

Evidence of source–sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout

DARRAGH J. WOODFORD¹ AND ANGUS R. MCINTOSH

School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140 New Zealand

Abstract. Introduced predators with patchy distributions can create demographic sinks within native prey populations. Such invasions may give rise to source–sink metapopulations if there are still sources of native species colonists in the landscape. In New Zealand, introduced brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are linked with declines in native non-diadromous galaxiids but co-occur with these galaxiids in some locations. We investigated whether trout create sinks in *Galaxias vulgaris* populations, and whether trout-free reaches could act as sources, allowing persistence in the sink habitat. We conducted quantitative seasonal monitoring of *G. vulgaris* population structure across two subcatchments of the Waimakariri River, South Island. Two trout-free and seven trout-invaded sites in the Porter River catchment and two trout-free and five trout-invaded sites in the Broken River catchment were monitored over two winters and the adjoining summer. Spatially continuous monitoring of young-of-the-year (YOY) galaxiid distributions and apparent survival across the Broken River catchment was also undertaken. *Galaxias vulgaris* YOY recruitment was high in trout-free reaches, indicating positive population growth. *Galaxias vulgaris* was absent from three trout-invaded sites, and the remaining invaded sites had significantly depleted juvenile recruitment. Information-theoretic model selection indicated that trout, rather than habitat, drove recruitment failure. Trout-invaded sites could be divided into “sinks” that retained no YOY galaxiids, indicating no local recruitment, and “pseudosinks,” which had very few recruits. Absence of small *G. vulgaris* at sink sites suggested population maintenance through immigration of adults from sources, whereas pseudosink sites appear capable of self-recruitment at low carrying capacities. Trout-free reaches appear to act as sources in a river network but are susceptible to future invasions by trout. Thus, not only may invasive species cause source–sink metapopulations in native species, but also the potential of refugia for natives (sources) to become future sinks highlights the vulnerability of these metapopulations when invasive predators are the principal demographic driver.

Key words: freshwater fish; *Galaxias vulgaris*; invasions; *Oncorhynchus mykiss*; predation; recruitment; refugia; riverscape; *Salmo trutta*; source–sink metapopulations; Waimakariri River, South Island, New Zealand.

INTRODUCTION

Effective conservation of species depends on adequately understanding the environmental and biotic pressures that structure populations (Shaffer 1981, Lande 1988). Variation in habitat suitability means that populations tend to be patchily distributed within landscapes (Turner 1989), and many species form source–sink metapopulations, in which extirpation from low-productivity sink patches is prevented by immigration from high-productivity source patches (Pulliam and Danielson 1991, Dias 1996). Although source–sink dynamics may be driven by differences in food availability or habitat for critical life-history stages among patches (Foppen et al. 2000, Nol et al. 2005,

Sulkava et al. 2007), they also can be driven by predators (Amezcuca and Holyoak 2000, Caudill 2005).

Invasions by nonnative predators may give rise to source–sink systems in native prey populations. Invasion is often patchy, negatively affecting vulnerable native prey species to varying degrees through the landscape (Maret et al. 2006). Consequently, invader-free patches may act as sources for adjacent predator-invaded sinks (Basse and McLennan 2003). To assess whether source–sink dynamics can facilitate predator–prey coexistence, we examined the population structuring of a vulnerable native fish species within river networks containing an introduced predator.

The patchy distribution of critical habitat and fish across the landscape of a river network, or “riverscape” (sensu Fausch et al. 2002), means that fragmented metapopulations can form within those networks (Rieman and Dunham 2000, Koizumi and Maekawa 2004, Slack et al. 2004). The patchy distribution of

Manuscript received 14 October 2008; revised 13 August 2009; accepted 26 August 2009. Corresponding Editor: K. B. Gido.

¹ E-mail: darraghwoodford@hotmail.com

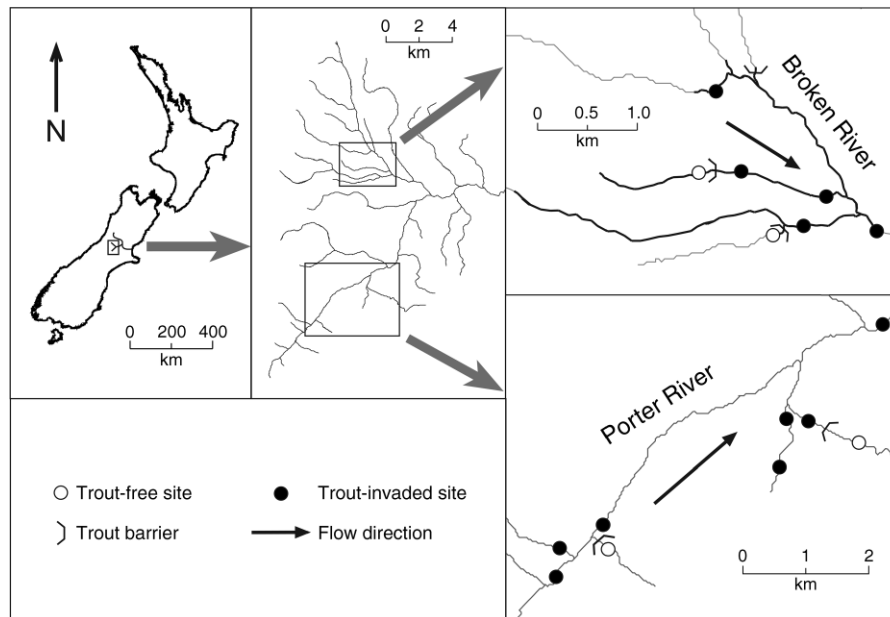


FIG. 1. Map of study area, showing the location and extent of the surveyed Porter and Broken riverscapes (subcatchments of the Waimakariri River, South Island New Zealand) and the position of quantitative monitoring sites within each riverscape. The reaches of Broken River monitored during fry surveys are drawn in bold.

introduced predatory fish may also be an important driver of such metapopulations, as they can fragment populations of vulnerable fish species (Labbe and Fausch 2000). Introduced fish have had severe impacts on native freshwater fish species around the world, sometimes resulting in local extinctions (Witte et al. 1992, Lintermans 2000, Woodford et al. 2005), and generally increasing overall extinction risks by fragmenting populations (Labbe and Fausch 2000, Fagan 2002). If sufficient individuals are able to disperse from refugia into predator-occupied habitat, populations that would normally go extinct may be rescued (Amezcuca and Holyoak 2000). Source-sink dynamics may therefore explain native fish coexistence with an introduced predator, if the river system still contains predator-free refugia.

