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Managing Isolation: Implementing In-Stream Barriers to Exclude Introduced Trout From Fragmented Native Freshwater Fish Refuges

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ABSTRACT

Fish invasions are a key driver of change in freshwater systems, impacting biodiversity and economies. The use of in-stream barriers to prevent or mitigate such invasions and protect native fish populations, known as isolation management (IM), has been increasingly reported. However, despite the need to secure vulnerable populations, trade-offs between isolation and invasion are likely, and it is unclear if current knowledge supports optimal long-term outcomes. Aotearoa New Zealand has a history of using exclusion barriers to prevent incursions of introduced sports fish into native river-resident galaxiid (RRG) refuges predominantly within the South Island. We assessed 37 structures and predicted successful exclusion would be due to a combination of barrier parameters and habitat. Additionally, we assessed global exclusion knowledge, conducting a systematic review and meta-analysis of peer-reviewed studies of trout barriers to examine the prevalence of quantitative barrier parameters in the literature. We found that drop height had the strongest relationship with exclusion in both field survey and meta-analysis, and downstream pool depth was also negatively correlated with exclusion in the field data. Less than a third (27%) of trout barrier studies identified by systematic review reported quantitative barrier parameters, and barrier height was the only parameter found to have a relationship with exclusion. Only six (11%) of the quantitative studies described deliberate exclusion of fish for ecological gain. Trout barriers had successful outcomes in New Zealand, with galaxiid densities higher above successful barriers than any other position; therefore, there is evidence supporting barrier use in conservation.

1 | Introduction

Freshwater invasions are a key driver of biodiversity loss, and their effects are exacerbated by other threats such as climate change and habitat loss (Blackburn et al. 2019; Dueñas et al. 2021; Roberts et al. 2017). Despite extensive evidence supporting the effect of invasions in freshwater, much remains to be learned about the application and outcomes of mitigation strategies, a key knowledge gap that hampers decision making in these situations (Homans and Smith 2013; Vander Zanden and Olden 2008). Reliable tools are needed to mitigate current invasions and prevent new incursions into vulnerable ecosystems to prevent ongoing biodiversity loss (Buckwalter et al. 2018; Cucherousset and Olden 2011). One strategy involves the placement of barriers to exclude non-desirable biota (Jones et al. 2021; Krieg and Zenker 2020; Noatch and Suski 2012). However, there is a need to untangle the barrier characteristics that lead to reliable exclusion by understanding how combinations of physical parameters, hydrology, habitat, and the biological traits of the invasive species can inform the long-term security of such refuges.

Exclusion barriers are a major tool in the prevention and mitigation of aquatic invasions globally (Britton et al. 2023; Jones et al. 2021; Krieg and Zenker 2020). Their use has increased significantly in the last 20 years, and they are especially useful to prevent the movement of invasive or non-desirable fish species (Altenritter et al. 2019; McLaughlin et al. 2007; Tempero et al. 2019). The term "isolation management" (IM) is used to describe this deliberate use of exclusion barriers in protecting desirable freshwater species, a niche use of exclusion barriers (Avenetti et al. 2006; Jones et al. 2021; Novinger and Rahel 2003). These barriers prevent upstream movement by the invader, and usually most other fish species, although downstream passage and/or dispersal tend to be possible. Species-selective barriers have been documented but may come with increased invasion risk (Frings et al. 2013; Morán-López and Uceda Tolosa 2017). Isolation management is used, for example, in the protection of native trout species in North America (e.g., Avenetti et al. 2006; Budy et al. 2021; Novinger and Rahel 2003), and in galaxiid protection from introduced trout in Australia and New Zealand, where such barriers have been used since the early 2000s (Franklin et al. 2024; Lintermans et al. 2014; Raadik et al. 2010). However, despite increased use, knowledge gaps, likely essential to long-term success, remain regarding the implementation, efficacy, and outcomes of IM (Fausch et al. 2009; Jolly et al. 2024; Jones et al. 2021).

It should be noted that "successful" IM comes with trade-offs for the protected population such as prevention of immigration or recolonisation following stochastic events. This disruption to dispersal may lead to genetic bottlenecking potentially reducing fitness or formation of sink populations where recruitment cannot keep up with losses (Hellmair and Kinziger 2014; Coleman et al. 2018). These populations are also at increased risk of extirpation during extreme events such as floods or drought due to limited habitat refuges in low-order, headwater fragments, often found above such barriers or used as man-made reserves (Grossman et al. 2016; Fausch et al. 2009).

Barrier characteristics are a key factor in excluding non-native salmonids from resident fish refuges. The introduction of salmonids such as trout for sport has impacted many global native fisheries and is a key driver of indigenous species declines, as well as other impacts such as land-use intensification, climate change, pollution, and habitat destruction (Budy and Gaeta 2017; Meredith et al. 2015; Rahel and Olden 2008). This pattern is true in the Southern Hemisphere where native river-resident galaxiids (RRG) species, a fish family with high levels of endemism and many threatened species, have been negatively impacted through predation and competition with nonnative and invasive fish (Jackson et al. 2004; McIntosh et al. 2010; Minett et al. 2023). These impacts remain ongoing, despite these interactions being documented for over three decades (Townsend and Crowl 1991). Southern Hemisphere researchers and practitioners have a history of interventions to protect RRG populations, such as exclusion barriers, non-native fish removal, and translocations, but drivers of success have often been difficult to evaluate (Lintermans 2013; Raadik et al. 2010). In Aotearoa New Zealand, RRG threat status (known as national "conservation status", Dunn et al. 2018) is closely linked to trout impacts. Therefore, tools for future mitigation are essential to prevent further decline and extinctions, particularly in small pockets of South Island catchments where remnant RRG populations remain and invasions continue to occur (Boddy and McIntosh 2017; Jellyman and Mcintosh 2010). Moreover, similar issues have been observed globally, making lessons from New Zealand IM useful in a much wider context (Hasegawa 2020; Lindegren et al. 2012; Woodford and Impson 2004).

Exclusion barriers rely on physical parameters combined with hydrology and habitat to prevent the passage of unwanted organisms (Stuart 1963). Barrier characteristics such as height, profile, and plunge pool depth are integral to conferring exclusion by preventing natural traits that allow upstream access, e.g., jumping (Castro-Santos 2006; Kondratieff and Myrick 1900), but it is not clear if current knowledge can accurately predict the exclusion of burst swimming fish such as trout, particularly when placed in "low head" (< 1–1.5 m drop height) situations, as occur in many low gradient streams where most RRG are most commonly found. It might also be assumed that the IM literature documents barrier metrics leading to exclusion, but this is not clear and may be a knowledge gap for practitioners attempting to prevent or mitigate invasions with engineered solutions. While still a principal intervention in native fish protection, much remains to be learned regarding the use of in-stream barriers excluding invasive fish, such as physical parameters and performance under varying flows and maintenance requirements long-term.

