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Flow Matters: Unravelling the Interactive Influences of Flow Variation and Non-Native Trout on Vulnerable Galaxiids

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ABSTRACT

Understanding the interactive effects of non-native species and alterations to flow regimes is important to combat threats to freshwater communities. Low-flow conditions may either exacerbate or offset influences of non-natives but the mechanisms determining the direction are poorly understood. We evaluated how stream drying affected interactions between vulnerable native stream-resident galaxiids and non-native trout in Aotearoa, New Zealand. We electrofished (December–March) paired perennial and drying reaches containing galaxiids (*Galaxias vulgaris* and *G. paucispondylus*) to compare abundance and growth rates in streams with high abundance ($n=2$), low abundance ($n=2$) or no brown trout ($n=3$; *Salmo trutta*). Low flows greatly reduced trout abundance and size, likely reducing predatory threats to galaxiids since risk is size-related. Galaxiid densities were consistently lower in drying compared to perennial reaches of troutless streams. However, galaxiids were less affected by low flows than trout, setting the scene for an interaction between trout and low flow. In streams with high numbers of trout, galaxiid numbers were very low in perennial reaches, whereas they were moderate in drying reaches. That meant galaxiid numbers increased with a decreasing flow in streams with many trout, an indirect positive effect, although their abundance never reached the high levels of trout-free perennial reaches. In low-density trout streams, there were no clear differences in galaxiid abundance between reaches of different flow types. Thus, the effects of trout on galaxiids depended on the flow regime, likely driven by harsh low-flow conditions suppressing large trout, which were more sensitive to low flow than galaxiids. Galaxiid growth rates actually increased with conspecific densities in trout streams, whereas growth rates decreased with increasing galaxiid densities in troutless streams. Thus, growth advantages for galaxiids in the presence of trout possibly helped drive these low-flow effects on their populations in trout streams, potentially via an attractive sink-type mechanism. Overall, although low-flow conditions likely reduced predatory effects of non-natives and may have indirectly bolstered growth rates of natives, populations of natives were also suppressed by low flow. Such interactive effects of flow reduction are likely common and appear controlled by relative vulnerability and size-structured interactions and will be key to balancing the maintenance of natural flows with minimising

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effects of non-native sports fish. Flow depletion might create some refuge for native fishes in the presence of a non-native, but net effects could still be worse than no flow depletion as we observed. Thus, it will be important to ascertain how flow-depleted reaches affect the long-term persistence of native fish populations before relaying on flow reduction to suppress non-natives.

1 | Introduction

Freshwater ecosystems are being increasingly affected by climate change–induced alterations to disturbance magnitudes and seasonality, especially low-flow occurrence (Vander Vorste et al. 2020; Tonkin 2022). Flow reductions affect stream physical characteristics like discharge, water temperatures and dissolved oxygen levels leading to water-quality deterioration and cascading effects on stream biota (Bunn and Arthington 2002; Dewson, James, and Death 2007; Rolls, Leigh, and Sheldon 2012; Mosley 2015). Flows are also being modified by flow regulation where even small dams and abstractions alter fish assemblages (Anderson, Freeman, and Pringle 2006; Boddy et al. 2020b). Relationships between flows and fish populations have been well studied (Murchie et al. 2008; Bradford and Heinonen 2008; Wheeler, Wenger, and Freeman 2018), but interactive effects between low flows and non-native species complicate these influences (Leprieur et al. 2006; Franssen, Gido, and Propst 2007; Moyle et al. 2013; Lennox et al. 2019).

The effects of low flows on relationships between native and non-native fishes are important because they involve multiple interacting global change drivers and highly threatened biota. Non-native fishes have been extensively introduced globally for aesthetic, recreational and aquaculture purposes (Casal 2006; De Leaniz, Gajardo, and Consuegra 2010; Tadaki et al. 2022). However, fish introductions are a main driver of native fish losses (Olden et al. 2022), making freshwater fish some of the most endangered vertebrates (Radinger et al. 2019). Habitat alteration and non-native species have sometimes been viewed as independent processes driving such biodiversity loss but likely interact to induce ecosystem change (Didham et al. 2007), so it is important to understand how these interactions will influence native fish assemblages.

Effects of interactions between non-natives and flow on native fishes are hard to predict because low flows could be either detrimental or beneficial to non-native fishes (Fausch et al. 2001; Rogosch et al. 2019). To advance beyond such contingent understanding, better knowledge of the factors driving the outcomes of interactive effects is needed. Habitat degradation can promote abundance and distribution of tolerant non-natives and at the same time cause native fish refugia loss, thus exposing natives to higher predation risk from invasives (Hermoso et al. 2011; Moyle et al. 2013; Rogosch et al. 2019). On the other hand, habitat alterations may benefit native species assemblages by disadvantaging non-natives species if the non-native fish is less tolerant than the native (Alcaraz, Bisazza, and García-Berthou 2008). For example, increased salinity in freshwater environments can mediate aggressive behaviour of invasive *Gambusia holbrooki* towards native species in Australia (Lopez, Davis, and Wong 2018). The direction of interactive effects is likely to depend in the first instance on the relative tolerances of the native vs. non-native species involved to flow alteration.

Where strong predatory or competitive interactions exist between a native and non-native fish, subsequent species interaction outcomes will likely depend on relative body sizes because competition and predation among fishes are almost always strongly size-structured (Jennings and Mackinson 2003). This is particularly important for salmonid fishes (Taniguchi, Fausch, and Nakano 2002) although non-natives are not always bigger; the presence of non-native perch can benefit native predatory eels in some situations because of the size advantage eels have over perch (Stewart et al. 2023). Thus, knowing how flow alteration affects fish size composition is important for predicting interaction outcomes.