The Canterbury galaxias (*Galaxias vulgaris* Stokell) (Salmoniformes: Galaxiidae), a benthic, stream-dwelling fish (McDowall 2000), is one of 15 non-diadromous galaxiids endemic to the rivers of New Zealand, and part of a species flock including several newly described taxa and genetically distinct lineages (Waters et al. 2000, McDowall 2006). All these galaxiid taxa are potentially threatened by predatory brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum), introduced for angling over a century ago (McDowall 2006). For example, three species within the galaxiid species group, *G. anomalus*, *G. pullus*, and *G. eldoni*, have restricted ranges in the Taieri River catchment, where they only survive above waterfall barriers that prevent further invasion by *S. trutta* (Townsend 1996). *Galaxias vulgaris*, in contrast, inhabits many trout-

invaded streams, often in sympatry with trout (Cadwallader 1975, Glova et al. 1992, McIntosh 2000, Davey and Kelly 2007). Avoidance behavior, microhabitat segregation, and disturbance-related reductions of large trout have all been proposed to explain their coexistence (McIntosh et al. 1992, Edge et al. 1993, Glova and Sagar 1993, McIntosh 2000).

We tested the hypothesis that source-sink metapopulation dynamics enable the persistence of *G. vulgaris* in invaded riverscapes, with trout-invaded reaches acting as sinks, but *G. vulgaris*-occupied reaches above barriers to trout invasion acting as sources. There is a paucity of studies empirically demonstrating source-sink dynamics in nature, because this generally requires estimates of both patch-specific population growth rates and individual dispersal rates (Diffendorfer 1998), and measuring these in freshwater fish is especially difficult (Dunham and Rieman 1999, Koizumi and Maekawa 2004). Instead, we used fish distributions and survivorship to infer population-structuring mechanisms, because it is possible to infer source-sink dynamics by monitoring the success of critical life-history stages (Caudill 2003, 2005). In addition, we considered the alternative possibility that apparent source-sink patterns were driven by habitat conditions.

METHODS

Study area

The study was undertaken in two subcatchments of the upper Waimakariri River, which drains the eastern slopes of the Southern Alps, South Island, New Zealand (Fig. 1). The subcatchments included four tributaries of

upper Broken River and three tributaries of upper Porter River, habitat-diverse riverscapes where both trout and galaxiids occur (McIntosh 2000, Jellyman and McIntosh 2008). A principal source of diversity of stream habitat in the system is flood-driven disturbance, which can be high and unpredictable in mountain-runoff streams, or low and predictable in spring-fed streams where the majority of instream flow is groundwater-derived (Jowett and Duncan 1990). Sixteen quantitative fish-monitoring sites were established on the mainstems and selected tributaries within these subcatchments (Fig. 1). These sites covered the full range of habitat variability and included four sites above and 12 sites below barriers to trout invasion (natural waterfalls, road culverts, and seasonally drying reaches that limited trout movement).

Continuous riverscape analysis of fry distribution and apparent survival

To investigate how *G. vulgaris* demography differs across a partially trout-invaded riverscape, we surveyed the distribution, density, and apparent survival of post-larval *G. vulgaris* across the Broken River network. Logistical and weather-related complications meant that a survey on the Porter River could not be completed. *Galaxias vulgaris* larvae are positively rheotactic immediately after hatching (Cadwallader 1976a), and disperse in the water column until swept into backwaters, where they remain until large enough to actively swim in the main channel (Jellyman and McIntosh 2008). The fry (post-larval fish trapped in backwaters, sensu Jellyman and McIntosh [2008]) are slow-swimming and constantly pelagic within the still and shallow backwaters, making visual density estimates possible. The fry appear in the austral spring (November), and leave the backwaters in autumn, especially from March to April (Jellyman and McIntosh 2008).

Fry were surveyed in summer (December 2007) and autumn (March 2008). This allowed the assessment of fry distributions at peak abundance and at the end of the summer, when they were close to leaving the backwaters. Because backwater fry densities decline in the latter part of the season, due to a likely combination of biotic, abiotic, and density-dependent drivers of mortality (P. G. Jellyman, unpublished manuscript), as well as possible early emigration, the numbers remaining in autumn could be interpreted as apparent survival of the fry cohort (sensu Coleman and Fausch 2007). Fieldwork consisted of one or two researchers walking upstream, estimating available backwater area, and counting *G. vulgaris* fry. Backwater area was visualized as squares of surface area that best covered the backwater. Visual estimates were highly correlated with measured backwater area ($n = 38$, $r = 0.96$, $P < 0.001$), with a fitted regression slope of 1. Rectangular measurements of backwater area provided a logistically feasible field measure, which we assumed had a small, consistent margin of error across the riverscape. To validate visual

counts in summer, fry numbers were estimated in a subset of backwaters and then fry were removed by hand with a dip net and re-counted in white trays. Due to the lack of cover-seeking behavior in summer fry, complete removal by dip netting was possible. Numbers counted in removal sampling were highly correlated with those from visual estimates ($n = 13$, $r = 0.93$, $P < 0.001$). The slope of the relationship between netting and visual counts was 0.71, indicating slight underestimation of fry numbers. Surveys therefore represented consistent minimum estimates of actual backwater densities. Fry counts could not be similarly verified in autumn, when the increased swimming ability of the fry made dip-net capture impractical. Because 89% of autumn fry counts were ≤ 5 fish per backwater, and fry remained pelagic within the backwaters, we assumed that survey estimates involved a small margin of error that was consistent across the riverscape.