Here, we investigated barrier characteristics important in excluding introduced trout from RRG refuges in New Zealand by examining physical parameters, habitat metrics, and hydrology of built and natural structures. To further assess global knowledge of the effectiveness of such barriers, we also conducted a systematic review and meta-analysis of peer-reviewed studies of trout barriers to complement the field data. We predicted that exclusion was mediated by a combination of physical parameters, hydrology, and habitat (H1), but that these quantitative data are likely missing from much of the global literature (H2). We also predicted that populations of RRG above successful trout barriers were more abundant or showed signs of better population health than other populations (H3).

2 | Materials and Methods

2.1 | Field Sampling

To assess in-stream structures preventing or allowing upstream trout passage in RRG habitat, we surveyed potential exclusion barriers. During the austral summer of 2022–2023, we evaluated 37 natural and built structures in the South Island. We chose these South Island locations due to the known presence of threatened RRG species (Boddy and McIntosh 2017; McDowall 2010; Stoffels 2022;), and the occurrence of deliberate IM projects. Of the 37 assessed, eleven barriers were identified as being deliberately built or augmented for trout exclusion from RRG populations, most of which were actively managed and monitored. The remainder were identified as potential trout barriers using the following criteria: (1) barrier comprised a known mechanism that was associated with exclusion, such as a physical drop, drying reach, or shallow velocity chute; (2) historical fish data were associated with the barrier, confirming the presence of trout downstream and RRG within the catchment; and (3) barrier sites were accessible to a field team to measure physical parameters, hydrology, habitat metrics, and perform fish surveys by electrofishing above and below each barrier. These selection criteria allowed the identification of this large sample of potential trout barriers in known RRG habitat. Two streams had more than one barrier present that was assessed ($n = 2$ and 3 respectively). Both had trout present above and below all barriers, and each barrier was treated as an independent replicate.

To compare barriers in multiple catchments, location metadata, physical barrier parameters and hydrological measurements were collected for each structure (Table 1). Metadata included location, altitude, district, catchment, stream name and land or structure owner. Flow measurements were taken using a Marsh 2000 Flo-Mate (Hach Company, USA). Dissolved oxygen and water temperature were measured with a YSI EcoSense DO 200 (YSI Inc., USA) and pH/Specific conductivity with a YSI Pro 1030 (YSI Inc., USA).

This approach allowed for a comprehensive assessment of all barrier characteristics critical to H1 (Brandt et al. 2005; Kondratieff and Myrick 1900; Stuart 1963). To document barrier success (H1) and test H3, fish surveys were conducted above and below each potential barrier. By surveying fish assemblages and densities above and below such barriers, we could assess metrics of RRG population health across multiple species in multiple catchments (Woodford 2009). Electrofishing, conducted using either a Smith-Root LR-24 backpack machine (Smith Root Inc., USA) or a NIWA Kianga 300 generating 300–400 V of pulsed direct current into handheld push nets, was used as an efficient capture method (Boddy et al. 2020; Woodford 2009). Fishing involved three passes of 2 m^2 in 10 lanes to give a total surface area of 20 m^2 total, working upstream, placing the push net just above the start of the last lane. Fishing reaches were placed at least 10 m from the barrier, if possible, to reduce any barrier effect on fish assemblage and abundance and were placed as close as possible to previous records (Stoffels 2022). Fishes were identified to species and measured by fork length for trout and total length for galaxiids. In combination with the physicochemical sampling, assessments allowed us to test H1 and H3. To allow for a strong test of H3, habitat and flows within fishing reaches were assessed so barrier effects on fish assemblages could be separated from habitat influences (Table 1). At each reach, three widths, three water depths per width, and mean substrate size (beta axis, Wolman Walk (Green 2003)) were measured (Brandt et al. 2005; Stuart 1963). Submerged vegetation, woody debris,

TABLE 1 | Parameters, units and their description measured from barriers, and reaches and fish populations associated with barriers, where: m, meters; m/s, meters per second; and °, degrees incline.

	Parameter	Units	Description
Barriers	Wetted width	m	Top of barrier
	Barrier width	m	Top of barrier
	Drop height	m	Three measures from top of barrier to top of pool
	Bottom pool depth	m	Three depths per width transect
	Bottom pool length	m	Barrier base to top of normal flow
	Water velocity lip	m/s	Three measurements from top of barrier
	Barrier profile/incline	°	Barrier slope
Reaches	Wetted width	m	Three transects
	Depth	cm	Three per transect
	Mesohabitat distribution	%	Proportion of riffle, run and pool habitat
	Substrate size	cm	30 randomly picked particles
	Woody debris	m^2	Within fishing reach
	Macrophyte cover	m^2	Within fishing reach
	Undercut bank	m	Length per bank
	Canopy cover	%	Densiometer
	Reach length	m	
	Discharge	cumecs (m^3/s)	
Fish populations	Fishing method		Stop nets or no nets
	Length	cm	Total length (galaxiids) Fork length (trout)
	Weight	g	

canopy cover, bank overhang, and mesohabitat distribution were estimated (Boddy and McIntosh 2017). Exclusion barriers were deemed "successful" if trout were confirmed below the barrier but not above it. "Unsuccessful" barriers had trout upstream also. All naturally occurring trout barriers were uninvaded at the time of sampling, whereas in several of the deliberate fragmentation projects with engineered barriers, trout removal above the barrier had been performed and "successful" barriers remained uninvaded following this removal.

2.2 | Field Data Analysis

To test H1, we selected seven ecologically relevant parameters potentially integral to exclusion (height, downstream pool depth, pool length, barrier slope, wetted width, discharge and lip velocity) (Brandt et al. 2005; Stuart 1963). We used principal components analysis (PCA) to reduce barrier parameters to a limited number for comparison across successful and non-successful barriers. Barrier height and discharge were $\log_{10}$-transformed to meet assumptions of normality. We conducted PERMANOVA with the adonis2 function in the Vegan package in R (Oksanen et al. 2022) to test if parameters or combinations of parameters (axis 1 and 2 from the PCA) differed between effective barriers, thereby testing H1.

To further assess which particular parameters were important in conferring exclusion, and further test H1, we used the same seven parameters as predictors in a global model, where the response variable was binomial; "effective" or "not effective". Lip velocity was removed as a predictor due to collinearity with discharge, leaving six parameters in the model. A generalized linear model (GLM) was used to interrogate the predictor relationship with trout exclusion (R Core Team 2022). Each predictor was included as a main effect (i.e., no interactions were included). These analyzes allowed barrier parameters or combinations of parameters with a significant relationship to exclusion to be identified. Probabilities were calculated using likelihood ratio tests (LRT). Plots were generated using the ggplot2 package (Wickham 2016) and 95% confidence intervals were extracted from our models using the effects package (Fox and Weisberg 2019).

