fishes

Article

The Influence of Rainbow Trout on Dwarf Galaxiid Habitat Preferences

Ami Coughlan [1,2] and Adam Canning [2,3,*]

[1] School of Natural Sciences—Ecology, Massey University, Private Bag 11 222, Palmerston North 4442, New Zealand; acoughlan@fishandgame.org.nz
[2] Wellington Fish and Game Council, P.O. Box 1325, Palmerston North 4440, New Zealand
[3] Centre for Tropical Water and Aquatic Ecosystem Research (TropWATER), James Cook University, 1 James Cook Drive, Townsville 4811, Australia
* Correspondence: adam.canning@jcu.edu.au

Abstract

Introduced salmonids are a major threat to New Zealand's non-migratory galaxiids, yet evidence for predator-driven habitat shifts remains limited. We experimentally tested whether dwarf galaxiids (*Galaxias divergens*) altered habitat use in response to rainbow trout (*Oncorhynchus mykiss*) presence or odour. Two habitat contrasts were offered: coarse versus fine substrate and open versus vegetated cover, under three predator treatments (trout-present, trout-odour-only, trout-absent). Generalised linear mixed models showed no significant effects of trout treatment on galaxiid habitat choice in either experiment. Substrate use was stable, with a consistent preference for coarse substrate regardless of predator cues, while vegetation cover had no detectable influence on behaviour. These results suggest that trout presence is unlikely to deter dwarf galaxiids from entire river reaches, but their limited behavioural response may leave them more exposed to predation where refuge is scarce. Habitat enhancement, particularly maintaining coarse substrate and reducing fine sediment, is likely to support the resilience of this short-lived, r-selected species.

Keywords: fish conservation; introduced species management; *Oncorhynchus mykiss*; *Galaxias divergens*; anti-predator behaviour; refuge use

Key Contribution: Dwarf galaxiids showed weak and inconsistent behavioural responses to trout presence or odour under controlled conditions, suggesting limited predator recognition. However, their consistent preference for coarse substrate highlights the importance of benthic structure for habitat quality, independent of predator cues.

check for updates

Academic Editor: Bror Jonsson

Received: 31 July 2025
Revised: 2 September 2025
Accepted: 4 September 2025
Published: 5 September 2025

Citation: Coughlan, A.; Canning, A. The Influence of Rainbow Trout on Dwarf Galaxiid Habitat Preferences. *Fishes* **2025**, *10*, 456. https://doi.org/10.3390/fishes10090456

1. Introduction

Managing undesirable interactions between native and introduced species has become a global conservation challenge [1,2]. Sayer et al. [3] estimated that globally, approximately one-quarter of freshwater fauna are threatened with extinction, with approximately one-third of threatened freshwater fish facing threats from invasive species and disease. Introduced species can affect natives through direct predation, competition for resources, habitat alteration, hybridisation, and transmission of novel pathogens, as well as indirect effects such as trophic cascades and altered nutrient dynamics [4,5]. However, not all introduced species are considered invasive or cause substantial ecological damage [6,7], with some introduced species considered beneficial depending on the desired ecological and/or human values [7–9]. Introduced fish may provide sustenance, support fisheries that provide recreation opportunities and attract tourism, or provide income for restorations and advocacy that benefits all freshwater fauna [10,11]. For example, while non-native fishes are associated with substantial economic costs, introduced sport fishes may generate economic returns an order of magnitude higher, as illustrated by recreational fisheries in the U.S.A. [12]. Decisions as to whether introduced species are suppressed, eradicated, or even enhanced are, therefore, dependent on local values and management objectives [13,14]. A large review has also highlighted a systematic and persistent bias in invasion biology, where introduced species are disproportionately framed as harmful regardless of evidence of actual impacts [15], highlighting the need for balanced, evidence-based evaluation when assessing ecological risks and management priorities.

New Zealand's freshwater fish biodiversity mirrors the global trend of an increasing decline in distribution, with 62% of native species experiencing significant declines [16]. Declines have largely been driven primarily by land use change, resulting in sedimentation and eutrophication, and compounding impacts from migration barriers and introduced species [16,17]. The introduction of salmonids (particularly rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*) has been implicated as a major driver of population fragmentation and decline of several species of native fish [18–20]. Trout have even been included in the IUCN Invasive Species Specialist Group's list of the "100 of the World's Worst Invasive Alien Species" [21], reflecting their ecological impacts in some regions. However, such designations are context-dependent, and in New Zealand, trout are also a valued recreational species [22,23]. The extent and severity of their impact on native fishes varies, with some native species observed coexisting with trout in certain locations but not others. Coexistence likely hinges on native fish species population resilience to predation, the abundance and availability of food, including the accessibility of habitat refuge to reduce predation, and the suitability of habitat to support dense trout populations [18–20]. Temporal changes in pressure further complicate impact quantification. A global meta-analysis of brown trout (*Salmo trutta*) introductions over the past 170 years found that impacts were strongly negative immediately after introduction but diminished over time, becoming, on average, non-significant more than a century later [24]. Given this variability across space and time, manipulative experiments are essential to disentangle correlation from causation and to clarify the mechanisms by which trout influence native fish populations.

The degree to which habitat refuge protects species from predation depends not just on habitat availability, but also on prey species' ability to use it [25–27]. New Zealand fishes, especially native species like bullies and non-diadromous galaxiids, seek refuge from predators and floods using various physical habitats, including benthic interstitial spaces [28–30]. Riparian vegetation also supports populations by offering cover and food [31,32]; for example, Graynoth [33] observed a sharp decline in dwarf galaxiids after riparian clear-felling. The use of refuge habitat by prey in experimental studies can vary with species, predator size, and experimental design [34–36]. Galaxiids avoid eel odour but not trout cues, even when experienced with trout, suggesting limited recognition of trout or a stronger response to eel dominance in New Zealand freshwater systems [35,37,38]. Their short evolutionary history with salmonids may explain the lack of specific avoidance behaviours [35,39]. Limited recognition of trout cues may leave galaxiids more exposed to predation, which has been linked to population fragmentation [40–42], and higher galaxiid densities upstream of trout presence [40,43,44]. However, learning is possible, as common bullies (*Gobiomorphus cotidianus*) learned to associate novel predator odours with risk after a single exposure [45], and inanga (*Galaxias maculatus*) showed strong responses to conspecific alarm cues [46]. It is plausible that the behaviour of other native fish has adapted in response to the presence of salmonids after 150 years of interactions.