Relative tolerance of environmental harshness and size-structured interactions are likely to be integral to the outcome of low-flow influences on interactions between threatened native galaxiid fishes and non-native salmonids. Brown and rainbow trout (*Salmo trutta*) were introduced to New Zealand from the late 1860s for a sports fishery (Crowl, Townsend, and Mcintosh 1992) and have been consistently associated with declines of native galaxiid fishes and alterations to ecosystems (Flecker and Townsend 1994; McIntosh and Townsend 1994; McDowall 2003; McIntosh et al. 2010). Similar salmonid-driven galaxiid declines have been observed throughout the Gondwanan range of galaxiids (Woodford and Impson 2004; McDowall 2006; Young et al. 2010; Chilcott et al. 2013; Minett et al. 2023), making Galaxiidae some of the most endangered fish (Cussac et al. 2020; Lintermans et al. 2020; Chakona et al. 2022; Lavery et al. 2022). However, suggestions that low-flow disturbances may favour native galaxiids over non-native trout (Leprieur et al. 2006; Boddy et al. 2020b) have been interpreted, at least in a New Zealand court, as indicating that the natives may benefit from such disturbances (Environment Court of New Zealand 2019). An interpretation that low-flow disturbances, and therefore water abstraction, could benefit galaxiid populations likely over-simplifies interactions among galaxiids, trout and flow, further emphasising the need for better understanding of interactive effects. In this case, although extreme low-flow events may benefit galaxiids by alleviating the negative effects of trout, low-flow effects on galaxiid population dynamics in troutless streams have largely been overlooked. To fully comprehend the influence of low flow on galaxiid populations, we need to understand how galaxiid populations are affected by flow changes in both the presence and absence of trout.

To investigate how trout and low flow interacted to affect river-resident galaxiids (i.e., non-diadromous galaxiids, referred to here as RRG), we compared RRG population abundance, biomass, size distributions and individual growth between perennial and drying reaches across streams with either high densities, low densities or no trout present. Overall, we hypothesised that low-flow characteristics that disadvantaged large trout would reduce their size-structured predation effects on non-migratory galaxiids (a positive indirect effect), but that low flow would still have net negative effects on RRG, compared to perennial flow situations. Specifically, we predicted that trout biomass and maximum fork length (mm) would decrease with low-flow disturbance (P1) because large salmonids are particularly vulnerable to the water-quality reductions that occur as flow decreases (a direct negative effect). We also expected that RRG abundance, biomass and growth would decrease with reduced flow when trout were absent (P2) because RRG are also likely disadvantaged by low-flow disturbance (also, direct negative effect). However, in streams where trout were abundant, we expected that RRG abundance, biomass and growth would increase with reduced flow relative to perennially flowing sections (P3), because the disturbance meant RRG were released from the influences of predation by large trout and some conspecific competition (indirect positive effects). Finally, we expected low RRG abundance and slow growth in perennial streams with abundant trout compared to equivalent troutless streams (P4) because of the direct negative consumptive and non-consumptive effects of predatory trout.

2 | Methods

2.1 | Study Sites

Seven streams (SI Figure S1) known to have seasonally drying reaches were sampled three times from December to March over the 2020–2021 austral summer in a well-studied area of the Canterbury High Country, South Island, New Zealand. In this area, major portions of streams naturally experience low flows and localised drying in areas of alluvial fans during summer and autumn. These low-flow conditions are largely due to reduced precipitation and snowmelt in headwaters across summer, combined with porous alluvial deposits creating perched channel conditions where seepage losses are substantial as streams flow from confined valleys across the alluvial fans (McHugh et al. 2015). Stream selection was based on the local knowledge of fish populations and drying, including previous drying stream studies (McHugh et al. 2015). There were no known human flow manipulations (such as abstraction), and rivers were ungauged. None of the streams are currently subject to trout stocking, the trout were introduced to the area > 100 years ago, and variations in trout density in perennial reaches mostly reflect variations in habitat conditions (Jellyman and McIntosh 2020).

All streams sampled contained river-resident galaxiids, and both perennially flowing and intermittently drying reaches 386–1500 m apart. Two streams had high-density trout populations, two had low-density trout populations and three had no trout. This design effectively formed a split-plot comparison with the two levels of flow nested within a stream (i.e., within the plots) and the three levels of trout density applied to streams (i.e., the whole plots). Although the extent and timing of drying varied because of local weather variations, these streams started to experience low flows from the beginning of the sampling period in December (the beginning of the austral summer).

To avoid confounded comparisons between stream categories, streams were broadly similar. They were 325–800 m above sea-level and within the same biogeographical area. Land use across sampled reaches consisted of low-intensity agricultural grassland such as pastoral beef and sheep or tussock grassland and forest reserve, and streams typically had wide riverbeds without substantial streamside vegetation (Cowie et al. 1986). Streams ranged in width from 1 to 11 m (1st to 4th order) and encompassed a range of mostly run-riffle habitat. The surrounding vegetation consisted mainly of native tussock or introduced pasture grasses mixed with native shrubland or beech forest.

2.2 | Field Sampling

Field sampling of the seven streams began in December as flows in drying reaches started to decline. Two 25-m reaches, between 386 and 1500 m apart with one in the drying section and one in the perennially flowing section, were sampled on each sampling occasion. The streams were sampled three times over the austral summer, in December, January and February, as drying reach flows declined.

We measured water temperature, pH, dissolved oxygen and conductivity using field meters (YSI Ecosense ODO 200 and YSI Pro 1030) and measured discharge at the bottom of each reach using a flow meter (Marsh McBirney Flo-Mate 2000) as well as substratum type, number of riffles and pools, and depth during sampling (following McIntosh 2000).