Fish survey data were also analyzed to test H3. This dataset included barriers that had never been invaded, those where deliberate barrier placement and trout removal had occurred, and barriers that were unsuccessful at excluding trout. Fish data were converted to a fish/m^2 density metric for each species at a site, and for some analysis, all RRG species were combined to create a galaxiid density response variable. We built a generalized linear mixed-effects model (GLMM) in the lme4 package (Bates et al. 2015), using galaxiid density as the response variable and position in relation to the barrier (above or below) and barrier success as predictors to test H3. The model included an interaction term between position and barrier success, and site was added as a random effect. Habitat parameters from upstream and downstream fishing reaches were also summarized by PCA and used to describe habitat above and below successful and non-successful barriers, allowing the habitat influences on invasion to be separated from barrier effects in testing H3. PERMANOVA was used to test for differences in habitat availability and complexity above and below successful and non-successful barriers. These analyzes allowed the effects of barriers and habitat on fish assemblages and abundance to be separated and quantified. All data analysis was performed in R Studio (R version 4.2.1).

2.3 | Systematic Review Methods

To further test H1 and evaluate H2, we performed a systematic review and subsequent meta-analysis of barriers to trout passage in the published global literature using a systematic approach (Haddaway et al. 2015). We aimed to corroborate our findings and assess what is commonly reported in deliberate exclusion practices worldwide. On 9 October 2023, we searched the Scopus scientific abstract and citation database for published material using the search string barrier* OR waterfall* OR weir* AND trout* OR galaxias OR salmonid AND exclu* OR passage OR swim OR "isolation management" OR "selective fragmentation". Additional results were added to these search results from author knowledge to expand the body of papers and cover as many deliberate exclusion studies as possible.

To conform with systematic review best practice, we used the Preferred Reporting of Items for Systematic Review and Meta-Analysis (PRISMA) guidelines, allowing replication of methods and robust reporting (Page et al. 2021). In accordance with PRISMA, the collection was screened, duplicates excluded, non-English text, and items where no full text was available were excluded. Further exclusion criteria were applied to remove articles that did not describe a barrier, fish-pass, or obstacle of some type, did not reference trout species, and finally, papers that did not report quantitative barrier parameters. We deliberately excluded large anadromous salmonids such as Atlantic salmon (*Salmo salar*) and Chinook salmon (*Oncorhynchus tshawytscha*) because these species have not been the target of IM projects to our knowledge. The remaining items that reported quantitative barrier metrics were then analyzed for metadata such as study type, date, and place of publication. Physical barrier parameters, equivalent to those measured in the field study, were extracted from each paper and used in our meta-analysis of barrier parameters described below.

2.4 | Data Analysis for the Systematic Review and Meta-Analysis

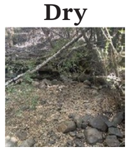
To assess parameters (H1) recorded in these studies in a similar way to the field survey data, extracted parameters were categorized. All possible barrier parameter combinations were calculated. Those parameters or combinations having 35 or more replicates were included in further analysis. This nominal cutoff point was chosen to equate to the New Zealand field barrier dataset and provide statistical robustness. Data were transformed to meet assumptions of normality. The same methodology used for the New Zealand barrier field data assessment was applied, i.e., barrier success was the binomial response and quantitative parameters were predictors in a GLM. A global model was impossible to build as each parameter or combination of parameters came from a different subset of studies, with variable and often inadequate replication, so individual GLMs were built for parameters that met the replication requirement. Thus, a similar protocol was applied to the quantitative data from the global studies, enabling further testing of H1 and assessment of H2.

3 | Results

We surveyed 37 potential New Zealand trout barriers. Eleven had been built to deliberately exclude trout for the purpose of RRG population protection, and the remainder were naturally occurring features such as waterfalls or were built for other purposes such as road culverts (Table 2). All deliberate IM barriers were assessed as impassable by trout, although one upstream reach was not designated "trout free" and trout removal was still ongoing. Two other populations above barriers had recently suffered new trout invasions during high flow events, most likely by overland flow from mainstems, which meant that trout removal was still being implemented. These barriers were therefore still categorized as "successful". Most barriers (34) had a physical drop as the main exclusion mechanism. The final three barriers included one with a shallow clay-based chute with high water velocities and two with ephemeral drying reaches (Table 2). These latter three were excluded from analysis because their exclusion mechanisms were different, reliant on flow rather than physical metrics, and less well understood (Table 2). Overall, most natural and built exclusion barriers had a drop as the primary exclusion mechanism (Table 2); hence, analyzing the characteristics of drop barriers was our focus for understanding trout exclusion success.

Assessment of parameters, or combinations of parameters, possibly conferring barrier success based on PCA, showed no separation between successful and non-successful barriers (Figure 1a). Drop height, pool depth, and pool length were all

TABLE 2 | Summary of potential trout exclusion barriers field audited in 2022–2023 summer from South Island streams categorized by type and exclusion mechanism.

Barrier type							**Likely exclusion mechanism**		
	Weir	**Culvert**	**Augmented**	**Waterfall**	**Dry**	**Chute**			
Barriers							**Drop**	**Velocity**	**Dry**
Deliberate exclusion ($n=11$)	8	3	1	0	0	0	12	0	0
Non-deliberate exclusion ($n=13$)	0	3	0	8	1	1	11	1	1
No exclusion ($n=12$)	0	5	0	6	1	0	10	0	2

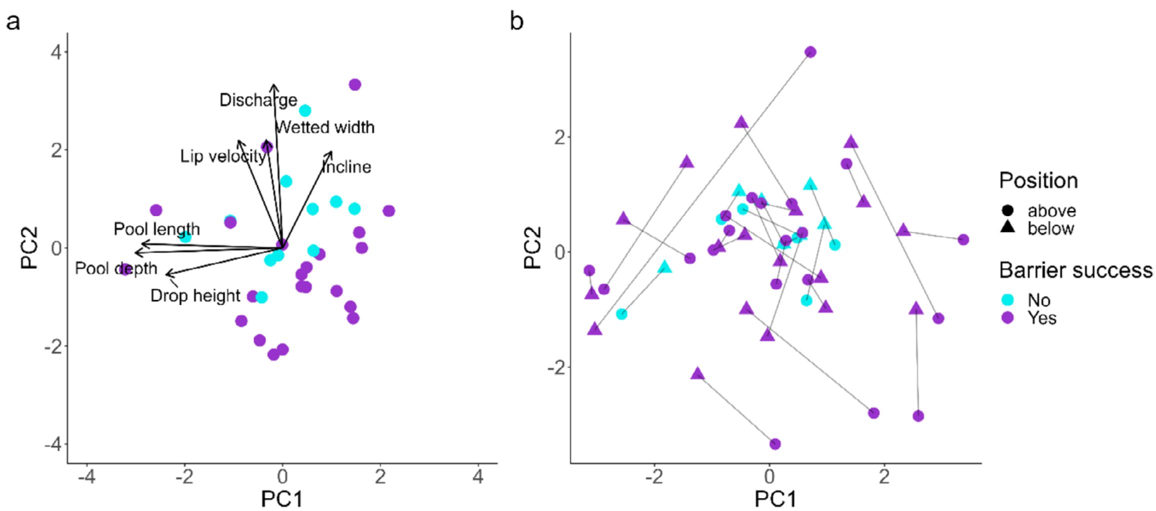


FIGURE 1 | Biplots of physical barrier parameters (a) and reach habitat variables (b) from two separate principal components analyzes with barrier success at excluding trout indicated by color, measured barrier parameters indicated by named vectors in (a), and for habitats in (b), positioning of the reaches indicated by symbol shapes connected by lines. The parameters represented in the vectors of (a) are described in more detail in Table 1. Upstream and downstream habitat reaches are linked by the barrier between them, hence the lines in (b) connect each pair of reaches above and below a barrier. [Color figure can be viewed at wileyonlinelibrary.com]

negatively associated with PC1, whereas discharge, lip velocity, wetted width, and barrier slope were positively associated with PC2. The two principal components (PC1 and PC2) accounting for 55% of total variation in physical and hydrological factors were not different between successful and non-successful barriers (PERMANOVA: $F_{1,33}=0.26$, $p=0.608$). Hence, general analysis of grouped barrier characteristics could not narrow down a consistent group of parameters that drove barrier success.

