Spawning and dispersal of *Salmo trutta* in a West Coast River, with specific reference to a proposed hydroelectric scheme

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Abstract

Understanding the spatial ecology of introduced brown trout (*Salmo trutta*) populations is essential for managing New Zealand's freshwater fisheries and for assessing the potential impacts of hydrological modification. This study applied otolith microchemistry to investigate the natal origins and dispersal patterns of S. trutta within the Ototutu (Rough) River catchment on the West Coast of New Zealand. Brown trout otoliths were analysed using quadrupole laser-ablation inductively coupled plasma mass spectrometry (Q-LA-ICP-MS) to measure seven element:Ca ratios (Mg, Al, P, Mn, Rb, Sr, Ba). A Linear Discriminant Analysis model was developed from juvenile reference samples to identify natal signatures and assign adult and juvenile individuals to their likely spawning tributaries.

All seven element:Ca ratios differed significantly among sampling sites ($p < 0.005$), confirming strong spatial variation in water chemistry. No variation was detected between the two Mawheranui River sites, so they were combined. The classification model achieved a reassignment accuracy of >90%, indicating that otolith elemental composition reliably distinguishes among tributaries. The majority of individuals were predicted to have originated from Mirfin Creek or the Mawheranui River, identifying these as key spawning and recruitment sources for the population. The Lower Ototutu River, previously assumed to represent a major spawning site, instead appeared to function primarily as a rearing or dispersal corridor. Sr:Ca profiles showed no evidence of marine migration, demonstrating that all sampled fish were potamodromous or resident. Juvenile dispersal was substantial, with approximately 58% of age-0 individuals moving away from their natal tributaries, emphasising the importance of maintaining connectivity across the catchment.

The findings have direct implications for the proposed hydroelectric development at the confluence of Mirfin Creek and the Ototutu River. Hydrological alteration, dewatering, and potential barriers to movement could threaten the ecological integrity of critical spawning and dispersal habitats. Consistent with section 7(h) of the Resource Management Act 1991, safeguarding the habitat of trout must be prioritised in any development decisions.

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1. Introduction

1.1. Life History Theory & Phenotypic Plasticity

Life history theory is a framework that explains how an organism should manage trade-offs and allocate time and energy to maximise its fitness (Kaplan & Gangestad 2015). It is the combination of life history traits that underpins a multitude of essential processes. These key life history traits are defined by Sterns (1992) as those with a direct influence on reproduction and survival. These include size at birth, growth pattern, age at maturity, size at maturity, number of offspring (Sterns 1992).

Phenotypic plasticity refers to a single genotype's capability to express more than one alternative morphological, physiological, or behavioural state in response to varying environmental conditions (West-Eberhard 1989). It allows for the adjustment of life-history traits. This ability is fundamental to the persistence of many taxa across heterogeneous environments, allowing organisms to optimise their fitness through trade-offs between life history traits. Phenotypic plasticity has been widely documented across the animal kingdom. For example, wing polymorphism in insects involves an evolutionary trade-off between reproduction and size at maturity, with individuals allocating resources towards either somatic growth or ovarian development (Zera & Denno 1997; Zera & Harshman 2001). Similarly, the lizard *Sceloporus jarrovi* also displays life history plasticity, trading off current and future reproductive prospects (Moore 1986). Bighead carp (*Hypophthalmichthys nobilis*) exhibit phenotypic plasticity in their spawning traits to accommodate invasion (Coulter et al. 2013), whilst brown trout (*Salmo trutta*) exhibit variations in migration strategy dependent on their habitat (Caballero et al. 2013). The plasticity observed in brown trout migration strategy is due to the combination of phenotypic traits and environmental cues (Thorpe & Metcalfe 1998; Källo et al. 2023).

1.2. Brown trout

Brown trout (*Salmo trutta* Linnaeus 1758) is a teleost fish belonging to the family *Salmonidae* (Linneaus 1758; Sanz 2017). This species is native to Europe, western Asia, and parts of North Africa (Elliott 1989), but has since been introduced to every continent except Antarctica

(Bagliniere 1999; McIntosh et al. 2010). Its widespread range has been driven largely by its popularity as a sport fish, and its perceived ecological resilience (Bagliniere 1999; Kos 2018).

In New Zealand, brown trout were first introduced in the mid-19th century by European settlers through acclimation societies who sought to recreate elements of the British lifestyle (Kos 2018). The first successful introduction occurred in Canterbury in 1867, followed by Otago in 1868, where live ova transported on ice were released (Kos 2018). Subsequent stockings and natural dispersal have enabled brown trout to spread across New Zealand, with densities increasing southwards (Jones & Closs 2017). Their success as invaders has been attributed to their highly plastic life histories and the lack of native predators in their invaded habitats, which have allowed them to invade far beyond their native range (Budy et al. 2013; Jones & Closs 2017).

Brown trout exhibit flexible habitat preferences, typically favouring cool, well-oxygenated waters with coarse substrates suitable for spawning (Budy et al. 2013). Spawning generally occurs during the autumn and winter months, with eggs deposited in gravel redds at an average depth of 31cm (Shirvell & Dungey 1983; Armstrong et al. 2003; Klemetson et al. 2003). These early life stages are strongly influenced by local environmental conditions such as temperature, substrate composition, and dissolved oxygen, which affect growth rates and survival (Shirvell & Dungey 1983; Armstrong et al. 2003).

A defining feature of brown trout is its exceptionally plastic life history, allowing individuals within the same population to adopt markedly different migratory strategies (Ferguson et al. 2019). Within the species, anadromous, potadromous, and resident forms coexist. Anadromous individuals migrate from freshwater to the sea and return to spawn (McDowall 1992), potadromous individuals migrate entirely within freshwater systems (Sammons 2015), and resident trout remain within a restricted section of river throughout their lives (Fry & Chumchal 2011). These alternative strategies are thought to arise from both genetic predispositions and environmental conditions, highlighting the importance of phenotypic plasticity in facilitating adaptive responses to heterogeneous habitats.

Migration is often an adaptive response to differences in resource availability between habitats. Both potadromy and anadromy are advantageous when natal rivers are less productive than downstream feeding areas (Ayer et al. 2018; Ferguson et al. 2019). Potadromous brown trout, for example, can attain significantly larger body sizes at maturity than resident conspecifics, particularly when they transition to piscivory (Campbell 1979; Wollebaek et al. 2018). However, this strategy carries trade-offs. While lentic systems often promote piscivory due to their slower flow and larger prey fish, they may support lower overall prey abundance than lotic systems (Hughes et al. 2016; Sánchez-Hernández 2020). Thus, brown trout populations demonstrate striking variation in growth rates, diet, and movement strategy depending on the productivity and structure of their habitats.

1.3. Otolith Microchemistry

Fish otoliths are paired aragonite structures found within the vestibular system of teleost fish (Pannella 1971; Payan et al. 2004; Thomas et al. 2020). Growth occurs incrementally through the deposition of discrete aragonite bands, where each band corresponds to a period of time in the fish's life (Morales-Nin 2000; Thomas et al. 2020). The aragonite is precipitated from endolymph fluid in which the otolith sits (Morales-Nin 2000). The crystalline aragonite structure allows for trace elements and various isotopes to become incorporated by substituting for calcium or attaching to the matrix (Campana & Thorrold 2001; Thomas et al. 2020).

Environmental factors such as water chemistry or catchment geology, and fish physiological processes, such as metabolism, influence the concentration at which these isotopes are incorporated into otolith growth (Campana & Thorrold 2001; Rodríguez Mendoza 2006). Once deposited, the trace elements act as markers of the water chemistry at that point in time. When the aragonite bands are deposited, they are not subject to reabsorption, and hence otoliths can provide accurate records of the individual fish's growth and environment (Campana & Thorrold 2001).

Otolith microchemistry has become a key tool in fisheries ecology for identifying natal origins, recruitment sources, and dispersal patterns of teleost fish (Thorrold et al. 1998; Vasconcelos et al. 2007; Avigliano et al. 2017; Mikheev et al. 2021). As well as their application in movement studies, otoliths have been successfully used in recruitment studies, to determine the natal sites of teleost fish, using a dataset of juvenile fish to infer natal origins and identify recruitment sources (Thorrold et al. 1998; Wells et al. 2003; Vasconcelos et al. 2007; Olley et al. 2011; Avigliano et al. 2017; Bouchoucha et al. 2018; Mikheev et al. 2021). Molar ratios of elements such as Sr:Ca, Ba:Ca, Mg:Ca are especially informative for distinguishing freshwater habitats and reconstructing fish movement histories as they often vary spatially due to catchment geology and water chemistry differences (Wells et al. 2003; Olley et al. 2011).