The river network was divided into contiguous reaches of 30–100 m, and reach ends were marked on a Trimble Geo-XM portable GPS. Coordinates were differentially corrected to a horizontal accuracy of 2–10 m, and estimated fry numbers and backwater area were summed for each reach. Stream width was measured at each reach end so that a continuous estimate of stream size could be used in assessing the effect of riverscape-scale habitat change on fry distributions. Dense forest fragments inhibited the GPS signal on two trout-free streams and prevented us from monitoring fry across all trout-free reaches. We consequently surveyed only trout-free reaches downstream of the forests, and focused our efforts on assessing fry distributions across the trout-invaded riverscape. At the conclusion of the autumn survey, we searched the trout-free reaches upstream of the forest fragments for fry to better assess the relative proportion of potential source and sink habitat occurring across the fish-occupied riverscape. In total 12.7 km of stream was traversed.

Fry density estimates in summer and autumn were mapped using ArcGIS 9.1 (ESRI 2005). The length of stream where fry did or did not persist until the end of autumn, in trout-invaded or trout-free reaches, was calculated using the cumulative lengths of digitized segments in the GIS. To examine whether trout distribution or stream width could best describe fry density, a range of candidate models was compared using the Akaike information criterion corrected for small sample sizes, AIC_c (Burnham and Anderson 2002). Candidate models were fitted via least squares and included: (1) univariate models with trout (presence-absence) and stream width as predictors; (2) an additive model including trout and width; and (3) a model including trout, width, and an interaction between trout and width, with fry density as the response. The AIC_c and AIC weights were computed for each model based on its residual sum of squares. The difference between each model's AIC_c and the best (lowest scoring) model's AIC_c , or ΔAIC_c , was calculated

(Burnham and Anderson 2002). Models with $|\Delta AIC_c| < 2$ were regarded as similarly informative as the best model. If the best model(s) included more than one parameter, the importance scores of each parameter were calculated from the combined AIC weights of models including the parameter (Burnham and Anderson 2002). Fry densities were square-root transformed to meet the normality and homoscedasticity assumptions required for regression analysis.

Quantitative fish monitoring

Depletion electrofishing with a Kainga EFM 300 backpack electrofisher (NIWA Instrument Systems, Christchurch, New Zealand) generating 400–600 V pulsed DC current was conducted at all monitoring sites in late winter (September 2006) and summer (February 2007), to quantify the population structuring of *G. vulgaris*. A second winter survey (August 2007), at all sites where *G. vulgaris* had been recorded previously, was used to assess survival of recruits. At each site, 20 m of stream were delineated by stop nets and three depletion passes were conducted. The surveyed area was fished using sequential sweeps downstream into a 1 m wide push net, ending at the downstream stop net. The stop net was checked for fish after every pass. This method is standard practice for collecting benthic galaxiids in New Zealand (McIntosh et al. 1994). All fish captured were weighed and measured (to the nearest 0.1 g and 1 mm, respectively) and returned to the stream. All native fish were measured to total length (TL), as they have square or rounded tails, whereas trout were measured to fork length (FL). The total abundance of each fish species was estimated from three-pass depletion data using the maximum weighted likelihood formula of Carle and Strub (1978) and was divided by stream surface area to obtain density per unit area. Fish densities were multiplied by the mean biomass per species per site to obtain biomass data.

Galaxias vulgaris individuals were grouped into three size classes: 0–60 mm, 61–90 mm, and >90 mm TL, corresponding to young-of-the-year (YOY), one-year-old fish, and 2+ year-old fish, respectively. These categories were based on the relationship between length and the formation of otolith annuli (Cadwallader 1973), and the maximum length of YOY fish previously recorded in the Waimakariri catchment in September (Benzie 1968). Both male and female *G. vulgaris* are sexually mature after one year (Cadwallader 1976b), so 1 and 2+ fish are referred to as small and large adults, respectively. The absence of YOY fish is a good indicator of sink habitat (Driver et al. 2005), whereas a population with some recruits could theoretically maintain itself in the absence of immigration at low carrying capacity, making the habitat a “pseudosink” (Dias 1996, Pulliam 1996). Consequently, trout-invaded sites that contained *G. vulgaris* were divided post hoc into sites with and without YOY recruits, distinguishing pseudosinks from sinks. Overall biomass of *G. vulgaris*

at source, sink, and pseudosink sites was compared using repeated-measures ANOVA. Seasonal densities of YOY, small adults, and large adults at source, sink, and pseudosink sites were compared using repeated-measures MANOVA, followed by one-way repeated-measures ANOVA. We chose to compare size classes using density rather than biomass because this gave a less biased assessment of cohort success, which was heavily skewed by the weight difference among size classes. The seasonal biomass of trout at sink and pseudosink sites was also compared using repeated-measures ANOVA.

Habitat analysis and model testing

After electrofishing in September 2006, discharge was measured on a transect using a Marsh-McBurney electromagnetic flow meter (Hach Flow, Loveland, Colorado, USA) mounted on a top-setting wading rod. Stream width and three depths were measured at downstream, middle, and upstream limits of the reaches, and 30 streambed particles were randomly selected from the site and their longest axis recorded. Percentage cover of submerged and emergent aquatic vegetation was visually estimated, as well as cover by overhanging riparian vegetation. The flow-related disturbance regime of the stream was assessed using the river disturbance index (Pfankuch 1975), a subjective index that uses upper, middle bank, and riverbed characteristics to assign a numerical disturbance rating that correlates strongly with substrate movement caused by flooding (Death and Winterbourn 1994, Greenwood and McIntosh 2008). Water temperature and stage were monitored in each tributary with WT-HR stage-height loggers (Trutrak, Christchurch, New Zealand).