Further assessment of influences on barrier success was performed using a global model incorporating the six previously described parameters in a GLM (Table 1). Of the six parameters analyzed, only two had a significant relationship with successful exclusion (Figures 2 and S1). Barrier height was strongly associated with exclusion (Likelihood ratio test, LRT: 21.5, $p<0.001$); no barrier greater than 1.2 m drop height allowed trout passage in our sample (Figure 2). A subset of barriers with a drop lower than 1.2 m also conferred exclusion, but there was no one variable associated with this exclusion (Figure 2a). Pool depth was negatively related to exclusion, likely because deeper pools at the foot of barriers made obstacles easier to breach (LRT $=6.8$, $p=0.009$; Figure 2b). No other analyzed parameter predicted successful exclusion (S1). Taken together, the results of both PERMANOVA and GLM of barrier characteristics suggest reliable exclusion is associated with drop height and pool depth, but any exclusion in addition to those parameters is likely nuanced and multifactorial.

Habitat characteristics in upstream and downstream fishing reaches were assessed in a similar way to barrier parameters, using PCA and PERMANOVA. No difference was found between habitat characteristics above and below all analyzed barriers (PERMANOVA: $F_{1,50}=0.15$, $p=0.721$), and likewise no difference was observed in available habitat above and below successful barriers (PERMANOVA: $F_{1,35}=0.038$, $p=0.85$), or unsuccessful barriers (PERMANOVA: $F_{1,12}=0.12$, $p=0.83$); (Figure 1b). Hence, there was no relationship between habitat and barrier success and no difference in habitat conditions above and below barriers. This means that habitat is unlikely to strongly affect fish species distribution in this comparison, adding weight to barriers being the key mechanism affecting fish community composition and abundance.

In addition to examining barrier success at excluding salmonids, we found that RRG populations above successful barriers had higher densities than those at any other position or barrier success combination (Figure 3a). Most sites surveyed supported either trout or RRG, with co-occurrence only happening in a handful of reaches and only involving three RRG species (*G. vulgaris*, *G. paucispondylus* and *G. macronasus*; Figure 3b, Jones 2014). Therefore, trout exclusion barriers supported more abundant native non-migratory fish populations than locations elsewhere.

4 | Results From a Global Literature of Trout Barriers

Our review of relevant global literature on obstacles to trout passage helped solidify these conclusions. The PRISMA approach returned 301 papers and with additional papers added, resulted in a total of 613 items for screening. Duplicates (25), no full text available (9) and text not available in English (10) papers were excluded, leaving 569 studies for topic-specific screening (Figure 4). A total of 370 items were filtered out because they did not refer to trout (226) or a barrier (144). Of the 199 items remaining, 54 (27%) contained quantitative barrier measurements equivalent to our New Zealand study and were included in the final review and meta-analysis (Figure 4). These studies covered a total of 101 barriers (considered replicates for our purposes).

Metadata from these included studies were used to categorize publication age, geographical origin, study type, and barrier types (Figure 5). Papers were published between 1991 and 2023, with an increase in studies from 2010 onwards. Geographically, studies came from North America (49%), Europe (33%), New

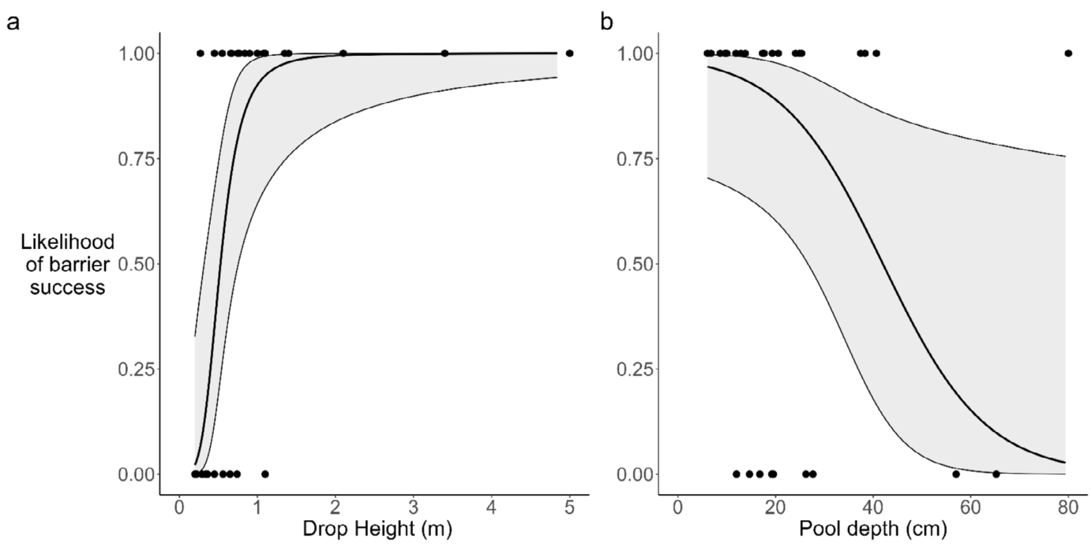


FIGURE 2 | Likelihoods of barrier success at preventing trout access in relation to drop height (a) and pool depth (b) for potential South Island trout barriers measured (points) with modeled fits (solid lines) and 95% confidence intervals (shaded areas) derived from generalized linear models. [Color figure can be viewed at wileyonlinelibrary.com]