1.4. Recreational Fishing in New Zealand

New Zealand has a strong recreational fishing culture, driven, in part, by the widespread distribution and abundance of brown trout (McDowall 1990). The activity now forms a significant component of both social and economic sectors of New Zealand (McDowall 1990; Teirney & Richardson 1992).

On the West Coast of the South Island of New Zealand, licence uptake is growing. For the 2023/24 season, the West Coast Fish & Game Council reported selling and distributing 2,158 whole season equivalent licences (West Coast Fish & Game Council 2024). This is an increase of 7.4% relative to the previous season, and a 26.7% increase on the 2019/20 season (West Coast Fish & Game Council 2024). The licence revenue is reported to generate roughly $306,000 New Zealand dollars in the West Coast for the 2023/24 season (West Coast Fish & Game Council 2024).

At a national scale, New Zealand requires anglers to hold a licence to access recreational fishery stocks, and these licences are administered by Fish & Game (Wildlife Act 1953; Conservation Act 1987). In addition, there is a growing focus on creating “Designated Waters” fisheries in pressure-sensitive rivers due to high angler demand.

Beyond economic value, angling contributes to wellbeing through exposure to green and blue natural spaces (White et al. 2020; Yang et al. 2021), as solitude and scenic beauty are well sought-after attributes of angling rivers (Teirney & Richardson 1992). When contextualised with the Te Whare Tapa Whā model, recreational trout fishing has the ability to enhance all aspects of holistic wellbeing (Stewart et al. 2025).

1.5. Hydroelectric Schemes

Hydroelectric schemes are a key component of New Zealand's renewable energy portfolio, contributing significantly to national electricity generation (EECA 2023). Despite their renewable energy generation, hydroelectric schemes often disrupt the ecological integrity of riverine systems and impact nearby fisheries (Reid et al. 2005; Bilotta et al. 2016). The construction and operation of hydroelectric infrastructure can alter natural flow regimes, water temperature, and habitat connectivity, resulting in changes to community structure and function (Bunn & Arthington 2002; Fullerton et al. 2010).

A major ecological effect of hydroelectric schemes is the regulation of flow. In run-of-river systems, the continual switching on and off of turbines causes dewatering and reduces minimum flow (Zdankus et al. 2008). These fluctuations cause rapid dewatering of shallow habitats and a reduction in minimum flow, leading to higher mortality rates in alevin (Casas-Mullet et al. 2016) and semi-buoyant eggs and larvae (Zeng et al. 2019). Furthermore, this results in intensive river-bed scour, causing significant reductions in fish community composition and abundance (Zdankus et al. 2008).

Hydroelectric schemes can also restrict fish migration and dispersal. Zhong & Power (1996) discovered a number of negative impacts of hydroelectric schemes on riverine fish; blocking of anadromous and semi-anadromous fish migrations and decreased fish species diversity. Further negative effects include spawning period delays and advances (Zhang et al. 2021), decreased capture from fisheries (Yoshida et al. 2020), and an increased risk of injury and immediate mortality risk as a result of passage through the scheme's infrastructure (Algera et al. 2020). Downstream thermal regimes may also be altered, influencing metabolism and growth in temperature-sensitive species such as salmonids (Olden & Naiman 2010).

On the West Coast of New Zealand, several new hydroelectric proposals have been put forward to support the regional transition to renewable energy (EECA 2023). One of these is the proposed hydroelectric scheme on the Otututu River, identified in 2004 as a potential site for hydroelectric resources (East Harbour Management Services 2004). While these projects are broadly supported by stakeholder groups, the West Coast Fish & Game Council has expressed concern about the potential effects of the scheme on the brown trout fishery in the river and the anglers who use it.

1.6. Resource Management Act 1991

The purpose of New Zealand's Resource Management Act 1991 (RMA) is "to promote the sustainable management of natural and physical resources". Included within this is "the protection of the habitat of trout and salmon", as outlined in section 7(h). Trout and salmon are the only species mentioned by name in the RMA 1991, affording them a unique protection and reflecting their recreational importance (RMA 1991; McIntosh et al. 2009). Consequently, any proposed development that could affect trout habitat, such as a hydroelectric scheme, must demonstrate that adverse effects on salmonid habitat are appropriately remedied in accordance with the RMA. This legislative framework provides the context for assessing potential ecological impacts of the proposed Otututu River hydroelectric scheme on the local brown trout population.

1.7. Objectives & Hypotheses

This research aims to evaluate the role of the Otututu (Rough) River and its tributaries as spawning and migratory habitat for both juvenile and adult brown trout, in the context of a proposed hydroelectric development. It will use otolith microchemistry and trace element analysis to address the following aims:

1) Determine the extent to which juvenile and adult brown trout originate from, disperse through or reside in sites within the Rough River and Mawheranui River system.
2) Assess whether certain tributaries serve as key spawning sites.
3) Evaluate the impact of the proposed hydroelectric scheme on migration and spawning of brown trout in the lower reaches of the Otututu (Rough) River.

These aims are used to test the following hypothesis: that there are significant differences in the use of sites as spawning grounds. Anecdotal evidence from West Coast Fish & Game and local anglers indicates that Rough River serves as a spawning site and is important for fish passage (Kersten 2024, personal communication). Given this, it was predicted that sites further upstream would have a higher number of individuals originating from them and that there would be high rates of dispersal between sites. Furthermore, as hydroelectric schemes have evidenced negative impacts on spawning and passage, there will be negative impacts to the *S. trutta* population.

