River Research and Applications

RESEARCH ARTICLE

Unearthing a New Approach to Gravel Extraction: Can It Restore Freshwater Fish Habitat and Improve Their Population Health?

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ABSTRACT

Despite their dynamic and resilient nature, river systems are degrading worldwide, with gravel extraction a key commercial activity that significantly threatens their integrity and natural functioning. However, extraction methods aiming to combine commercial aggregate harvesting and riverbed ecosystem restoration are being trialled. To evaluate one such approach, we compared the environmental effects of an experimental gravel and overburden skimming technique, designed for restoration, with those of traditional pit mining. Population health indicators—diet, parasite load and growth rate—were assessed in a generalist fish, the upland bully (*Gobiomorphus breviceps*), across three treatments: pit-mined ponds, gravel and overburden skimming river restoration sites, and unmodified river reaches, all located in a section of the Aparima River, New Zealand. Fish in pit mining ponds had higher parasite loads and faster growth rates than those in the river treatments. These differences are likely due to more suitable conditions for fish growth and parasites in pit-mined ponds, including elevated nutrient levels, higher temperatures and a lack of flow. Sites harvested via experimental gravel and overburden skimming (restoration) and unmodified river reaches (control) showed minimal differences, leaving the efficacy of the experimental gravel and overburden skimming method as a restoration technique for native fish conservation uncertain, but showing that extraction using this method did not have a negative effect on the fish population health variables assessed. This contrasts with pit mining, which, as indicated by fish population health, was more environmentally disruptive. Further regulation, monitoring, and development of integrative gravel extraction and river restoration methodologies could potentially enhance the ecosystem functioning and native biodiversity of river systems.

1 | Introduction

River corridors, characterised by both terrestrial and aquatic landscape elements, are dynamic, heterogeneous, and diverse ecosystems that support a range of rare and threatened species (Ward et al. 2002; Scott et al. 2022). However, human-induced degradation of riverine habitats presents a significant threat to the ecosystem functions and biodiversity they support (Caruso 2006b; Holdaway et al. 2012; Kuiper et al. 2014; Feio et al. 2023). Gravel extraction from river corridors to provide aggregates for infrastructure such as roads, pipelines and concrete, is a practice carried out worldwide (Kondolf 1994; Wishart et al. 2008). This activity is generally considered to have negative environmental effects (Brown et al. 1998; Kelly et al. 2005; Rinaldi et al. 2005; Rentier and Cammeraat 2022), however, its impacts vary depending on the extraction methods used and the regulatory and management regimes in place (Collins and Dunne 1990; Damseth et al. 2024; Gopal and Chauhan 2025).

Both pit mining and beach skimming are practised in New Zealand river corridors, although consents for these gravel extraction activities (especially pit mining) have become increasingly rare, due to their negative environmental implications. Pit mining occurs adjacent to, but separate from, the active river channel, yielding considerable quantities of gravel and leaving behind large, isolated ponds with steep uniform edges and low structural complexity (Kondolf 1997). These pit-mined ponds typically have no surface water connection to the river, and are filled by groundwater and precipitation, although substantial flooding events can temporarily connect them to the river's surface water (Kondolf 1994, 1997). Pit-mined ponds can become stagnant over time, as the lack of a surface flow regime allows sediment and organic matter to accumulate, reducing groundwater inflow and leading to elevated temperatures and nutrient concentrations. Beach skimming is an alternative gravel extraction method that can be executed in various ways, with the methodology, volume of gravel in the riverbed, and specific location along the river influencing the outcome of the activity. Generally, only the top layer of gravel is removed, without excavating below water level, and the volumes extracted are less than those removed by pit mining (Rinaldi et al. 2005). Disregarding floodplain dynamics during beach skimming can result in a shallow streambed, elevated water temperatures, reduction in bar area, and changes to the amount of pool, riffle, and run habitats (Kondolf 1994, 1997; Church et al. 2001). However, if thorough consideration is given to river functioning and hydrological connectivity, well-designed, restoration-focused riverbed excavation techniques could potentially increase the diversity and heterogeneity of riverine habitats (Amoros 2001).

Experimental methods to improve and restore the ecological functioning and natural character of river corridors are being trialled (Palmer et al. 2010; Kondolf et al. 2014; Chardon et al. 2021). The general aims are to expand their width, increase the formation of gravel bars, and improve habitat heterogeneity. Evaluating these restoration methods involves monitoring their effects on river ecosystems and biodiversity (Naiman et al. 2012) and examining their impacts on populations and individuals of key taxa within these habitats (Marshall Adams and Ryon 1994). The health of relatively long-lived fish populations is influenced by habitat and resource availability, making these species valuable indicators of environmental conditions (Munkittrick and Dixon 1989; Naiman et al. 2012), especially in the context of river restoration and management (Chovanec et al. 2003). The ecosystem and community-level effects of gravel extraction on fish have been well studied (Kondolf 1994; Brown et al. 1998; Rinaldi et al. 2005), but less research has investigated the population-level effects of gravel extraction on fish (Cote et al. 1999; Dunn and O'Brien 2006). This study aims to improve understanding of river restoration and gravel extraction practices within a river corridor by using fish population health indicators to assess the biological, hydrological, morphological, and physicochemical integrity of the receiving ecosystem.

