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Effects of introduced trout predation on non-diadromous galaxiid fish populations across invaded riverscapes

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Department of Conservation
Te Papa Atawhai

Cover: Canterbury galaxias, *Galaxias vulgaris* Stokell. *Photo: Angus McIntosh.*

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Abstract

We assessed the landscape-scale effect of predation pressure from trout on the population integrity and distributions of non-diadromous galaxiids in high-country streams of the South Island, New Zealand. The effects of trout (brown trout, *Salmo trutta*, and rainbow trout, *Oncorhynchus mykiss*) on two widespread species, the Canterbury galaxias (*Galaxias vulgaris* Stokell) and the alpine galaxias (*G. paucispondylus* Stokell) were assessed. Experiments confirmed that both species were vulnerable to trout predation and that habitat (size and disturbance regime) may be a factor in local co-occurrence. Quantitative electrofishing surveys indicated that *G. paucispondylus* distributions were less affected by trout than *G. vulgaris* distributions and that the species' range was limited by temperature. Trout created demographic sinks for *G. vulgaris* across most invaded reaches, while refuge populations in streams above barriers to trout acted as demographic sources for this species. *G. vulgaris* was consistently absent from small, stable stream reaches far from sources, indicating that trout predation pressure and propagule pressure (driven by immigration from sources) interact to drive local *G. vulgaris* persistence in trout-invaded reaches. Predation pressure is likely to be highest in areas where infrequent flooding allows high densities of large trout (>150 mm FL) to occur and where there are few refugia for galaxiids. A spatial model was developed to predict exclusion of galaxiids by trout across invaded networks. If used appropriately, the model could be used to find new refuge populations of non-diadromous galaxiids and to aid planning of active rehabilitation of trout-invaded river networks.

Keywords: non-diadromous galaxiids, trout, predation, refugia, source-sink dynamics, riverscapes, spatial exclusion

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1. Introduction

The Galaxiidae family is the largest grouping in New Zealand's endemic fish fauna. It contains the diadromous galaxiids, a group that includes the well-known whitebait species kōkopu and inanga, as well as the lesser-known non-diadromous species that do not travel to the sea. This group (Salmoniformes: Galaxiidae) contains at least 17 species, and more are in the process of being described (McDowall 2006).


Figure 1. The Canterbury galaxias, *Galaxias vulgaris* Stokell. Fish length c. 100 mm. *Photo: Angus McIntosh*


Figure 2. The alpine galaxias, *Galaxias paucispondylus* Stokell. Fish length c. 100 mm. *Photo: Angus McIntosh*

Galaxias vulgaris (Fig. 1) was once considered to be a single species with local phenotypic variations, widely distributed across the South Island, New Zealand (Townsend & Crowl 1991; Waters & Wallis 2001). Recent taxonomic revisions now recognise this '*G. vulgaris* sensu lato' species complex as a group of distinct species and as-yet undescribed taxa, which are collectively referred to as 'flathead' and 'roundhead' galaxiids (Waters & Wallis 2001; McDowall 2006; Burridge et al. 2007; Crow et al. 2009). Little is known about specific differences in ecology between these taxa. *Galaxias paucispondylus* (Fig. 2) belongs to a group known as the 'pencil galaxiids'.

In fresh waters worldwide, introduced predators have had a disproportionately large effect on local diversity (Cox & Lima 2006), and introduced predatory sports fish (Cambray 2003) have resulted in local extinctions, community shifts, trophic cascades and alterations to ecosystem functioning (Hall & Mills 2000; Donald et al. 2001; Simon & Townsend 2003, Finlay & Vredenburg 2007). Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) were introduced to New Zealand rivers from the late 1860s (Walrond 2009) and are now well-established, sharing the same preference for cold, fast-flowing habitats in spring-fed or high-altitude streams as the non-diadromous galaxiids (McDowall 2006).

Trout have long been assumed to pose both a predatory and competitive threat to non-diadromous galaxiids, due to their dietary overlap and widespread distribution (McIntosh et al. 2010), but only in the last 20 years has quantitative evidence of their impact been available (Townsend & Crowl 1991; Townsend 1996; McIntosh 2000; McDowall 2003a; McDowall 2006). Previous studies, conducted in artificial channels and aquaria, have shown that roundhead and flathead galaxiids are vulnerable to competitive displacement by small trout (<150 mm fork length (FL)) and direct predation by large trout (>150 mm FL) (Glova et al. 1992; Glova & Sagar 1993; McIntosh et al. 1994; McIntosh 2000).

We investigated the effects of trout on the distribution and structure of non-diadromous galaxiid populations using two species—the Canterbury galaxias (*Galaxias vulgaris* Stokell) and the alpine galaxias (*Galaxias paucispondylus* Stokell). Both sporadically co-occur with trout and are found in a variety of stream habitats (McIntosh 2000; Elkington & Charteris 2005). Our studies were based on the landscape-scale invasion patterns and habitats of trout, a scale in freshwater fish ecology that has been referred to as the 'riverscape scale' (Fausch et al. 2002). This scale of study allows the importance of configuration of critical habitats for fish within the river network to be taken into account. While the impacts of trout on *G. vulgaris* detected in this study have been published in the scientific literature and are referred to, where appropriate, in the results and discussion, the results of predation experiments conducted during the study are presented here in full.

Appropriate management plans based on local-scale mechanisms, as well as large-scale 'landscape' effects, must be developed for the effective conservation of native species threatened by introduced species (Hulme 2006). In this report we explore the implications of our findings for the conservation management of non-diadromous galaxiids within trout-dominated riverscapes.

2. Methods

2.1 Study areas

Most field studies on *G. vulgaris* were carried out in Broken River and Porter River of the Waimakariri River catchment. These networks were chosen because their streams contain both *G. vulgaris* and trout, as well as several trout-free populations above natural barriers. The Acheron riverscape in the Rakaia River catchment was used to assess the spatial interactions between *G. paucispondylus* and trout.

Quantitative fish sampling was conducted at five sites in the Acheron rivescape, nine sites in the Porter riverscape and seven sites in the Broken riverscape (Fig. 3A–C). Details of the locations of these sites are provided in Table 1. The sites were chosen to provide a combination of large, small, stable and disturbed habitats that were both near to and far away from trout-free galaxiid populations, which were also sampled. The Waimakariri River and the Rakaia River drain the eastern slopes of the Southern Alps / Kā Tiritiri o te Moana and flow into the sea north and south of Christchurch, respectively. The surveyed Porter, Broken and Acheron riverscapes are third-order streams and include fish-occupied headwater tributaries.

2.2 Sampling methods

Electrofishing surveys were conducted at two different sampling scales: riverscape-scale spot-fishing and reach-scale quantitative fishing. Riverscape-scale surveys were initially conducted in the Broken (Fig. 3A), Porter (Fig. 3B) and Acheron (Fig. 3C) riverscapes. Riverscape-scale surveys were also later used in the Otamatapaio River (Fig. 3D) and Fraser River (Fig. 3E) tributaries of Waitaki River in the South Island, New Zealand, to test GIS-based predictive models of galaxiid distributions.

2.2.1 Quantitative electrofishing

To assess relative abundances and size-class structuring in trout and galaxiids, quantitative electrofishing was used at key locations across the study riverscapes (Table 1). Electrofishing was performed using a Kainga EFM 300 backpack electrofisher (NIWA Instrument Systems) generating 400–600 V pulsed DC current. The quantitative sites (each 20 m long) were surveyed using three-pass depletion electrofishing, with stop nets placed upstream and downstream of each site. Stunned fish were collected in a push net, as well as in the downstream stop net at the end of each pass. Fish were measured and weighed before being returned to the stream, and abundances were determined using the Maximum Weighted Likelihood model of Carle & Strub (1978). Biomass per unit area was calculated as the mean weight (g) of each species captured at a site multiplied by abundance and divided by the surface area of the site.