Furthermore, it is unclear whether the extent to which the lack of overlapping distributions between trout and some galaxiids is because of predator avoidance, competitive exclusion or natural differences in habitat preference. Some argue that observed differences in native species presence between sites with and without trout may overstate causation, instead reflecting underlying differences in habitat suitability or land use rather than direct impacts of trout [17,18,47]. Most existing evidence is, therefore, based on correlative field studies, with only limited experimental work directly testing predator-driven behavioural shifts in galaxiids. Controlled manipulative experiments are needed to disentangle predator effects from environmental variability and provide a mechanistic understanding of habitat use.

New Zealand's dwarf galaxiids (*Galaxias divergens*) are likely highly susceptible to salmonid predation due to their small size, poor predator recognition, and frequent overlap with trout [48]. This benthic, non-migratory species is endemic to New Zealand and reaches a maximum length of ~90 mm. They are largely benthic and occur in cobble and gravel riffles of small streams and river margins, particularly in foothill catchments, and feed diurnally on benthic and drifting invertebrates [48,49]. With a lifespan of ~3 years, females typically mature within 1–2 years and spawn in spring and possibly autumn, producing moderate numbers of relatively large eggs [43,49]. Listed as endangered on the International Union for Conservation of Nature (IUCN) red list, the species faces multiple threats, including predation by trout and birds, and ongoing habitat fragmentation and range contraction due to both human impacts and natural barriers [17,50,51]. Nevertheless, trout have clear potential to influence dwarf galaxiids, as both rely heavily on aquatic macroinvertebrates as a primary food source [48,49], creating scope for strong dietary overlap and competition in addition to predation. The small body size, benthic habits, and frequent co-occurrence of dwarf galaxiids with trout make them especially vulnerable to both direct mortality and resource limitation. Their persistence alongside trout in some systems suggests that local habitat features, prey availability, or behavioural adjustments may mediate these interactions, yet the underlying mechanisms remain unresolved.

Given this habitat overlap and potential vulnerability to trout, dwarf galaxiids represent a suitable model for testing predator-driven habitat selection. However, the role of trout predation in structuring native fish populations remains debated. Long-term field data indicate that hydrological variability can outweigh predator effects in some systems. In a South Island stream, Hayes [52] found no consistent evidence that juvenile trout reduced native fish abundance; instead, flood events were the primary driver of temporal changes in fish populations. Yet, correlative evidence suggests reduced dwarf galaxiid populations in locations overlapping with trout [20]. Given the numerous ways that species interactions are dependent on abiotic factors, understanding the importance of how species interactions affect the use of habitat is, therefore, critical to the effective management of species interactions.

This study experimentally tested whether dwarf galaxiids alter their habitat preferences in response to trout presence (providing visual and chemical cues) or chemical cues only released from upstream trout. Two contrasting habitat choices were offered: (1) sandy vs. cobbly substrate and (2) absence vs. presence of overhanging vegetation—each providing one option with greater refuge potential. We hypothesised that galaxiids would prefer cobbly or vegetated habitats when exposed to trout or their cues, but not when these cues were absent.

2. Materials and Methods

2.1. Dwarf Galaxiids and Their Collection

The dwarf galaxiids used in this experiment were sourced from the Manga-o-nuku Stream, Hawkes Bay, North Island, New Zealand, using a combination of backpack electric fishing and herding via foot shuffling into stop nets. Approximately 400 fish (~70–90 mm in fork length (FL)) were collected and transported to the Fish and Game hatchery facility in Napier, North Island, New Zealand, where the experiment was conducted. The galaxiids were acclimatised to the hatchery facility within a large, aerated tank, where they were liberally fed Ridley 4 mm Tasman Freshwater palleted fish food (47% protein, 24% fat), which they readily consumed. The galaxiids were then allowed to adjust to changes in temperature, light, and location for seven days prior to the experiment beginning.

2.2. Habitat Preference Experiment

Two separate experiments were run: (i) a riparian cover preference experiment and (ii) a substrate preference experiment. These were independent and conducted on different days, with troughs flushed overnight between experiments to eliminate residual cues.

The entire experiment was conducted within the Hawkes Bay Fish and Game hatchery facility, which ensured all treatments were of the same size and had the same water flow, light, temperature, and water quality. All rainbow trout (*Oncorhynchus mykiss*) used in this experiment were approximately two years old and between 190 and 290 mm long (FL) and reared on-site in large exterior ponds. Selecting trout larger than 150 mm ensured they were of piscivorous length [53]. The trout were fed with their usual food pellets for the duration of the experiment to reduce any risk of direct predation on the galaxiids, as the focus of this experiment was on changes in habitat preference, not predation, as per animal ethics requirements (ethics protocol number 19/75; Massey University Ethics Committee). We note that providing trout with pellet food may have influenced their aggressive behaviour towards galaxiids. Food abundance is known to modify aggression and territory size in salmonids, with aggression generally peaking at intermediate food levels but persisting even under high rations [54]. Aggression in trout persists across densities and size structures, and rainbow trout frequently outcompete native salmonids for feeding stations regardless of food supply [55,56]. Thus, while supplemental feeding may have reduced hunger-driven chasing, it is unlikely to have removed competitive or aggressive interactions entirely.

Each experimental replicate was a channel system consisting of three troughs (or zones) in series, each trough measuring 2 m in length, approximately 50 cm in depth and width, with a constant water flow of ~0.18 m^3 from the uppermost trough to the lowest (water depth = 30 cm, temperature = 11 °C, dissolved inorganic nitrogen concentration = 0.11 mg N/L, dissolved reactive phosphorus concentration = 0.04 mg/L). All troughs were supplied from a single header tank with evenly split inflows, ensuring consistent current velocity across zones (Figure 1). The header tank was fed continuously from groundwater to ensure constant pressure remained. Each trough contained material (vegetation or substrate) that either provided or denied the dwarf galaxiids places to hide. The two habitats were clearly delineated within a trough but randomly ordered. Within each trough, zones were separated by notched concrete dividers, which prevented fish from observing fish in adjacent zones. Mesh screens (2 mm aperture) were placed over drains to prevent fish loss (Figure 1).