2. Study Site

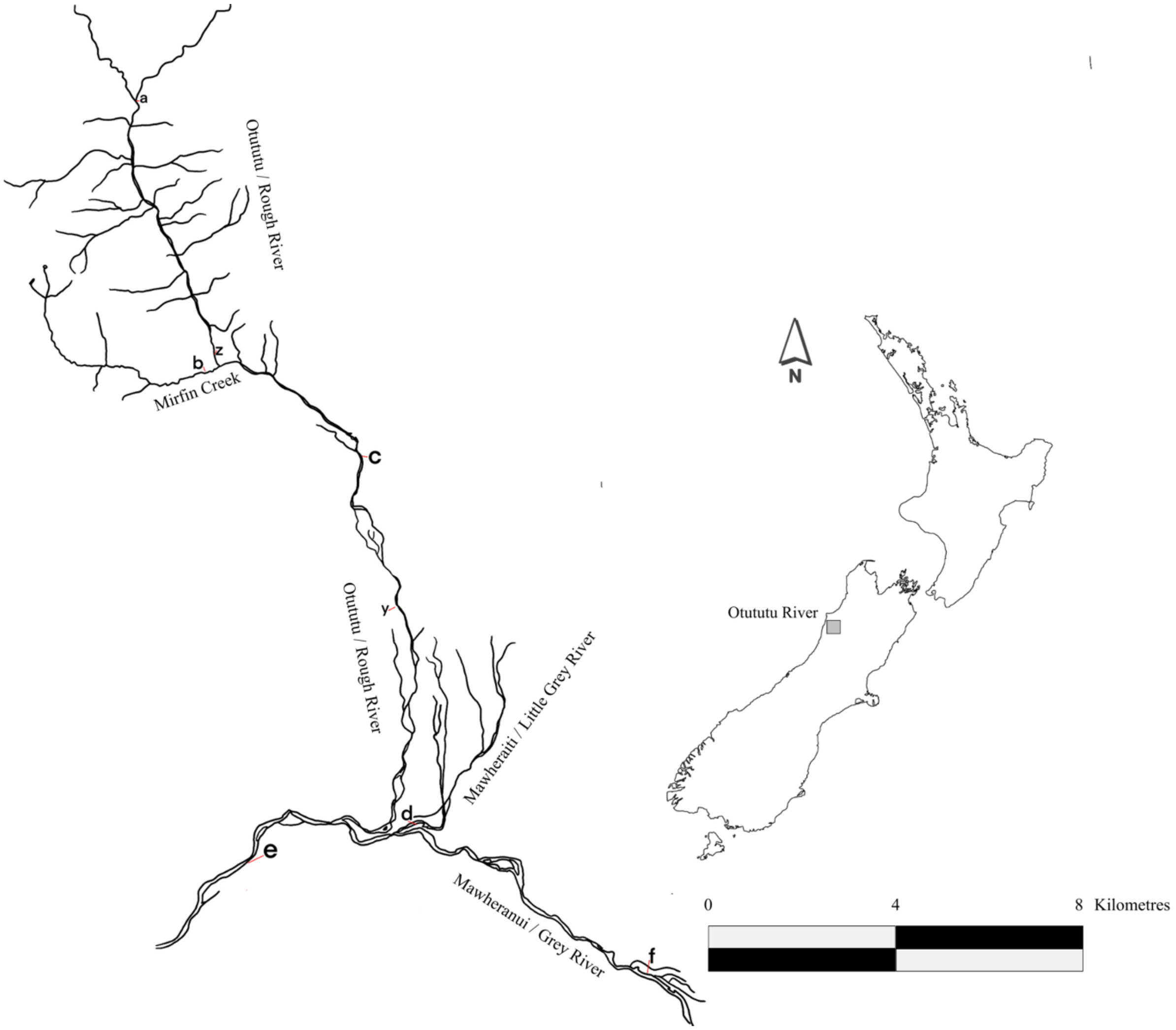

Figure 2.1. Map depicting the sampling locations throughout the Otututu River. Letters denote sampling locations and infrasctructure sites for the proposed hydroelectric scheme. a is Upper Otututu River. b is Mirfin Creek. c is Lower Otututu River. d is Mawheraiti River. e is Mawheranui River. f is Lower Mawheranui River. z is the site of the proposed intake gallery for the Otututu River hydroelectric scheme. y is the estimated site where abstracted water would be returned to.

The study was conducted in Otututu (Rough) River, and its tributaries and distributaries, located in the Grey District on the West Coast of New Zealand's South Island. The Otututu River is headwatered on the slopes of Mount Uriah, in the Paparoa Range and flows south-east through predominantly native forest, before joining the Mawheranui River near the township of

Ikamatua. Major tributaries include Morrison Creek, Mills Creek, Gordon Creek, and Mirfin Creek, all of which are headwatered in the Paparoa Range.

Otututu River has a rock, gravel and boulder bed, with sections of cobble and coarse sand. Most reaches are shaded by native riparian vegetation, contributing to cool, well-oxygenated water that provides suitable habitat for brown trout (Sievers et al. 2017). The Otututu River is recognised locally as a high-value recreational fishery, supporting populations of large, trophy-sized brown trout (West Coast Fish & Game Council, unpublished data).

The river is classified as a fourth-order stream, with Mirfin Creek representing a second-order stream (Strahler 1957). The catchment experiences a temperate, high-rainfall climate typical of the West Coast. According to the Earth Sciences New Zealand DataHub (Reefton climate station), mean annual precipitation between 1961 and 2024 was 1926mm, distributed over an average of 187.3 days per year. The mean annual air temperature for the same period was 11.5°C.

The catchment is underlain predominantly by Haast Schist, with inputs of granite-derived garnet, containing elevated MgO concentrations (Mason 1981). The geology contributes to the region's distinct water chemistry and may influence trace element signatures in fish otoliths.

A proposal for a hydroelectric scheme has been underway since mid-2022. This would be situated in the Otututu (Rough) River in the Grey Valley and generate 11.1MW of electricity. The scheme would involve an intake gallery above the confluence of Mirfin Creek and Otututu River, 8km of conveyance pipe and infrastructure to return the abstracted water to the Otututu River 8km downstream from the intake gallery. This activity poses a serious concern to the West Coast Fish & Game Council, as the Otututu River is an important fishery and home to trophy-sized brown trout.

Six sites were sampled in the Otututu River and Mawheranui River. These streams were chosen based on their significance to the Otututu River fishery and their perceived significance in spawning. To date, the Otututu River is relatively unstudied, with only West Coast Fish & Game Council reports available, and no published literature.

3. Methods

3.1. Sample Collection & Storage

Juvenile and adult *S. trutta* were obtained from West Coast Fish & Game. Juveniles were provided as whole preserved specimens, while adults were supplied as extracted left and right sagittal otoliths. 6 adults were caught from the Upper Otututu River, 31 juveniles caught from Mirfin Creek, 20 juveniles and 6 adults from the Lower Otututu River, 19 juveniles from the Mawheraiti River, 11 juveniles from the Mawheranui River and 19 juveniles from the Lower Grey River.

Juveniles were stored at -20°C before processing in the laboratory. In the laboratory, fish were thawed and total length (mm; snout to caudal fin) was measured and recorded. Individuals were stored in 50mL Falcon^{TM} tubes containing 100% ethanol. Sagittal otoliths were extracted from juvenile trout under a dissecting microscope (Olympus SZ61) and stored in Milli-Q® ultrapure water (18mΩ/cm) in 1.5mL Eppendorf^{TM} tubes.

3.2. Cleaning and preparation of juvenile otoliths

Juvenile otoliths were ultrasonically cleaned in Milli-Q® water for 5 minutes to remove any residual biological material (Olley et al. 2011). Following cleaning, the water was removed with a pipette, and otoliths were left to air-dry in their respective tubes under sterile laboratory conditions.

Previous studies have shown no significant difference in isotopic composition between the left and right sagittal otoliths (Campana et al. 1994); therefore, only one otolith from each individual was selected for analysis.

3.3. Preparation of adult otoliths

Each adult otolith was adhered to the centre of a glass microscope slide with a thin layer of Crystalbond^{TM} thermal adhesive, with the sulcal groove facing up. These otoliths were ground using a combination of wet/dry sandpaper of descending grit (P1500, P2000 and P2500 grit) and lapping film (40, 30 and 3µm, 3 M). The otoliths were sanded until the sulcal groove was removed, then flipped over and the distal face sanded until its core could be seen. The core was visually identified using a dissecting microscope (Olympus SZ61)

3.4. Mounting for analysis

Two slides were prepared for subsequent analysis.

Slide A

The central 48 x 24mm of a glass microscope slide was demarcated, and transparent, double-sided tape (Pomona) was applied. Juvenile otoliths were mounted on the tape with the proximal surface facing down. Otoliths were arranged in vertical columns in ascending order of fish total length (mm). Polished adult otoliths from the Upper Otututu River were also affixed to this slide using double-sided tape.

Slide B

The central 48 x 24mm of a second glass microscope slide was demarcated. Adult otoliths from the Lower Otututu River were adhered to a second glass microscope slide using Crystalbond^{TM} thermal adhesive.

3.5. Laser Ablation Inductively Coupled Plasma Mass Spectrometry

To establish the elemental signatures of sites and adult natal sites, trace element analysis was performed using Quadrupole laser ablation inductively coupled plasma mass spectrometry (Q-LA-ICP-MS; Agilent 7500 cs/ce Quadrupole ICP-MS coupled to a Resonetics RESOlution M-50-LR excimer (193nm) laser ablation system) at the Centre for Trace Element Analysis, University of Otago. Seven isotopes of seven elements were measured: ^{24}Mg, ^{27}Al, ^{31}P, ^{55}Mn, ^{85}Rb, ^{88}Sr, ^{138}Ba. These elements were selected because they have previously been demonstrated to vary systematically with water chemistry and are effective discriminators of habitat or natal origin in freshwater fish otoliths (Wells et al. 2003; Brazner et al. 2004; Friedrich & Halden 2008; Olley et al. 2011; Mikheev et al. 2020; Akland et al. 2025).

For each juvenile otolith, a vertical transect was ablated for 45 seconds, with the laser beam focused over the primordium on the distal surface. For each adult otolith, a horizontal transect was ablated across the distal surface, extending from the primordium to the edge. Each sample was ablated with a laser firing rate of 10Hz, an on-sample fluence of 2.5J/cm^2, and a beam diameter of 75µm. The sample stage translated at a rate of 10µm/s to ensure a continuous ablation path across the otolith. Helium was used as the carrier gas to transport ablated material from the sample chamber into the ICP-MS where element concentrations were calculated (Eggins et al. 1998; Olley et al. 2011).

Otoliths were analysed in batches of 12. The international glass reference materials NIST610 and NIST612, and MACS-3 pellets (Jochum et al. 2019) were ablated at the beginning and end of each sequence, as well as between each batch to correct for potential instrumental drift. Background samples were collected for 20 seconds with the laser shutter closed before each standard or otolith was ablated.

Longerich et al. (1996) set out Q-LA-ICP-MS protocols for data reduction, which were followed in this study. NIST610 was used as the reference material and external calibration standard, and ^{43}Ca as the internal standard to account for variation in ablation yield (Eggins et al. 1998). Mean background counts were subtracted from all element intensities before conversion to element:Ca molar ratios. Calcium was used as the internal normalising element because it constitutes the majority of the aragonite matrix in otoliths and provides a stable reference for the trace element concentrations. Raw data was processed using IOLITE Version 4.0 (Paton et al. 2011). Subsequent data processing took place in Microsoft Excel (2025), and the resulting element:Ca ratios were plotted against ablation distance (µm) to visualise spatial variation across otolith transects.

