	0.13
	Eels + elevation + length + snails	103.53	756.23	3.02	0.12
T. opisthorchis	Distance + eels + elevation + flow + length + snails	88.79	533.53	0.00	0.36
	CPUE + distance + eels + elevation + length + migratory + snails	88.79	535.98	2.45	0.11
	CPUE + eels + elevation + flow + length + migratory + snails	88.79	535.98	2.45	0.11
	CPUE + distance + elevation + flow + length + migratory + snails	88.79	535.98	2.45	0.11
	CPUE + distance + eels + elevation + flow + length + snails	88.79	535.98	2.45	0.11
	Distance + eels + elevation + flow + length + migratory + snails	88.79	535.98	2.45	0.11
	CPUE + distance + eels + flow + length + migratory + snails	88.79	535.98	2.45	0.11

Since more than one model was within 4 AIC_C of the top model, all models were sorted by the AIC_C

AIC_C small size-corrected Akaike information criterion, ΔAIC_C difference in AIC_C from the best model, AIC_W weight value of the model

[a] Predictor variables in the models are explained in the text

Table 4 Predictor variables from top models for each response variable, i.e. infection by *S. anguillae* and by *T. opisthorchis*

Response	Predictor variable	$w_+(I)$	Estimate	SE	95% CI
S. anguillae	Intercept	–	−0.376	1.570	−3.460 to 2.710
	Presence of eels	**1.00**	**−2.650**	**0.972**	**−4.560 to −0.735**
	Elevation	**1.00**	**−0.008**	**0.003**	**−0.015 to −0.002**
	Body length	**1.00**	**0.428**	**0.040**	**0.350 to 0.506**
	Snail abundance	**1.00**	**0.005**	**0.001**	**0.004 to 0.007**
	CPUE	**0.88**	**−4.080**	**1.780**	**−7.600 to −0.563**
	Migratory status	**0.75**	**2.910**	**0.968**	**0.984 to 4.830**
	Flow	**0.75**	**19.100**	**6.980**	**5.230 to 33.000**
	Distance inland	0.23	0.021	0.021	−0.020 to 0.063
T. opisthorchis	Intercept	–	0.031	3.88e + 03	−7.71e + 03 to 7.71e + 03
	Body length	**1.00**	**0.554**	**0.005**	**0.457 to 0.651**
	Snail abundance	1.00	0.039	8.180	−16.20 to 16.30
	Elevation	0.89	−0.072	11.60	−23.10 to 22.90
	Presence of eels	0.89	−29.20	7.66e + 03	−1.53e + 04 to 1.52e + 04
	Distance inland	0.89	0.422	54.30	−1.08e + 02 to 1.08e + 02
	Flow	0.89	51.50	1.78e + 04	−3.53e + 04 to 3.54e + 04
	Migratory status	0.53	−30.80	7.49e + 03	−1.49e + 04 to 1.49e + 04
	CPUE	0.53	38.20	9.49e + 03	−1.88e + 04 to 1.89e + 04

Variables are ranked by relative importance weights [$w_+(I)$], with coefficient estimates, their SE and 95% confidence interval (CI) after model averaging also shown

Significant main effects are given in bold

1 *G. brevipinnis*) were found to harbour an unidentified myxozoan parasite; because these parasites can multiply rapidly within their host and be pathogenic, these fish were excluded from the study. Among the 92 fish that were included, 17 harboured between one and 45 individual *Coitocaecum parvum* (*trematode*), two harboured a single *Deretrema minutum* (*trematode*), and six harboured unidentified nematodes, all in their gastrointestinal tract. In contrast to these trophically acquired parasites, both the percentage of fish infected and the numbers of parasites per fish were much higher for the two skin-penetrating trematodes considered in this study (Table 2).

For the trematode *Stegodexamene anguillae*, model analysis resulted in four top models within four AIC_C of the best model (Table 3). All predictor variables considered in the global model were included in at least one model in the top model set, and all predictors except distance from the sea had significant effects on numbers of *S. anguillae* per fish, i.e. their 95% CIs were bounded away from zero (Table 4). The focal predictor of this study, i.e. the migratory status of the fish, was one of the factors that significantly influenced infection levels: for any given body length, fish that underwent migration tended to harbour fewer *S. anguillae* metacercariae than non-migratory fish