2 | Study Location and Treatments

The erosion and precipitation produced by New Zealand's Southern Alps give rise to extensive river systems with distinct hydrological regimes (Caruso 2006a; Kerr 2013). These ecosystems provide critical habitats for threatened native species (Gray and Harding 2010; Caruso et al. 2013) but are also subjected to significant gravel extraction. Formerly flowing across a large floodplain, with sections harboring braided channels and bare gravel bars (Figure 1), the Aparima River, located in Southland on New Zealand's South Island, has undergone significant degradation, and is now characterised by a weed-covered bed and a constricted single channel. The Aparima River Restoration Project (ARRP), led by the New Zealand Department of Conservation, and operational since 2016, aims to restore a 4-km section of the river's natural character and functionality. So far, the project has focused on restoring terrestrial riverbed habitat for avian species, yielding overall positive results (Rossiter and Lagrue 2024). A commercial gravel extractor employs a gravel and overburden skimming technique, adapted from beach skimming, as part of an experimental approach aimed at simultaneously restoring the natural river system and extracting gravel for human use. Excavation is undertaken on the dry bank of the channel which is isolated from the water by a bund. Vegetation and accumulated fine sediments (i.e., overburden) are first removed and transported out of the river corridor. Gravel aggregates are then harvested. When flows increase, the excavated trenches are naturalised by flowing water, creating a new braid, and widening the active riverbed. The removal of overburden alleviates river constriction, allowing the water to flow more freely and remobilise the gravel uncovered by overburden removal. This enables substrate deposition within the widened corridor, forming new habitats such as gravel bars that expand shoreline ecosystems, and shallow riffles that enhance habitat heterogeneity.

In floodplain environments, structural heterogeneity creates a broad range of depths, flow velocities, thermal conditions and substrate sizes. This complexity supports resting, spawning, nursery and feeding functions for a wide variety of fish species, particularly those whose habitat preferences shift across life stages (Rosenfeld et al. 2008; Wang et al. 2022; Amat-Trigo et al. 2024). Habitat complexity is a key determinant of ecosystem processes, functions and stability, shaping aquatic systems at multiple levels, including individuals, species and communities (Kovalenko et al. 2012; Soukup et al. 2022). It influences population health through its impacts on resource availability, behaviour (Soukup et al. 2022), morphological variation (Costa-Pereira et al. 2016), brain development (Axelrod et al. 2018) and disease susceptibility (Falke and Preston 2021).

To gain an understanding of the environmental effects of the gravel and overburden skimming technique, fish population health was compared amongst three treatments: sites within the ARRP area where the gravel and overburden skimming