For edge measurements from juvenile otoliths, the first 5µm of the vertical ablation path was treated as a pre-ablation segment and excluded from analysis to eliminate any potential surface contamination from handling or storage. Mean element:Ca ratios were calculated from the subsequent 5µm of each transect. This portion of the otolith corresponds to the most recently deposited material prior to fish capture, thereby representing the elemental composition of the environment in which the fish resided immediately before sampling (Olley et al. 2011).

For adult and juvenile otoliths, the primordium was identified along the horizontal transect using two indicators: symmetry in element:Ca ratios across the otolith core, and the presence of a distinct Mn:Ca spike characteristic of the early larval growth zone (Macdonald et al. 2008). Element:Ca ratios were averaged from two 50µm regions, located 200µm on either side of the primordium. These regions, referred to collectively as the natal region, correspond to otolith material deposited soon after fry emergence and early rearing in the natal tributary (Olley et al. 2011).

30 juvenile individuals were unable to be used in the dataset, as their primordium's could not be identified. A total of 82 individuals were used; 12 adults and 70 juveniles.

3.6. Data Analysis

Data analysis was carried out in R Studio (R Core Team 2025).

One-way ANOVAs were run to assess differences between element:Ca ratios from the juvenile otoliths, and the sampling site. Tukey's HSD test was used for post-hoc testing for these ANOVAs to identify statistically significant differences between specific pairs of sites for each element:Ca ratio. Omega-squared was also calculated to determine the biological significance of the result.

Literature suggests that there are interactive effects between the incorporation of different elements and their concentrations into otoliths, specifically Sr and Ba (Tian et al. 2019). Therefore, to determine differences in elemental fingerprints between sites, a MANOVA was run. Subsequent pair-wise testing was undertaken to determine the relationships between the combined element:Ca ratios and site. There were no significant differences found between single element:Ca ratios between the two sites in the Mawheranui River (Mawheranui River and Lower Grey River), nor between elemental fingerprints and sites for the same sites. As both sites were both part of the Mawheranui River and could not be differentiated, they were combined into one site called the Mawheranui River. One-way ANOVAs and the MANOVA were re-run with this data set.

To assign natal sites to individuals, linear discriminant analysis (LDA) was used. This allowed for group separation to be visualised and identify the element:Ca ratios that best differentiated between sites. Element:Ca ratios with both statistically significant differences between sites, and biological significance were included in the LDA. Thirteen juveniles from each site were randomly selected to be used in this model. The LDA models underwent jack-knife cross-validation, to prevent overconfidence in classifying data points. The cross-validated LDA model was run separately for the Mawheranui River sites and then combined; the only difference between the two models was the proportion of individuals incorrectly classified between the two Mawheranui River sites.

The element:Ca ratios from both the adult and juvenile brown trout (those not included in the cross-validated model) were entered into the LDA. The model then classified these data points into one of the four spawning sites. These predicted sites were added to the original data frame, and the squared Mahalanobis distance was calculated for each individual. For an individual to be correctly classified in the model, the posterior probability had to be larger than the mean of the posterior probabilities of the other individuals predicted back to the site, minus two standard deviations. The squared Mahalanobis distance from the group centroid had to be less than the mean squared Mahalanobis distance of the group centroids of the other individuals, plus two standard deviations (Olley et al. 2011). The posterior probability indicated the site it was most likely caught it and the Mahalanobis distance measured the likelihood of the predicted site membership.

To ensure that the data met assumptions of normality and equal variances, an LN transformation from Mikheev et al. (2021) was applied:

$$I_{i,j} = \frac{\ln C_{i,j} - \overline{\ln C_j}}{\sigma_{\ln C_j}}$$

Iij - standardised i measurement of j fish. Cij - i measurement of j fish. $\overline{lnCj}$ - average of LN-transformed measurements of j fish. $\sigma lnCj$ - standard deviation of LN-transformed measurements of j fish (see Mikheev et al. 2021).

4. Results

4.1. Elemental variation among juvenile otoliths

From the juvenile training dataset, all seven element:Ca ratios were found to have significant variation among sites. The strongest site effect were detected for Sr:Ca($F_{(3,51)} = 39.85, p < 0.001, \omega^2 = 0.68$) and Ba:Ca($F_{(3,51)} = 29.54, p < 0.001, \omega^2 = 0.61$), indicating pronounced spatial differences in these elements among sites. Phosphorus, magnesium, manganese, rubidium and aluminium also varied significantly between sites: P:Ca ($F_{(3,51)} = 18.37, p < 0.001, \omega^2 = 0.49$), Mg:Ca ($F_{(3,51)} = 11.56, p < 0.001, \omega^2 = 0.37$), Mn:Ca ($F_{(3,51)} = 8.80, p < 0.001, \omega^2 = 0.30$), Rb:Ca ($F_{(3,51)} = 8.08, p < 0.001, \omega^2 = 0.28$) and Al:Ca ($F_{(3,51)} = 5.47, p = 0.0025, \omega^2 = 0.20$).

Table 4.1. The cross-validated LDA classification of juvenile brown trout to their sample site. 13 measurements of seven elements (^{24}Mg, ^{27}Al, ^{31}P, ^{55}Mn, ^{85}Rb, ^{88}Sr, ^{138}Ba) for each site were taken from vertical ablations of juvenile otoliths. The reclassification rate is 92.3%.

Spawning Site		***a***	***b***	***c***	***d***	**% Correct**
Predicted		**Actual**				
Mirfin Creek	*a*	12	1	0	0	92.3
Lower Otututu River	*b*	0	12	1	0	92.3
Mawheraiti River	*c*	1	0	11	0	84.6
Mawheranui River	*d*	0	0	1	13	100

When sites 5 and 6 were combined due to similar water chemistry and proximity, a multivariate test confirmed that elemental fingerprints remained significantly distinct among all sampling sites ($Wilks'\Lambda = 0.0304, F(3,51) = 17.70, p < 0.001$).

Table 4.2. The cross-validated LDA classification of juvenile and adult brown trout to their natal site. A total of 82 measurements of seven elements (^{24}*Mg,* ^{27}*Al,* ^{31}*P,* ^{55}*Mn,* ^{85}*Rb,* ^{88}*Sr,* ^{138}*Ba) were taken from vertical ablated transects of juvenile otoliths and horizontal ablated transects of adult otoliths.*

Predicted Site	Total	Matched	Proportion matched	Proportion remained	Proportion dispersed
Mirfin Creek	37	33	0.892	0.364	0.636
Lower Otututu River	7	6	0.857	0.500	0.500
Mawheraiti River	3	3	1.000	1.000	1.000
Mawheranui River	35	31	0.886	0.290	0.710

4.2. Classification of juvenile otoliths

The linear discriminant analysis (LDA) successfully re-classified juveniles to their site of capture with a cross-validated accuracy of 92.3% (*Table 4.1*), indicating that otolith chemistry effectively reflected local habitat conditions. Al was excluded from the LDA model as it was collinear with Rb and was the least biologically significant. The discriminant model was then able to predict natal sites for 73 of the individuals (64 juveniles, 9 adults) with an overall classification rate of 90.1%. The Mawheraiti River had a precision of 100%, whilst sites 2, 3 and 5 returned rates of 89.2%, 85.7% and 88.6% respectively (*Table 4.2*).

4.3. Prediction of natal origin

The discriminant model was applied to both juvenile and adult otoliths to predict natal origins based on elemental fingerprints. The model correctly assigned 73 individuals (64 juveniles, 9 adults) to a natal site, with an overall classification success of 89.0%. Among adults, six were assigned to the Mawheranui River, and three to Mirfin Creek, indicating that these tributaries were the most probable natal environments for mature individuals (*Figure 4.1*). No adults were assigned to sites 3 or 4, implying limited recruitment from these areas in the sample population.

Most individuals were associated with natal origins in Mirfin Creek and the Mawheranui River, suggesting that these tributaries serve as key spawning and early rearing habitats within the Otututu River system. The classification results also suggest evidence of bidirectional dispersal.

Table 4.3. Concentrations of seven elements (μmol/mol^{43}Ca) across the ablated section of brown trout otolith sampled from the Otututu River. Element:Ca ratios are showed as mean (±SE). Superscript letters next to mean (±SE) values indicate a significant difference between the element:Ca ratios of individuals at different sites.