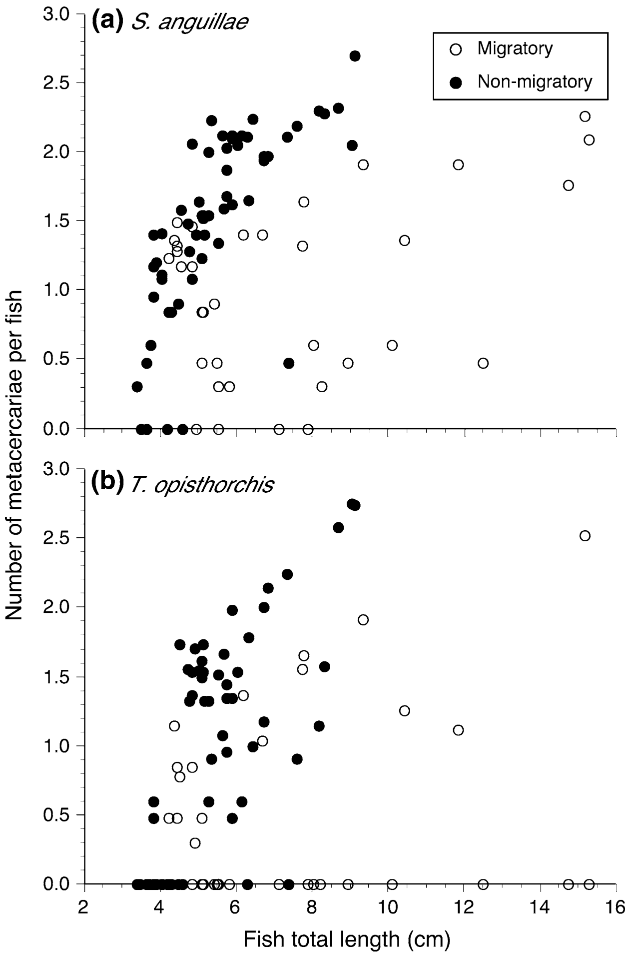

Fig. 1 Number of metacercariae of the trematodes *Stegodexamene anguillae* (**a**) and *Telogaster opisthorchis* (**b**) encysted in individual migratory (*open circles*) and non-migratory (*solid circles*) *Galaxias* spp. fish, as a function of fish length. For clarity, the numbers of metacercariae have been $\log_{10}$ (x + 1) transformed

(Fig. 1). As indicated by the analysis, local habitat characteristics also played a role (see Table 4). For instance, numbers of *S. anguillae* metacercariae per fish also covaried positively with local snail abundance (Fig. 2). However, the influence of migratory status was independent from these other predictors.

In contrast, for the trematode *Telogaster opisthorchis*, model analysis yielded seven top models within four $\mathrm{AIC_C}$ of the best model (Table 3), with all predictor variables considered in the global model being included in at least five models in the top model set. However, only fish body length had a 95% CI not overlapping zero, indicating that it was the only variable affecting the numbers of *T. opisthorchis* per fish (Table 4). Although for a given body length, migratory fish appear to harbour fewer *T. opisthorchis* metacercariae than non-migratory fish (Fig. 1), this effect was not significant when the 'averaged' effect of other predictors from the top model set were also taken into account.

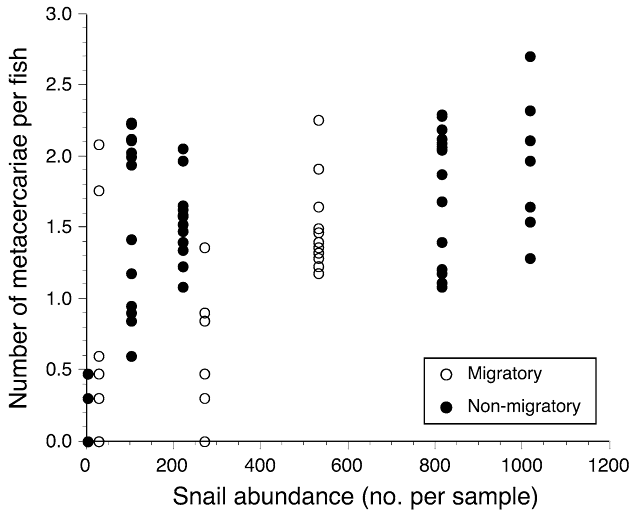

Fig. 2 Number of metacercariae of the trematode *S. anguillae* encysted in individual migratory (*open circles*) and non-migratory (*solid circles*) *Galaxias* spp. fish, as a function of the local abundance of the snail *Potamopyrgus antipodarum*. Snail abundance is the average number of snails recovered from three kick-samples per locality. For clarity, numbers of metacercariae have been $\log_{10}$ (x + 1) transformed