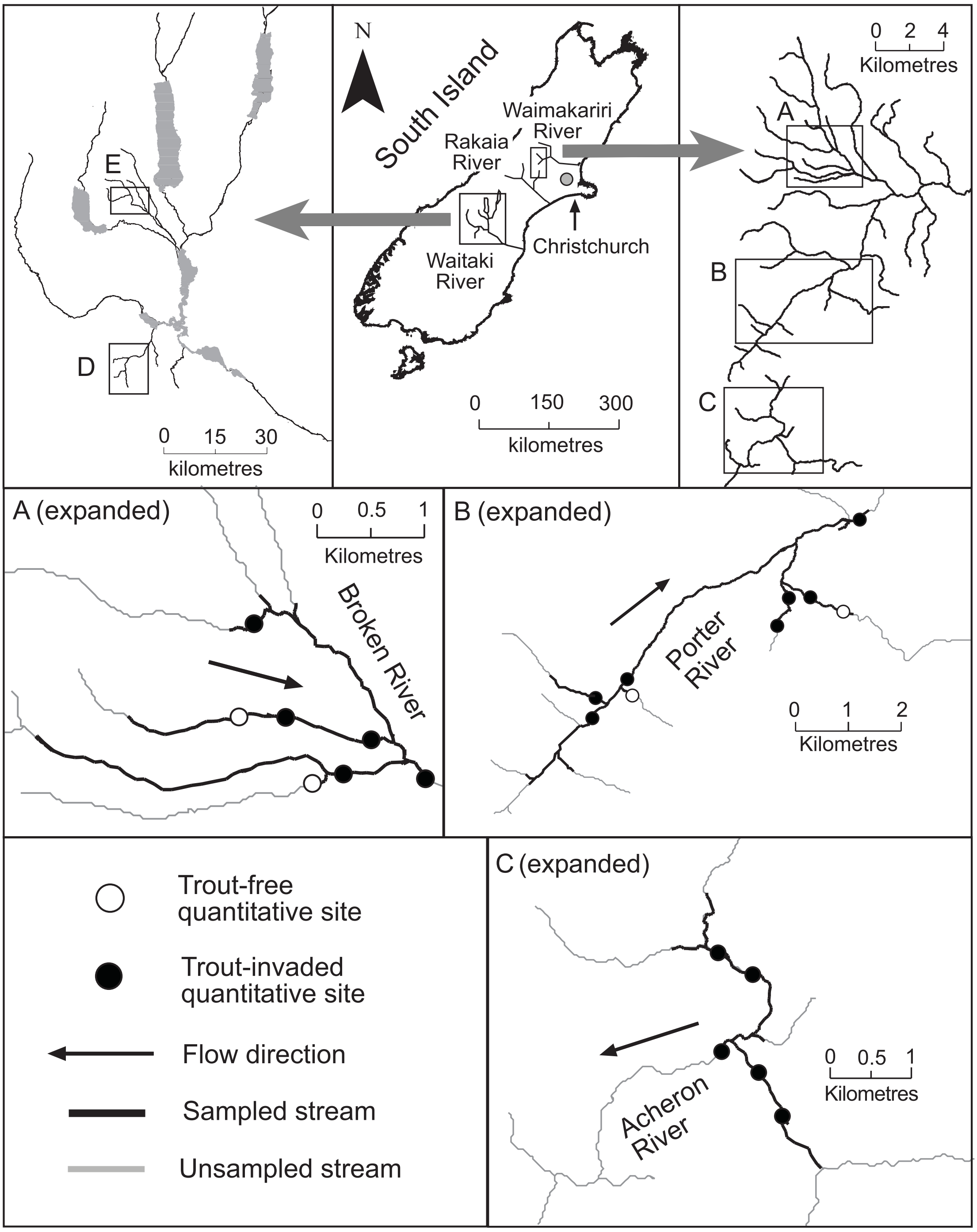

Figure 3. Map of river networks surveyed during the study. The Broken River (A) and Porter River (B) networks were surveyed to assess *G. vulgaris* population structure. Quantitative monitoring sites are shown in the expanded maps of the Broken (A), Porter (B) and Acheron (C) River networks. Riverscape-scale surveys were also later used in the Otamatapaio River (D) and Fraser River (E) tributaries of the Waitaki River.

2.2.2 Spot fishing

To achieve a highly extensive, low-intensity assessment of fish species presences and absences across the riverscape, a rapid 'spot-fishing' technique was used. The technique involved subsampling three separate micro-habitats within a stream reach (30–80 m, normally denoted by major bends in the river) to assess the presence or absence of galaxiids and trout (Woodford & McIntosh 2011). For each subsample, a section of stream measuring 3 m × 1 m in area was electrofished downstream into a push net in a single pass. Sub-sampling areas that contained high levels of in-stream cover, either from benthic structure or from aquatic macrophytes, were

Table 1. List of quantitative fish monitoring sites and their coordinates.

RIVERSCAPE	SITE NAME	LATITUDE	LONGITUDE
Broken River	Upper Bradley	43°11′26.67″S	171°42′28.08″E
Broken River	Middle Bradley	43°11′25.02″S	171°42′44.20″E
Broken River	Lower Bradley	43°11′25.02″S	171°42′44.20″E
Broken River	Hogs Back Creek	43°11′43.13″S	171°43′12.35″E
Broken River	Thunder Creek	43°11′46.31″S	171°43′03.14″E
Broken River	Broken River	43°11′33.08″S	171°43′32.58″E
Broken River	Tims Stream	43°10′59.14″S	171°42′39.60″E
Porter River	Upper Slip Spring	43°15′41.10″S	171°42′30.14″E
Porter River	Lower Slip Spring	43°15′21.01″S	171°42′29.89″E
Porter River	Upper Dry Stream	43°15′42.72″S	171°43′32.31″E
Porter River	Lower Dry Stream	43°15′25.36″S	171°42′45.83″E
Porter River	Skifield Stream	43°16′24.70″S	171°40′16.61″E
Porter River	McNulty Stream	43°16′31.82″S	171°39′58.62″E
Porter River	Upper Porter	43°16′46.09″S	171°39′44.39″E
Porter River	Lower Porter	43°14′38.40″S	171°43′41.67″E
Acheron River	Upper Acheron	43°19′27.39″S	171°40′07.17″E
Acheron River	Middle Acheron	43°19′35.15″S	171°40′21.52″E
Acheron River	Lower Acheron	43°20′01.81″S	171°40′04.42″E
Acheron River	Upper Helm Stream	43°20′31.40″S	171°40′36.84″E
Acheron River	Lower Helm Stream	43°20′04.28″S	171°40′12.09″E

chosen. All fish captured were identified to species, measured to the nearest mm and released. The ability of the spot-fishing technique to detect galaxiids and trout was assessed by comparing results from selected sites where quantitative depletion electrofishing was also performed. Habitat characteristics were measured at all surveyed reaches, including maximum depth, mean width, vegetative cover and riverbed disturbance (see Woodford & McIntosh (2011) for full details on habitat assessment). Riverscape-scale surveys were conducted at multiple reaches in each trout-invaded riverscape, as follows: Acheron River—21 reaches; Porter River—57 reaches; and Broken River—23 reaches. For GIS model analyses, a further 40 sites in the Otamatapaio and 34 sites in the Fraser riverscapes were also surveyed using this technique (Woodford et al. 2011) (Fig. 3).

2.2.3 Young-of-year studies

Quantitative electrofishing was used to assess the effects of habitat and trout biomass on the biomass of young-of-year (YOY) galaxiids. The presence of YOY fish is an indication of successful recruitment (Driver et al. 2005), and their absence could indicate the impact of trout on the viability of galaxiid populations in the area.

YOY were defined as all individuals < 60 mm total length (TL) for both *G. vulgaris* (Benzie 1968; Cadwallader 1973) and *G. paucispondylus* (Bonnett 1990). These fish were a cohort spawned in the previous spring that had spent their larval stage in a backwater and later moved to the stream. We estimated the number of YOY for each species separately and calculated their biomass per m^2.

2.3 Predation experiments

Three experiments were conducted to test the differing predatory threats posed by large and small trout, and how vegetative cover and trout species (*S. trutta* v. *O. mykiss*) affected the survival of *G. vulgaris* and *G. paucispondylus*. One experiment was carried out in a natural stream and two were conducted in aquaria (mesocosms) at the University of Canterbury's Cass Field Station in the Waimakariri basin. The mesocosm experiments were conducted during the summer of 2008/09 in an array of eight (1.2 m^2 diameter) circular tanks at Cass Field Station.

2.3.1 Natural stream experiment

This experiment was conducted on Binser Stream, a small tributary (discharge 0.02–0.05 m^3/s) of Waimakariri River, which is populated by *S. trutta*. The stream was divided into 20 experimental reaches (each 20 m^2) by placing fences across the stream. Each fence was constructed of nylon netting with an aperture size of 4 mm. The experiment used six replicates of three treatments: a no trout control, small trout (100–120 mm FL) and large trout (150–220 mm FL). Resident trout were removed, and experimental trout and *G. vulgaris* and *G. paucispondylus* were added to each reach. All experimental trout were taken from the nearby Peacock Stream. After 3 weeks, each pen was electrofished four times to retrieve fish and the proportion of the original biomass of each galaxiid species was calculated. We used ANCOVA to test survival of galaxiids across the treatments, using distance downstream from the first pen as a continuous covariate to account for any non-random effect of the order of treatments along the stream.

2.3.2 Mesocosm experiment 1

This trial assessed the predation of large (>150 mm FL) *S. trutta* on large and small *G. paucispondylus* in tanks with and without vegetative cover. Vegetative cover (such as aquatic macrophytes, e.g. *Nasturtium* sp.) can reduce predation of galaxiids in lakes (Stuart-Smith et al. 2007) and was common in stable reaches of the surveyed rivers.

The base of each tank was covered with a single layer of gravel and half of the tanks were planted with stands of *Nasturtium* sp., harvested from the nearby Grasmere Stream. A single large *S. trutta* (172–187 mm) was added to four of the eight tanks, creating treatments of trout only, trout and macrophytes, macrophytes only, and no trout and no macrophytes. Three small (56–75 mm) and three large (82–96 mm) *G. paucispondylus* were added to each tank, and the number of galaxiid mortalities recorded after 48 hours. The experiment was run twice, to obtain four replicates per treatment blocked by time. Galaxiid densities for the experiment were 5 fish/m^2, which is approximately 10× the maximum density of *G. paucispondylus* recorded in field surveys for this study. We used a factorial ANOVA with treatment and time as factors to assess the effect of vegetation on galaxiid survival in the mesocosm.

2.3.3 Mesocosm experiment 2

A second experiment compared the relative ability of the two trout species (*S. trutta* and *O. mykiss*) to prey on small (YOY or 1+) *G. vulgaris* and *G. paucispondylus* in a controlled environment. Four *G. vulgaris* (58–75 mm) and four *G. paucispondylus* (59–79 mm) were placed in each tank, which contained a standardised assortment of cobbles and gravel for benthic cover. One large *S. trutta* (169–187 mm) or *O. mykiss* (179–195 mm) was added to six of the eight tanks. The trout treatments, with both species of galaxiid in each tank, created a six replicate split-plot design. The two remaining tanks served as trout-free monitoring controls, which were not used in statistical analyses, but were used to verify that the tanks themselves were not a likely source of mortality for the fish. Galaxiid mortalities were recorded after 48 h. While overall galaxiid densities were far above natural levels for this experiment, this was seen more as an experiment to compare the innate ability of the two trout species to prey on galaxiids, rather than to estimate real-world predation levels. Results of all three experiments were tested using a nested ANOVA, with differences in galaxiid species mortality nested within the effect of trout species on overall galaxiid mortality.

2.4 GIS modelling

As riverscape-scale spatial patterns were identified over the course of the research, it became increasingly clear that a GIS-based model of these patterns could be developed to predict the spatial interactions between galaxiids and trout. These analyses were performed using the programme ArcGIS 9 (ESRI, 2009) and are described in detail in Woodford et al. (2011). The validation and potential applications of this model are developed further in the discussion of this report.