	Element						
Spawning Tributary	**^{24}Mg**	**^{27}Al**	**^{31}P**	**^{55}Mn**	**^{85}Rb**	**^{88}Sr**	**^{138}Ba**
Mirfin Creek ^{a}	186.462 (29.870)	22.115 (5.344)	1019.931 (188.702)	12.777 (6.816)	0.551 (0.156)	745.382 (19.002)	12.207 (0.629)
	b, c, d	c, d	b	b	b	c, d	b, d
Lower Otututu River ^{b}	107.984 (21.035)	19.594 (6.256)	1097.929 (747.259)	3.808 (1.191)	0.505 (0.064)	683.157 (82.739)	11.978 (1.417)
	a		a, c, d	a, c, d	a, c	c, d	a, c
Mawheraiti River ^{c}	90.326 (7.978)	9.693 (2.131)	1693.333 (449.006)	4.430 (0.686)	0.183 (0.039)	1422.003 (96.114)	21.240 (1.022)
	a	a	b	b	b	a, b, d	a, b, d
Mawheranui River ^{d}	82.053 (6.141)	8.703 (1.630)	1545.320 (431.698)	3.024 (0.265)	0.178 (0.016)	1518.469 (25.933)	14.271 (0.553)
	a	a	c	c		a, b, c	a, c

Visual examination of Sr:Ca ratios in adult otolith transects found no inconsistencies, suggesting freshwater residency (Arai et al. 2002). Therefore, all adults analysed were classified as potadromous migrants or residents.

4.4. Movement patterns

These results suggest that the Otututu River supports both local and dispersing brown trout populations. Most juveniles appear to recruit from tributaries such as Mirfin Creek and the Mawheranui, with subsequent downstream dispersal as they mature. The combination of strong elemental discrimination among sites and high reclassification success highlights the accuracy achievable with otolith microchemistry in this system.

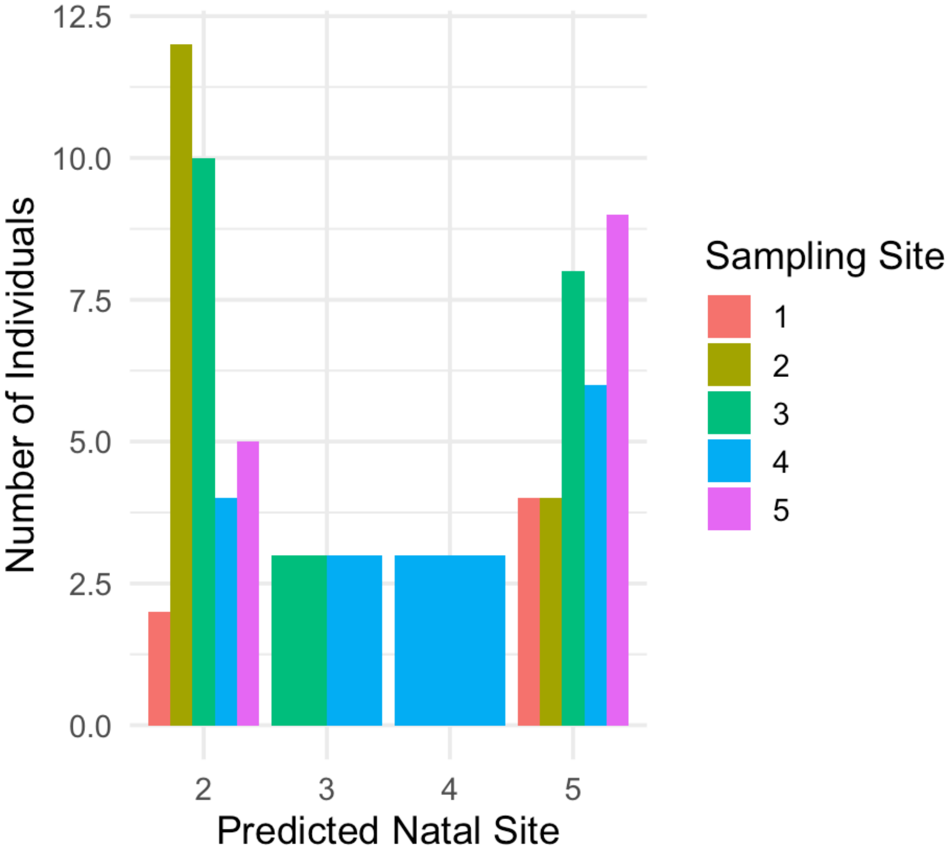

Figure 4.1 Barplot of the number of individuals accurately predicted to each natal site. Bar colour denotes the site at which the individual was sampled from. Mirfin Creek (Site 2) natal n = 33, Lower Otututu River (Site 3) natal n = 6, Mawheraiti (Site 4) natal n = 3, Mawheranui River (Site 5) natal n = 31.

5. Discussion

5.1. Overall

Otolith microchemistry analysis revealed clear spatial variation in elemental composition among sampling sites within the Otututu (Rough) River catchment. All seven measured element:Ca ratios (Mg:Ca, Al:Ca, P:Ca, Mn:Ca, Rb:Ca, Sr:Ca, Ba:Ca) differed significantly among sites, confirming that water chemistry varies sufficiently across the system to produce distinct elemental fingerprints in brown trout otoliths. These results support the use of otolith elemental composition as a reliable indicator of natal origin and habitat use for brown trout in this region.

The linear discriminant analysis (LDA) developed from the juvenile training dataset was highly effective, correctly reclassifying 92.3% of juveniles to their site of origin and aligning with similar studies (Thorrold et al. 1998; Wells et al. 2003; Vasconcelos et al. 2007; Olley et al. 2011; Avigliano et al. 2017; Bouchoucha et al. 2018). These results demonstrate that elemental ratios in otoliths can reliably discriminate between even closely connected tributaries in the Otututu River system.

Predicted natal origins based on the discriminant model showed that the majority of individuals, both juveniles and adults, were assigned to either Mirfin Creek or Mawheranui River. This suggests that these two tributaries function as the primary spawning and early rearing habitats for brown trout within the catchment. Lower Otututu River and Mawheraiti River contributed fewer individuals, indicating either lower spawning activity or reduced juvenile survival in these areas during the study period.

5.2. Movement & dispersal

Distinct natal origins were detected for brown trout in the Otututu River, confirming that multiple tributaries function as spawning habitats within the catchment. Individuals originated from several sites, with Mirfin Creek and Mawheranui River emerging as key spawning areas. A small proportion of individuals (11.0%) could not be confidently assigned to a natal site. This may indicate that they originated from unsampled spawning sites or poor differentiation in elemental fingerprint.

Natal dispersal rates among brown trout are highly variable across systems and are influenced by both environmental and genetic factors (Jonsson & Jonsson 2011). Previous studies have reported limited movement among age-0 trout within tributary networks (Vatland & Caudron 2015), whereas others have observed extensive dispersal, with up to 40% of age-0 trout emigrating from their natal tributaries (Akland et al. 2025). In the current study, 57.8% of juveniles were classified as having dispersed from their natal tributaries, suggesting a relatively high level of early-life mobility. Such dispersal rates are ecologically meaningful, particularly in heterogenous river systems where habitat quality, flow and resource availability vary at fine spatial scales (Cucherousset et al. 2005; Taal et al. 2018).

Brown trout in Zealand typically hatch during winter and emerge in spring (Klemetsen et al. 2003; Wood & Budy 2009). The juveniles captured in this study were collected in summer and measured under 100 mm total length, allowing them to be confidently classified as age-0 individuals (Taube 1976; Lobón-Cerviá 2000). This indicates that dispersal must have occurred during the spring or early summer months, coinciding with increasing water temperatures, variable flows and seasonal peaks in invertebrate prey abundance (Tortenson & Shaw 2025). Environmental cues such as these are known to trigger movements in juvenile salmonids (Jonsson & Jonsson 2011).

Parr and age-0 migrations are less studied than smolt or adult migrations, but are typically density-dependent and resource-driven (Jonsson & Sandlund 1979). When local competition intensifies or rearing habitat becomes saturated, juveniles may disperse downstream or laterally into adjacent tributaries (Grant & Kramer 1990; Cucherousset et al. 2005). Therefore, the comparatively high dispersal rate observed here likely reflects behavioural responses to spatial variation in food and habitat availability.