Table 5 Number and body length of juvenile *G. brevipinnis* sampled in spring from three localities

Site	Number of fish sampled	Total length[a] (cm)
2	6	4.87 (4.7–5.0)
6	10	4.95 (4.7–5.4)
8	28	4.85 (4.4–5.3)

[a] Data are presented as the mean, with the range in parenthesis

Spring samples

A total of 44 juvenile *Galaxias brevipinnis* were captured from three streams in October 2010. These not only differed morphologically from adult fish, but they were also smaller in size than fish collected from the same site in autumn (Table 5). No trematode metacercariae were found in these fish, as well as no other parasites of any kind.

Discussion

At a time when human-induced climate and habitat changes are greatly altering the migratory patterns of many species (Wilcove and Wikelski 2008) as well as the distribution and dynamics of parasitic diseases (Mouritsen and Poulin 2002; Brooks and Hoberg 2007; Lafferty 2009), we need to better understand the link between parasitism and migration. Our results suggest a direct link between parasitism and migration in *Galaxias* fishes, showing that migratory fish incur lower infection levels by trematode metacercariae than non-migratory ones. These parasites accumulate in an individual fish over time, and therefore body size, as a surrogate for age, is a universally strong predictor of metacercarial infection levels among conspecific fish (Poulin 2000). We show that for a given size, migratory *Galaxias* harbour fewer parasites than non-migratory *Galaxias*. More importantly, we found that juvenile migrants returning from their pelagic marine phase were completely parasite-free. These fish only began to accumulate metacercariae from a size (>4 cm body length) and age when these infections are mostly benign. Small juvenile *Galaxias* (1–2 cm body length) incur severe malformations and high mortality from even low infection levels, but these impacts are much weaker at sizes of >2 cm (Kelly et al. 2010). Therefore, whether through adaptation or coincidentally, migration takes juveniles away from high-exposure stream habitats during a critical window of developmental susceptibility.

The main caveat applying to our study is that comparisons are made among different species and localities. However, several arguments support the validity of our conclusions regarding the effect of migratory status on infection levels. First, in comparisons among localities, our statistical models include several local factors thought a priori to influence galaxiid infections by skin-penetrating trematodes. Therefore, the higher numbers of *Stegodexamene anguillae* metacercariae in non-migratory *Galaxias* than in migratory ones are independent of local variation in the abundance of other essential hosts for the parasite (snails, eels) or of local variation in flow characteristics. We are aware of one study that compared conspecific migratory and non-migratory fish: Bouillon and Curtis (1987) found that all anadromous Arctic charr, *Salvelinus alpinus*, sampled from a river and fjord in Labrador were uninfected by trematode metacercariae, whereas lake resident charr in a nearby lake were heavily infected. However, unlike our study, the potential influence of other factors was not considered in the charr study. Second, our analysis revealed that, when all other factors are taken into account, there is no significant difference in infection levels by either trematode species between the two non-migratory *Galaxias* species included in our study. The trematodes *S. anguillae* and *Telogaster opisthorchis* truly appear to be generalists in their choice of second intermediate fish hosts. They are frequently found in fish from different orders (Hine et al. 2000), for instance also achieving high infection levels in fish of the family Eleotridae (Poulin and Lefebvre 2006; Herrmann and Poulin 2011). Also, the *Galaxias* species we compared are closely related (Allibone and Wallis 1993; Waters et al. 2010) and offer the best alternative to intraspecific comparisons since the latter are not possible. Therefore, the difference in infection levels between migratory and non-migratory *Galaxias*, observed after correcting for local variation in confounding variables, is most likely associated with the contrasting migratory behaviours of the fish.

Our findings are also corroborated by studies on coral reef fishes. The migration of pelagic larval stages of coral reef fishes followed by their settlement on the reef is analogous to the amphidromous migration of galaxiids: both are akin to habitat switching from one life stage to the next. This general life history strategy may serve to take juveniles away from the high infection risk associated with adult habitats. For example, in the damselfish *Pomacentrus moluccensis*, parasite infections are negligible in pelagic larval stages (prevalence 0–4%, all metazoan parasites combined), but increase sharply to approximately 50% in recently settled juvenile stages (Grutter et al. 2010). Like migratory *Galaxias* in this study, larval damselfish avoid the high risk of parasitism in the adult habitat through a pelagic phase.