3. Results

3.1 Spatial patterns in galaxiid and trout distributions

Galaxias vulgaris was recorded in many trout-invaded reaches, but recruitment of post-larval galaxiid fry was limited to 9% of trout-invaded reaches in Broken River (Woodford & McIntosh 2010). Fry recruitment was high in trout-free refuge streams where trout were excluded from upstream movement by physical barriers (65% of all trout-free reaches retained fry). Juvenile galaxiids were recorded at all trout-free quantitative monitoring sites, but only at a few highly disturbed trout-occupied monitoring sites where the densities of both trout and galaxiids were extremely low (Woodford & McIntosh 2010). These sites were designated as 'pseudosinks', as they demonstrated a capacity to allow local recruitment at a seemingly low carrying capacity. Other trout-invaded sites, where no juveniles and very few small adults were present, were seen as true sinks, where trout predation had effectively prevented local recruitment by *G. vulgaris* (Fig. 4).

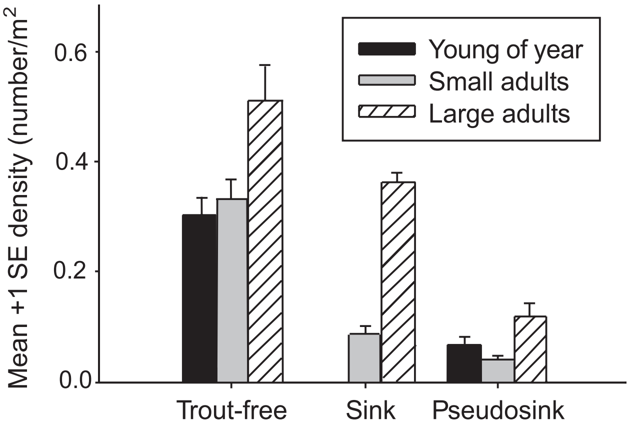

Figure 4. Size-class structuring in *G. vulgaris* populations in trout-free refuge sites, and trout-occupied sink and pseudosink sites in the Broken and Porter riverscapes in winter. Modified from Woodford & McIntosh (2010).

Spot-fishing detected *G. vulgaris* at 72% of the quantitative survey reaches where they occurred, while *G. paucispondylus* was detected at 78% of the quantitative reaches where they occurred by the low-intensity technique. Spot-fishing successfully detected trout at 92% of the quantitative sampling sites, although large trout (>150 mm FL) were only detected at 44% of the quantitatively sampled sites where they occurred. We may therefore assume that false absences (caused by the low intensity of the sampling method) of galaxiids and trout were probably rare in the riverscape surveys, but that large trout were more difficult to detect with this method. Spot-fishing revealed a distinct pattern of *G. vulgaris* absence at trout-occupied sites that were far from trout-free refuge streams and either narrow or with a highly disturbed flow regime (Woodford & McIntosh 2011). These results indicate that the trout-occupied riverscapes could be divided into co-occurrence zones, where immigration from trout-free sources allows the persistence of *G. vulgaris* in the presence of trout, and exclusion zones where dispersal distance and habitat variability interact to exclude *G. vulgaris* from trout-occupied waters. When stream size was used as the primary habitat variable, the division between exclusion and co-occurrence could be plotted as a linear limit response (Fig. 5).

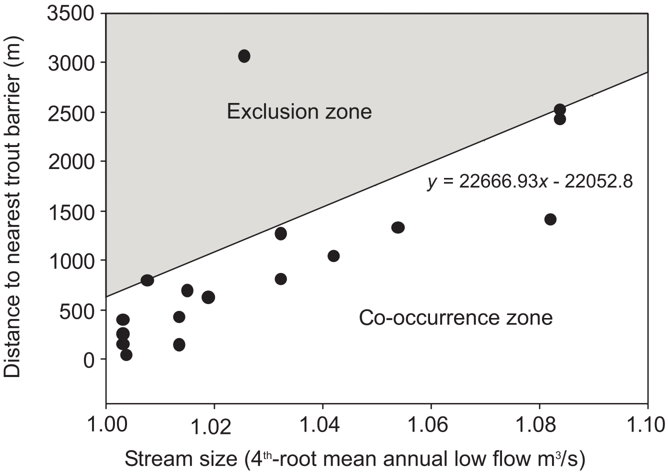

Figure 5. Graphic representation of the exclusion zone phenomenon detected in *G. vulgaris* distributions across trout-occupied habitats of the Broken and Porter riverscapes. Dots represent localities of *G. vulgaris* records within the trout-invaded riverscape relative to the nearest trout-free barrier population. The function that divides the exclusion zone from the co-occurrence zone is a 90th quantile regression that plots the maximum distances of 90% of *G. vulgaris* occurrences from the nearest trout barrier in the river network across the stream size gradient, and was calculated using geo-referenced fish records and the Freshwater Environments of New Zealand (FWENZ) river model. The 90th quantile makes the regression robust to the random outlier *G. vulgaris* record in the modelled exclusion zone, which probably represents a fish in a pseudosink habitat (Woodford & McIntosh 2011). Stream size is estimated using a 4th root transformed estimate of river segment discharge (m^3/s) obtained from the FWENZ. Modified from Woodford et al. (2011).

Galaxias paucispondylus did not show similar patterns of absence in trout-occupied reaches relative to trout-free refugia, and juvenile recruitment was not negatively associated with trout (Woodford 2009). The species was, however, only recorded in reaches where temperature loggers recorded maximum summer temperatures below 18°C, suggesting a temperature limitation to their distribution.

3.2 Experimental results

In this study, a fish manipulation experiment in a natural stream and two mesocosm experiments indicated that *O. mykiss* and *S. trutta* pose a significant predatory threat to both *G. vulgaris* and *G. paucispondylus*, despite the field evidence implying *G. paucispondylus* might be considerably less vulnerable.

The stream experiment showed that large trout had depleted a significant proportion of the biomass of both species relative to the other treatments (Table 2, Fig. 6). While this indicated a clear predation effect on *G. vulgaris*, the role of predation was uncertain for *G. paucispondylus*, as relatively few fish were recaptured overall and several were found in different pens from the ones they had been placed in, suggesting that many fish had burrowed under the fences and left the experimental reaches, especially those with large trout (Fig. 6).

In the vegetation experiment, *G. paucispondylus* showed significant mortality in both vegetated and non-vegetated treatments containing trout, while no fish were lost from the trout-free treatments. A significant interaction between treatment and time (whether the data came from the first or second run of the experiment) was recorded (Table 2) as a result of many galaxiids surviving in the trout with vegetation treatment in the first run, and few surviving in this treatment in the second run. This means that the ability of aquatic macrophytes to protect *G. paucispondylus* from trout predation could not be proven. In the trout species experiment, *O. mykiss* and *S. trutta* did not show a significant difference in their ability to consume galaxiids of either species (Table 2), even though galaxiid mortalities were recorded in most trout treatments and none in the two monitoring controls. This result suggests that there is no difference in the threat posed by either trout species to non-diadromous galaxiids.

Table 2. Statistical analyses for three predation experiments conducted to assess the predatory threat posed by *Salmo trutta* (Exp.1, 2), and *S. trutta* and *Oncorhynchus mykiss* (Exp. 3) on *Galaxias vulgaris* and *G. paucispondylus*. Experiment 1 compared galaxiid survival in no trout, small (< 150 mm) trout and large (> 150 mm) trout treatments in a fenced natural stream with ANCOVA, using longitudinal distance of pens from the upstream end of the array of pens as a continuous covariate to account for any bias in the sequence of treatments. Experiment 2 compared *G. paucispondylus* survival in vegetated and non-vegetated mesocosms with and without a single large (> 150 mm) trout. Experiment 3 compared the relative threat posed by the two trout species to the galaxiids, using a split-plot design that compared survival of the two galaxiid species, nested within the effect of trout species (*S. trutta* or *O. mykiss*) within mesocosms.

EFFECT	df	*F*	*P*
Experiment 1: Fenced stream (ANCOVA)			
G. vulgaris			
Trout size treatment	2	4.16	0.04
Distance	1	0.67	0.42
Error	14		
G. paucispondylus			
Trout size treatment	2	4.89	0.02
Distance	1	0.12	0.73
Error	14		
Experiment 2: Vegetation (factorial ANOVA)			
Treatment	3	35.41	< 0.0001
Time	1	7.23	0.03
Treatment x time	3	15.20	0.001
Error	8		
Experiment 3: Trout species (nested ANOVA)			
Trout species	1	0.50	0.49
Galaxiid species (trout species)	2	0.72	0.51
Error	8		

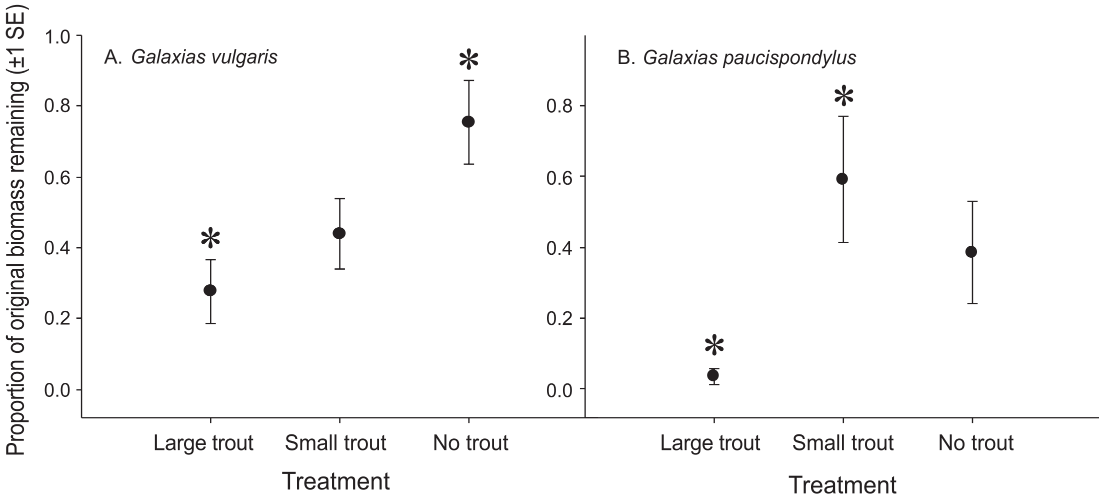

Figure 6. Mean proportion of original biomass of *G. vulgaris* and *G. paucispondylus* recaptured in pens containing large (>150 mm), small (<150 mm) and no trout, in the Binser Stream after 3 weeks. Asterisks show significant differences between treatments as calculated by post-hoc Tukey tests ($P < 0.05$).