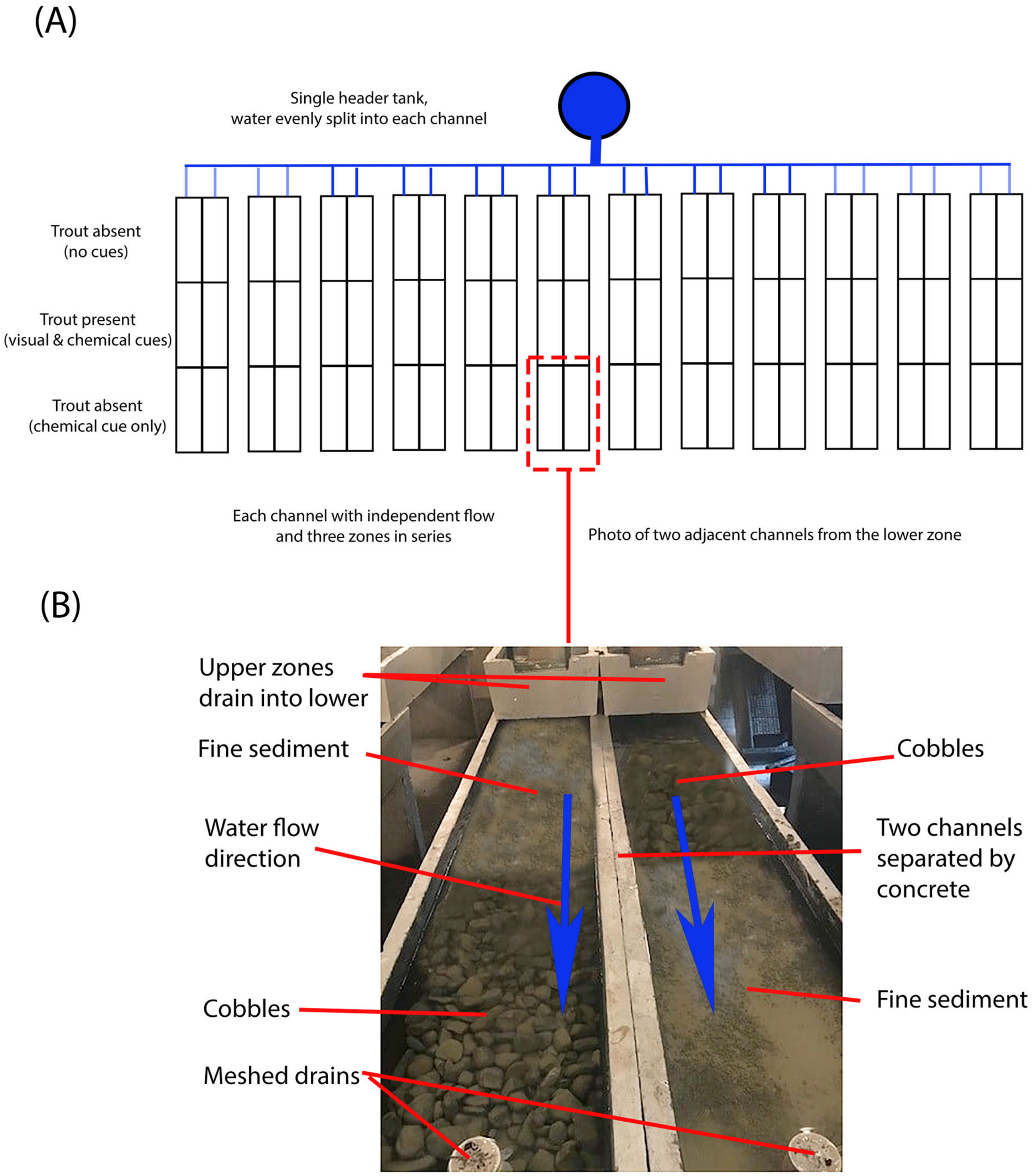

Figure 1. (**A**) Overall experimental facility layout with a header tank continuously feeding twelve replicate concrete channels. Each channel contained three flow-through zones: the upper zones contained no trout or odour, the middle zones contained a single trout to provide both visual and chemical cues, while the lower zone contained no trout but received the chemical cues from the middle zone. Panel (**B**) shows a photo of two adjacent zones (separate channels), with the zone evenly split into two contrasting habitats (cobbles and fine sediment). The vegetation experiment did not have contrasting substrates but instead had artificial macrophytes floating over half of the zone. All zones contained six dwarf galaxiids.

Six randomly selected dwarf galaxiids (regardless of sex or any apparent colouration or behavioural differences) were introduced into each section of the trough; this corresponds to a high stocking density typically observed when schooling [52,57,58]. Galaxiids were fed palleted fish food and allowed to adjust to the new troughs, which contained the same water supply they had been acclimated to. In accordance with the approved ethics protocols, feed was available for the entire duration, including during the acclimatisation phase. After the adjustment period, a single rainbow trout was placed in the middle trough section of each replicate. This created three treatments: the upper sections with dwarf galaxiids only (no trout cues), the middle sections where galaxiids were directly exposed to both the physical presence and chemical cues of trout, and the lower sections where galaxiids experienced trout odour alone without any physical presence. The number of dwarf galaxiids in each habitat were recorded immediately before trout addition, approximately every hour after trout addition, and then after trout were removed. Observations were made by two observers randomly assigned to each trough in each instance to minimise observer bias. Fish were observed to rapidly mobilise when startled by observers, so each observer waited two minutes beside the trough before beginning counts to allow fish behaviour to normalise, consistent with Hay [49].

2.2.1. Riparian (Vegetation) Experiment

The riparian experiment used twelve replicates and ran with trout present for five hours (between 16:30 and 21:30 h) over dusk when trout are most actively foraging. One-half of each of the three sections of each replicate was draped with artificial leafy vine, forming floating riparian refuges. Riparian coverage was randomly allocated to moderate any possible impact of differences in lighting and other variables. The bottoms of each of the troughs were lined with white paper to assist with dwarf galaxiid visibility, as some of the fish were small (~3 cm) and dark, and thus difficult to spot against the concrete. Following completion, the system was flushed overnight to reset conditions, and the substrate preference experiment was run the next day. This ensured independence between trials and eliminated residual cues from the previous treatment. This produced 7 observations per replicate (one pre-trout, five hourly during, and one post-trout), giving a total of 84 observations across all replicates.