Of the 33 individuals assigned to Mirfin Creek as their natal origin, only 12 were captured there, while 21 (19 juveniles and two adults) were caught downstream. This pattern suggests substantial downstream movement, consistent with observations by Jonsson & Sandlund (1979) that young trout disperse when doing so enhances growth opportunities. The Otututu River supports a well-known recreational fishery and large-bodied brown trout have been reported from lower reaches (West Coast Fish & Game Council pers. comm.), implying that individuals originating in smaller tributaries may migrate into larger channels as they grow.

No Sr:Ca ratios consistent with anadromous (sea-run) behaviour were observed in any individuals (Arai 2002; Walther & Limburg 2012), confirming that all detected movements occurred within freshwater. Of those dispersing, the proportion dispersing downstream in this study (47.8%) aligns closely with recent estimates by Grant & Weir (2025; 56.6%), and is lower than the 70–80% downstream dispersal reported in older European studies (Daufresne et al. 2005; Palm et al. 2023). These similarities suggest that the movement dynamics in the Otututu River are broadly consistent with global patterns of freshwater trout movement.

Flow velocity, discharge fluctuations, and substrate composition likely influence the direction and magnitude of dispersal. Higher discharge events during spring may act as proximate triggers for downstream movement (Daufresne et al. 2005), though further research is needed to confirm this mechanism under local flow conditions.

All juveniles (<100 mm) were assumed to be age-0 and therefore not yet sexually mature (Lobón-Cerviá 2000). Their observed movements represent dispersal rather than spawning migrations. While migratory distance often increases with body size (Aarestrup & Koed 2003; Cucherousset et al. 2005), the predominance of small dispersers here indicates that early movement is not size-limited. Instead, dispersal may reflect opportunities for uncompetitive feeding sites, or reduced competition in their current stream (Grant & Kramer 1990; Imre et al. 2024).

The distance of dispersal seen in the juvenile brown trout is markedly different to that documented in literature. Juvenile brown trout in my study are dispersing kilometres downstream or upstream. Vatland & Caudron (2015) observed low rates of dispersal of age-0 brown trout from their tagging site; of those that did disperse, this was mainly downstream and at most, ~300m from their tagging site. These maximum range limits were extended in Jorgenson & Berg's (1991) study, where maximum distance was 600m upstream and 700m downstream. The key piece to note here is that these studies looked at a smaller window of time than this study does. The key distinctions lie in the temporal scale and location of these studies. Vatland & Caudron (2015) recorded data for two months each in consecutive years and undertook their study in France. Jorgensen & Berg (1991) followed fish movements for 60 days, in tributaries of a Norwegian stream. Their data represents a significantly shorter time period in the juvenile's life, whereas the current study encompasses a broader developmental window in which individuals have had greater opportunity to disperse during a range of life stages. Furthermore, brown trout are native to Europe (Elliot 1989), and stocked populations have reportedly high straying rates (Degerman et al. 2012; Mikheev et al. 2020). Brown trout were introduced and stocked in New Zealand from 1867, meaning that the Otututu River population has had little time on an evolutionary scale to adapt to the catchment. Mikheev et al. (2021) was conducted in the South Island of New Zealand and suggest that their focus population in the Taieri River may have been unable to adapt entirely to the conditions of the catchment. As the individuals in this study have a similar evolutionary background to that of Mikheev et al. (2020), the same conclusion can be applied here.

Extended dispersal distances may also reflect differences in habitat availability and flow regime. In spatially constrained systems, juvenile trout often remain close to their natal redds due to abundant cover and food (Elliot 1993; Armstrong et al. 2003). However, in rivers with limited suitable rearing habitat, individuals may undertake extensive movements to locate optimal territories or feeding opportunities (Keeley 2001; Lobón-Cerviá 2000). Density-dependent mechanisms are another likely factor; when juvenile densities are high, subordinate fish are often forced to disperse in search of unoccupied feeding areas (Grant & Kramer 1990; Imre et al. 2004). Thus, the larger dispersal range observed here may indicate competitive displacement or habitat limitation rather than purely behavioural choice.

Adult trout sampled at the Upper Otututu River were assigned primarily to Mirfin Creek and the Mawheranui as their natal origins, suggesting upstream migration within the catchment. Such movement is typical of potamodromous trout seeking suitable spawning substrates or increased flows (Jonsson & Jonsson 2011). The absence of elevated Sr:Ca ratios in these otoliths confirmed that these individuals were freshwater-resident.

The concentration of natal assignments to Mirfin Creek and the Mawheranui River likely reflects habitat heterogeneity. Mirfin Creek contains gravel–cobble substrates and moderate flow velocities conducive to egg deposition and incubation, whereas the Mawheranui River has been identified by anglers and managers as a productive spawning reach (Kersten 2021).

Ciepala & Walters (2019) reported that approximately 57% of trout migrated between natal and resident locations, consistent with a flexible movement strategy in which only a subset of individuals return to natal areas. Källo et al. (2023) similarly concluded that the costs and benefits of autumn migration and straying differ depending on an individual's home river and environmental context. In this study, such variability in movement may explain why some individuals from the Mawheranui migrated upstream to the Upper Otututu, while others remained closer to their natal areas.

From a fisheries perspective, these patterns suggest that juvenile trout in the Rough River may contribute to recruitment across a much broader spatial scale than previously appreciated. This has important implications for how populations and fisheries are managed. Maintaining connectivity between tributaries and mainstem habitats is therefore crucial for sustaining recruitment and genetic diversity (Hutchings & Fraser 2008). Disruption of these dispersal pathways through hydroelectric development or dewatering could reduce resilience and lead to localised depletion of the fishery (Cattanéo et al. 2002). Future studies could quantify dispersal in relation to flow dynamics, density and habitat structure to better identify the environmental threshold that drives large-scale juvenile movement in brown trout.

The combination of weak natal site fidelity and moderate straying suggests that the Otututu River brown trout population is semi-structured, with partially connected subpopulations linked by dispersal among key tributaries. This structure promotes both local adaptation and demographic resilience but depends on unimpeded movement to allow juveniles to disperse through the river network.

From a management perspective, these findings highlight the importance of maintaining connectivity between tributaries and the mainstem to sustain recruitment and gene flow. Hydroelectric development, water abstraction, or dewatering could fragment the system and disrupt these movement pathways (Cattanéo et al. 2002; Hutchings & Fraser 2008). Protecting access to spawning tributaries such as Mirfin Creek and Mawheranui River should therefore be a priority in environmental planning and impact assessments.

5.3. Spawning

One of the more notable outcomes of this study was the contrast between the high number of individuals originating from Mirfin Creek and the comparatively low number from the Lower Otututu River. Although anecdotal reports and angler observations have long suggested that the

Lower Otututu River is a primary spawning reach for brown trout in the Otututu (Rough) River, only 14.3% of the individuals captured there were classified as having originated from that site. This discrepancy indicates that the Lower Otututu River may function primarily as a juvenile rearing or transitional habitat rather than a major spawning location. Similar patterns have been documented in other salmonid populations, where shallow tributaries provide nursery habitat but contribute relatively few recruits to the overall population (Lobón-Cerviá 2000; Armstrong et al. 2003).

In contrast, Mirfin Creek stood out as a key spawning and dispersal source. This site is positioned at the confluence of Mirfin Creek and the Otututu River, an area characterised by pronounced hydrological and geomorphic heterogeneity. Confluences are widely recognised as ecological hotspots of productivity and biodiversity, particularly where tributaries with contrasting physical regimes meet (Boddy et al. 2019). The combination of Mirfin Creek's shallow, cobbled substrate and the deeper, more stable flows of the mainstem of the Otututu River likely provides an optimal balance of conditions for egg deposition, incubation, and early fry rearing (Elliott 1993; Kondolf et al. 2003).

The observed importance of Mirfin Creek aligns with the predictions of the Intermediate Disturbance Hypothesis (IDH; Connell 1978), which proposes that biodiversity and productivity peak at intermediate levels of environmental disturbance. At the confluence of Mirfin Creek and the Otututu River, the two separate flows likely disturb sediments enough to maintain spawning gravel quality, while the relatively stable flow of the mainstem prevents excessive scour or siltation. This intermediate disturbance regime may therefore sustain a balance between habitat renewal and stability, supporting both spawning adults and early-life survival (Resh et al. 1988).

The juvenile brown trout analysed here were all classified as age-0 and hence not sexually mature (Taube 1976). Consequently, direct evidence of homing or spawning return behaviour cannot be inferred. However, the disproportionately high number of individuals originating from Mirfin Creek, combined with its inferred habitat characteristics, suggests that this area functions as one of the principal spawning and recruitment hubs in the Otututu River system.