To compare habitat among monitoring sites, principal components analysis (PCA) was performed on physical habitat variables, producing factors that summarized variation in habitat (PCA 1 and 2 hereafter). The potential status of trout-free sites as outliers in overall habitat variation was tested using Student *t* tests between the factor coordinates of trout-free and all other sites. To assess whether habitat was a stronger predictor of source–sink dynamics at monitoring sites than trout, regression models describing biomass of YOY *G. vulgaris* in the two winter surveys were fitted and compared using ΔAIC_c . We only compared sites where *G. vulgaris* occurred. The summer survey was not used, as fry were still transitioning from backwaters to the river channel at the time of the survey, making electrofishing results potentially spurious. Candidate models included: (1) univariate models with trout presence, PCA 1 or PCA 2; (2) additive models with trout and either PCA axis; and (3) an additive model with just the PCA axes. To avoid over-parameterization, given our small sample size, we limited models to a maximum of two predictors and did not consider interactions. All biomass data were square-root transformed, continuous habitat data were \log_e -transformed, and all percentage data were arcsine-square root transformed to meet statistical assumptions. All

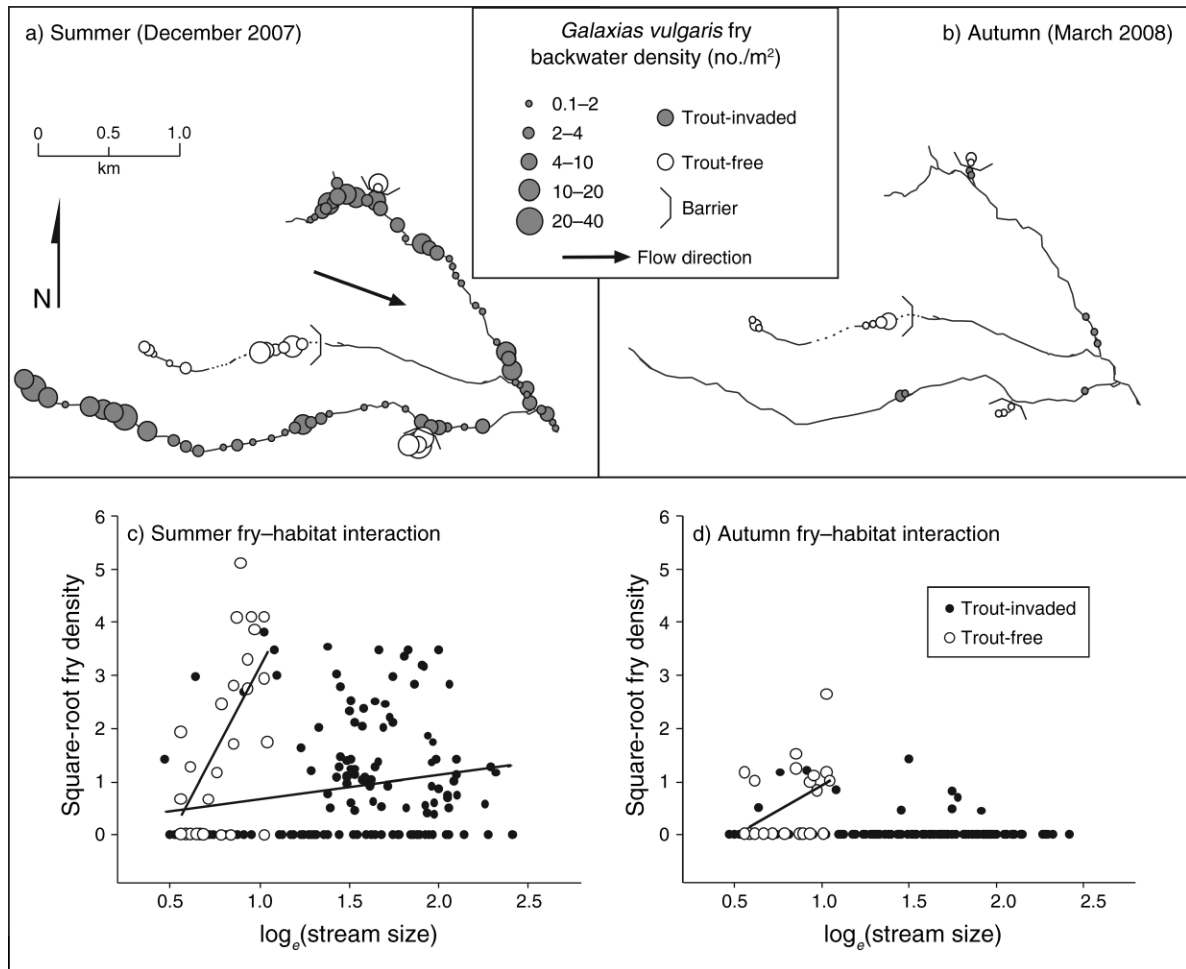


FIG. 2. Maps of density estimates and distribution of fry of the native fish *Galaxias vulgaris* recorded across the monitored Broken River network in (a) summer (December 2007) and (b) autumn (March 2008), as well as the interaction between square-root transformed fry density (originally measured as no./m²) and log-transformed stream size (width, originally measured in m) within trout-free and trout-invaded reaches in (c) summer and (d) autumn. Dashed lines in the stream network represent seasonally drying reaches. Lines on density graphs indicate significant ($P < 0.05$) relationships between fry density and stream size above and below trout barriers, fitted by least-squares regression.

statistical analyses were performed in Statistica 8 (Statsoft 2007).

RESULTS

Fry distribution and interactions with trout and habitat

In summer 2007, the period of peak galaxiid fry abundance (Jellyman and McIntosh 2008), *G. vulgaris* fry were found in high densities across most of the surveyed riverscape of the Broken River (Fig. 2a). Backwaters were recorded in 86% of trout-free segments, with a mean estimated area of 2.83 m² per segment. Backwaters occurred in 96% of trout-invaded reaches (2.28 m² per segment). By autumn 2008, fry were no longer present in most trout-invaded reaches, but persisted in most trout-free reaches (Fig. 2b). Although estimated backwater area in trout-free reaches decreased to 1.7 m² per reach (63% of reaches retained backwater)

and 1.36 m² in trout-invaded reaches (89% retained backwater), there was no significant difference in backwater area per segment between trout-invaded and trout-free reaches in summer ($t = 1.4$, $df = 171$, $P = 0.16$) or autumn ($t = 1.21$, $df = 171$, $P = 0.23$). Apparent fry survival (estimated autumn density) was higher among trout-free reaches than trout-invaded reaches ($t = 7.48$, $df = 171$, $P < 0.0001$). Trout-free reaches retaining fry (including previously unmonitored reaches upstream of forest fragments) made up 16% of the surveyed river network, whereas trout-invaded reaches retaining fry made up 7% of the surveyed network (Table 1). Invaded segments that retained fry were scattered across the riverscape, often isolated from each other by more than 1 km (Fig. 2b).