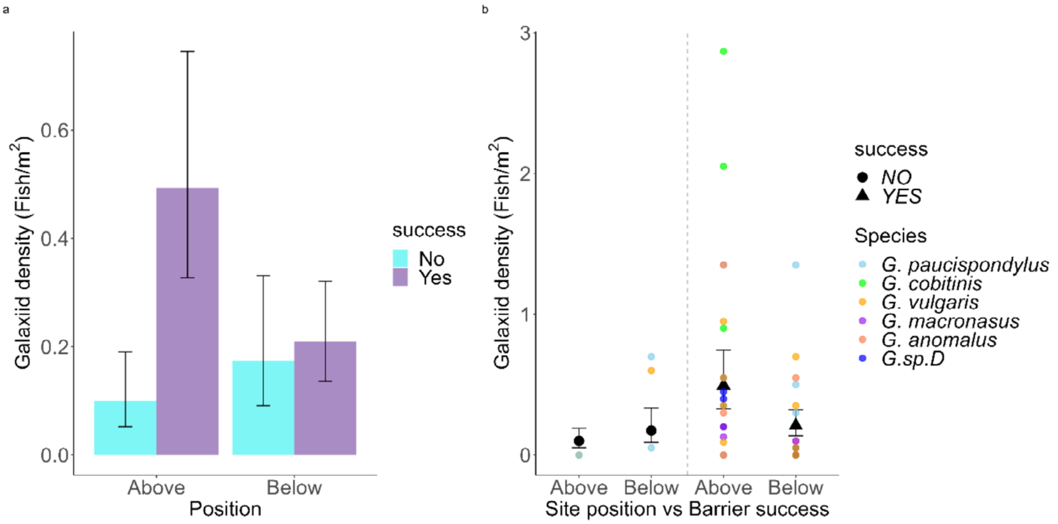


FIGURE 3 | Modeled means and 95% confidence intervals from GLMM models of non-migratory galaxiid densities above and below successful and non-successful South Island trout barriers (a), with the raw densities of different species (colored circles) (b). [Color figure can be viewed at wileyonlinelibrary.com]

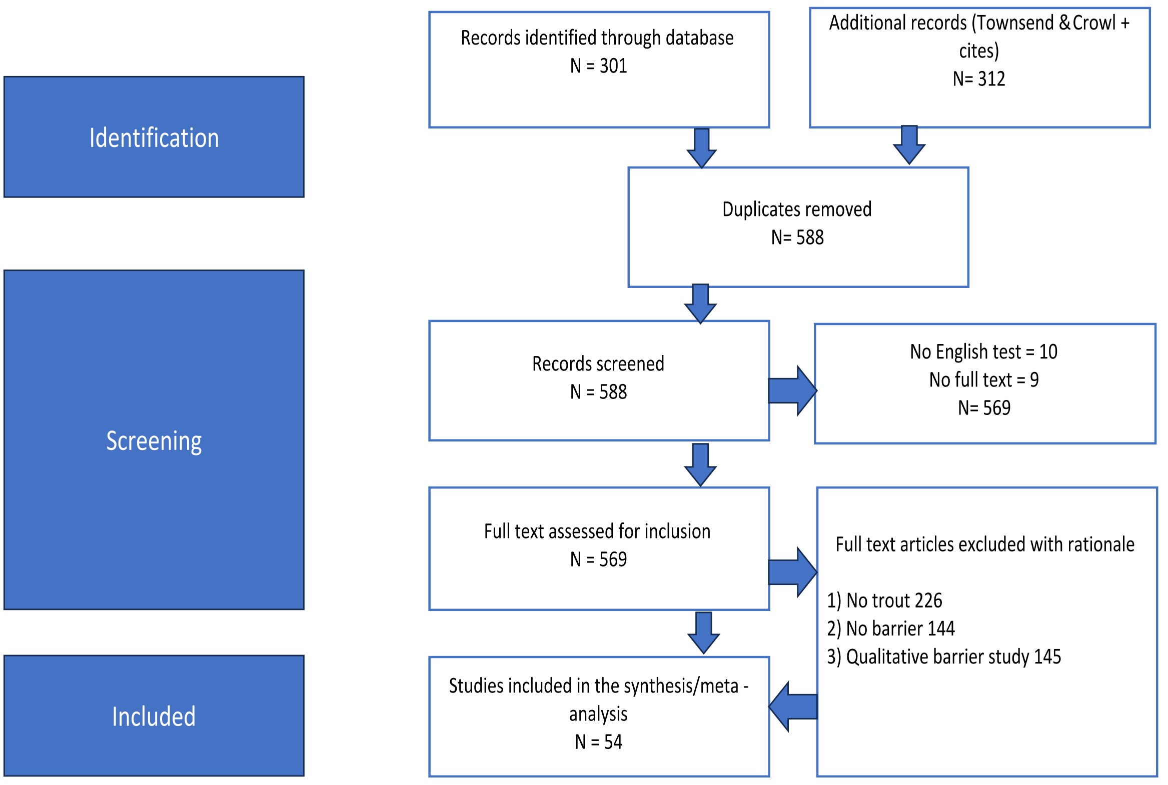


FIGURE 4 | Numbers of studies identified and screened at different stages from the global fish barrier literature by systematic review to include in the final synthesis and meta-analysis ($n = 54$) of parameters driving trout barrier success. Items were screened using the preferred reporting for systematic reviews and meta-analysis (PRISMA) framework. Studies were identified by using a search string in the Scopus database, added to additional items, and screened to remove those that did not report quantitative metrics of potential trout barriers. [Color figure can be viewed at wileyonlinelibrary.com]

Zealand (9%), South America (5%), Australia (3%) and Asia (1%). Barrier types were varied, but potential obstacles allowing passage were dominated by fish passes and culverts, whereas those conferring exclusion were more likely to be waterfalls or weirs (Figure 5), and field studies (81%) were more common than laboratory or modeling studies.

To evaluate study aims and outcomes, papers were scanned and categorized into either passage or exclusion studies. Study aims varied but were skewed toward improving passage over prioritizing exclusion. Most potential obstacles allowed trout passage (79) rather than exclusion (36). Most papers (56%) aimed to document improved fish passage (e.g., Aarestrup

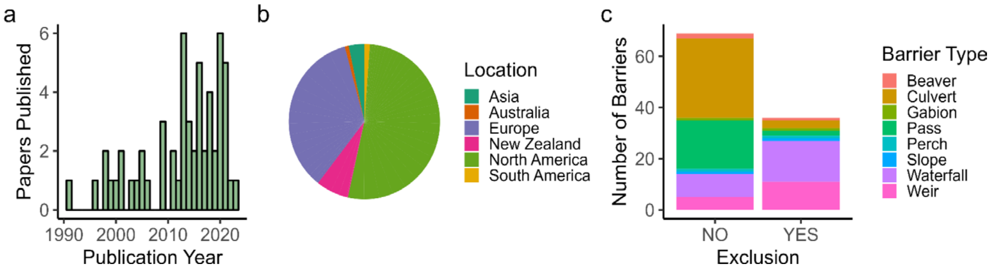


FIGURE 5 | Quantitative barrier publications identified by systematic review categorized by year (a), publication location (b) and barrier type by exclusion success (c). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 | Studies on deliberate fish exclusion using in-stream barriers reporting quantitative barrier metrics discovered by systematic review.