To sample fish, we delineated 25-m reaches with stop-nets (mesh size 5 mm) and made three consecutive downstream electrofishing passes (following McIntosh 2000). We calculated densities using a three-pass depletion (Cowx 1983) and reached dimensions, implemented using the FSA package (Ogle et al. 2023) in R. We anaesthetised fish with AQUI-S (20 mg/L) for identification, and individual weight and length measurement (total length for RRG, bullies and eels; fork length for salmonids).

Prior to release, we uniquely marked anaesthetised subadult and adult galaxiids greater than 59 mm (range 60–110 mm) with visual implant elastomer (Northwest Marine Technology Inc.; White et al. 2015) on the ventral side, where the lighter underbelly ensured that any marks could be clearly identified on recapture. Within each stream, we uniquely marked galaxiids using visual implant elastomer colour(s) and mark location(s), so recaptured individuals could be identified, and associated changes in length (total length) and weight (g) were recorded.

We calculated instantaneous (specific) growth rates, using

$$G_w = \left[\left(\ln \mathrm{W}_{\mathrm{final}} - \ln W_{\mathrm{initial}}\right) / t\right] \times 100 \quad (1)$$

where G_w was the specific growth rate of the individual fish each day, W_{final} and W_{initial} were the length of the individual fish at the end and start of the experiment, respectively, and t was the elapsed time in days (Ricker 1979).

2.3 | Statistical Analyses

To summarise and visualise major stream environmental gradients, we ran a principal component analysis (PCA) on scaled measurements using *prcomp* (Sigg and Buhmann 2008) in R (version 4.3.3). We then assessed whether physical site characteristics varied depending on flow or trout density using PERMANOVA in *Adonis2* from the vegan package (version 2.6.4; Oksanen et al. 2022).

Drying and trout density were treated as categorical variables in analyses, with the two levels of flow (perennial and drying) nested within the three levels of trout (high, low and none). Response variables were RRG biomass (g/m^2, log$_{10}$-transformed to remove skewness) and abundance (No./25 m of linear stream log$_{10}$-transformed), trout biomass (log$_{10}$-transformed g/m^2) and trout maximum length (FL mm). *Salmo trutta* (hereafter 'trout') was the only salmonid species caught, but we grouped both *G. vulgaris* and *Galaxias pauscispondylus* into a 'galaxiid' variable for some biomass and abundance analyses to improve statistical power. To test the relationships between both galaxiid abundance and biomass, and trout density, across each flow type and sample month, we ran general linear mixed effects models implemented using *lme4* (version 1.1.35.2; Bates et al. 2015) and deriving probabilities using type II sums of squares with Satterthwaite's method using *lmerTest* (version 3.1.3; Kuznetsova, Brockhoff, and Christensen 2017). Stream was used as a random effect to account for the multiple sampling periods per stream. Marginal ($R^2{}_m$) and conditional ($R^2{}_c$) model pseudo R^2 metrics were calculated using *MuMIn* (version 1.47.5; Bartoń 2024).

Galaxiid density was affected by both drying and trout and was in turn likely to affect individual galaxiid growth, so for evaluations of RRG growth rates, we used RRG abundance as a continuous predictor and trout presence/absence as a fixed variable, with a random effect of stream. We took this approach to begin to separate the various influences based on the assumption that lethal or emigration-inducing effects of both trout and low flow would be reflected in RRG density. Thus, our analysis assessed the non-lethal effects of trout, low flow and conspecific density on resident fish.

We initially used a combination of both *G. vulgaris* and *G. paucispondylus* growth rates to observe overall patterns and then tested *G. vulgaris* separately to check if patterns matched; there were not enough *G. paucispondylus* replicates for individual analysis. This growth analysis was performed with an ANCOVA general linear mixed model (glmm) in a mixed effects framework using *lme4*.

All statistical analyses were carried out in R, version 4.3.3 (R Core Team 2021), and we followed recommendations from Muff et al. (2022) for reporting statistical results where a gradual notion of evidence was presented rather than simply stating if the results were statistically significant. Graphical results of lme4-modelled responses were plotted with the *emmeans* package (version 1.10.2; Lenth 2024) in *ggplot2* (version 3.5.0; Wickham 2016).

3 | Results

3.1 | Stream Characteristics

Two principal component axes collectively explained ~66% of variation in stream physico-chemical characteristics reflecting the main dimensions associated with flow variation across locations and times (SI, Figure S2). Based on the evaluation of these two axes with PERMANOVA, drying and perennial reaches had different physico-chemical conditions (Table 1), indicating important differences between reaches from the same stream. For example, cross-sectional area and flow discharge consistently reduced from perennial to drying reaches (SI, Table S1). However, there were no consistent differences between streams of differing trout densities and there was also no interaction between the flow type and trout density (Table 1). Therefore, differences between perennial and drying sites were not confounded by measured physical differences associated with trout density treatments.

TABLE 1 | Results of permutational multivariate analysis of variance (PERMANOVA) on combined environmental variables to evaluate differences between flow types (perennial vs. drying) and trout densities (high, low and none) in Canterbury high country streams.

Source	*df*	Mean Sq	*f* model	*p*	R^2
Flow type	1	11.27	11.27	0.047	0.0458
Trout density	2	54.17	27.09	0.180	0.2202
Flow type × trout density		5.011	2.505	0.874	
Residuals	36	175.5			0.7136
Total	41				

3.2 | Trout Abundance and Size

There was strong evidence (model $R^2{}_m = 0.78$) for negative effects of low flow on the trout body size; trout were consistently larger in perennial reaches compared to those in intermittently drying reaches (Table 2, Figure 1). There was also a strong interaction between trout density treatment and flow affecting trout biomass (Table 2, model $R^2{}_m = 0.67$). When trout density was high, trout biomass was much higher in perennially flowing reaches than that of drying reaches, but when trout density was low, trout biomass was similar between flow types (Figure 1). This partially supports P1 since trout were consistently smaller in drying reaches but densities were only reduced in drying reaches relative to perennial reaches when at high density.