4. Discussion

4.1 Riverscape-scale effects of trout on galaxiid populations in the Waimakariri River catchment

Trout are estimated to occupy >95% of all fish-occupied habitat in the Waimakariri River catchment (McIntosh et al. 2010). Our riverscape-scale surveys found trout in the majority of surveyed habitats in all tributaries of the Broken and Porter Rivers (Table 3). Since this work focussed on the headwaters of these rivers, the number of trout-free habitats encountered is proportionally higher than would be found across the entire Waimakariri River catchment.

Table 3. Comparison of length of fish-occupied habitat upstream and downstream of trout barriers in the upper Broken and Porter Rivers.

	TOTAL LENGTH OF STREAM (km)	PROPORTION OF STREAM LENGTH (%)
Trout-free	5.1	14
Trout invaded	30.1	85

4.1.1 Predation

Our experimental results show that both *O. mykiss* and *S. trutta* prey on *G. vulgaris* and *G. paucispondylus*. It should therefore be assumed that wherever trout occur in sufficient numbers in a river network, the threat of predation on non-diadromous galaxiids will be high.

Most trout-inhabited streams can be considered as 'demographic sinks' for *G. vulgaris*, with negative population growth. Juvenile fish were found in very few trout-occupied reaches during depletion electrofishing surveys, and large adult *G. vulgaris* were proportionally more abundant than small adults in trout-occupied reaches compared with trout-free sites. This would suggest that the presence of galaxiids in these areas is dependent on the immigration of adult fish from trout-free reaches (Woodford & McIntosh 2010). Trout-free reaches (which have high juvenile recruitment—65% of reaches retained fry) appear to act as sources of immigrants for the trout-invaded sink reaches (Woodford & McIntosh 2010). Broken and Porter Rivers both have well-established trout populations, so the effect on *G. vulgaris* recruitment was predictably severe. The effect of trout in other catchments will depend on the population density and distribution of large trout in those areas.

Even in systems such as Broken River, where most of the river network is suitable for trout, local reach-scale factors reduce the impact of predation on galaxiids. Predation is dependent on encounter rates, which are affected by predator and prey densities, as well as habitat complexity (Crowder & Cooper 1982; Morin 1986; Beukers & Jones 1998; Seitz et al. 2001). Habitats that support high numbers of predators will be hostile for prey species, unless local factors can disrupt predator feeding or provide refugia (microhabitats) that are inaccessible to the predator (Crowder & Cooper 1982; Steele 1999; Kauffman et al. 2007). As fish grow, different types of stream habitat are likely to provide refugia for different life-history stages (Schlosser 1987; Schlosser 1988).

At the post-larval or fry stage, *G. vulgaris* are confined to backwaters with low flow and are extremely vulnerable to predation by trout of all sizes (McIntosh et al. 2010; Woodford & McIntosh 2010). In a riverscape context, a backwater may act as a refuge for *G. vulgaris* fry if it is temporarily disconnected from the main channel, or if low trout densities in the main stream mean that the backwater is not populated during the summer. Most (91%) of the trout-inhabited reaches of Broken River contained no fry at the end of summer and were demographic sinks for *G. vulgaris*. The few reaches where some *G. vulgaris* recruitment did occur were considered 'pseudosink' habitats (after Pulliam 1996), as they appeared to support low densities of both trout and galaxiids. The populations in these marginal reaches would be highly susceptible to extinction when compared with trout-free source populations (Woodford & McIntosh 2010), since pseudosink sites are often disturbed by flooding and have few invertebrate food resources, and therefore have a low carrying capacity for galaxiids and trout (Death & Winterbourn 1994; Suren & Jowett 2006). Frequent flooding or drying events will also affect fish populations in these reaches by increasing the displacement and mortality of individual fish, and disrupting spawning (Detenbeck et al. 1992; Allibone 2000).

4.1.2 Effects of flooding, drying and habitat complexity

Habitats disturbed by seasonal flooding and drying have fewer trout (McIntosh 2000; Woodford & McIntosh 2011) and, in this study, large trout were seasonally restricted to hydrologically stable reaches (Woodford & McIntosh 2011). Since trout densities are affected by these events (Jowett & Richardson 1989; Woodford & McIntosh 2011), their effect on galaxiids in streams with regular disturbances is likely to fluctuate over time. In Cass River, a tributary of Waimakariri River, trout densities decreased after rainfall and consequent flooding (McIntosh et al. 2010). Regular hydrologic disturbance appears to be important in allowing trout and galaxiids to co-exist in streams (Closs & Lake 1996; Leprieur et al. 2006), and river networks that offer these conditions are less likely to act as demographic sinks for galaxiids.

By contrast, *G. paucispondylus* recruitment does not appear to be as severely affected by the presence of trout. The fry may be more agile and benthic in behaviour, and more resistant to predation from trout entering a backwater, but further investigation is required. *Galaxias paucispondylus* achieved maximum juvenile recruitment in disturbed sites with few trout (Woodford 2009). Juveniles co-occurred with trout in streams of varying sizes and stabilities, provided water temperatures were below an apparent physiological limit of 18°C. The elongated shape of *G. paucispondylus* may make them less visible to trout in areas of interstitial and vegetative cover in the riverbed, but more research into the effects of trout on *G. paucispondylus* populations is required to establish the mechanisms controlling their co-existence.

Adults of *G. vulgaris* and related flathead species may also avoid larger trout by occupying different microhabitats in a stream reach (McIntosh et al. 1992; Glova & Sagar 1993). The more varied habitats in larger streams could decrease encounters between predators and prey (Angermeier & Schlosser 1989), and enable *G. vulgaris* to live in trout-occupied sink habitats. Persistence therefore depends on successful immigration from trout-free tributaries, and a matrix of biotic and abiotic factors that dictate the availability of predation refugia for juvenile and adult galaxiids in the trout-invaded riverscape (Fig. 7).

4.1.3 Refuge streams

Although trout-free reaches made up only a small percentage of the surveyed stream habitat (Table 3), they still appeared to act as demographic sources in the riverscape. Even relatively small trout-free habitats (Table 4) supported large, healthy galaxiid populations relative to those in invaded reaches (Woodford & McIntosh 2010).

The number and location of trout-free streams in a river network may be far more important than their physical size. These refuge streams are not easy to locate without fieldwork, as they often appear indistinguishable from trout-inhabited streams on a map. The barriers that protect them from trout are also physically variable and can easily be overlooked. Trout barriers in the Waimakariri catchment were not always physically substantial, and trout breached some long-established barriers during the course of this study. For example, the upper reaches of Coach Stream, a tributary of the Waimakariri River that is crossed by the trans-alpine highway at the base of Porters Pass, were thought to be inaccessible to trout due to a road culvert, but in 2007, trout were discovered there. This incident highlights the need to monitor existing barriers, look for new ones and to engage in restoration to ensure non-diadromous galaxiid populations are preserved.

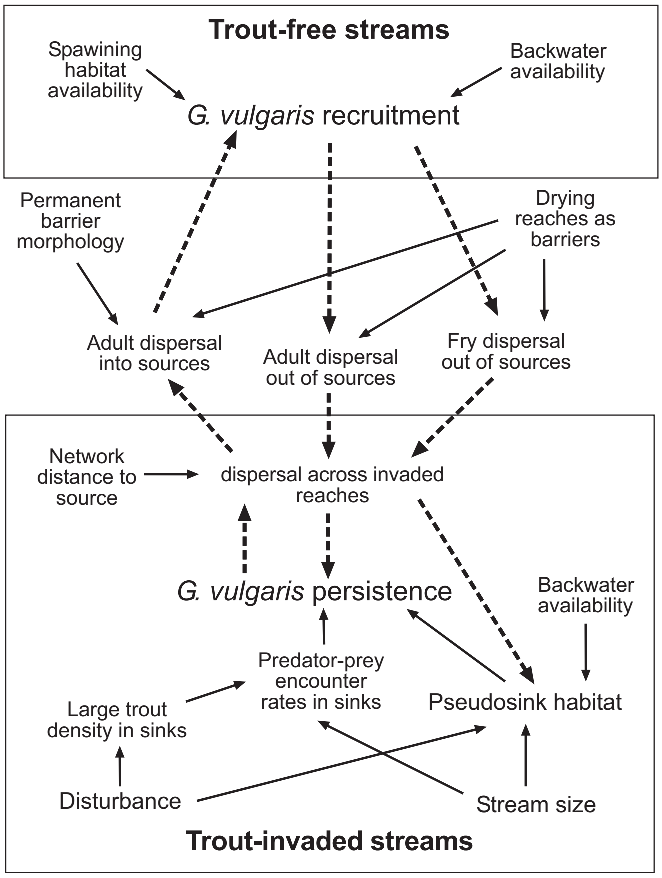

Figure 7. Processes that drive *G. vulgaris* occurrence patterns in trout-invaded riverscapes. Solid arrows depict mechanisms affecting *G. vulgaris* dispersal and persistence, while dashed arrows represent dispersal pathways between trout-free and trout-invaded habitats. Circles represent habitat drivers of these ecological processes.

Table 4. Length and dimensions of trout-free streams above trout barriers that appear to have functioned as demographic sources for *G. vulgaris*.