AIC_c model selection indicated that a model containing trout, stream width, and trout \times width interactions best described overall fry density in summer (Table 2,

TABLE 1. Cumulative lengths of Broken River (South Island, New Zealand) network segments where galaxiid fry were retained or not retained through to March in barrier or trout-invaded reaches.

| Stream length measure | Trout-free reaches | | Trout-invaded reaches | |
|--|---------------------------------|-------------------------|--------------------------|-----------------------------|
| | No fry recruitment or retention | "Sources" retaining fry | "Sinks" retaining no fry | "Pseudosinks" retaining fry |
| Cumulative surveyed segment length (m) | 1069 | 2026 | 8773 | 877 |
| Percentage of trout-free or trout-invaded network surveyed | 29 | 65 | 91 | 9 |
| Percentage of total river network surveyed | 8 | 16 | 69 | 7 |

Notes: Surveyed reaches included trout-free reaches upstream of forest fragments not initially monitored in December but checked for the presence of fry in March. Segments monitored in December and March are shown in Fig. 2.

model a). The interactive model had an AIC weight several orders of magnitude higher than either trout-only or stream-width-only models. Given the overwhelming weight of this model, the importance of individual trout or habitat effects could not be assessed. Trout presence negatively affected the strength of the relationship between initial fry densities and stream width (Table 3, model a; Fig. 2c). Although there was no overall correlation between fry density and stream width ($r = 0.06$, $P = 0.43$), densities were positively associated with stream width when trout-invaded and trout-free reaches were examined separately (i.e., $r = 0.66$, $P < 0.001$ above trout barriers and $r = 0.21$, $P = 0.01$ below barriers; Fig. 2c). In autumn, fry density was again best described by a model including additive and interactive trout and stream width effects (Table 2, model b), but the relationship of fry density to width differed from that observed in summer (Fig. 2d). Autumn density above barriers was still positively associated ($r = 0.47$, $P = 0.01$) with stream width, whereas fry in the trout-invaded riverscape were randomly distributed across the stream width gradient (Fig. 2d).

Monitoring sites: Fish and habitat patterns

Galaxias vulgaris was recorded at all trout-free sites in all three sampling seasons. At least one species of trout

(*O. mykiss*) was recorded at all sites below trout barriers, and both *O. mykiss* and *S. trutta* were recorded at two sites (Table 4). *Galaxias vulgaris* was never recorded at three trout-invaded sites, while one or more size classes of *G. vulgaris* were present at the other nine sites containing trout. Other fish species encountered at both trout-free and trout-invaded sites were the New Zealand longfin eel (*Anguilla dieffenbachii* Gray) and the alpine galaxias (*G. paucispondylus* Stokell). Only one species, the upland bully (*Gobiomorphus breviceps* Stokell), was recorded only at trout-invaded sites.

The first two PCA factors explained most of the variability in habitat structure among quantitative monitoring sites (58.8% and 18.9%, respectively). PCA 1 was positively associated with width, depth, discharge, and disturbance, and was negatively associated with bank vegetative cover. PCA 2 was positively associated with disturbance and negatively associated with habitat depth, substrate particle size, and aquatic vegetative cover (Fig. 3b). Trout-free sites tended to be small and shallow with relatively high flow stability, but were not outliers in the overall spread of sites in ordination space (for PCA 1, $t = 1.41$, $df = 14$, $P = 0.18$; for PCA 2, $t = -0.33$, $df = 14$, $P = 0.74$) and overlapped with sites containing trout (Fig. 3a).

TABLE 2. Selection of linear models to describe fry backwater density and YOY biomass through residual sum of squares and ΔAIC_c analysis.

| Analysis and model | RSS | AIC | AIC _c | ΔAIC_c | AIC _w |
|---|--------|---------|------------------|----------------|------------------|
| Fry density (summer 2007) | | | | | |
| a) Trout + width + (trout \times width) | 201.61 | 36.48 | 36.84 | 0.00 | 1.00 |
| Fry density (autumn 2008) | | | | | |
| b) Trout + width + (trout \times width) | 14.63 | -417.32 | -416.96 | 0.00 | 1.00 |
| YOY biomass (winter 2006) | | | | | |
| c) Trout | 0.07 | -55.53 | -52.53 | 0.00 | 0.56 |
| d) Trout + PCA2 | 0.05 | -56.77 | -51.06 | 1.47 | 0.27 |
| e) Trout + PCA1 | 0.06 | -55.29 | -49.57 | 2.95 | 0.13 |
| YOY biomass (winter 2007) | | | | | |
| f) Trout | 0.11 | -50.77 | -47.77 | 0.00 | 0.72 |
| g) Trout + PCA2 | 0.09 | -50.02 | -44.31 | 3.46 | 0.12 |
| h) Trout + PCA1 | 0.10 | -49.38 | -43.66 | 4.10 | 0.09 |

Notes: All candidate models with an Akaike information criterion (AIC) weight $w \geq 10\%$ of the best model's weight are shown. For each analysis, top models were regarded as those with a $\Delta AIC_c < 2$. Width refers to stream width.