2.2.2. Substrate Experiment

The substrate preference experiment was conducted independently on the following day, after the riparian experiment. Troughs were flushed overnight to remove residual cues. An experiment malfunction meant the substrate experiment had ten replicates that ran for four hours (18:20–22:20 h) instead of the twelve replicates for five hours used in the vegetation experiment. Substrate within each trough section was divided into two habitat types: half cobbles and larger stones providing interstitial cover, and half fine gravel lacking interstitial spaces. Dwarf galaxiids were added as per the riparian experiment, and trout were introduced only into the middle trough section to generate the three treatments (control, odour, trout-present). Observations followed the same schedule as in the riparian experiment (pre-trout, hourly, post-trout). This produced 6 observations per replicate (one pre-trout, four hourly during, and one post-trout), resulting in a total of 60 observations across all replicates.

2.3. Statistical Analysis

For each experiment separately, we modelled the number of dwarf galaxiids observed in open habitat (no cover or fine substrate without interstitial spaces) as the response variable. Treatment (control, trout-present, trout-odour), observation time, and their interaction were included as fixed effects. Replicate through identity was included as a random intercept to account for repeated observations within troughs. Generalised linear mixed models (GLMMs) with a negative binomial error distribution and log link were fitted using the R package glmmTMB (v1.1.11) [59]. Model assumptions and fit were evaluated using the DHARMa package (v0.4.7) [60], including simulation-based residual diagnostics, dispersion tests, and zero-inflation tests. No evidence of overdispersion or zero-inflation was detected. All analyses were carried out in R version 4.4.3 [61].

3. Results

3.1. Vegetation Choice Experiment

In the vegetation choice experiment, there were no significant effects of trout treatment, time, or their interaction on the number of dwarf galaxiids observed in open water (all $p > 0.1$; Table 1). The final model had an AIC of 182.8, BIC of 202.8, log-likelihood of −83.4, and 82 residual degrees of freedom. Model diagnostics confirmed a good fit, with no overdispersion ($p = 0.896$) and no zero-inflation ($p = 0.944$).

Table 1. Fixed-effect estimates from generalised linear mixed models (GLMMs, negative binomial distribution) testing the effects of trout treatment (control, odour, trout-present), time, and their interaction on the number of dwarf galaxiids observed in open habitat. Analyses were conducted separately for the vegetation and substrate experiments, with replicate trough as a random effect.

Experiment	Term	Estimate	Std. Error	Z Value	*p* Value
Vegetation	Intercept	−0.627	0.617	−1.016	0.31
	Treatment Odour	−0.804	0.898	−0.896	0.37
	Treatment Present	0.577	0.988	0.584	0.559
	Time	0.071	0.268	0.267	0.789
	Treatment Odour: Time	0.371	0.388	0.957	0.339
	Treatment Present: Time	−0.795	0.534	−1.489	0.137
Substrate	(Intercept)	−0.7	0.672	−1.042	0.298
	Treatment Odour	0.836	0.857	0.976	0.329
	Treatment Present	−1.249	1.212	−1.031	0.303
	Time	0.08	0.301	0.267	0.789
	Treatment Odour: Time	−0.179	0.394	−0.454	0.65
	Treatment Present: Time	0.261	0.526	0.496	0.62

3.2. Substrate Choice Experiment

In the substrate choice experiment, there were no significant effects of trout treatment, time, or their interaction on the number of dwarf galaxiids observed over fine substrate (all $p > 0.3$; Table 1). The final model had an AIC of 198.8, BIC of 218.8, log-likelihood of −91.4, and 82 residual degrees of freedom. Model diagnostics confirmed a good fit, with no overdispersion ($p = 0.896$) and no zero-inflation ($p = 0.904$).

4. Discussion

In the substrate experiment, there were no significant effects of trout presence or odour on the number of dwarf galaxiids observed over fine or coarse substrates, suggesting that substrate use was not influenced by predator cues under our conditions. This is consistent with studies showing that galaxiid substrate preferences are often stable despite trout presence. For example, McIntosh et al. [62] found that *G. vulgaris* consistently used coarse substrate during the day regardless of trout, although at night galaxiids shifted to slower-flow areas in the presence of trout, indicating altered space use under competition rather than direct avoidance. Howard [37] also reported no change in refuge-seeking by *G. vulgaris* in response to trout odour, supporting the view that predator cues do not universally trigger microhabitat shifts. In contrast, Sowersby, Thompson, and Wong [27] found that *G. arcanus* actively avoided trout on sand but cohabited with them on cobble, suggesting that habitat complexity mediates predator perception. Woodford and McIntosh [63] reported higher disappearance rates of galaxiids in pens with large trout, but interpretation was confounded because many fish escaped between pens and trout densities and size classes were unintentionally altered. These design issues make it difficult to separate true predation effects from artefacts. In contrast, our experiment used individually housed trout of known size with physical separation between treatments, reducing both actual and perceived predation risk. Overall, the absence of predator effects and consistent substrate use in our experiment suggests dwarf galaxiids prefer structured habitat regardless of trout presence.

In the vegetation experiment, GLMM testing indicated dwarf galaxiids showed no difference in their use of open versus vegetated habitat across trout-present, trout-absent, or odour-only treatments. This indicates that submerged vegetation (such as from floating macrophytes or overhanging riparian) had little influence on habitat selection under the conditions tested, contrary to expectations that visual cover would provide refuge from predators (both avian and fish). One possibility is that, as benthic dwellers, dwarf galaxiids rely more on substrate-associated cover than on floating or overhead structure. Further trials using rooted macrophytes or woody debris could help clarify how dwarf galaxiids use physical habitat to mitigate predation risk.

Behavioural responses to trout may also vary with environmental context or between galaxiid populations. Edge et al. [34] found that three genetically distinct *G. vulgaris* populations within the Taieri River system, which also contains a brown trout (*Salmo trutta*) fishery, differed markedly in posture, activity, and feeding behaviour in response to brown trout. While one type adopted cryptic postures and reduced feeding, another remained active and continued foraging despite predator presence. These differences occurred under identical experimental conditions, indicating innate or population-specific variation in risk sensitivity. Our observed lack of vegetation effects and generally weak responses may similarly reflect lineage-specific behavioural traits or low responsiveness to the particular predator or conditions tested. This highlights the importance of considering intraspecific variability when assessing anti-predator behaviour in galaxiids.