STREAM	BARRIER TYPE	FISH-OCCUPIED LENGTH (m)	MEAN WIDTH (m)	MEAN DEPTH (cm)
Skifield Stream*	Road culvert	168	1.5	20
Dry Stream	Drying reach + culvert	788	2.9	24
Bradley Stream*	Drying reach	1051	1.1	25
Thunder Creek*†	Bedrock chute	1476	1.6	31
Parapet Stream*†	Waterfall	1089	1.8	30
Otamatapaio River (terrace tributary)†	Waterfall	50	1.3	22
Otamatapaio River (headwater tributary)†	Waterfall	Unknown	1.8	46
Fraser River (unnamed spring creek)†	Culvert	Unknown	0.7	30

* Unofficial name.

† Dimension data represent electrofished reaches only, not all fish-occupied habitat.

4.1.4 Spatial exclusion patterns

We analysed the relationship between the occurrence of *G. vulgaris* and the presence or absence of various habitats in the Porter and Broken riverscapes (Woodford & McIntosh 2011). Our research revealed a pattern of spatial exclusion, where *G. vulgaris* was consistently absent from small, undisturbed streams that were distant from the nearest trout-free tributary in the network (Fig. 5). The combination of narrow, stable habitats occupied by large trout, and minimal immigration of adult galaxiids drove this pattern (Woodford & McIntosh 2011).

Stream size and disturbance patterns may affect the exclusion zone in Broken and Porter Rivers, as the large sink reaches where *G. vulgaris* occurred also flooded regularly (Woodford & McIntosh 2011). The impact of disturbance and stream size in trout-occupied sink streams requires further investigation, especially where large stable reaches and small disturbed reaches occur far from source streams.

A sink reach located close to a source will contain proportionately more immigrating adults than a more distant reach. Further research is needed to confirm and quantify the mechanisms of dispersal and estimate dispersal rates across barriers and through sink reaches. Previous mark-recapture and PIT tagging studies have helped understand dispersal patterns, although they have logistical challenges (Labbe & Fausch 2000; Homel & Budy 2008). Mark-recapture has been used in a limited capacity on *G. vulgaris* and has demonstrated that mobility is strongly linked to spawning behaviour (Cadwallader 1976). The use of molecular markers such as microsatellites (e.g. Hänfling & Weetman 2006) could also provide information about dispersal rates between sources and across sink reaches.

4.1.5 Comparison of sampling methods

Our low-intensity extensive spot-fishing sampling regime enabled the exclusion pattern for *G. vulgaris* to be detected (Woodford & McIntosh 2011). Standard fish diversity and distribution monitoring protocols, such as the United States Environmental Protection Agency (US EPA) wadeable stream guidelines, call for a limited number of long (e.g. 40 × stream width) sampling reaches to capture the maximum fish diversity in a river (Peck et al. 2001). This method could potentially misrepresent the presence or prevalence of galaxiids in a trout-invaded river if the single representative site happened to be far from a source. Our technique, while far less intensive than the EPA approach, was able to detect the effects of habitat through the high number and dispersion of sample sites across the river network. Conservation managers should consider less-intensive, but more spatially extensive sampling when planning surveys or monitoring threatened fish.

4.1.6 Source-sink dynamics

The stability and persistence of source-sink metapopulations within a landscape depends on sink patches (populations in sink reaches) being renewed via dispersal from source patches (Dias 1996). Increasing the number of galaxiid source populations in a river network may not only increase metapopulation stability, but could also affect their persistence in trout-invaded reaches through the increased supply of fish. Because dispersal through sink habitats can decrease extinction risk in both source and sink populations (Foppen et al. 2000), the viability of *G. vulgaris* populations in both trout-invaded and trout-free habitats could depend on dispersal to and from sources, and across sink reaches (Fig. 7). Maintaining routes to allow dispersal between sources and sinks is therefore also a fundamental driver of metapopulation stability (Namba et al. 1999; Fagan 2002; Hilderbrand 2003). Thus, habitat disruption, like abstraction which disrupts metapopulation connectivity, could have disproportionately large effects on the riverscape persistence of galaxiids.

4.1.7 Barriers to trout

The shape of trout barriers (Fig. 8) will directly affect connectivity in *G. vulgaris* source-sink metapopulations (Fig. 7). The fry of *G. vulgaris* are likely to move from sources to sinks across waterfall and culvert barriers, as passive drift is their primary mode of dispersal (Cadwallader 1976; Jellyman & McIntosh 2008). Adult fish are less likely to disperse over waterfalls and cannot re-enter a source if the waterfall prevents upstream movement (Figs 7 & 8). Bedrock chutes (Fig. 8) may be scalable by galaxiids (such as *G. vulgaris* and *G. depresseceps*) that climb by crawling up the edges of the flow (Allibone & Townsend 1997; McDowall 2003b), but these barriers are not passable by trout, as they must leap from a deep pool to scale the barrier (Bjornn & Reiser 1991). Chutes may allow more exchange between source and sink populations of galaxiids than waterfalls, while being equally impervious to trout.

Seasonally dry barriers may help adult *G. vulgaris* disperse as they tend to colonise wetted reaches of intermittent streams rapidly (Davey & Kelly 2007). However, the timing and duration of stream drying may be critical to trout invasion and galaxiid dispersal, and barriers may be breached if wetting occurs when adult trout are migrating upstream during spawning (Ovidio et al. 1998). Conversely, erratic flows during peak fry dispersal times could seriously reduce their dispersal downstream. Although habitat drying can favour galaxiids by reducing their interactions with trout, benefits are delicately balanced with negative impacts such as the loss of spawning habitat and mortality (Allibone 2000; Dunn 2003; Leprieur et al. 2006).

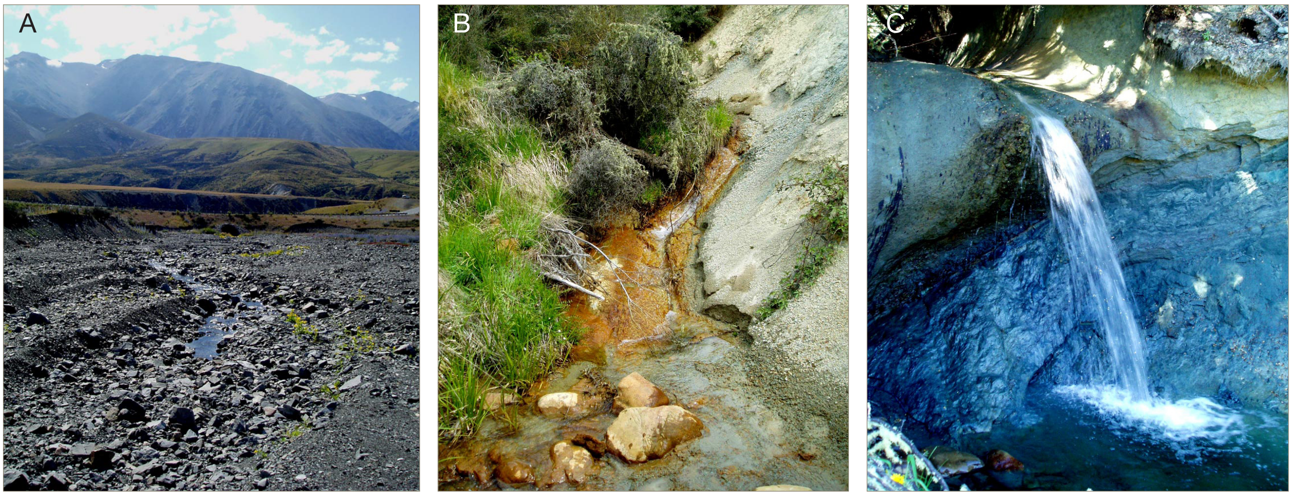

Figure 8. Three examples of trout barriers, each differing in permeability for dispersing galaxiids. Shown from left to right are A. a seasonally drying reach (Dry Stream, Porter River catchment), B. a bedrock chute passable by climbing galaxiids (*G. vulgaris*, *G. depresseceps*) but not leaping trout (Thunder Creek, Broken River catchment), and C. an overhanging waterfall that is unlikely to be scalable by trout or non-migratory galaxiids (Parapet Stream, Broken River catchment). Further details of these streams are listed in Table 4.

4.2 GIS modelling and applications

4.2.1 Galaxiid Exclusion Model—development and validation

We developed a GIS-based model that used riverscape-scale habitat data and distances to predict where trout would exclude galaxiids in a source-sink metapopulation network, based on interaction between distance to source and stream size (Fig. 5; see Woodford et al. (2011) for a full description of the model structure). The objective was to find out if the parts of the riverscape where *G. vulgaris* was excluded by trout could be predicted outside the Waimakariri River catchment. The model correctly predicted *G. vulgaris* distributions in Otamatapaio River in the Waitaki River catchment (Woodford et al. 2011), and indicated that this form of exclusion by trout is likely to be generally encountered.

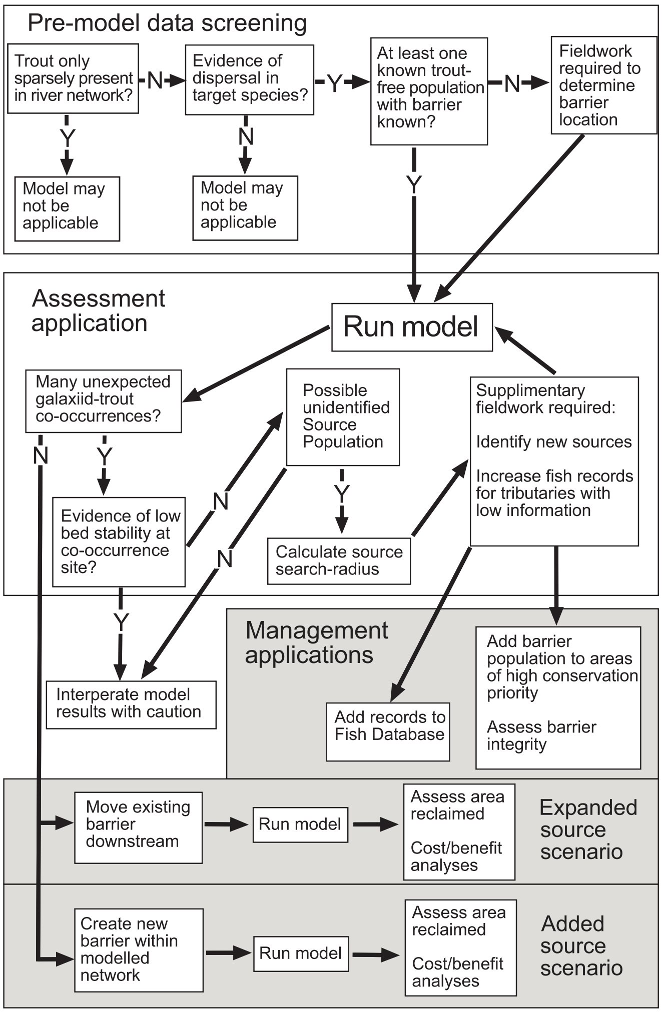

Figure 9. Procedures for using the Galaxiid Exclusion Model as a management tool to conserve galaxiids in trout-occupied riverscapes. Steps with direct management application are boxed in grey.