TABLE 3. Parameter estimates for top models predicting *G. vulgaris* fry densities across the riverscape and YOY biomass across quantitative monitoring sites.

| Model and parameter | Estimate | 95% confidence limits | |
|-----------------------------|----------|-----------------------|-------|
| | | Lower | Upper |
| Fry density summer 2007 (a) | | | |
| Intercept | -1.75 | -2.84 | -0.68 |
| Trout presence | 1.88 | 0.80 | 2.96 |
| Width | 3.59 | 2.30 | 4.89 |
| Trout \times width | -3.10 | -4.39 | -1.81 |
| Fry density autumn 2008 (b) | | | |
| Intercept | -0.51 | -0.79 | -0.21 |
| Trout presence | 0.54 | 0.26 | 0.83 |
| Width | 0.99 | 0.65 | 1.34 |
| Trout \times width | -0.99 | -1.34 | -0.65 |
| YOY biomass winter 2006 (c) | | | |
| Intercept | 0.11 | 0.05 | 0.17 |
| Trout presence | -0.11 | -0.17 | -0.05 |
| YOY biomass winter 2006 (d) | | | |
| Intercept | 0.09 | 0.04 | 0.16 |
| Trout presence | -0.12 | -0.17 | -0.06 |
| PCA2 | 0.03 | -0.01 | 0.08 |
| YOY biomass winter 2007 (f) | | | |
| Intercept | 0.13 | 0.06 | 0.20 |
| Trout presence | -0.08 | -0.15 | -0.01 |

Note: Letters in parentheses refer to models in Table 2; only models with $\Delta AIC < 2$ are presented.

AIC_c model selection indicated that YOY biomass was best described by trout presence alone in winter 2007, whereas models with trout only and trout + PCA 2 were equally informative predictors of YOY biomass in 2006 (Table 2). Trout presence had a negative effect on YOY biomass in both analyses, and had a higher importance score than either habitat factor in the 2006 data set (trout = 0.96, vs. PCA 1 = 0.14 and PCA 2 = 0.27); the trout effect was three times more important than habitat in the 2006 model. In terms of habitat variables captured in PCA 1 and PCA 2, trout-invaded sites that retained recruits (i.e., pseudosink sites) were large, disturbed, or both (Fig. 3).

Biomass and size structuring of *Galaxias vulgaris*

Galaxias vulgaris biomass was significantly different among putative source, sink, and pseudosink sites (Table 5). Post hoc Tukey hsd tests indicated that *G. vulgaris* biomass at trout-free sites was higher than at

pseudosink sites ($P < 0.02$). Trout biomass differed significantly between sinks and pseudosinks, as well as among seasons (Table 5). Post hoc Tukey hsd tests indicated that trout summer biomass was higher in sinks than at pseudosinks in winter ($P < 0.02$). Although large trout (>150 mm FL) were rarely captured in pseudosink sites, they were captured at all sink sites, as well as all sites where *G. vulgaris* was entirely absent. Densities of *G. vulgaris* size classes varied among the demographic categories of trout-free, sinks, and pseudosinks, showing a significant interaction with sampling season (Table 5). The interaction between demographic categories and season indicates that differences in YOY and small-adult *G. vulgaris* density among trout-free and trout-invaded sites fluctuated as the seasons changed. Post hoc Tukey hsd tests showed that YOY density was significantly higher at trout-free sites than at either sink or pseudosink sites ($P = 0.04$; Fig. 4). Likewise, small adults (61–90 mm) were found in significantly higher densities at trout-free sites than at either sinks or pseudosinks (Table 5, Fig. 4). Large-adult (>90 mm) densities were not significantly different across the three demographic categories (Table 5), although they were usually highest in source sites and lowest in pseudosink sites (Fig. 4).

DISCUSSION

Our results provide several lines of evidence for source-sink metapopulation dynamics in a freshwater fish species, linked to the introduction of a nonnative predator. Trout were associated with decreases in YOY recruitment, both among backwater-occupying fry and free-swimming juveniles. The effect of trout presence on *G. vulgaris* size structuring indicates a shift in demographic processes that can best be explained by source-sink dynamics.

Model selection indicated that an interaction between the effect of trout invasion and stream width best described *G. vulgaris* fry densities in summer and autumn. Stream width was closely associated with other habitat size variables in the PCA and is therefore a good proxy for habitat size across the riverscape. Fry densities were positively correlated with stream size within trout-free sites in summer, even though these reaches were uniformly small in the context of the overall riverscape. Initial *G. vulgaris* fry densities have been linked to the local densities of adults (Jellyman and McIntosh 2008),

TABLE 4. Galaxiid-trout species co-occurrence scenarios at sites above and below trout barriers, indicating whether or not young-of-year *G. vulgaris* were recorded at any sites in two years of sampling.

| Location relative to trout barriers | Species present | <i>Galaxias vulgaris</i> | |
|-------------------------------------|--|--------------------------|-----------|
| | | YOY present | No. sites |
| Above barrier | <i>G. vulgaris</i> only | yes | 4 |
| Below barrier | <i>G. vulgaris</i> + <i>O. mykiss</i> | yes | 4 |
| Below barrier | <i>G. vulgaris</i> + <i>O. mykiss</i> | no | 3 |
| Below barrier | <i>G. vulgaris</i> + <i>O. mykiss</i> + <i>S. trutta</i> | no | 2 |
| Below barrier | <i>O. mykiss</i> only | not applicable | 3 |