Juvenile non-migratory *Galaxias* start acquiring metacercariae from an early age when they are just over 1 cm in length (Kelly et al. 2010), whereas juvenile migratory fish clearly return to streams parasite-free, and parasite accumulation only starts in fish of >4 cm in total length (present results). It is somewhat intriguing that the difference between older migratory and non-migratory *Galaxias* sampled during the autumn is limited to infections by *S. anguillae*, and not to those by *T. opisthorchis*. The effects of other predictors, such as snail abundance or stream flow, also differ between trematode species. There is no obvious biological reason for these contrasting patterns. Both trematodes have perfectly identical life cycles, with the same snail first intermediate host, the same set of small fish species used as second intermediate hosts and the same eel definitive hosts. The infective stages of both trematodes have roughly the same dimensions. In *S. anguillae*, the cercarial body is approximately 0.22 mm long by 0.13 mm wide, and the tail is 0.34 mm long (Macfarlane 1951); in *T. opisthorchis*, the cercarial body is 0.27 mm long by 0.11 mm wide, and the tail is 0.34 mm long (Macfarlane 1945). The metacercariae of both species also grow to the same extent once inside a fish, reaching body lengths of 0.5–1.0 mm. Although their dimensions are comparable, cercarial swimming and host-finding behaviour differ between the two species, with cercariae of *S. anguillae* being less phototactic and less active swimmers than those of *T. opisthorchis* (Macfarlane 1952). Perhaps these differences mean that, for *T. opisthorchis* and not for *S. anguillae*, certain local factors are key determinants of infection success and obscure any influence of host migratory behaviour. Alternatively, since migratory *Galaxias* appear to harbour fewer *T. opisthorchis* metacercariae for a given body size than non-migratory ones, just as seen for *S. anguillae* metacercariae (see Fig. 1), the lack of significance for the former parasite species may be attributed to statistical issues. Only eight fish out of 92 were uninfected by *S. anguillae*, whereas 35 were uninfected by *T. opisthorchis*; the greater number of zeros leads to more variable coefficient estimates for the predictor variables in our models (see Table 4), possibly masking a true effect of migratory behaviour on infection levels by *T. opisthorchis*.

If migration to pelagic marine habitats by larval galaxiids has evolved as an adaptation to escape from parasitism during a sensitive life stage, then the benefits of this strategy must outweigh its costs. There are several physiological costs associated with migration (Dingle 1996), and the benefits of avoiding parasitic infection can easily eclipse those costs. Metacercarial infections in fish are commonly associated with elevated mortality, especially in young fish or those exposed to other stress (Gordon and Rau 1982; Lemly and Esch 1984; Jacobson et al. 2008; Ferguson et al. 2011). In *Galaxias*, infection by even a few metacercariae of *T. opisthorchis* at an early age results in pronounced spinal malformations. Not only does the rapid disappearance of malformed fish from field cohorts suggest parasite-induced mortality, but the causal arrow from infection to death, through malformation, has also been demonstrated experimentally (Kelly et al. 2010). There is no reason why the other trematode species, *S. anguillae*, which is equally as abundant, has the same size and the same infection mode as *T. opisthorchis*, should not have roughly similar deleterious effects on young galaxiids. Therefore, we might speculate that ancestral populations of migratory *Galaxias* lived in habitats with a particularly high local risk of infection. Through either frequency- or intensity-dependent selection, parasitism may outweigh any cost of migration and favour individuals with a larval pelagic phase, thus promoting the evolution of migration.

This scenario is plausible because in a range of animals several other life history strategies appear to have evolved as adaptations to avoid parasitism (e.g. Fredensborg and Poulin 2006; Ohlberger et al. 2011) and because the restlessness associated with migratory behaviour may be controlled by very few genes (Mueller et al. 2011) and thus liable to rapid evolution under local selection. Our data do not allow us to distinguish between a parasite-driven adaptive explanation for the historical adoption of a migratory strategy in some *Galaxias* and a coincidental protection from infection gained as a side-effect of larval migration. Nevertheless, our findings add to the growing realization that migration and parasitism are far from independent of each other (Folstad et al. 1991; Loehle 1995; Piersma 1997; Altizer et al. 2011). Whether as a cause or a consequence of migratory behaviour, infection risks are influenced by animal movements, and so parasitism should routinely be included as a potential factor in future studies of animal migration.

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