3.3 | Galaxiid Abundance

Flow effects on galaxiid density varied according to trout treatment because there was a strong interaction between flow and trout density affecting galaxiid density (Table 3A). In streams with no trout, galaxiid density was highest in perennial reaches and lower in drying reaches (Figure 2A). By contrast, in high-density trout streams, galaxiid density was consistently higher in drying reaches than in associated perennially flowing reaches (Figure 2A). The same patterns were evident for galaxiid biomass (Figure 2B, Table 3B). In comparison, there was no difference between drying and perennial sites for both galaxiid density and biomass in low-trout density streams (Figure 2A,B). Across all treatments, the highest abundance of

TABLE 2 | Results of linear mixed effects models for the influences of flow (perennial vs. drying) and trout density (none, low and high) on (A) maximum trout fork length (mm) and (B) $\log_{10}[y+1]$-transformed trout biomass (g/m^2) in Canterbury high country streams, with a random effect of stream.

Response and model $R^2_{\mathrm{m,c}}$	Variable	Num. and den. *df*	Mean sq	*F* value	*Prob.*
(A) Maximum trout fork length (mm)	Flow type	1, 16.3	40,611	58.20	<0.001
0.78, 0.80	Trout density	1, 3.4	7254	10.39	0.040
	Flow type × trout density	1, 16.9	370	0.753	0.47
(B) Log trout biomass (g/m^2)	Flow type	1, 20	4.396	23.7	<0.001
0.67, 0.75	Trout density	1, 4	1.654	8.92	0.041
	Flow type × trout density	1, 20	2.309	12.4	<0.01

Note: Numerator and denominator degrees of freedom (Num. and den. *df*), mean squares (Mean sq), *F*-value and probabilities obtained from Satterthwaite's method, as well as marginal and conditional pseudo R^2 for the model are shown.

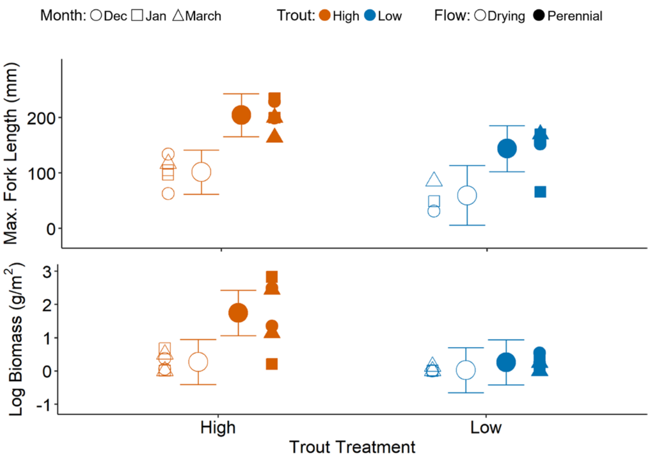


FIGURE 1 | Maximum trout fork length (top) and trout biomass ($\log_{10}[y+1]$; bottom) in perennially flowing and intermittently drying reaches, from four different streams, categorised by high- ($n=2$) and low ($n=2$)-trout densities. Larger circles are fits from mixed effects models with 95% confidence intervals, and smaller points are raw measures shaped by sample month and coloured by trout treatment. [Color figure can be viewed at wileyonlinelibrary.com]

galaxiids occurred in perennially flowing reaches with no trout (Figure 2A,B). In summary, RRG populations were more abundant in the perennial flow, but when trout were present at high densities, galaxiids were largely only found in low-flow reaches (supporting P2, P3 and P4).

3.4 | Galaxiid Growth

For both *G. vulgaris* and *G. paucispondylus* combined, there was a strong interaction between trout presence and galaxiid abundance affecting galaxiid growth rate (Table 4). When trout were absent, the galaxiid growth rate decreased slightly as galaxiid abundance increased (Figure 3, solid lines). In contrast, when trout were present, the galaxiid growth rate increased with galaxiid abundance (Figure 3, dashed lines). This trout-stream pattern occurred because galaxiid growth rates from low-trout-density situations (blue points and dashed line, Figure 3) were often above those from troutless sites (green points and solid line, Figure 3). These results also show that compared to trout-free sites, galaxiid growth was both negatively affected by trout at high densities (i.e., in perennially flowing sites; orange points in Figure 3; P3) and positively affected by low-density trout in drying reaches (blue points in Figure 3; P4). Moreover, there was little evidence for RRG growth rate altering as RRG density changed across the drying gradient in sites without trout (no support for P2). Thus, the influences on galaxiid growth reflect the net influences of trout density/size and conspecific density.

4 | Discussion

Understanding how interactions between native and non-native species are modulated by reduced flow is important in the face of increasing drought conditions associated with climate change and the associated redistribution of species globally (Vander Vorste et al. 2020; Tonkin 2022; Datry et al. 2023). We examined how stream drying modulated the impacts of non-native brown trout on native non-migratory galaxiids in New Zealand streams. Although galaxiids, which generally have much smaller adult body sizes than trout, escaped the negative consequences of trout through a positive indirect effect of low-flow disturbance in drying streams, they fared much better off in perennial sites when trout were absent. Galaxiids only benefited from reduced flows because the disturbance supressed large trout, and in line with our hypothesis, low-flow conditions also suppressed non-migratory galaxiid populations relative to trout-free perennial conditions. Thus, the indirect positive effect on galaxiids via trout suppression was countered by a direct negative effect of low flow on galaxiids such that only moderately abundant galaxiid populations occurred in low-flow reaches of trout streams. These results demonstrate how the effects of non-native species can be influenced by flow reductions, point to predictability in those interactions based on the relative sensitivities and sizes of species involved and highlight the challenges confronting flow management given this situation.