Authors	Title	Year	Publication
Holthe, E., Lund, E., Finstad, B., Thorstad, E.B. &McKinley, R.S.	A fish selective obstacle to prevent dispersion of an unwanted fish species based on leaping capabilities.	2005	Fisheries Management and Ecology
Larson, E.E., Meyer, K.A. & High, B.	Incidence of spinal injuries in migratory Yellowstone cutthroat trout captured at electric and waterfall- velocity weirs.	2014	Fisheries Management and Ecology
Lintermans, M.	Recolonisation by the mountain galaxias *Galaxias olidus* of a montane stream after the eradication of rainbow trout *Oncorynchus mykiss*.	2000	Marine and Freshwater Research
Lintermans, M. & Raadik, T.	Local eradication of trout from streams using Rotenone: the Australian experience.	2001	Managing Invasive Freshwater Fish in New Zealand
Tews, J.M., Adams, J.V., Mann, K.A., Koon, E.M. &Heinrich, J. W.	A review of an electric weir and fishway in a Great Lake tributary from conception to termination.	2021	Journal of Great Lakes Research
Thompson, P.D. & Rahel, F.J.	Evaluation of artificial barriers in small Rocky Mountain streams for preventing the upstream movement of brook trout.	1998	North American Journal of Fisheries Managment

et al. 2003; Ghimire and Jones 2014; Meixler et al. 2009), while a third investigated how in-stream obstacles affected distribution patterns, often by examining the genetic diversity of fragmented fish populations (e.g., Horreo et al. 2011; Kelson et al. 2020; Winans et al. 2018). Only six papers reported deliberate fish exclusion. Two papers reported non-salmonid exclusion while allowing for trout passage (Holthe et al. 2005; Tews et al. 2021). Two North American studies documented introduced trout species exclusion from native trout populations (Larson et al. 2014; Thompson and Rahel 1998; Table 3). The final two papers documented deliberate eradication of, and prevention of reinvasion by, *Oncorhynchus mykiss* (rainbow trout) and *Salmo trutta* (brown trout) into Australian streams where RRG species, *Galaxias olidus* and *G. fuscus*, had been found (Lintermans 2000; Lintermans and Raadik 2001). Both studies used the piscicide rotenone to eliminate trout before augmenting current barriers to prevent reinvasion. Overall, deliberate exclusion is much less reported in the literature than any other facet of fish passage management.

To test H1, that exclusion is conferred by a combination of physical characteristics and hydrology, we extracted the quantitative barrier data from these 54 studies, containing 105 parameter replicates. From these studies, we identified eight physical parameters that were recorded repeatedly: height, slope, length, wetted width, discharge, water velocity, pool depth, and pool length. This equated to 255 possible metric combinations of single or multiple parameters. The number of metrics recorded per study varied from one to five, with most studies recording three or fewer metrics. No study recorded all eight.

To analyze barrier parameters with a similar method to the field data from New Zealand, we picked parameters or combinations of parameters with 35 or more data points and used them in a generalized linear model with a binomial response variable (exclusion or non-exclusion). We found eight parameter combinations were reported 35 or over times (Table 4). The most reported barrier metric was height (72), followed by slope (58), wetted width (54) and barrier length (48). The results from this analysis concur with those of the New Zealand field study; barrier height was highly predictive of trout exclusion ($p = 0.0001$, McFadden's $R^2 = 0.26$) (Figure 6). No other parameter or combination of parameters had a significant relationship with exclusion, although the length of the barrier was weakly correlated with exclusion.

TABLE 4 | Eight GLM models of different barrier parameter combinations analyzed using data extracted from the global literature in a systematic review.

Model	Replicates	*p* value (> chi) GLM	AIC	McFadden's R^2
Height	72	< 0.001***	77.44	0.26
Slope	58	0.62	50.3	0.005
Wetted width	54	0.05	27.8	0.14
Length	48	0.056	28.9	0.13
Slope + length	49	0.46/0.025*	23.2	0.24
Slope + width	41	—	—	—
Length + width	38	—	—	—
Incline + length + width	38	—	—	—

Note: The final three models were not completed due to all barriers in these data sets allowing trout passage.

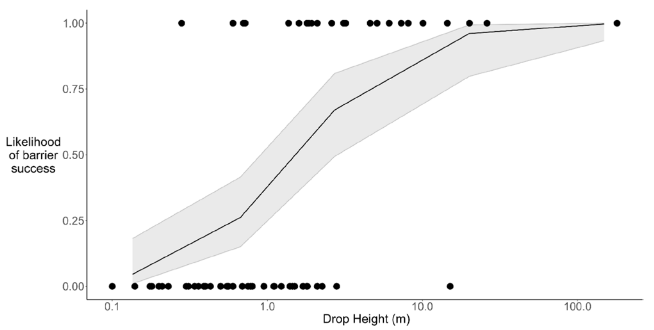


FIGURE 6 | Modeled likelihood of barrier exclusion success (line and gray 95% confidence interval) in relation to drop height from the meta-analysis of papers included in the systematic review of barrier height and barrier effect with points indicating individual barriers used as replicates in the analysis. Note height is $\log_{10}$ scaled to account for the large spread of barrier heights. [Color figure can be viewed at wileyonlinelibrary.com]

Hence, beyond height, exclusion is complex and likely relies on more than physical parameters alone.

5 | Discussion

As imperiled freshwater fish populations continue to decline in the face of invasions, tools preventing further losses and mitigating ongoing incursions are needed (Reid et al. 2019; Strayer 2010; Williams-Subiza and Epele 2021). In-stream barriers preventing incursion into headwater fish populations have been used primarily in Australia and New Zealand to protect threatened RRG species, and in North America to secure native trout populations from invasion by introduced salmonids such as brown trout (Budy et al. 2021; Lintermans 2000; Novinger and Rahel 2003). However, there remains a lack of evidence and confirmation regarding what factors drive successful exclusion by such structures. We hypothesized barrier parameters, or combinations of parameters, would exclude trout from headwater streams that form current RRG refuges (H1) (Franklin et al. 2024). Across all barrier types, drop height had the strongest relationship with successful exclusion; this was reflected in both field survey and meta-analysis results, and is most often highlighted in management advice (Holthe et al. 2005; Meixler et al. 2009). Beyond drop height, hydrological conditions associated with plunge pool depths appear to predict some exclusion, at least in the field survey data, although this was not reflected in the meta-analysis. Below, we examine what these results mean for securing vulnerable headwater populations from unwanted species, likely to be an essential tool in safeguarding vulnerable species survival and longevity, at least in the short to medium term.

Drop-height best explained exclusion in both the field survey and the global meta-analysis. We found that all barriers greater than 1.2 m high protected upstream reaches from trout incursion across a range of catchments, and with varying types and hydrology in the field survey. Interestingly, of the 72 barrier height data points analyzed in the meta-analysis, 50 potential obstacles allowed passage, while 22 did not. All obstacles that allowed trout passage were less than 2.2 m in drop height apart from one outlier, a 15 m waterfall with documented *Oncorhynchus mykiss* passage during spawning migration (Twardek et al. 2019). The study does not describe the waterfall topography; however, it is probably safe to assume a combination of gradients and multiple pools to allow resting space for burst swimmers throughout the cascade. The smallest barrier that conferred exclusion was 0.18 m in a laboratory study of juvenile brown trout (Binder and Don Stevens 2004). It has been well documented that the jumping ability of trout depends on fish length and water temperature (Bowersox et al. 2016; Kondratieff and Myrick 1900). New Zealand streams are cold, and trout found in headwaters are usually small (less than 150 mm); therefore, an exclusion cut-off of over 1.2 m will be a conservative estimate for other systems. However, these results do increase collective knowledge and are particularly useful for practitioners planning exclusion barrier implementation.