While galaxiids and trout are often negatively associated in field surveys [20], our results suggest caution in interpreting such patterns. Naive correlations between trout presence and galaxiid absence risk conflating correlation with causation: displacement is often assumed, yet our experiment indicates that dwarf galaxiid behaviour did not change in the presence of trout. Instead, other pressures may drive local absences, such as habitat loss or cumulative effects. Alternatively, these patterns could reflect fundamentally different habitat preferences, with the two species overlapping only at the margins of their ecological niches.

Our experimental conditions inevitably simplify the natural environment. In the wild, dwarf galaxiids and trout interact in larger, more complex habitats with variable flow, depth, and cover, which may create stronger or more diverse cues than those available in tanks. Nonetheless, the presence of visually exposed, free-swimming trout in our design provided a direct predation risk that galaxiids could perceive. Another consideration is whether dwarf galaxiids and trout overlap strongly in habitat use. Trout are typically larger, water-column-oriented predators, whereas dwarf galaxiids are small, benthic species that use coarse substrate as cover. This separation may reduce direct competition for space, with interactions driven more by predation risk than habitat displacement. This separation in size and microhabitat use means that direct competition for space is likely limited, with dwarf galaxiids occupying benthic refuges within coarse substrates while trout dominate the water column. Interactions, therefore, arise primarily through predation rather than overlap in habitat demand. Such ecological partitioning may partly explain why behavioural responses were weak in our study and why field associations should not be assumed to reflect competitive exclusion. Although simplified, the presence of visually exposed, free-swimming trout meant that dwarf galaxiids were exposed to a direct predation risk comparable to what they might perceive in the wild, ensuring that the core predator–prey dynamic was preserved even without the full complexity of natural streams.

These findings also have implications for habitat management. Although dwarf galaxiids did not shift substrate use in response to trout, their consistent use of coarse substrate across treatments aligns with previous studies showing that non-migratory galaxiids are strongly benthic and rely on coarse interstitial spaces for refuge and foraging [64–67]. Fine sediment inputs reduce this habitat quality by filling interstices, suppressing macroinvertebrate prey, and increasing exposure to predators and high flow [68,69]. A lack of behavioural response to trout may leave dwarf galaxiids more exposed to predation where coarse substrate is scarce, reinforcing the importance of maintaining habitat structure.

Conservation actions that enhance coarse benthic habitat and overall stream condition are, therefore, critical. Measures include reducing sediment and nutrient inputs, restoring riparian vegetation, stabilising banks, excluding livestock, and re-establishing physical habitat complexity. Trials removing deposited fine sediment in New Zealand streams have improved macroinvertebrate density and fish habitat, benefiting both native fish and trout [70]. In some catchments, conservation programmes have also used trout barriers or targeted headwater reaches to protect vulnerable galaxiid populations [42,44]. More broadly, improving native fish habitat irrespective of trout presence may be the most effective approach to building resilience, considering widespread habitat degradation and the cumulative nature of disturbance impacts [71,72]. For dwarf galaxiids, which are short-lived and rely on high reproductive output (R-selected), habitat enhancement that increases refuge, food availability, and resilience to multiple pressures will likely provide the greatest conservation gains.

At the policy level, the National Policy Statement for Freshwater Management 2020 requires regional councils to maintain or improve freshwater condition to at least minimum standards, including those relating to fish habitat and both deposited and suspended sediment. The Resource Management (National Environmental Standards for Freshwater) Regulations 2020 set enforceable requirements for activities affecting freshwater, including specific standards for fish passage that are critical for maintaining galaxiid connectivity. In addition, the Conservation (Indigenous Freshwater Fish) Amendment Act 2019 provides for the development of native freshwater fish management plans, thereby providing the Department of Conservation with tools to address key threats to non-migratory galaxiids through habitat restoration and species-specific management. Collectively, these instruments strengthen the mandate for the protection and enhancement of habitat that will improve the resilience of dwarf galaxiids and must be retained or further strengthened over time to reduce their extinction risk and support long-term population recovery.

5. Conclusions

In conclusion, dwarf galaxiids showed no significant shifts in habitat use in response to either trout presence or predator odour under controlled experimental conditions. While they consistently used coarse substrate, this preference was unaffected by predator cues, and overhead vegetation had no detectable influence on habitat use. The absence of a clear predator response may leave dwarf galaxiids more exposed to predation, reinforcing the importance of habitat preference in mediating risk. As an R-selected species, their persistence is likely to depend on the availability of high-quality habitat that buffers multiple pressures. Maintaining or restoring coarse benthic habitat and reducing fine sediment inputs, therefore, remain key priorities for supporting dwarf galaxiid populations and improving their resilience to both land use impacts and predation.

Author Contributions: Conceptualization, A.C. (Ami Coughlan) and A.C. (Adam Canning); methodology, A.C. (Ami Coughlan) and A.C. (Adam Canning); formal analysis, A.C. (Ami Coughlan) and A.C. (Adam Canning); writing—original draft preparation, A.C. (Ami Coughlan) and A.C. (Adam Canning); writing—review and editing, A.C. (Ami Coughlan) and A.C. (Adam Canning); funding acquisition, A.C. (Ami Coughlan) and A.C. (Adam Canning). All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Wellington Fish and Game Council.

Institutional Review Board Statement: The animal study protocol was approved by the Ethics Committee of Massey University (protocol code 19/75; 10 June 2019).

Data Availability Statement: Data available upon reasonable request.

Acknowledgments: The authors thank Russell Death for his guidance throughout the study; Phil Teal, Matt Kavermann and Corinne Deans for their support and proofreading; and Hawkes Bay Fish and Game Council for providing the experiment facilities.

Conflicts of Interest: The authors were employed by the funder (Wellington Fish and Game Council), a statutory organisation which includes responsibility for the conservation and management of New Zealand's freshwater sports fisheries in accordance with the Conservation Act 1987 and the Freshwater Fisheries Regulations 1983.