The model can be a useful management tool for galaxiid conservation and is based on a sequence of procedures (Fig. 9). Trout occupancy and the location of all known galaxiid demographic sources are entered, as well as fish occurrence data from inside and outside the modelled exclusion zone (Woodford et al. 2011). Next, the locations of trout barriers and *G. vulgaris* populations are entered, and exclusion zones based on the interactions between distance-to-source and stream size can then be predicted.

If many occurrences are later found within the modelled exclusion zone, this could indicate the presence of previously unknown source populations within the network. Physical factors such as disturbance, which may limit trout density, could also result in inaccurately modelled zones, so the physical attributes of a river and the consistency of trout occupancy should be considered when applying the model (Fig. 9; Woodford et al. 2011).

4.2.2 Use of the model for population management and conservation

Since the model is a useful tool for detecting previously unknown source populations, it could inform management plans for galaxiids. If new populations are found, a barrier will exist that must be identified and secured, and the landowners or relevant authorities (if on Crown land) made aware of the need to keep the stream trout-free.

Creating new, large conservation structures (national parks, conservation areas) specifically to protect newly discovered populations may be impractical or inappropriate, and other methods of protecting their habitats may be required. One approach could be to declare such streams as Freshwater Protected Areas (FPAs), independent of the established status of the surrounding land (following Abell et al. 2007), and so conserve the population regardless of whether the river network flows through public or private land. Alternatively, a conservation covenant or easement (Kabii & Horwitz 2006) could be set up with the landowner, whereby the landowner agrees to maintain riparian habitat and existing fish dispersal barriers. Such mechanisms have legal precedent in New Zealand (Norton 2007) and would allow managers greater wherewithal to enforce the protection of critical habitats and prevent future invasions without having to purchase the land surrounding the streams. This solution would enhance the overall security of *G. vulgaris* and other non-diadromous galaxiids threatened by trout.

Another use of the model is in testing possible management scenarios, such as expanding an existing source population by moving a trout barrier, or eradicating trout from a tributary and translocating galaxiids. Projects with the best outcomes from the model could then be implemented. Both refuge habitat expansion (Lintermans 2000) and translocation (Harig & Fausch 2002) would have positive effects for native fish populations threatened by trout, if managed correctly.

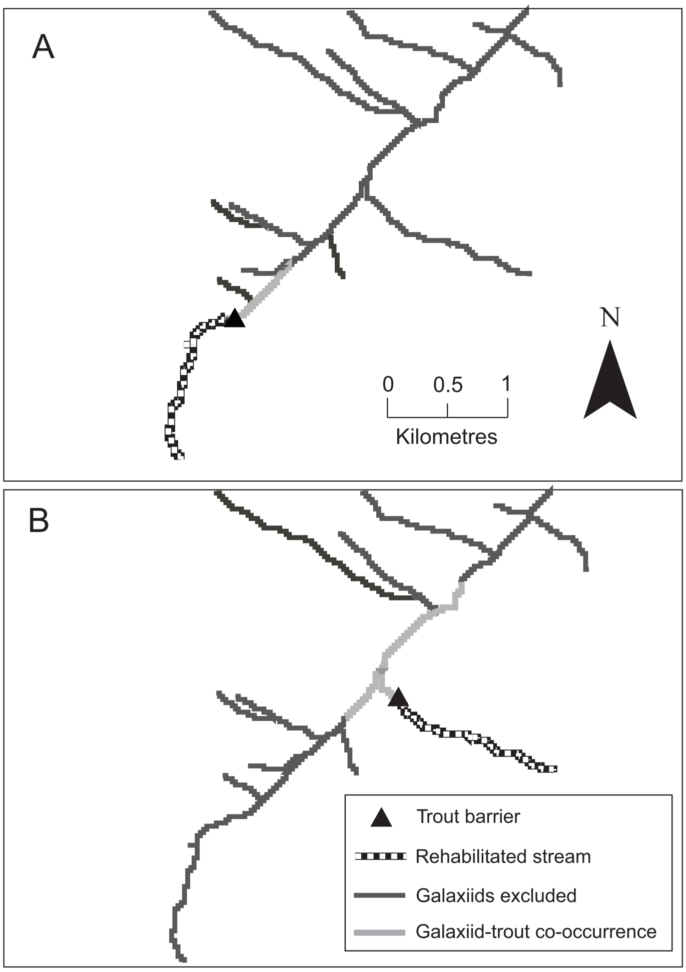

Figure 10. Maps of modelling scenarios generated by the Galaxiid Exclusion Model showing lengths of potential galaxiid-trout co-occurrence habitat created by A. removing trout and restoring galaxiids to the headwaters of the Porter River and B. restoring the identical amount of habitat on a downstream tributary.

Figure 10 illustrates two such scenarios of trout eradication and galaxiid translocation in the headwaters of Porter River. In the first, 1.5 km of stream is cleared of trout and a barrier placed on the headwater tributary draining Coleridge Pass. The model predicts that this source would support co-occurrence of galaxiids and trout for 730 m downstream (Fig. 10A). In a second scenario, a downstream tributary of Porter River is cleared of trout for 1.5 km. Because Porter River is larger downstream from the confluence with this tributary, the model predicts co-occurrence could be enabled over as much as 1.85 km (Fig. 10B). Source streams that flow into large rivers are likely to have a bigger effect on overall co-occurrence, as increased area, habitat heterogeneity and the potential for high-energy flood events would lower the predation pressure, compared with smaller headwaters (Woodford & McIntosh 2011). A short, narrow tributary that flows into a large, physically heterogeneous river is therefore ideal for a rehabilitation project. Regardless of the choice of management strategy, when dealing with trout removals it will be crucial for managers to keep landowners and other stakeholders involved in the planning process. Such measures would counteract public negative sentiment against trout removals, which can hinder the success of such projects (McIntosh et al. 2012).

4.2.3 Applying the spatial metapopulation model to other galaxiids

The galaxiid exclusion model may be of value in the management of other threatened non-diadromous galaxiids in need of conservation action. For the model to be applicable to roundhead and flathead galaxiid populations, trout must occupy most of the riverscape and some dispersal from trout-free streams into trout-occupied streams must occur (Fig. 7). *Galaxias vulgaris* and *G. paucispondylus* appear to differ in their spatial interactions with trout, and we consider that 'pencil' galaxiids (e.g. *G. prognathus*, *G. cobitinis*, *G. macronasus* and *G. divergens*) probably interact with trout in similar ways to *G. paucispondylus*, due to their similar morphology (in contrast to 'roundhead' and 'flathead' galaxiids). However, further research is needed to model the spatial interactions between trout and these galaxiid species.

Fieldwork in Otamatapaio and Fraser Rivers in the Waitaki catchment seldom found *G. cobitinis* and *G. macronasus* in the same stream as trout, and never in the same microhabitat. These species are restricted, both by their habitat requirements and by trout (McDowall & Allibone 2004; Elkington & Charteris 2005), and their few interactions with trout were not suitable for modelling.

We trialled the model on threatened galaxiid species in the southern South Island using fish distribution records from the New Zealand Freshwater Fish Database (NZFFDB) and known trout barriers recorded by the Department of Conservation Otago Regional Office. It was difficult to create datasets for any roundhead species, due to their extremely low levels of co-occurrence with trout. The species with the highest rate of co-occurrence, *G. anomalus*, is generally found where trout densities are extremely low, often because of human habitat alteration (Leprieur et al. 2006).

Other roundhead species (e.g. *G. pullus* and *G. eldoni*) are only found where trout densities are low, such as immediately below trout barriers (Simon Madill, DOC, pers. comm.). As there is only limited overlap of the galaxiids with trout in this case, the model was ineffective in predicting spatial exclusion of roundhead galaxiids by trout.

We tested the model in three catchments where populations of other flathead galaxiids occur—the 'Clutha flathead galaxias' (an undescribed taxon also known as '*Galaxias* sp. D') in Coal Creek and Cardrona River (Clutha catchment), as well as *G. depressiceps* in Nenthorn River in the Taieri catchment (Table 5). The model successfully predicted galaxiid exclusion in Coal Creek, with the only co-occurrence of galaxiid and trout found in the zone predicted. However, galaxiids were only found in the predicted exclusion zones in Cardrona and Nenthorn Rivers, a result that caused a model validation failure (Table 5). These failures may indicate the presence of multiple unknown barrier populations, but the rather sparse NZFFDB records suggest that patchy trout distributions rather than unknown galaxiid sources could explain the unexpected galaxiid occurrences.

Table 5. Validation of spatial model predicting exclusion of 'flathead' galaxiids by trout using occurrence records from the New Zealand Freshwater Fish Database. Statistical results include: binomial test of deviation from the predicted proportion of *G. vulgaris* occurrences in the exclusion zone (non-significant result indicates successful validation); binomial test for negative predictive power (NPP) in exclusion zone being significantly different from random (significant result indicates successful validation). Significant test results in bold. More details on the rationale behind these statistical tests are provided in Woodford et al. (2011).