4.1 | Trout Effects on Galaxiids Depended on Flow Conditions

In streams with abundant trout, galaxiids were rare in perennial flow and moderately abundant in drying reaches.

TABLE 3 | Results from linear mixed effects models testing the influence of flow (perennial vs. drying) and trout density (none, low and high) on (A) $\log_{10}[y+1]$-transformed RRG abundance (No./25 m) and (B) $\log_{10}[y+1]$-transformed RRG biomass (g/m^2) in Canterbury high country streams, with a random effect of stream.

Response and model $R^2_{m,c}$	Variable	Num. and den. *df*	Mean Sq	*F* value	*Prob.*
(A) Log RRG abundance (No./25 m)	Flow type	1, 35	0.9385	10.11	0.003
0.50, 0.61	Trout density	2, 7	0.2191	2.361	0.16
	Flow type × trout density	2, 35	1.384	14.90	< 0.001
(B) Log RRG biomass (g/m^2)	Flow type	1, 35	0.8895	7.635	< 0.01
0.47, 0.69	Trout density	2, 7	0.1550	1.330	0.32
	Flow type × trout density	2, 35	2.401	20.61	< 0.001

Note: Numerator and denominator degrees of freedom (Num. and den. *df*), mean squares (Mean sq), *F*-value and probabilities obtained from Satterthwaite's method, as well as marginal and conditional pseudo R^2 for the model are shown.

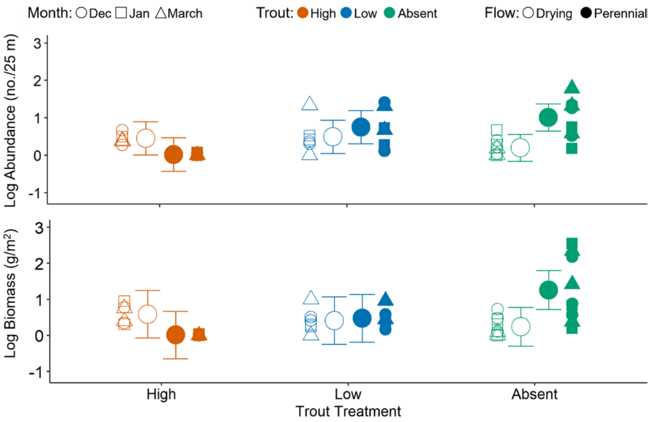


FIGURE 2 | River-resident galaxiid (RRG) abundance ($\log_{10}[y+1]$, no./25 m; top) and biomass ($\log_{10}[y+1]$, g/m^2; bottom) in perennially flowing and intermittently drying reaches, from seven different streams, categorised by high- ($n=2$) and low ($n=2$)-trout densities or with trout absent ($n=3$). Larger circles are fits from mixed models with 95% confidence intervals, and points are raw measures shaped by sample month and coloured by trout treatment. [Color figure can be viewed at wileyonlinelibrary.com]

The opposite was found when trout were absent; galaxiid densities were high in perennially flowing reaches and declined with low flow. This reflects a positive indirect effect of low-flow disturbance on galaxiids driven by negative low-flow effects on trout. The low galaxiid abundance observed in perennial reaches with abundant trout is consistent with predation-driven negative effects of trout, with non-migratory galaxiids being a main contributor to galaxiid declines (McDowall 2006; McIntosh et al. 2010; Jones and Closs 2018). By reducing trout numbers, especially the large piscivorous individuals (McHugh et al. 2015), reduced flow likely created refuges from trout, thereby allowing more galaxiids to persist in trout streams. Leprieur et al. (2006) also observed that galaxiids, mostly *Galaxias anomalus*, only co-occurred when the galaxiids had access to reaches unsuitable for trout due to localised drying. Similarly, flood disturbance also enhances the co-occurrence of non-migratory galaxiids and trout in streams in our study area (McIntosh 2000; McHugh et al. 2012; Boddy, Booker, and McIntosh 2019). Overall, both high- and low-flow hydrological disturbances are likely to enhance trout–galaxiid co-occurrence by creating refuges from trout.

Differential physiological tolerances likely underlie this flow-based interaction involving non-natives. Galaxiids have a larger physiological tolerance to instream water-quality changes than salmonids (Cussac et al. 2020). Galaxiidae have been recorded in water temperatures exceeding 28°C, for example (Leprieur et al. 2006; Cussac et al. 2020). In comparison, large trout were likely excluded from low-flow reaches, either because they are sensitive to changes in water quality, due to a narrow physiological tolerance range (Moore et al. 2012), or because drying conditions typically do not have resources to support larger predatory fish (Dekar, Magoulick, and Huxel 2009; Lynch and Magoulick 2016) since larger fish require bigger foraging areas (McIntosh et al. 2018). Field observations also suggest that flood disturbances deleteriously influence the more sensitive trout compared to the less sensitive galaxiids (Jellyman et al. 2017; Boddy, Booker, and McIntosh 2019, 2020a; Jellyman and McIntosh 2020). Some galaxiids have also evolved burrowing capabilities to persist in the substrate to avoid desiccation during short-term extreme low-flow events (Chakona, Swartz, and Magellan 2011; Urbina et al. 2014). Thus, differential tolerance of the two types of fish, which ultimately reduced size-structured interactions, was likely the basis for the indirect effect.