Abbreviations

The following abbreviations are used in this manuscript:

IUCN	International Union for Conservation of Nature
GLMM	Generalised linear mixed model
DF	Degrees of Freedom
U.S.A.	United States of America
FL	Fork Length
Std.	Standard

References

1. Boltovskoy, D.; Correa, N.M.; Burlakova, L.E.; Karatayev, A.Y.; Thuesen, E.V.; Sylvester, F.; Paolucci, E.M. Traits and impacts of introduced species: A quantitative review of meta-analyses. *Hydrobiologia* **2021**, *848*, 2225–2258. [CrossRef]
2. Pyšek, P.; Hulme, P.E.; Simberloff, D.; Bacher, S.; Blackburn, T.M.; Carlton, J.T.; Dawson, W.; Essl, F.; Foxcroft, L.C.; Genovesi, P.; et al. Scientists' warning on invasive alien species. *Biol. Rev.* **2020**, *95*, 1511–1534. [CrossRef]
3. Sayer, C.A.; Fernando, E.; Jimenez, R.R.; Macfarlane, N.B.W.; Rapacciuolo, G.; Böhm, M.; Brooks, T.M.; Contreras-MacBeath, T.; Cox, N.A.; Harrison, I.; et al. One-quarter of freshwater fauna threatened with extinction. *Nature* **2025**, *638*, 138–145. [CrossRef]
4. Bernery, C.; Bellard, C.; Courchamp, F.; Brosse, S.; Gozlan, R.E.; Jarić, I.; Teletchea, F.; Leroy, B. Freshwater Fish Invasions: A Comprehensive Review. *Annu. Rev. Ecol. Evol. Syst.* **2022**, *53*, 427–456. [CrossRef]
5. Britton, J.R. Contemporary perspectives on the ecological impacts of invasive freshwater fishes. *J. Fish Biol.* **2023**, *103*, 752–764. [CrossRef] [PubMed]
6. Belnap, J.; Ludwig, J.A.; Wilcox, B.P.; Betancourt, J.L.; Dean, W.R.J.; Hoffmann, B.D.; Milton, S.J. Introduced and Invasive Species in Novel Rangeland Ecosystems: Friends or Foes? *Rangel. Ecol. Manag.* **2012**, *65*, 569–578. [CrossRef]
7. de Carvalho-Souza, G.F.; Kourantidou, M.; Laiz, I.; Nuñez, M.A.; González-Ortegón, E. How to deal with invasive species that have high economic value? *Biol. Conserv.* **2024**, *292*, 110548. [CrossRef]
8. Goodenough, A. Are the ecological impacts of alien species misrepresented? A review of the "native good, alien bad" philosophy. *Community Ecol.* **2010**, *11*, 13–21. [CrossRef]
9. Vimercati, G.; Kumschick, S.; Probert, A.F.; Volery, L.; Bacher, S. The importance of assessing positive and beneficial impacts of alien species. *NeoBiota* **2020**, *62*, 525. [CrossRef]
10. Canning, A.D.; Jarvis, D.; Costanza, R.; Hasan, S.; Smart, J.C.R.; Finisdore, J.; Lovelock, C.; Greenhalgh, S.; Marr, H.; Beck, M.W.; et al. Financial incentives for large-scale wetland restoration: Beyond markets to common asset trusts. *One Earth* **2021**, *4*, 937–950. [CrossRef]
11. Gozlan, R.E.; Britton, J.R.; Cowx, I.; Copp, G.H. Current knowledge on non-native freshwater fish introductions. *J. Fish Biol.* **2010**, *76*, 751–786. [CrossRef]
12. Bjergo, C.; Boydstun, C.; Crosby, M.; Kokkanakis, S.; Sayers, R. Non-native aquatic species in the United States and coastal water. In *Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of US Plants, Animals and Ecosystems*; US Department of the Interior, National Biological Service: Washington, DC, USA, 1995; pp. 428–430.