DATASET	PROBABILITY FROM BINOMIAL TEST OF 90TH QUANTILE MODEL CONSISTENCY*	CORRECT EXCLUSION (NPP) (%)	PROBABILITY FROM BINOMIAL TEST OF NPP†
Coal Creek (*G.* sp. D)	1	100	0.008
Cardrona River (*G.* sp. D)	< 0.0001	63	0.13
Nenthorn River (*G. depresseceps*)	< 0.0001	27	0.36

* H0: Proportion of *G. vulgaris* occurrences above limit = 0.1.

† H0: Proportion of exclusion zone sites containing *G. vulgaris* = 0.5.

4.3 Dispersal routes

We have investigated the influence of riverscape configuration on interactions between trout and non-diadromous galaxiids and highlighted the importance of dispersal pathways when assessing population structures. The role of size and isolation of habitats in metapopulation stability is well known (Namba et al. 1999; Ficetola & De Bernardi 2004; O'Brien et al. 2008). This study has clarified how the configuration and connection of refugia can affect threatened populations, especially in the confined structure of a river network. High and low productivity habitats in networks have previously been linked to source-sink dynamics in fish populations (Pringle 2001; Fagan 2002; Schick & Lindley 2007), and our research now demonstrates that those dynamics are particularly important for prey populations in networks dominated by invasive predators.

When source-sink dynamics are operating, identifying and protecting dispersal routes between the source and sink populations is crucial for restoring threatened fish populations (Schick & Lindley 2007). Preserving connectivity between predator-free sources and predator-dominated sinks may be just as important for overall population stability as improving conditions in individual habitats. It is still unknown what the minimum size and habitat requirements of source populations are for most non-diadromous galaxiids (DOC 2004). The correct management of sink and source streams must be informed by further research into recruitment in the absence of predators, such as adult spawning and fry recruitment habitats, which affect population growth (Jellyman & McIntosh 2008).

5. Conclusion

Management of native fish in areas threatened by invasive fish must address how to prevent invasion without also disrupting connectivity between fish sources and sinks (Fausch et al. 2009). In the case of galaxiids and trout, sufficient differences in morphology and locomotion should allow the design of barriers that prevent passage by salmonids but allow passage by galaxiids (Woodford & McIntosh 2011). To ensure the survival of galaxiids, trout-free source populations must be maintained and new sources created. Source populations will need legislative protection from habitat degradation and the deliberate introduction of trout. While terrestrial conservation areas seldom protect river networks from introduced species (Pringle 2001; Saunders et al. 2002), such protection could be achieved in streams designated as FPAs. This is a key advantage of FPAs over relying on the streams' inclusion in terrestrial conservation areas for protection of instream habitat (Saunders et al. 2002). Designating trout-free source streams as freshwater conservation 'focal areas' (following Abell et al. 2007) would allow authorities to protect these habitats without the need to buy surrounding land from a landowner. Alternatively, by deploying tools such as covenants or easements, protection of the waterways may not necessarily restrict the use of surrounding land, as long as protection of riparian habitats is enforced and the introduction of predators is prevented.

Small, stable trout-invaded streams, which have low habitat heterogeneity and many resident trout, are the least favourable environments for *G. vulgaris* in the long term (Woodford & McIntosh 2011). They are also the easiest streams from which to remove trout, due to their size (Moore et al. 1986). Management plans for galaxiids should assess the costs and benefits of active rehabilitation projects (Peterson et al. 2008). For example, creating a new barrier on a tributary, removing trout upstream and introducing galaxiids could be a feasible way to add a demographic source. The position of the barrier and upstream length to be treated, the structure and permeability of the barrier to galaxiids, as well as its location relative to other sources in the network, should be considered when assessing various options.

Creating new trout-free source populations is our favoured method for protecting threatened galaxiids, as removing trout from streams can be logistically difficult (Moore et al. 1986; Shepard et al. 2002) and may fail if the habitats are unsuitable for native fish recruitment (Harig & Fausch 2002). Only through active management and practical responses to new invasions will we conserve non-diadromous galaxiids in trout-dominated riverscapes.

6. Recommendations

We recommend that the following points be considered for future work:

Barriers

- Analyse the structure of trout barriers that allow galaxiids to pass.
- Research the effectiveness of naturally drying barriers by measuring the timing and duration of drying and its effects.
- Upgrade existing barriers to ensure long-term trout exclusion.
- Design new trout barriers based on the ability of galaxiids to climb.

Modelling

- Further develop the galaxiid exclusion model to more reliably predict the presence or absence of galaxiids in trout-occupied, small, high-country tributaries, by exploring the interaction between disturbance and stream size.
- Develop models that can predict how habitat variability limits trout densities in streams, which would further improve the Galaxiid Exclusion Model.

Conservation

- Identify suitable sites from which to remove trout. For flathead galaxiids, the Galaxiid Exclusion Model can be used to select sites that would maximise trout-galaxiid co-occurrence in the surrounding riverscape.
- Determine the legislative requirements needed to set up freshwater conservation focal areas on refuge streams.
- Investigate the possibility of using covenants or easements to protect sensitive refuge streams on private land.

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8. References

Abell, R.; Allan, J.D.; Lehner, B. 2007: Unlocking the potential of protected areas for freshwaters. *Biological Conservation 134*: 48–63.

Allibone, R.M. 2000: Water abstraction impacts on non-migratory galaxiids of Otago streams. *Science for Conservation 147*. Department of Conservation, Wellington. 45 p.

Allibone, R.M.; Townsend, C.R. 1997: Distribution of four recently discovered galaxiid species in the Taieri River, New Zealand: the role of macrohabitat. *Journal of Fish Biology 51*: 1235–1246.

Angermeier, P.L.; Schlosser, I.J. 1989: Species-area relationships for stream fishes. *Ecology 70*: 1450–1462.

Benzie, V. 1968: The life history of *Galaxias vulgaris* Stokell, with a comparison with *G. maculatus attenuatus*. *New Zealand Journal of Marine and Freshwater Research 2*: 628–652.

Beukers, J.S.; Jones, G.P. 1998: Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia 114*: 50–59.

Bjornn, T.C.; Reiser, D.W. 1991: Habitat requirements of salmonids in streams. Pp. 83–138 in Meehan, W.R. (Ed.): Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

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

Burridge, C.P.; Craw, D.; Waters, J.M. 2007: An empirical test of freshwater vicariance via river capture. *Molecular Ecology 16*: 1883–1895.

Cadwallader, P.L. 1973: The ecology of *Galaxias vulgaris* (Pisces: Salmoniformes: Galaxiidae) in the River Glentui, Canterbury, New Zealand. Unpublished PhD thesis, University of Canterbury, Christchurch. 211 p.

Cadwallader, P.L. 1976: Home range and movements of the common river galaxias, *Galaxias vulgaris* Stokell (Pisces : Salmoniformes), in the Glentui River, New Zealand. *Australian Journal of Marine and Freshwater Research 27*: 23–33.

Cambray, J.A. 2003: Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. *Hydrobiologia 500*: 217–230.

Carle, F.L.; Strub, M.R. 1978: A new method for estimating population size from removal data. *Biometrics 34*: 621–630.

Closs, G.P.; Lake, P.S. 1996: Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes 47*: 17–26.

Cox, J.G.; Lima, S.L. 2006: Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution 21*: 674–680.

Crow, S.K.; Waters, J.M.; Closs, G.P.; Wallis, G.P. 2009: Morphological and genetic analysis of *Galaxias* 'southern' and *G. gollumoides*: interspecific differentiation and intraspecific structuring. *Journal of the Royal Society of New Zealand 39*: 43–62.

Crowder, L.B.; Cooper, W.E. 1982: Habitat structural complexity and the interaction between bluegills and their prey. *Ecology 63*: 1802–1813.

Davey, A.J.H.; Kelly, D.J. 2007: Fish community responses to drying disturbances in an intermittent stream: a landscape perspective. *Freshwater Biology 52*: 1719–1733.

Death, R.G.; Winterbourn, M.J. 1994: Environmental stability and community persistence: a multivariate perspective. *Journal of the North American Benthological Society 13*: 125–139.

Detenbeck, N.E.; DeVore, P.W.; Niemi, G.J.; Lima, A. 1992: Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. *Environmental Management 16*: 33–53.

Dias, P.C. 1996: Sources and sinks in population biology. *Trends in Ecology and Evolution 11*: 326–330.

DOC (Department of Conservation) 2004: New Zealand non-migratory galaxiid fishes recovery plan 2003–13. Threatened Species Recovery Plan 53. Department of Conservation, Wellington. 45 p.

Donald, D.B.; Vinebrooke, R.D.; Anderson, R.S.; Syrgiannis, J.; Graham, M.D. 2001: Recovery of zooplankton assemblages in mountain lakes from the effects of introduced sport fish. *Canadian Journal of Fisheries and Aquatic Sciences 58*: 1822–1830.

Donlan, C.J.; Wilcox, C. 2008: Diversity, invasive species and extinctions in insular ecosystems. *Journal of Applied Ecology 45*: 1114–1123.

Driver, P.D.; Harris, J.H.; Closs, G.P.; Koen, T.B. 2005: Effects of flow regulation on carp (*Cyprinus carpio* L.) recruitment in the Murray-Darling Basin, Australia. *River Research and Applications 21*: 327–335.

Dunham, J.B.; Rieman, B.E. 1999: Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications 9*: 642–655.

Dunn, N.R. 2003: The effects of extremes in flow on alpine (*Galaxias paucispondylus*) and Canterbury (*G. vulgaris*) galaxias. Unpublished MSc thesis, University of Canterbury, Christchurch 174 p.

Elkington, S.; Charteris, S. 2005: Species and distribution of freshwater fish of the upper Waitaki River. Department of Conservation, Christchurch (unpublished). 27 p.

Fagan, W.F. 2002: Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology 83*: 3243–3249.

Fausch, K.D.; Rieman, B.; Dunham, J.B.; Young, M.K.; Peterson, D.P. 2009: Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology 23*: 859–870.

Fausch, K.D.; Torgersen, C.E.; Baxter, C.V.; Li, H.W. 2002: Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience 52*: 483–498.

Ficetola, G.F.; De Bernardi, F. 2004: Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation 119*: 219–230.