Hydrological modification from the proposed hydroelectric development could disrupt this balance. The construction of an intake gallery and associated weir at the confluence is expected to alter local flow velocity, sediment transport, and depth variability. Excessive disturbance or prolonged dewatering may push the site beyond the "intermediate" threshold predicted by the IDH, leading to habitat homogenisation and reduced reproductive success (Resh et al. 1988; Bilotta et al. 2016). Preserving the current hydrological variability at Mirfin Creek should therefore be considered a management priority to maintain its role as a spawning and dispersal hub.

All adult trout that could be confidently assigned to a natal tributary were traced to either Mirfin Creek or Mawheranui. This finding reinforces the conclusion that these locations serve as the primary spawning habitats within the catchment. The Mawheranui River (being a braided river (DOC 2025)) with its wider channel and coarser substrate, likely provides suitable gravel for egg deposition and ample oxygen exchange (Armstrong et al. 2003).

Several adults captured at the Upper Otututu River were predicted to have originated from Mawheranui, implying upstream migration within the system. The absence of elevated Sr:Ca ratios in their otoliths confirms that these individuals were potamodromous rather than anadromous (Arai 2002; Walther & Limburg 2012). Upstream migrations of this nature are commonly observed in brown trout seeking suitable spawning habitat or cooler summer refugia (Jonsson & Jonsson 2011; Keefer & Caudill 2014).

5.4. Impacts of a Hydroelectric Scheme

The proposed hydroelectric scheme at the confluence of Mirfin Creek and Otututu River would cause significant disturbance to local hydrology and habitat connectivity. This may shift the equilibrium of disturbance, making disturbance events too frequent and negatively impacting species diversity at the site. (Resh et al. 1988). The proposed site of the intake gallery for the run-of-river scheme is located at the confluence of Mirfin Creek and the Otututu River. The Mirfin Creek sampling site, which is located just upstream of this confluence, is a key spawning site for brown trout. Otolith trace element analysis indicated that of the 33 individuals predicted to have originated from Mirfin Creek, 21 were caught downstream in the Otututu River. This highlights the ecological importance of Mirfin Creek as a spawning site for the population, contributing recruits to downstream populations, including the Mawheraiti and the Mawheranui Rivers.

At the time of sampling, there were no significant anthropogenic barriers in the Otututu River, allowing for natural dispersal. However, construction of the proposed intake gallery and necessary associated weir, would likely form a significant barrier to fish movement upstream in the Otututu (Rough) River, especially for juvenile trout (Aarestrup & Koed 2003).

The New Zealand Fish Passage Guidelines (Version 2.0; NIWA 2024) explicitly recommends against the installation of new weirs. The guidelines emphasise that weirs restrict both upstream and downstream migration and reduce the connectivity of riverine habitats; in turn decreasing trout abundance and recruitment (Gosset et al. 2006; NIWA 2024).

In the Otututu River, juvenile trout disperse throughout the river. These juvenile trout are particularly vulnerable to partial barriers and velocity thresholds exceeding their swimming capability (Stuart & Mallen-Cooper 1999; Baker & Votta 2021). Even low-head weirs can prevent passage by small fish due to excessive turbulence and hydraulic jumps (Franklin & Bartels 2012). Given that juvenile trout in this system must move from Mirfin Creek downstream to the Mawheraiti and the Mawheranui, any reduction in connectivity would directly compromise natural dispersal and recruitment.

Operation of the proposed scheme would involve abstraction of flow into a headpond, effectively dewatering a section of the Otututu River downstream of the intake (Ministry for the Environment 2024). Because the Otututu catchment is substantially larger than that of Mirfin Creek, diversion would result in a disproportionate reduction in discharge, particularly during periods of low flow.

Dewatering has been repeatedly shown to cause habitat degradation, increased water temperature, and reduced dissolved oxygen concentrations (Hayes et al. 2020; Pander et al. 2022). It also eliminates shallow marginal zones that serve as nursery habitats for juvenile fish (Pander et al. 2022). Small-bodied fish are especially prone to stranding and mortality during rapid drawdown events (Halleraker et al. 2003; Pander et al. 2022). Pander et al. (2022) observed significantly higher stranding rates among fish 44–90 mm in length compared to larger conspecifics, the size range that encompasses most juveniles in this study.

In addition, Halleraker et al. (2003) reported that brown trout fry (>60 mm fork length) were twice as likely to strand during daytime dewatering as at night, with an overall 100 mm critical threshold below which stranding risk increased sharply. In the present study, 53 trout moved through the reach that would be affected by the proposed diversion, and 46 of these fell within the vulnerable size range. This indicates that even brief or partial dewatering events could result in substantial mortality and recruitment failure.

Dewatering also reduces refuge availability and disrupts the fine-scale hydraulic diversity that supports feeding and predator avoidance (Bunn & Arthington 2002). Collectively, these effects would transform a heterogeneous, productive reach into a simplified and unstable environment.

Halleraker et al. (2003) reported significant negative impacts on brown trout fry during dewatering events, with larger fry (>60mm fork length) being twice as likely to be stranded during daytime dewatering events than nighttime dewatering events. When in a heterogeneous mix of brown trout life history stages, trout fry were then three times more likely to be stranded during a dewatering event than their parr conspecifics (Halleraker et al. 2003). Furthermore, a 100mm critical limit for brown trout stranding risk was identified; all juvenile trout sampled in the Otututu River fall outside of this threshold and would be at high risk of stranding. Of the individuals sampled in the Otututu River, 53 of them moved through the section of river that would be affected by the proposed dewatering, 46 individuals fall in the vulnerable size range.

Interruptions to both upstream and downstream dispersal will likely lead to a reduction in recruitment to downstream populations. Dispersal is a key demographic process that sustains trout populations, allowing juveniles to colonise suitable habitats as they grow. Increases in discharges are known to stimulate upstream dispersal within river systems (Jonsson & Jonsson 2011; Aarestrup et al. 2017), and thus alterations in flow dynamics can disrupt the environmental cues that drive movement.

Dewatering and hydropeaking events can have severe consequences for early life stages of brown trout, which are particularly sensitive to hydrological instability (Molony 2001). Periods of fluctuating flow have been shown to inhibit growth and increase mortality among brown trout fry, largely due to elevated energetic demands and disrupted feeding opportunities (Addo et al. 2023). While the Lower Otututu River contributed relatively few individuals of natal origin, it serves as a critical corridor facilitating connectivity between major spawning and rearing areas such as Mirfin Creek and the Mawheranui. Maintaining consistent flow through this reach is therefore essential not only for the survival of resident fry but also for ensuring longitudinal connectivity throughout the Otututu River catchment.

Fluctuating flows, whether from dewatering or hydropeaking, have well-documented negative effects on salmonid reproduction and juvenile survival. Repeated drawdown and refilling of channels can expose redds to desiccation, disrupt the thermal regime, and physically dislodge developing embryos (Halleraker et al. 2003; McMichael et al. 2005; Casas-Mulet et al. 2016). Addo et al. (2023) further demonstrated that repeated water-level fluctuations suppress fry growth and elevate mortality rates, attributing these effects to reduced feeding efficiency and high energetic costs associated with re-adjustment to changing velocities. Over time, this physiological stress can divert energy away from somatic growth and towards maintenance metabolism, producing smaller, energetically depleted fry (Forseth et al. 1999). Smaller fry entering winter experience higher overwinter mortality and delayed maturation, ultimately constraining recruitment success (Taube 1976; Elliott 1993).

In addition to direct mortality, hydropeaking can indirectly reduce survival by altering microhabitat structure and food availability. Rapid changes in discharge modify substrate stability and invertebrate drift density, key determinants of feeding success in juvenile salmonids. Such disturbance can desynchronise fry emergence and growth between affected and unaffected tributaries, resulting in heterogeneous size structures across the catchment (Vollset et al. 2016; Hajiesmaeli et al. 2023). Vollset et al. (2016) found that frequent low-flow periods delayed fry emergence, exposing later-emerging cohorts to increased predation and competition. In the Otututu River, asynchronous emergence among sites could translate into population-level consequences, including reduced survival, slower growth, and lower recruitment rates. These biological changes would also diminish the river's reputation as a high-quality recreational trout fishery, which depends on consistent recruitment of large, fast-growing individuals. Furthermore, hydropeaking-induced fluctuations could desynchronise growth rates and emergence timings between sites affected by the hydroelectric scheme and those not affected (Vollset et al. 2016; Hajiesmaeli et al. 2023). Growth is negatively affected by hydropeaking events (Hajiesmaeli et al. 2023) and as not all sites in the Otututu River would be severely affected by changing flows, there may be noticeable changes in size of brown trout. This would negatively affect the reputation of the Otututu River as an excellent trout fishery. Changes in flow then affect the time of spawning; with frequently low flow periods due to the hydroelectric scheme, emergence of fry from redds may be delayed (Vollset et al. 2016). There are strong selection pressures on the timing of emergence by fry, and those emerging later are at a higher risk of mortality (Skogland et al. 2011). The energetic stress imposed on the trout by repeated adjustments to the water flow can divert energy away from somatic growth and towards maintaining higher metabolic rates (Forseth et al. 1999). This can lead to smaller fry at the onset of winter, bottlenecking salmonid survival and potentially delaying sexual maturation (Taube 1976; Elliot 1993).