13. Woodford, D.J.; Richardson, D.M.; MacIsaac, H.J.; Mandrak, N.E.; van Wilgen, B.W.; Wilson, J.R.U.; Weyl, O.L.F. Confronting the wicked problem of managing biological invasions. *NeoBiota* **2016**, *31*, 63–86. [CrossRef]
14. Simberloff, D. Non-native invasive species and novel ecosystems. *F1000Prime Rep.* **2015**, *7*, 47. [CrossRef]
15. Pereyra, P.J.; de la Barra, P.; Amione, L.L.D.; Arcángel, A.; Marello Buch, B.M.; Rodríguez, E.; Mazzolari, A.; Maldonado, M.A.; Hünicken, L.; Wallach, A.D. Systematic and persistent bias against introduced species. *BioScience* **2024**, *74*, 44–53. [CrossRef]
16. Joy, M.K.; Foote, K.J.; McNie, P.; Piria, M. Decline in New Zealand's freshwater fish fauna: Effect of land use. *Mar. Freshw. Res.* **2019**, *70*, 114–124. [CrossRef]
17. Canning, A. Predicting New Zealand riverine fish reference assemblages. *PeerJ* **2018**, *6*, e4890. [CrossRef]
18. McIntosh, A.; McHugh, P.; Dunn, N.; Goodman, J.; Howard, S.; Jellyman, P.; O'Brien, L.; Nyström, P.; Woodford, D. The impact of trout on galaxiid fishes in New Zealand. *N. Z. J. Ecol.* **2010**, *34*, 195–206.
19. Jones, P.; Closs, G.P. The introduction of Brown Trout to New Zealand and their impact on native fish communities. In *Brown Trout: Biology, Ecology and Management*, 1st ed.; Lobon-Cervia, J., Sanz, N., Eds.; John Wiley & Sons Ltd.: West Sussex, UK, 2018.
20. Jellyman, P.G.; McHugh, P.A.; Simon, K.S.; Thompson, R.M.; McIntosh, A.R. The effects of brown trout on the trophic webs of New Zealand streams. In *Brown Trout: Biology, Ecology and Management*, 1st ed.; Lobon-Cervia, J., Sanz, N., Eds.; John Wiley & Sons Ltd.: West Sussex, UK, 2018.
21. Lowe, S.; Browne, M.; Boudjelas, S.; De Poorter, M. *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database*; Invasive Species Specialist Group Auckland: Auckland, New Zealand, 2000; Volume 12.
22. Tadaki, M.; Holmes, R.; Kitson, J.; McFarlane, K. Understanding divergent perspectives on introduced trout in Aotearoa: A relational values approach. *Kōtuitui N. Z. J. Soc. Sci. Online* **2022**, *17*, 461–478. [CrossRef]
23. Stewart, C.; Bennett-Fakahau, I.; Nada-Raja, S.; Stewart, K. Exploring the relationship between trout fishing and wellbeing: Insights from Aotearoa New Zealand trout anglers. *Kōtuitui N. Z. J. Soc. Sci. Online* **2025**, *20*, 98–115. [CrossRef]
24. Závorka, L.; Buoro, M.; Cucherousset, J. The negative ecological impacts of a globally introduced species decrease with time since introduction. *Glob. Change Biol.* **2018**, *24*, 4428–4437. [CrossRef]
25. Boon, J.S.; Keith, S.A.; Exton, D.A.; Field, R. The role of refuges in biological invasions: A systematic review. *Glob. Ecol. Biogeogr.* **2023**, *32*, 1244–1271. [CrossRef]
26. Selwood, K.E.; Zimmer, H.C. Refuges for biodiversity conservation: A review of the evidence. *Biol. Conserv.* **2020**, *245*, 108502. [CrossRef]
27. Sowersby, W.; Thompson, R.M.; Wong, B.B.M. Invasive predator influences habitat preferences in a freshwater fish. *Environ. Biol. Fishes* **2016**, *99*, 187–193. [CrossRef]
28. McEwan, A.; Joy, M. Responses of three PIT-tagged native fish species to floods in a small, upland stream in New Zealand. *N. Z. J. Mar. Freshw. Res.* **2013**, *47*, 225–234. [CrossRef]
29. Davey, A.; Kelly, D. Fish community responses to drying disturbances in an intermittent stream: A landscape perspective. *Freshw. Biol.* **2007**, *52*, 1719–1733. [CrossRef]
30. Jowett, I.G.; Richardson, J. Comparison of habitat use by fish in normal and flooded river conditions. *N. Z. J. Mar. Freshw. Res.* **1994**, *28*, 409–416. [CrossRef]
31. Meijer, C.G.; Warburton, H.J.; McIntosh, A.R. Disentangling the multiple effects of stream drying and riparian canopy cover on the trophic ecology of a highly threatened fish. *Freshw. Biol.* **2021**, *66*, 102–113. [CrossRef]
32. Pusey, B.J.; Arthington, A.H. Importance of the riparian zone to the conservation and management of freshwater fish: A review. *Mar. Freshw. Res.* **2003**, *54*, 1–16. [CrossRef]
33. Graynoth, E. Effects of logging on stream environments and faunas in Nelson. *N. Z. J. Mar. Freshw. Res.* **1979**, *13*, 79–109. [CrossRef]
34. Edge, K.A.; Townsend, C.R.; Crowl, T.A. Investigating anti-predator behaviour in three genetically differentiated populations of non-rnigratory galaxiid fishes in a New Zealand river. *N. Z. J. Mar. Freshw. Res.* **1993**, *27*, 357–363. [CrossRef]
35. McLean, F.; Barbee, N.C.; Swearer, S.E. Avoidance of native versus non-native predator odours by migrating whitebait and juveniles of the common galaxiid, galaxias maculatus. *N. Z. J. Mar. Freshw. Res.* **2007**, *41*, 175–184. [CrossRef]
36. Albariño, R.J.; Closs, G.P.; Matthaei, C.D.; Townsend, C.R.; Zamorano, D. Substrate size modifies stream grazer–biofilm interactions in the presence of invertivorous fish. *Ecology* **2022**, *103*, e3828. [CrossRef]
37. Howard, S.W. Effects of Trout on Galaxiid Growth and Antipredator Behaviour. Master's Thesis, University of Canterbury, Christchurch, New Zealand, 2007.
38. Jellyman, D.J.; Crow, S.K.; Robinson, P. Impacts of longfin eels (*Anguilla dieffenbachii*) on the behaviour of common bullies (*Gobiomorphus cotidianus*) held in captivity. *Ecol. Freshw. Fish* **2012**, *21*, 57–63. [CrossRef]
39. Milano, D.; Lozada, M.; Zagarese, H.E. Predator-induced reaction patterns of landlocked Galaxias maculatus to visual and chemical cues. *Aquat. Ecol.* **2010**, *44*, 741–748. [CrossRef]
40. McDowall, R.M. When galaxiid and salmonid fishes meet–a family reunion in New Zealand. *J. Fish Biol.* **1990**, *37*, 35–43. [CrossRef]