Finlay, J.C.; Vredenburg, V.T. 2007: Introduced trout sever trophic connections in watersheds: consequences for a declining amphibian. *Ecology 88*: 2187–2198.

Foppen, R.P.B.; Chardon, J.P.; Liefveld, W. 2000: Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conservation Biology 14*: 1881–1892.

Glova, G.J.; Sagar, P.M. 1993: A further assessment of trophic and spatial inter-relations of galaxiids and salmonids in New Zealand. *Ecology of Freshwater Fish 2*: 132–140.

Glova, G.J.; Sagar, P.M.; Naslund, I. 1992: Interaction for food and space between populations of *Galaxias vulgaris* Stokell and juvenile *Salmo trutta* L. in a New Zealand stream. *Journal of Fish Biology 41*: 909–925.

Hall, S.R.; Mills, E.L. 2000: Exotic species in large lakes of the world. *Aquatic Ecosystem Health and Management 3*: 105–135.

Hänfling, B.; Weetman, D. 2006: Concordant genetic estimators of migration reveal anthropogenically enhanced source-sink population structure in the river sculpin, *Cottus gobio*. *Genetics 173*: 1487–1501.

Harig, A.L.; Fausch, K.D. 2002: Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications 12*: 535–551.

Hilderbrand, R.H. 2003: The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. *Biological Conservation 110*: 257–266.

Homel, K.; Budy, P. 2008: Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. *Transactions of the American Fisheries Society 137*: 869–880.

Hulme, P.E. 2006: Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology 43*: 835–847.

Jellyman, P.G.; McIntosh, A.R. 2008: The influence of habitat availability and adult density on non-diadromous galaxiid fry settlement in New Zealand. *Journal of Fish Biology 72*: 143–156.

Jowett, I.G.; Richardson, J. 1989: Effects of a severe flood on instream habitat and trout populations in seven New Zealand rivers. *New Zealand Journal of Marine & Freshwater Research 23*: 11–17.

Kabii, T.; Horwitz, P. 2006: A review of landholder motivations and determinants for participation in conservation covenanting programmes. *Environmental Conservation 33*: 11–20.

Kauffman, M.J.; Varley, N.; Smith, D.W.; Stahler, D.R.; MacNulty D.R.; Boyce, M.S. 2007: Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters 10*: 690–700.

King, T.M.; Wallis, G.P. 1998: Fine-scale genetic structuring in endemic galaxiid fish populations of the Taieri River. *New Zealand Journal of Zoology 25*: 17–22.

Labbe, T.R.; Fausch, K.D. 2000: Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications 10*: 1774–1791.

Leathwick, J.R.; Julian, K.; Elith, J.; Chadderton, L.; Ferrier, S.; Snelder, T. 2008: A biologically optimised environmental classification of New Zealand rivers and streams: reanalysis excluding human impact variables. NIWA client report HAM2008–027, NIWA, Hamilton. 47 p.

Leprieur, F.; Hickey, M.A.; Arbuckle, C.J.; Closs, G.P.; Brosse, S.; Townsend, C.R. 2006: Hydrological disturbance benefits a native fish at the expense of an exotic fish. *Journal of Applied Ecology 43*: 930–939.

Lintermans, M. 2000: Recolonization by the mountain galaxias *Galaxias olidus* of a mountain stream after the eradication of rainbow trout *Oncorhynchus mykiss*. *Marine and Freshwater Research 51*: 799–804.

McDowall, R.M. 2003a: Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Transactions of the American Fisheries Society 132*: 229–238.

McDowall, R.M. 2003b: The key to climbing in koaro. *Water and Atmosphere 11*: 16–17.

McDowall, R.M. 2006: Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Reviews in Fish Biology and Fisheries 16*: 233–422.

McDowall, R.M.; Allibone, R.M. 2004: Threatened fishes of the world: *Galaxias cobitinis* McDowall & Waters, 2002 (Galaxiidae). *Environmental Biology of Fishes 70*: 42.

McIntosh, A.R. 2000: Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences 57*: 2140–2151.

McIntosh, A.R.; Crowl, T.A.; Townsend, C.R. 1994: Size-related impacts of introduced brown trout on the distribution of native common river galaxias. *New Zealand Journal of Marine and Freshwater Research 28*: 135–144.

McIntosh, A.R.; McHugh, P.A.; Budy, P. 2012: *Salmo trutta* L. (brown trout). Pp. 285–296 in Francis R.A. (Ed): A handbook of global invasive fishes. Earthscan, Oxon, UK.

McIntosh, A.R.; McHugh, P.A.; Dunn, N.R.; Goodman, J.; Howard, S.W.; Jellyman, P.G.; O'Brien, L.K.; Nyström, P.; Woodford, D.J. 2010: The impact of trout on galaxiid fishes in New Zealand. *New Zealand Journal of Ecology 34*: 195–206.

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, S.E.; Larson, G.L.; Ridley, B. 1986: Population control of exotic rainbow trout in streams of a natural area park. *Environmental Management 10*: 215–219.

Morin, P.J. 1986: Interactions between intraspecific competition and predation in an amphibian predator-prey system. *Ecology 67*: 713–720.

Namba, T.; Umemoto, A.; Minami, E. 1999: The effects of habitat fragmentation on persistence of source-sink metapopulations in systems with predators and prey or apparent competitors. *Theoretical Population Biology 56*: 123–137.

Norton, D.A. 2007: Using biodiversity offsets to obtain 'win-win' outcomes for biodiversity conservation and economic production. *New Zealand Journal of Forestry 52*: 36–40.

O'Brien, C.M.; Crowther, M.S.; Dickman, C.R.; Keating, J. 2008: Metapopulation dynamics and threatened species management: why does the broad-toothed rat (*Mastacomys fuscus*) persist? *Biological Conservation 141*: 1962–1971.

Ovidio, M.; Baras, E.; Goffaux, D.; Birtles, C.; Philippart, J. 1998: Environmental unpredictability rules the autumn migration of brown trout (*Salmo trutta* L.) in the Belgian Ardennes. *Hydrobiologia 371–372*: 263–274.

Peck, D.; Lazorchak, J.; Klemm, D. 2001: EMAP-Surface Waters: Western pilot study field operations manual for wadeable streams. U.S. Environmental Protection Agency, Office of Research and Development, Corvallis, Oregon. 275 p.

Peterson, D.P.; Rieman, B.E.; Dunham, J.B.; Fausch, K.D.; Young, M.K. 2008: Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). *Canadian Journal of Fisheries and Aquatic Sciences 65*: 557–573.

Pringle, C.M. 2001: Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecological Applications 11*: 981–998.

Pulliam, H.R. 1996: Sources and sinks: empirical evidence and population consequences. Pp 45–69 in Rhodes, E.R.; Chesser, R.K.; Smith, M.H. (Eds): Population dynamics in ecological space and time. University of Chicago Press, Chicago.

Ricciardi, A. 2007: Are modern biological invasions an unprecedented form of global change? *Conservation Biology 21*: 329–336.

Saunders, D.L.; Meeuwig, J.J.; Vincent, A.C.J. 2002: Freshwater protected areas: strategies for conservation. *Conservation Biology 16*: 30–41.

Schick, R.S.; Lindley, S.T. 2007: Directed connectivity among fish populations in a riverine network. *Journal of Applied Ecology 44*: 1116–1126.

Schlosser, I.J. 1987: The role of predation in age- and size-related habitat use by stream fishes. *Ecology 68*: 651–659.

Schlosser, I.J. 1988: Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. *Oikos 52*: 36–40.

Seitz, R.D.; Lipcius, R.N.; Hines, A.H.; Eggleston, D.B. 2001: Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology 82*: 2435–2451.

Shepard, B.B.; Spoon, R.; Nelson, L. 2002: A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. *Intermountain Journal of Sciences 8*: 193–214.

Simon, K.S.; Townsend, C.R. 2003: Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology 48*: 982–994.

Steele, M.A. 1999: Effects of shelter and predators on reef fishes. *Journal of Experimental Marine Biology and Ecology 233*: 65–79.

Stuart-Smith, R.D.; Stuart-Smith, J.F.; White, R.W.G.; Barmuta, L.A. 2007: The impact of an introduced predator on a threatened galaxiid fish is reduced by the availability of complex habitats. *Freshwater Biology 52*: 1555–1563.

Suren, A.M.; Jowett, I.G. 2006: Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. *Freshwater Biology 51*: 2207–2227.

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.; Crowl, T.A. 1991: Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? *Oikos 61*: 347–354.

Vitousek, P.M.; D'Antonio, C.M.; Loope, L.L.; Westbrooks, R. 1996: Biological invasions as global environmental change. *American Scientist 84*: 468–478.

Walrond, C. 2009: Trout and salmon—Brown trout. Te Ara—the Encyclopedia of New Zealand www.TeAra.govt.nz/en/trout-and-salmon/1 (viewed 15 April 2011).

Waters, J.M.; Wallis, G.P. 2001: Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. *Journal of Fish Biology 58*: 1166–1180.

Witte, F.; Goldschmidt, J.; Wanink, K.; van Oijen, M.; Goudswaard, K.; Witte-Maas, E.; Bouton, N. 1992: The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes 34*: 1–28.

Woodford, D.J. 2009: Riverscape-mediated effects of introduced trout on non-diadromous galaxiid fishes in New Zealand. Unpublished PhD thesis, University of Canterbury, Christchurch. 144 p.

Woodford, D.J.; Cochrane, T.A.; McHugh, P.A.; McIntosh, A.R. 2011: Modelling spatial exclusion of a vulnerable native fish by introduced trout in rivers using landscape features: a new tool for conservation management. *Aquatic Conservation: Marine and Freshwater Ecosystems 21*: 484–493.

Woodford, D.J.; McIntosh, A.R. 2010: Evidence of source-sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout. *Ecological Applications 20*: 967–977.

Woodford, D.J.; McIntosh, A.R. 2011: Location of demographic sources affects the distributions of a vulnerable native fish in invaded river networks. *Freshwater Biology 56*: 311–324.