Considering the barriers that prevent passage at heights lower than this conservative cut-off is also useful. A small subset of barriers less than 1.2 m drop height ($n = 8$) in the New Zealand survey also conferred protection from trout incursion. There are several factors that may aid exclusion when optimum drop height is not present, and which potentially explain the usefulness of these barriers. The barriers deliberately engineered to exclude trout from low gradient spring systems, many supporting critically endangered RRG species like *Galaxias cobitinis*, are necessarily lower than this optimum because of a lack of hydraulic head height. These low-head situations meant that larger barriers may have caused excessive back pooling, sediment capture, or upstream habitat loss in protecting reaches that were already short. In these cases, further exclusion criteria were frequently added, such as downstream shallow splashpads (aprons) to prevent pool formation that prevent trout from being able to jump, and anti-jump screens and overhanging or perched culvert pipes to exclude jumping fish. The natural features in this low head subset of barriers had very low flow and in some cases were supported by an ephemeral reach with no flow preventing incursion. Hence, exclusion may still be possible in situations where drop heights greater than 1.2 m cannot be attained and involve the addition of artificial exclusion mechanisms. In natural systems, such low-head barriers protecting vulnerable RRG populations must be viewed as susceptible to breach and may benefit from augmentation or more intensive monitoring, particularly where rapid changes in flow are possible. Thus, predictable exclusion where optimum barrier height is not possible may still be achieved by combining barrier features with an understanding of system hydrology, such as reducing downstream pool depth. Exclusion "success" however, cannot be thought of as a permanent state and requires regular monitoring, preferably by combining fishing surveys with environmental DNA.

In the barrier field survey, a negative relationship between the pool depth at the barrier foot and successful exclusion was also demonstrated, meaning that pool depth increased the probability of barrier failure. This relationship was not assessed in the meta-analysis because only 10 replicates of pool depth were reported, highlighting how inconsistent parameter reporting was across published papers. The effect of pool depth has been well documented in both laboratory and field studies of trout ascending drop barriers such as waterfalls. Salmonids are burst swimmers, requiring a "run up" from the pool to propel themselves out of the water and over the barrier crest (Brandt et al. 2005; Stuart 1963). It is therefore reasonable to suggest that smaller barriers may be secured by manipulating the pool depth, for example, by placing a smooth, concrete splashpad, known as an apron, downstream of the barrier. This dramatically reduces pool depth immediately and prevents scouring that might re-form a pool in natural barriers. Therefore, susceptible barriers could be altered by managers to maintain non-desirable fish exclusion by minimizing downstream pool depth.

Both the field data and meta-analysis identified physical drops as the main exclusion mechanism. However, other structures also prevent fish passage (Burford et al. 2009; Goerig et al. 2017; Olsen and Tullis 2013). Barrier mechanisms identified in the review were typically velocity barriers rather than drops. Velocity barriers comprise a high velocity section of water that requires sustained swimming in a constant velocity range to ascend the barrier (Goerig et al. 2016; Rogers et al. 2021; Shahabi et al. 2021). As with burst swimming used to tackle drop barriers, sustained swimming ability is dependent on variables such as fish size and identity (Castro-Santos et al. 2013; Goerig et al. 2017). Hence, obstacles such as road culverts typically comprise two exclusion mechanisms, the downstream drop and the culvert chute velocity. We found one natural velocity barrier in New Zealand that appeared to have prevented trout incursion over time, comprising high-water velocities and shallow depths (a clay-based chute in a first order stream). A remnant population of *Galaxias vulgaris* survives upstream of this reach, but the barrier was excluded from the analysis due to being the only obstacle with this mechanism. Two barriers consisting of ephemeral drying reaches were also excluded by the same reasoning. Thus, naturally occurring trout barriers may vary in form and effectiveness, and their mechanisms remain poorly understood such that longevity and reliability are difficult to predict (Jolly et al. 2024; Twardek et al. 2019). Some of these characteristics are reflected in the global literature, such as fish-pass metrics analogous to water velocities and depths in such chutes (Seidl and Schneider 2023; Shahabi et al. 2021). This means that documented, vulnerable fish populations are protected by multiple exclusion mechanisms, the future of which is at risk of change. Current knowledge on such outcomes is not necessarily reflected in the literature.

The above evaluations suggest that barrier infrastructure can reliably improve exclusion at normal stream flows; however, system hydrology can be prone to rapid changes such as floods or droughts. Stream flows affect the ability of barriers to prevent incursions (Belford and Gould 1989; Dodd et al. 2017; Goerig et al. 2016; Reiser et al. 2006). In large floods, even the best-designed barriers (i.e., adequate height and shallow pool) may become passable by non-desirable fish, via barrier over-topping or overland flow from nearby streams. Reliable exclusion is likely to be commonly compromised by extreme flows (Thomaz 2022). These circumstances make most IM projects, regardless of drop height, velocities, and pool depths, vulnerable to catastrophic hydrological changes. This vulnerability is a good example of why barrier and upstream reach monitoring are essential for securing populations, particularly after high-flow events. Such events tend to not be represented in field data collected at one time point, such as our New Zealand surveys. Thus, as much as understanding that height and pool depth are crucial to trout exclusion, holistic consideration of system hydrology, combined with appropriate barrier maintenance monitoring, will be required to create successful population refuges for vulnerable species.

We predicted that the global literature lacked explicit quantitative barrier metrics (H2). Through the systematic review process, this lack of reporting was highlighted by only 54 studies of 199 (27%) stating measured barrier parameters. Furthermore, only 6 of these quantitative studies documented deliberate exclusion, meaning that passage seems to be much better documented than exclusion, and quantitative parameters of all barrier types are underreported in the scientific literature. Catchment fragmentation is a known driver of biodiversity decline and loss of ecosystem services; hence, barrier removal is frequently prioritized (Franklin et al. 2022). Laboratory studies have been used to parameterize complex mathematical models used for the prioritization of barrier removals for ecological and economic gain (Barry et al. 2018; Bonetti et al. 2016; King et al. 2017). These models frequently estimate barrier "passability" as a percentage or proportion of organisms able to swim past the obstacle upstream. In the case of IM to protect vulnerable native species, one or two invasive organisms may have a catastrophic effect on the protected population, demonstrated by trout exclusion barrier breaches in New Zealand (Jolly et al. 2024). We can learn from fish passage literature and tools, but it is not as simple as "back-engineering" solutions because our analysis suggests whole system and holistic approaches are required. A careful approach to barrier removals or repair in catchments with valued native fish populations is essential and requires multi-agency awareness and compliance. One aspect of the understanding of barrier removal, augmentation, or deliberate placement for ecological gain appears to be a lack of consistent terminology or outcome measures not only globally but within countries and even organizations. A cohesive approach to interventions such as isolation management will be essential in securing vulnerable fish populations and reversing species decline and loss in future.