In low-density trout streams, galaxiid abundance, biomass and growth were similar across both drying and perennial reach types. As trout size and biomass reduce, the negative interactions occurring between trout and RRG also likely decreased, because smaller fish are generally not as effective competitors or predators (Paszkowski et al. 1990; Thornton, Duda, and Quinn 2017). Trout and natives can co-occur when trout are smaller (< 150 mm) (McIntosh 2000), possibly because smaller trout are less effective predators, but once larger trout are present (> 150 mm), and depending on life history variations, RRG can be eliminated or sink populations created (McIntosh, Townsend, and Crowl 1992; McIntosh, Crowl, and Townsend 1994; Woodford and McIntosh 2010; Jones and Closs 2015). Therefore, the extent of detrimental impacts of non-native trout on native fish assemblages is likely to be mediated through trout size. Thus, small trout were likely less effective predators than larger trout and at low densities had a reduced non-consumptive influence, alleviating effects on galaxiids. This intermediate situation in low-density trout streams (RRG population: drying = perennial) compared to that in high-density trout streams

TABLE 4 | Analysis of co-variance results for the effects log$_{10}$-transformed RRG abundance (No./25 m) and trout presence vs. absence on RRG mean instantaneous growth rate in length (%/day) for both *G. vulgaris* and *G. paucispondylus* combined (A) and *G. vulgaris* only (B) in Canterbury high country streams.

Response	Variable	*df*	Sum Sq	*f* value	*p* value
(A) RRG growth rate (Gw)	Log RRG abundance (No./25 m)	1	131.2	2.312	0.130
	Trout presence	1	169.5	2.986	0.086
	Log RRG abundance (No./25 m) × trout presence	1	401.1	7.067	0.009
	Residuals	129	7322.6		
Observations	133				
(B) *G. vulgaris* growth rate (Gw)	Log RRG abundance (No./25 m)	1	7.1	0.121	0.73
	Trout presence	1	55.3	0.943	0.34
	Log RRG abundance (No./25 m) × trout presence	1	217.7	3.713	0.058
	Residuals	66	3869.6		
Observations	70				

Note: Degrees of freedom (*df*), sum of squares, *F*-ratio and *p*-value are all shown.

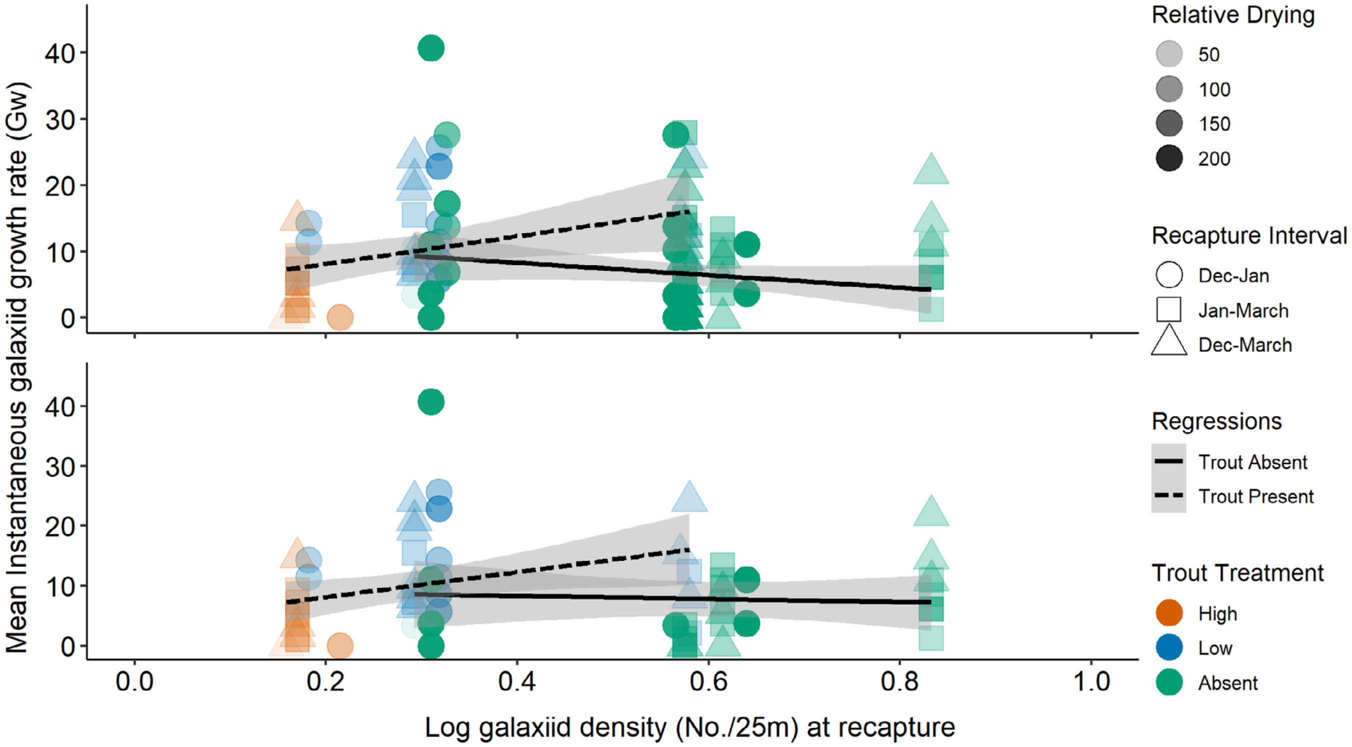
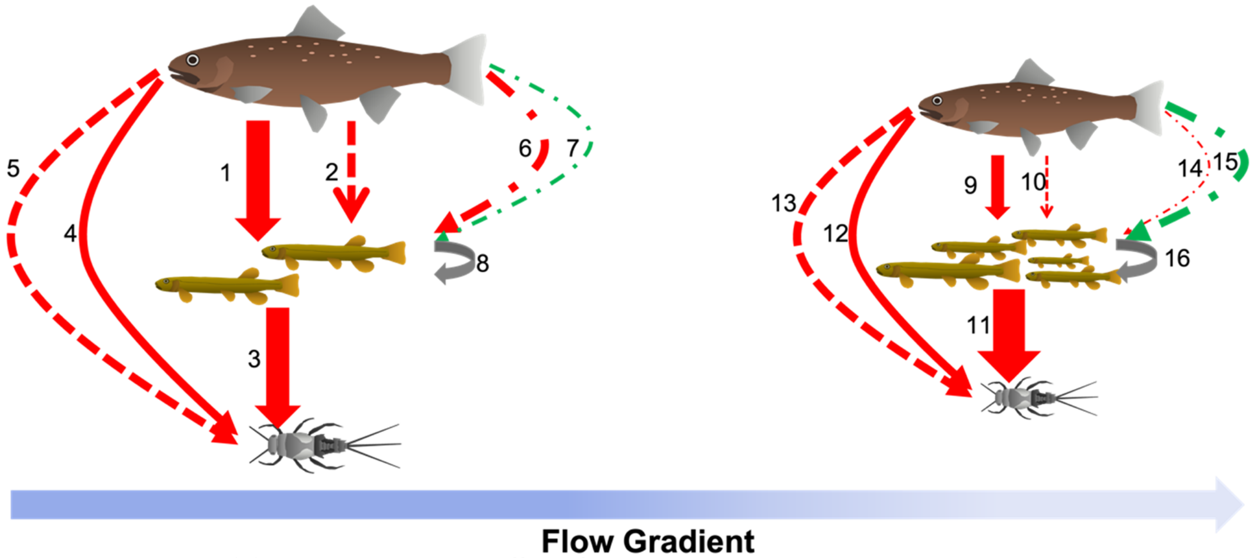