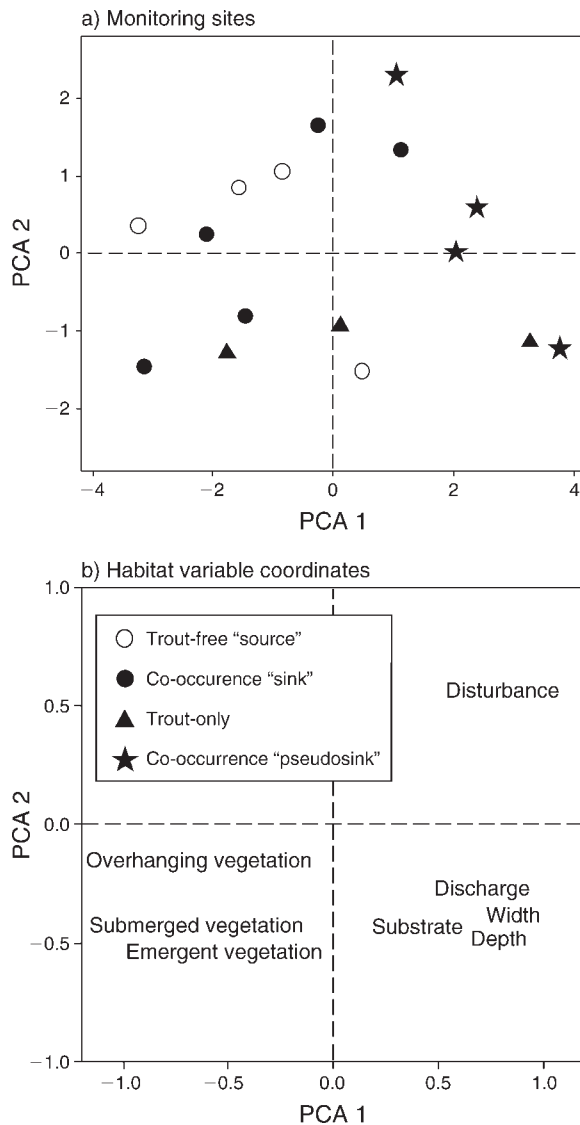


FIG. 3. Principal components analysis of monitoring sites showing (a) the coordinates of monitoring sites across the first two PCA factors, and (b) the coordinates of habitat variables across these factors. PCA 1 is positively associated with width, depth, discharge, and disturbance and is negatively associated with bank vegetative cover. PCA 2 is positively associated with disturbance and negatively associated with habitat depth, substrate particle size, and aquatic vegetative cover. Coordinates indicate the strength and directionality of each site or habitat variable's relationship to PCA factors.

and it is possible that very small headwater reaches contained limited habitat for *G. vulgaris* compared to larger reaches, resulting in increases in fry production with stream size. The positive association between fry density and stream size remained intact in trout-free streams through autumn, suggesting that apparent fry survival did not change with increasing stream size in trout-free reaches.

In contrast to most trout-free reaches of the same size, small trout-invaded reaches had few or no fry in

summer. This pattern suggests that predation by trout had an overriding effect on fry recruitment in small streams. In a field experiment conducted on a small trout-invaded stream in the area, trout rapidly eliminated *G. vulgaris* fry inside backwaters to which they had access, whereas backwaters fenced to prevent trout access (but allowing fry emigration) retained many fry (McIntosh et al. 2010). Although most trout-free reaches retained fry into autumn, few fry remained in trout-invaded reaches, and mostly occurred in backwaters and side braids that were disconnected from the main channel. Whether or not trout gained access to the backwaters during the course of the summer appears to be a better predictor of apparent fry survival than stream size in trout-invaded reaches.

Trout presence was the most important predictor of YOY *G. vulgaris* biomass at monitoring sites in each winter survey. This result, together with the patterns of apparent fry survival, indicates that trout were the cause of YOY recruitment failures. The presence of large (>100 mm) trout has been linked to the loss of recruits in a congeneric species (McIntosh et al. 1994) and the complete loss of galaxiids from invaded streams both in our study system and other regions of the South Island (Townsend 1996, McIntosh 2000). Furthermore, a mesocosm experiment showed that large (>150 mm) trout prey on all sizes of *G. vulgaris* (McIntosh 2000). Trout of this size or larger were present within all sink sites, which also supported the highest biomass of trout. This high predator biomass appears to have depleted all but the largest *G. vulgaris* individuals.

TABLE 5. Repeated-measures univariate and multivariate ANOVAs testing differences in seasonal biomass of trout and *G. vulgaris*, as well as seasonal densities of YOY, small, and large adult *G. vulgaris* between putative sources, sinks, and pseudosinks.

| Effect | Wilks' lambda | df | F | P |
|-----------------------------------|---------------|-------|-------|------|
| <i>G. vulgaris</i> biomass ANOVA | | | | |
| Source-sink | | 2 | 6.06 | 0.02 |
| Error | | 8 | | |
| Trout biomass ANOVA | | | | |
| Sink-pseudosink | | 1 | 10.55 | 0.02 |
| Season | | 2 | 4.73 | 0.03 |
| Error | | 5 | | |
| <i>G. vulgaris</i> density MANOVA | | | | |
| Source-sink | 0.13 | 6, 14 | 4.21 | 0.01 |
| Source-sink × season | 0.02 | 12, 8 | 4.53 | 0.02 |
| YOY density | | | | |
| Source-sink | | 2 | 6.04 | 0.02 |
| Source-sink × season | | 4 | 3.29 | 0.03 |
| Error | | 8 | | |
| Small-adult density | | | | |
| Source-sink | | 2 | 7.02 | 0.01 |
| Error | | 8 | | |

Note: Only significant effects are shown; large-adult density had no significant effects.

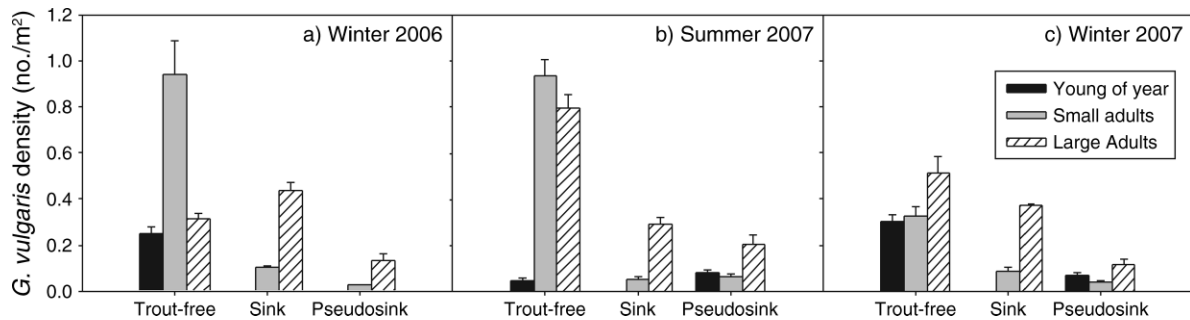


FIG. 4. Density (mean + SE) of three size classes (young-of-year, YOY, 30–60 mm; small adult, 61–90 mm; large adult, >90 mm) of *G. vulgaris* recorded at trout-free sites, trout-invaded “sink” sites where *G. vulgaris* occurred, and all invaded “pseudosink” sites in winter 2006, summer 2007, and winter 2007.