The term isolation management, used to describe a niche application of in-stream barriers, is not limited to exclusion alone, but considers the protection of a valued species above such barriers (Avenetti et al. 2006; Budy et al. 2021; Novinger and Rahel 2003). In the field, we found native fish densities were higher above successful barriers, thus validating IM as a conservation tool (H3). This was true across catchments, RRG species, and native fish conservation status. Additionally, these protected populations were identified through historical fish survey records and previous research datasets, some being documented several decades ago, thus lending understanding to population persistence in such refuges (Woodford 2009; Stoffels 2022; Townsend and Crowl 1991). Despite an increase in the reporting of in-stream barriers used to prevent aquatic invasions and protect upstream species, success has not been explicitly documented in many cases. In a recent review, most exclusion barriers placed for the mitigation of aquatic invasions were monitored for short periods of time (87% less than 5 years), and only 25% took into consideration barrier effects on native species (Jones et al. 2021). It is therefore crucial that robust reporting of both success and failures of these interventions becomes standard practice in the future to inform practitioners and managers considering implementing such barriers for native fish protection. Such reporting could be used to build a "best-practice" framework covering consistent terminology, science-based implementation, and evidence to inform feasibility, projected success, and resources required, including follow-up monitoring, essential to any IM project. Such a framework would require support by statutory protection for indigenous freshwater fish both in New Zealand and globally.

Finally, our study highlights knowledge limitations and key gaps for future consideration. Despite there being a wealth of laboratory data spanning over six decades, prediction of exclusion barrier success in the field is lacking, as are frameworks that aid decision making through planning, implementation and post-intervention monitoring (Figure 7), although a solid base of government agency work exists within New Zealand (Charters 2013; Franklin et al. 2024). According to the New Zealand Fish Passage Assessment Tool (FPAT), an open-source application allowing recording in-stream structures (NIWA 2024), there are over 150,000 recognized in-stream structures in New Zealand possibly preventing fish passage. Of these around 11,000 (7%) should be considered being maintained to protect valued native species. The New Zealand dataset is useful by specifically examining the exclusion of introduced salmonids from vulnerable RRG populations as a field study, with a control cohort of barriers that do not exclude trout. Our study also provides the first documented data from New Zealand that these interventions can be successful over time, although longevity of populations in the future cannot be predicted by these data. It is likely that barriers secure populations in the short to medium-term but reversing population declines will need holistic intervention and whole ecosystem thinking (Britton et al. 2023; Harper et al. 2021). Broader implementation might include intense proliferation of protected reaches such as multiple barriers in multiple reaches protecting many fragmented populations. Other mechanisms such as reclaiming habitat downstream to potentially link such reserves, fish rescues, translocations and captive breeding are likely to be increasingly necessary if RRG vulnerability is to be adequately addressed (Buckley et al. 2023; Lintermans 2013; Pavlova et al. 2017). Thought must also be given to non-desirable

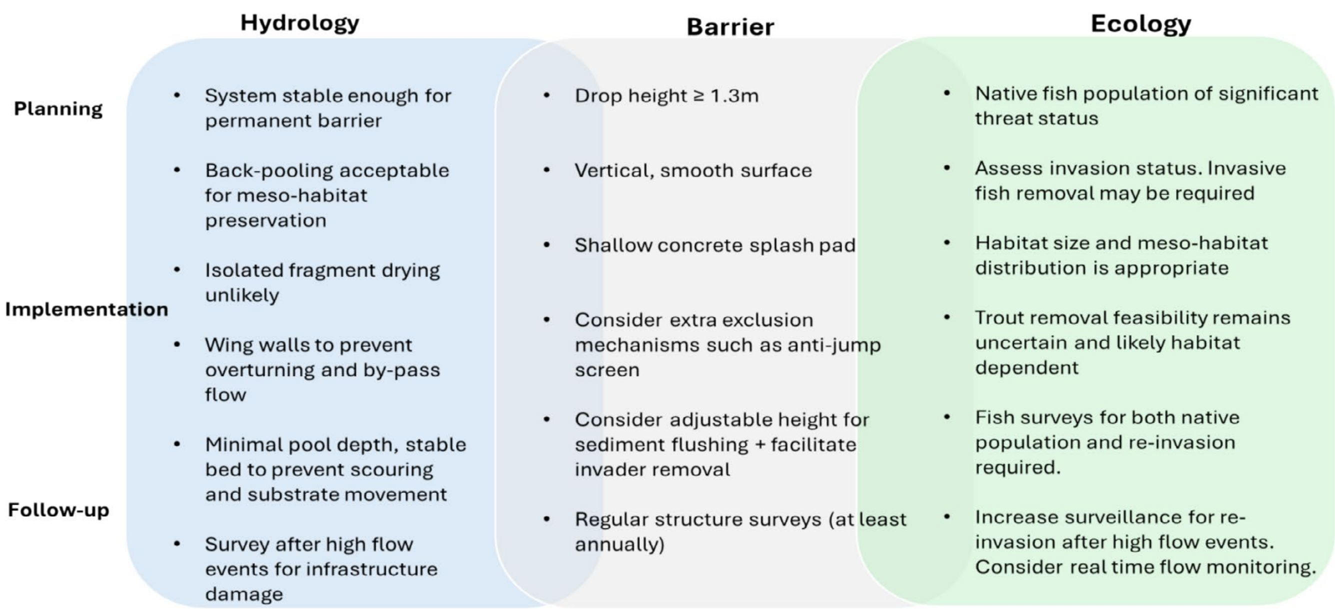


FIGURE 7 | Components of successful exclusion barriers used in preventing trout incursions into RRG populations. Lack of explicit barrier details in the global literature is one impediment to successful IM projects. If criteria cannot be met, then consideration of other options such as population translocations with or without captive breeding is necessary. Statutory protection of both fish and habitats will also be required. (Figure summarizes barrier implementation from multiple sources including Franklin et al. 2024). [Color figure can be viewed at wileyonlinelibrary.com]

fish removal as part of invasion mitigation. Both mechanical and chemical fish removal is frequently required to provide safe habitat for native fish species and feasibility of total invader removal is still poorly understood (Rytwinski et al. 2019; Tiberti et al. 2021). As acknowledged in many restoration efforts, success can only be documented by allocating resources to post intervention monitoring and rapid responses to population threats such as reinvasion or droughts. Deliberate fragmentation should therefore be thought of as a dynamic, ongoing process, requiring adaptive management rather than a "set and forget" intervention, reaching beyond barrier placement and physical parameters and encompassing who ecosystem thinking.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data is now open source on Figshare https://doi.org/10.6084/m9.figshare.28836986.

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Supporting Information

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