FIGURE 3 | Mean instantaneous galaxiid total length growth rate (Gw, % day^{-1}) of both *G. vulgaris* and *G. paucispondylus* (top) and *G. vulgaris* only (bottom), as a function of RRG abundance (log$_{10}$, No./25 m) at recapture, in perennially and drying reaches, from seven different streams, categorised by high ($n=2$), low ($n=2$) and absent ($n=4$) trout densities, and with regressions for trout (dashed line) and troutless (solid line) streams. Points are raw growth measures shaped by their recapture interval (circle, December–January; square, January–March; triangle, December–March) and coloured by trout treatment, with colour gradient representing the amount the site had dried (darker colour is more relative flow). The units of the relative drying gradient are percentages (calculated as: $[Q_t/Q_{\text{Dec perennial}}] \times 100$, where Q_t is the discharge at the time of recapture and $Q_{\text{Dec perennial}}$ was the discharge at the perennial site in December), so that 200 and 50 reflect a doubling and halving of flow, respectively. Regression lines were fit using formula $y \sim x$, and the troutless regression included all green points (i.e., trout absent sites), whereas the trout present regression included orange and blue points (i.e., measurements from both high- and low-density trout sites). [Color figure can be viewed at wileyonlinelibrary.com]

(drying > perennial) and troutless streams (drying < perennial) highlights the importance of size-structured interactions on the outcome of these flow-driven interactions.

Direct and indirect effects involving both consumptive and non-consumptive influences likely underlay the interactive effects of low-flow disturbance and native and non-native



1. Strong size-structured direct -ve consumptive effect of T on G (McIntosh et al 2010).
2. Direct -ve non-consumptive effect of T on G behaviour (McIntosh et al 1992) leading to reduced growth.
3. Direct consumptive effect of G on invertebrates.
4. Direct consumptive effect of T on invertebrates (Flecker & Townsend 1995) potentially leading to an indirect effect (6.).
5. Direct non-consumptive effect of T on invertebrate behaviour (McIntosh & Townsend 1994).
6. Indirect -ve effect of T on G due to T consuming NMG food.
7. Indirect +ve non-trophic effect of T on G growth (facilitation) due to T-induced changes to invertebrate behaviour making foraging easier for G (5., McIntosh et al 2010, McDowall 2003).
8. Density-dependent effects of conspecifics on G.
9. Reduced direct consumptive effect of T on G due to indirect effect of low flow on T.
10. Indirect reduction in the effect of interaction 2 due to drying reducing T.
11. Increased consumption of invertebrates by G potentially due to the combination of stronger indirect facilitation (15 vs. 7) and weaker non-consumptive effects (10 vs 2).
12. Same as interaction 4 but in drying reaches.
13. Same as interaction 5 but in drying reaches.
14. Weakened indirect –ve effects of T on G via T consuming NMG food due to low flow reduction in T.
15. Stronger (c.f. 7) indirect facilitation of G by T.
16. Density-dependent effects of conspecifics on G.

FIGURE 4 | Our observations provide insights useful for hypothesising about the types of interactions involved (numbered pathways) supported by previous studies (listed). The type of the arrow represents the type of interaction (dot-dash, indirect; unbroken, direct consumptive; dash, direct non-consumptive), the colour of the arrow represents the sign of interaction (red, negative; green, positive; grey, indeterminant), with cartoon sizes corresponding to observed effects on fish population density and possible effects on invertebrates and arrows corresponding to hypothesised magnitudes and directions. Firstly, there was likely a large direct negative consumptive size-specific effect of trout (T) predation on galaxiids (G) in perennial conditions (1) that was greatly reduced in drying flow (9) because of reductions in trout size and biomass in drying reaches. Growth of the few galaxiids occurring in high-density trout streams was very low, probably partly due to effects of trout predation risk restricting galaxiid foraging, a direct non-consumptive interaction (2). Such effects are difficult to separate from potential indirect negative effects on RRG of trout consuming their macroinvertebrate food (4 and 6). Increased galaxiid growth in low-density trout streams across both perennial and drying reaches, compared to both troutless streams and high-trout density treatments, could potentially be explained by facilitation of galaxiid growth at low densities of trout (7 and 15) if, for example, trout cause invertebrates to become more nocturnal, increasing their vulnerability to nocturnally foraging galaxiids. Because enhanced galaxiid growth in the presence of trout only occurred in low-density trout situation, such a facilitation was likely only important when the direct trophic and non-trophic interactions (1 and 2) were weak. Finally, density-dependent intraspecific interactions could have supressed galaxiid growth at high conspecific densities (8 and 16), but our evidence for this is weak. Slight declines in galaxiid growth with conspecific density were observed in troutless stream when galaxiid taxa were combined, but not when *G. vulgaris* were considered individually. [Color figure can be viewed at wileyonlinelibrary.com]