Energetic stress imposed by repeated flow fluctuations can also affect long-term life-history trajectories. Flodmark et al. (2006) demonstrated that juveniles exposed to variable flows allocate less energy to growth and more to maintaining metabolic stability. Such shifts can lead to stunted growth prior to winter and delay the onset of sexual maturity. In systems subjected to frequent hydropeaking, this can create a demographic bottleneck where small, slow-growing cohorts dominate, further reducing the resilience of the population (Elliott 1993).

The ecological role of the Lower Otututu underscores the importance of maintaining stable hydrological conditions across connecting reaches. Although relatively few individuals were identified as originating from this site, its position between Mirfin Creek and the Mawheranui River makes it an essential dispersal pathway. Flow fluctuations or localised dewatering could fragment this corridor, creating intermittent dry reaches or hydraulic barriers that small-bodied fish are unable to traverse (Nilsson et al. 2005; Lothian et al. 2020). The resulting loss of connectivity would impede downstream recruitment from Mirfin Creek and limit gene flow within the catchment.

From a fisheries management perspective, these findings reinforce the need to minimise extreme flow fluctuations during critical developmental stages. Protection of consistent flow conditions in recognised trout habitats is consistent with section 7(h) of the Resource Management Act 1991, which requires particular regard to “the protection of the habitat of trout and salmon.” Any hydroelectric operation that compromises hydrological stability, particularly during spawning and emergence periods, would therefore be inconsistent with the intent of the RMA and the National Policy Statement for Freshwater Management 2020. Avoiding such impacts is critical to safeguarding both the ecological integrity of the Otututu River and its continued value as a regionally significant trout fishery.

5.5. Limitations of the study

While this study successfully identified spatial variation in otolith microchemistry and demonstrated high classification accuracy, several methodological and contextual limitations should be acknowledged.

A risk with micro-sampling 5µm of each juvenile otolith is that the sample is not representative of the water chemistry at the site of capture. Olley et al. (2011) considered this a potential confounding factor in their study, but because their reclassification rates were consistently above 90%, it was deemed unlikely. The methods used in this study do not allow recent fish immigration to be quantified, and therefore, the juvenile trout may have visited a number of tributaries immediately prior to being caught. However, as the reclassification rates most all sites were greater than 90%, this scenario is unlikely to occur here.

As this study focused solely on otolith microchemistry and trace element analysis, no habitat measurements were taken of sampled sites; it was out of scope for the study. This made it difficult to determine the extent to which environmental factors influenced the trout's spawning and migration habits. This meant that no conclusions could be drawn based on the appropriateness of spawning sites and the correct environmental conditions.

The limited number of sites may have stunted the ability to classify individuals to their natal tributary correctly. Under this model, 90.1% of individuals were correctly classified to their natal tributary. A wider range of sites may have allowed for higher classification rates for individuals.

Although seven elements were analysed, there may be other trace elements or isotopes that could enhance site discrimination, in particular discrimination between the two Mawheranui River sites. Elements such as lithium (Li), zinc (Zn), or rare earth elements have recently been shown to improve discrimination power in freshwater otolith studies (Hamer et al. 2006; Hamer et al. 2012; Izzo et al. 2018). The detection limits and matrix effects associated with quadrupole ICP-MS systems also introduce small degrees of measurement uncertainty, particularly for elements present in low concentrations (Longerich et al. 1996).

While otolith chemistry provides a powerful indirect measure of movement, it does not capture behavioural or physiological context. The methods used in this study cannot differentiate between individuals that permanently dispersed and those that made multiple trips between tributaries. For instance, juveniles may have briefly entered other tributaries prior to capture without leaving a clear geochemical signal, leading to potential underestimation of short-term dispersal. Complementary methods such as PIT-tag telemetry or stable isotope analysis, or could provide a deeper understanding of movement pathways and strengthen ecological understanding (Cucherousset et al. 2007; Crook et al. 2020)

All adults that could be successfully assigned to a natal tributary were traced to either Mirfin Creek or Mawheranui, suggesting that the individuals residing at the Upper Otututu River originate downstream of the site. Of those adults caught at the Lower Otututu River, only 3 of the 6 individuals could be accurately predicted to a natal tributary.

There are two plausible explanations for these unclassified fish. Firstly, it may have originated from a tributary not included in the current study and therefore could not be predicted back to it because there was no juvenile reference set for the site. Alternatively, there may have been significant interannual variability in the environmental concentrations of the element:Ca ratios. There does not appear to be a consensus on the degree of interannual variability in elements in otoliths in literature. Olley et al. (2011) suggests that the Sr:Ca and Rb:Ca ratios remain stable over time, whilst Gillanders (2002) found significant temporal variation for Sr. The conclusion in Olley et al. (2011) is that variation between catchments should override any effects of interannual variability.

Current literature has reported significant temporal variation in element:Ca ratios in fish otoliths from re-sampled sites in lacustrine (Schaffler & Winkelman 2008), estuarine (Gillanders 2002; Reis-Santos et al. 2012) and coastal (Hampton et al. 2018) systems. However, studies focusing on lotic systems (Olley et al. 2011; Nazir & Khan 2019) did not find significant interannual variation in element:Ca ratios. This study did not look at temporal variation in the otoliths sampled.

Martin et al. (2013) found interannual differences in otolith element fingerprints, but this was negligible when compared to the variation between sites. Thorrold et al. (1998) saw more problematic rates of interannual variation, but were still able to classify adults to their rivers of origin. Morissette & Sirois (2021) came to similar conclusions, adding that the method could only be applied within regional tributary groups.

5.6. Future Research & Recommendations

In line with the New Zealand Fish Passage Guidelines (NIWA 2024) and recent ecological studies, the installation of any structure that impedes movement should be avoided where alternative designs are feasible. If construction proceeds, incorporation of effective fish passage structures, such as a low gradient, roughened channel rather than a traditional weir, should be prioritised. However, fish ladders often have limited effectiveness for small-bodied fish and require specific hydraulic conditions to function properly; passage success is typically low for trout under 100mm (Lothian et al. 2020). As such, the proposed scheme poses a substantial risk to trout dispersal, recruitment, and the long-term viability of local populations.

This study is the first application of otolith microchemistry to assess natal origins and dispersal patterns of brown trout within the Otututu River catchment. There was clear variation in elemental signatures among tributaries, and high rates of reclassification of juveniles (>85%), supporting the use of otolith trace-element analysis to predict juvenile spawning sites.

The results revealed that Mirfin Creek and the Mawheranui are key spawning and recruitment sources for the Otututu River trout population. Most individuals were assigned to these two tributaries, while relatively few originated from the Lower Otututu River and the Mawheraiti, suggesting that it functions primarily as a rearing or dispersal corridor rather than a spawning site. Movement patterns indicated that juveniles often dispersed downstream following emergence, with some evidence of upstream migration among both juveniles and adults. All individuals displayed otolith Sr:Ca profiles consistent with freshwater residency.

These findings have important ecological and management implications. The strong reliance on a small number of tributaries for spawning highlights the population's vulnerability to localised disturbance. The proposed hydroelectric development at the confluence of Mirfin Creek and the Otututu River poses particular risk, as hydrological alteration and dewatering could disrupt key spawning and dispersal habitats. Reduced flow stability and physical barriers could impede juvenile migration, fragment population structure, and undermine recruitment to downstream reaches.

In accordance with section 7(h) of the Resource Management Act 1991, the protection of trout habitat must be prioritised when evaluating such developments. Maintaining river connectivity, stable flows, and suitable spawning conditions in tributaries such as Mirfin Creek will be critical to sustaining the ecological integrity and recreational value of the Otututu River fishery.

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