41. Woodford, D.J.; McIntosh, A.R. Evidence of source-sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout. *Ecol. Appl.* **2010**, *20*, 967–977. [CrossRef]
42. Jolly, M.E.; Warburton, H.J.; Bowie, S.; Challies, E.; Jellyman, P.G.; McIntosh, A.R. Isolation management to protect threatened native galaxiid fish species: Lessons from Aotearoa New Zealand. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2024**, *34*, e4220. [CrossRef]
43. Jowett, I.G.; Richardson, J. Fish communities in New Zealand rivers and their relationship to environmental variables. *N. Z. J. Mar. Freshw. Res.* **2003**, *37*, 347–366. [CrossRef]
44. Jolly, M.E.; Warburton, H.J.; Bowie, S.; McIntosh, A.R. Managing Isolation: Implementing In-Stream Barriers to Exclude Introduced Trout From Fragmented Native Freshwater Fish Refuges. *River Res. Appl.* **2025**, *41*, 1347–1361. [CrossRef]
45. Kristensen, E.A.; Closs, G.P. Anti-predator response of naïve and experienced common bully to chemical alarm cues. *J. Fish Biol.* **2004**, *64*, 643–652. [CrossRef]
46. Thomas, O.R.B.; Barbee, N.C.; Hassell, K.L.; Swearer, S.E. Smell no evil: Copper disrupts the alarm chemical response in a diadromous fish, Galaxias maculatus. *Environ. Toxicol. Chem.* **2016**, *35*, 2209–2214. [CrossRef]
47. Townsend, C.R. Invasion biology and ecological impacts of brown trout Salmo trutta in New Zealand. *Biol. Conserv.* **1996**, *78*, 13–22. [CrossRef]
48. Hopkins, C.L. Life history of *Galaxias divergens* (salmonoidea: Galaxiidae). *N. Z. J. Mar. Freshw. Res.* **1971**, *5*, 41–57. [CrossRef]
49. Hay, J. *Effects of Low Flow on Dwarf Galaxias and Their Habitat in the Wairau River*; Department of Conservation: Wellington, New Zealand, 2009; pp. 1–20.
50. West, D.; Allibone, R.; Franklin, P.; Ling, N.; David, B.; Closs, G.; Crow, S. Galaxias divergens, Dwarf galaxiid. The IUCN Red List of Threatened Species 2014: e.T197291A2481541. 2014. Available online: https://www.iucnredlist.org/species/197291/2481541 (accessed on 1 September 2025).
51. Dunn, N.R.; Allibone, R.M.; Closs, G.P.; Crow, S.K.; David, B.O.; Goodman, J.M.; Griffiths, M.; Jack, D.C.; Ling, N.; Waters, J.M.; et al. *Conservation Status of New Zealand Freshwater Fishes, 2017*; New Zealand Threat Classification Series 24; Department of Conservation: Wellington, New Zealand, 2018; 11p. Available online: https://www.doc.govt.nz/Documents/science-and-technical/nztcs24entire.pdf (accessed on 1 September 2025).
52. Hayes, J.; Goodwin, E.; Clapcott, J.; Shearer, K. The influence of natural flow and temperature and introduced brown trout on the temporal variation in native fish abundance in a "reference" stream. *Can. J. Fish. Aquat. Sci.* **2019**, *76*, 705–722. [CrossRef]
53. Sánchez-Hernández, J. Drivers of piscivory in a globally distributed aquatic predator (brown trout): A meta-analysis. *Sci. Rep.* **2020**, *10*, 11258. [CrossRef]
54. Toobaie, A.; Grant, J.W.A. Effect of food abundance on aggressiveness and territory size of juvenile rainbow trout, Oncorhynchus mykiss. *Anim. Behav.* **2013**, *85*, 241–246. [CrossRef]
55. Wipf, M.M.; Barnes, M.E. Competitor density and size effects on aggression and feeding in cutthroat trout: Implications for aquaculture. *Open Fish Sci. J.* **2011**, *4*, 62–66. [CrossRef]
56. Seiler, S.M.; Keeley, E.R. A comparison of aggressive and foraging behaviour between juvenile cutthroat trout, rainbow trout and F1 hybrids. *Anim. Behav.* **2007**, *74*, 1805–1812. [CrossRef]
57. Jowett, I.G.; Richardson, J.; McDowall, R.M. Relative effects of in-stream habitat and land use on fish distribution and abundance in tributaries of the Grey River, New Zealand. *N. Z. J. Mar. Freshw. Res.* **1996**, *30*, 463–475. [CrossRef]
58. Jowett, I.G.; Hayes, J.W.; Deans, N.; Eldon, G.A. Comparison of fish communities and abundance in unmodified streams of Kahurangi National Park with other areas of New Zealand. *N. Z. J. Mar. Freshw. Res.* **1998**, *32*, 307–322. [CrossRef]
59. Brooks, M.E.; Kristensen, K.; Van Benthem, K.J.; Magnusson, A.; Berg, C.W.; Nielsen, A.; Skaug, H.J.; Machler, M.; Bolker, B.M. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **2017**, *9*, 378–400. [CrossRef]
60. Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models, R Package Version 0.4.7. 2024. Available online: https://cran.r-project.org/web/packages/DHARMa/index.html (accessed on 1 September 2025).
61. R Core Team. R: A Language and Environment for Statistical Computing. 2024. Available online: https://www.r-project.org/ (accessed on 1 September 2025).
62. McIntosh, A.R.; Townsend, C.R.; Crowl, T.A. Competition for space between introduced brown trout (*Salmo trutta* L.) and a native galaxiid (*Galaxias vulgaris* Stokell) in a New Zealand stream. *J. Fish Biol.* **1992**, *41*, 63–81. [CrossRef]
63. Woodford, D.J.; McIntosh, A.R. *Effects of Introduced Trout Predation on Non-Diadromous Galaxiid Fish Populations Across Invaded Riverscape*; Department of Conservation: Wellington, New Zealand, 2013; pp. 1–23.
64. Sepulveda, A.J.; Sechrist, J.; Marczak, L.B. Testing Ecological Tradeoffs of a New Tool for Removing Fine Sediment in a Spring-fed Stream. *Ecol. Restor.* **2014**, *32*, 68–77. [CrossRef]
65. Owens, P.N.; Batalla, R.J.; Collins, A.J.; Gomez, B.; Hicks, D.M.; Horowitz, A.J.; Kondolf, G.M.; Marden, M.; Page, M.J.; Peacock, D.H.; et al. Fine-grained sediment in river systems: Environmental significance and management issues. *River Res. Appl.* **2005**, *21*, 693–717. [CrossRef]

66. Roni, P.; Hanson, K.; Beechie, T. Global Review of the Physical and Biological Effectiveness of Stream Habitat Rehabilitation Techniques. *N. Am. J. Fish. Manag.* **2008**, *28*, 856–890. [CrossRef]
67. Knott, J.; Mueller, M.; Pander, J.; Geist, J. Effectiveness of catchment erosion protection measures and scale-dependent response of stream biota. *Hydrobiologia* **2019**, *830*, 77–92. [CrossRef]
68. Jones, J.I.; Murphy, J.F.; Collins, A.L.; Sear, D.A.; Naden, P.S.; Armitage, P.D. The impact of fine sediment on macroinvertebrates. *River Res. Appl.* **2012**, *28*, 1055–1071. [CrossRef]
69. Kemp, P.; Sear, D.; Collins, A.; Naden, P.; Jones, I. The impacts of fine sediment on riverine fish. *Hydrol. Process.* **2011**, *25*, 1800–1821. [CrossRef]
70. Ramezani, J.; Rennebeck, L.; Closs, G.P.; Matthaei, C.D. Effects of fine sediment addition and removal on stream invertebrates and fish: A reach-scale experiment. *Freshw. Biol.* **2014**, *59*, 2584–2604. [CrossRef]
71. Fraley, K.M.; Warburton, H.J.; Jellyman, P.G.; Kelly, D.; McIntosh, A.R. The influence of pastoral and native forest land cover, flooding disturbance, and stream size on the trophic ecology of New Zealand streams. *Austral Ecology* **2021**, *46*, 833–846. [CrossRef]
72. Pingram, M.A.; Collier, K.J.; Williams, A.K.; David, B.O.; Garrett-Walker, J.; Górski, K.; Özkundakci, D.; Ryan, E.F. Surviving Invasion: Regaining Native Fish Resilience Following Fish Invasions in a Modified Floodplain Landscape. *Water Resour. Res.* **2021**, *57*, e2020WR029513. [CrossRef]