The high densities of fry retained in trout-free reaches, together with the consistently high densities of YOY fish occurring at trout-free monitoring sites, suggest positive net recruitment and therefore positive population growth rates within these reaches, a prerequisite for a demographic source (Pulliam 1996, Diffendorfer 1998). It is unknown how far downstream from the nest *G. vulgaris* fry drift before settling in backwaters, but long-distance dispersal is possible for the species (Benzie 1968). Consequently, trout-free populations are likely exporters of passively dispersing fry into downstream, mostly invaded, reaches. Conversely, it is physically impossible for the invaded reaches to export fry to trout-free reaches upstream.

It may be tempting to think that the one-way dispersal of galaxiid fry could lead to a source–sink dynamic in *G. vulgaris* independent of trout. Under this scenario, upstream sites would be natural sources (net exporters of individuals) and downstream sites natural sinks (net importers of individuals) if there were insufficient reciprocal upstream migration of adults (Slack et al. 2004, Hänfling and Weetman 2006), but we think this is unlikely. Adult *G. vulgaris* are potentially highly mobile, rapidly dispersing to recolonize habitat left vacant after drying disturbance (Davey and Kelly 2007). Moreover, three sink sites that contained adults but never YOY recruits were located on tributaries upstream of the nearest source stream, and must have been sustained by adult immigration from downstream. It is therefore unlikely that a source–sink metapopulation based on one-way dispersal existed in *G. vulgaris* in our study system prior to the introduction of trout.

The four pseudosink sites that retained YOY fish also contained the lowest biomasses of *G. vulgaris* and trout. These patterns suggest the potential for positive *G. vulgaris* population growth, but at a lowered carrying capacity, two defining features of pseudosinks (Pulliam 1996). These reaches were also large, disturbed, or both. Carrying capacity for galaxiids and trout could therefore be limited by flood disturbance, which would reduce invertebrate food resources (Death and Winterbourn 1995, Suren and Jowett 2006). In contrast, greater habitat complexity within the large, often braided

pseudosink reaches may enhance *G. vulgaris* survival by enabling selection of different microhabitats than trout (McIntosh et al. 1992, Glova and Sagar 1993, Leprieur et al. 2006). Thus, conflicting biotic and abiotic controls at pseudosink sites may enable sporadic positive population growth despite the presence of trout.

If one assumes that all trout-invaded reaches where *G. vulgaris* fry survived until autumn within the Broken River network are true pseudosinks, they amount to only 7% of the surveyed riverscape. In contrast, trout-free source reaches comprised only 16%, whereas trout-invaded sink habitat made up 69%. These figures suggest that *G. vulgaris*, while seemingly common across the riverscape as a whole, may in fact be quite vulnerable to extinction within these networks. If trout were introduced into the trout-free reaches of these streams, galaxiids in both the source and linked sink populations would probably be eliminated (Townsend 1996, McIntosh 2000, McDowall 2006). Only in the pseudosink habitats, where self-recruitment is maintained despite the presence of trout, would *G. vulgaris* populations likely survive over several generations.

Because pseudosink habitats tended to have elevated disturbance and supported low numbers of galaxiids, they are also inherently susceptible to local extinction (Dunham and Rieman 1999, Hilderbrand 2003). Demographic modeling of isolated salmonid populations elsewhere suggests that limiting immigration to populations with low carrying capacity can severely increase extinction risk (Hilderbrand 2003). Thus, by removing source populations and consequently isolating pseudosink reaches, invasive predators like trout could drastically reduce the viability of the prey metapopulation despite its apparent size and potentially high patch connectivity, normally earmarks of low extinction risk (Dunham and Rieman 1999, Fagan 2002).

Conservation implications

Our findings suggest that the viability of *G. vulgaris* populations in New Zealand streams may not be evident from their current size and extent, because much of their distribution comprises trout-induced sink habitat. *Galaxias vulgaris* is not currently considered a conser-

vation priority (Department of Conservation 2004), due in part to its wide distribution and co-occurrence with trout. This case study highlights the challenge of managing populations for which demographic data are difficult or costly to obtain, despite the fact that incorrect management decisions could be made in the absence of such data (Lande 1988, Cooper and Mangel 1999). We recommend that managers of native species threatened by patchy invaders consider whether instances of co-occurrence are, in fact, invader-driven source-sink metapopulations dependent on refuge populations.

Invasive predators have the potential not only to create sinks within prey metapopulations but also, through continued invasion, to convert old sources into new sinks, potentially destabilizing the entire metapopulation. In particular, continual invasion of new freshwater habitats by predatory sport fish, often through illegal human introductions, is an ongoing process that continues to have negative consequences for aquatic biodiversity around the world (Cambray 2003). It is therefore critical that management effort be directed toward the identification and preservation of invader-free habitat, because these habitat patches may act as linchpins in controlling the persistence of threatened species throughout riverscapes or landscapes. Such fragile metapopulations, in turn, could be stabilized through the removal of the invader to expand existing invader-free populations (Lintermans 2000). New demographic sources could also be created through translocation of threatened species to invader-free habitats within the landscape (Harig and Fausch 2002), reinforcing metapopulation stability.

ACKNOWLEDGMENTS

This study was jointly funded by a Department of Conservation (DoC) research grant (to D. J. Woodford and A. R. McIntosh) and an NZ-AID Commonwealth Scholarship (to D. J. Woodford). We thank S. Howard, P. Jellyman, R. Bishop, H. Greig, R. Campbell, D. Campbell, A. Sinton, and V. Nock for assistance in the field. We thank P. McHugh for statistical advice and DoC staff L. Chadderton, B. David, and D. Kelly for support and advice. Thanks also to L. Morris and N. Etheridge for technical support, and to members of the Freshwater Ecology Research Group, University of Canterbury, for helpful discussion and feedback. DoC and the landowners of Castle Hill Station granted land access, and fieldwork was performed in accordance with University of Canterbury Animal Ethics guidelines. We thank M. Winterbourn, J. Harding, D. West, K. Fausch, and an anonymous referee for valuable comments on the manuscript.

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