fish we observed (Figure 4). There was potential for facilitation from trout to have resulted in increased galaxiid growth, for example, when trout were small and at low densities, so consumptive and non-consumptive direct effects on galaxiids were weak but trout presence was still influencing invertebrate behaviour (Figure 4). This could happen because trout cause invertebrates to become more nocturnal (McIntosh and Townsend 1994), potentially increasing their vulnerability to nocturnally foraging galaxiids. Such an interaction involving trout and invertebrate behaviour will be important to investigate because the growth advantages it potentially provides could encourage galaxiids to occupy drying reaches in trout streams, possibly leading to an attractive population sink (Delibes, Ferreras, and Gaona 2001). The lack of strong negative relationships with conspecifics also suggests that local galaxiid populations in troutless streams, regardless of reach, were well matched to local invertebrate food supplies, and deviations from that matching like the possible facilitation only occurred when trout altered those patterns. These are just hypotheses for what might have been occurring, but understanding the details of these sorts of interactions better will help predict the global outcomes of flow-regime changes and associated redistributions of species. Studies that identify the specific occurrence of such interactions will enhance our ability to predict the outcome of future changes and will be particularly useful when they measure the actual vital rates of species affected across contexts. That will help parameterise mechanistic models with greater transferability to flow conditions associated with non-stationarity under climate change (Rogosch et al. 2019; Tonkin et al. 2019; Lewis et al. 2023).

Finally, our study design was integral to detecting these interactive effects. Knowledge of the study streams over more than 20 years meant we could accurately delineate drying and perennial reaches. Although there was variation in stream order and altitude of sites, for example, that did not confound our comparison because there were no consistent trout-related differences in physical comparisons. This reflects that trout occupy all habitats they can get to, and their abundance is driven by local habitat conditions (Jellyman and McIntosh 2020). Moreover, that the interactive effects were observed despite variations among streams means that the drying effects on trout body size and abundance were very strong.

4.2 | Conservation Implications and Future Directions

Even though galaxiids may find refuge from trout in low-flow conditions, they were still negatively affected by low flow because densities were still lower compared to those in perennial trout-free streams. Galaxiids might have higher tolerance ranges than trout, but they were still likely to have been stressed by both reductions in water quality associated with declines in flow and associated reductions in their macroinvertebrate food (Drummond, McIntosh, and Larned 2015). RRG generally feed on macroinvertebrates, and as flow reduces so does long-term food production (Young, Smart, and Harding 2004). The net effect of low flow will depend on its long-term effects on galaxiid populations, so human-driven low flows, through water abstraction for extended periods, for example, could harm galaxiid populations. If low-flow conditions become too extreme and long-lasting, individuals and entire populations could be at risk of extinction (Dunn 2003; Meijer et al. 2019). Thus, river-resident galaxiids like those studied, and especially headwater-adapted species (Jones and Closs 2016), may be particularly vulnerable to low-flow disturbances.

In evaluating the effects of low flow on galaxiid populations, dynamics in troutless streams have been largely overlooked. Suggestions that extreme low-flow disturbances may favour native galaxiid populations over trout populations (Leprieur et al. 2006; Boddy et al. 2020b) have been interpreted as indicating that natives may benefit from low flows (Environment Court of New Zealand 2019). Our work suggests that such interpretations over-simplify a more complicated interaction among galaxiids, trout and flow. Removing water to maintain a threatened fish in the face of predation is only slightly better than not removing water because the natives are still disadvantaged, and the best solution is to manage the predatory threat of the trout. Importantly, low-flow vulnerabilities of native fish will only be obvious when controlled comparisons are made using streams where trout are completely absent.

When assessing conservation strategies for threatened fish like galaxiids, we should consider the breadth of interactions involved (Figure 4), especially the relative tolerances of species and the potential for size-specific interactions. Using flow manipulation techniques in the realm of adaptive ecosystem management is a tool that should be carefully considered because there is potential for negative consequences for the ecosystem (Propst and Gido 2004; Poff 2018; Tonkin et al. 2021; Stein et al. 2022). Our work indicates that outcomes are highly dependent on relative tolerance and size-structured interactions; therefore, it is necessary to understand the characteristics of individual species and ecosystems and their requirements before implementing altered flow as a management strategy (Franssen, Gido, and Propst 2007; Propst, Gido, and Stefferud 2008; Rolls, Leigh, and Sheldon 2012; Gido et al. 2013).

Our results indicate that some native fish could exploit changes to flow regime to aid in population recovery in the face of predatory threats from non-natives. Once specific species and catchment knowledge have been achieved, the manipulation of flow can be a potentially powerful tool for managing native fish species requirements (Gido and Propst 2012; Stein et al. 2022), when used in conjunction with other restoration efforts and in the context of ecosystem restoration. However, it is important to recognise that trade-offs are inherent in such decision-making (Chen and Olden 2017; Tonkin et al. 2021). Indeed, our study shows that galaxiids only perform *relatively* better in low-flow conditions in the presence of trout, and in the absence of trout, they perform worse in low-flow conditions compared to that in perennial conditions. Further climate change will make trout-free populations particularly important to retain because they are likely to be more resilient.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.28245695.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.