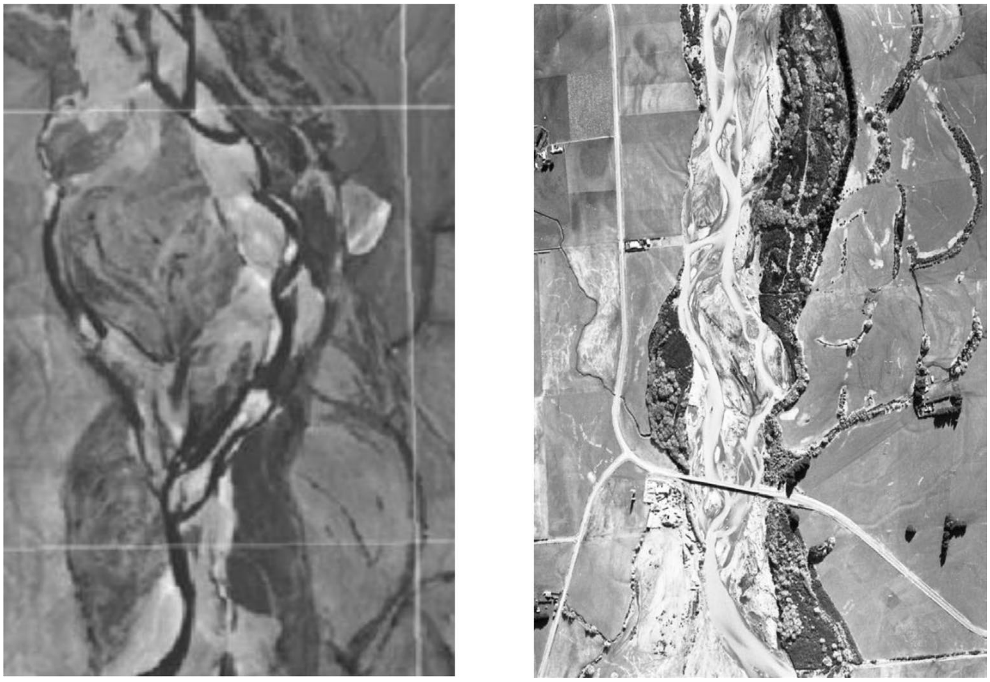

FIGURE 1 | Aerial photographs of the Aparima River in the 1950's (left) and in the 1980's (right). The river in the 1950's exhibits complex morphology, including multiple braiding channels, backwaters, and exposed gravel bars. In the 1980's, the river has braided channels and some exposed gravel bars; however, constriction of the river corridor is evident. *Source*: Hudson 2015 (left) and ArcGIS Online (n.d.) (right).

FIGURE 2 | Aerial photographs of the Aparima River. Left, 2016: Prior to application of the experimental gravel and overburden skimming technique—the river is constricted and channelized, and gravel bars are covered in exotic vegetation. Right, 2020: The experimental gravel and overburden skimming technique (RES treatment) has been applied in the top section; overburden has been removed, multiple channels and bars are visible, and conditions are intended to be more representative of the natural river, and, therefore, impact fish population health positively. The pit mining/POND treatment can be seen in the bottom left of the photo. The lower right section of the river channel is representative of the unrestored/UNRES treatment. *Source:* Department of Conservation. [Color figure can be viewed at wileyonlinelibrary.com]

methodology, intended to be restorative, is being trialled (RES), pit mining ponds, which are homogenous in structure and located on the riverbed, but separated from the active channel (POND), and unmodified, degraded river reaches that were used as 'controls' (UNRES) (Figure 2). Prior to restorative measures, the condition of RES sites was largely comparable to unrestored

UNRES sites. The gravel and overburden skimming technique (RES) was designed not merely to be less ecologically harmful than pit mining, but to restore degraded, weed- and sediment-dominated single-channel river sections to a more natural form with braids and gravel bars.

3 | Fish Population Health

Fish population health can encompass multiple aspects of their life history, resource use and interspecific interactions. Generalist fish species, with broad environmental tolerances, are useful for studying population health responses across habitats of varying ecological integrity. Despite their ability to tolerate diverse abiotic stressors, they remain susceptible to conditions that can impact their health and fitness (Schulte 2014; Dala-Corte et al. 2017). Parasite infection, growth rate, behaviour and swimming performance of generalist fish are influenced by environmental conditions and can therefore provide insights into ecosystem health (Vanderpham et al. 2013; Schulte 2014; Canosa and Bertucci 2023). Similarly, the opportunistic feeding habits of generalist fish mean that their diet largely reflects the diversity of local macroinvertebrate communities, which can serve as useful bioindicators (Heatherly et al. 2007; Bonacina et al. 2023).

Floodplain ecosystems support a wide range of macroinvertebrate taxa that, influenced by heterogeneity, hydrological conditions, substrate, nutrient levels, temperature and dissolved oxygen (Burgherr et al. 2002; Woodward and Hildrew 2002; Hill et al. 2017; Thornhill et al. 2017; Garrett-Walker and Collier 2021), can be distinctly distributed along floodplain lateral gradients (Starr et al. 2014). Macroinvertebrate diversity is often negatively impacted by lentic floodplain habitats that are hydrologically isolated and have elevated temperatures, and by nutrient-rich artificial pond habitats that feature hard-engineered edges (Starr et al. 2014; Kraft et al. 2015; Thornhill et al. 2017; Chanut et al. 2019; White et al. 2021). In contrast to the more uniform POND and UNRES treatments, the increased surface area and habitat complexity within the RES treatment are anticipated to provide shelter from physical disturbances and create mosaics of microhabitats that support greater species abundance and diversity, as per Soukup et al. (2022). Based on the negative effects of expected elevated temperature and nutrient enrichment in artificial pond habitats, and the heterogeneity and flow patterns intended to result from gravel and overburden skimming in the RES treatment, we hypothesised that fish populations in RES sites would have a more diverse diet compared to those in the POND and UNRES treatments.

Parasite transmission and load are key aspects of fish population health, often negatively affecting host physiology, reproduction, body condition, behaviour and survival (Lemly and Esch 1984; Ferguson et al. 2011; Timi and Poulin 2020). Parasites can respond to factors including warmer temperatures (Poulin 2006; Macnab and Barber 2012), pollution (Timi and Poulin 2020), host population density (Sonnenholzner et al. 2011; Lagrue and Poulin 2015) and water velocity (Samsing et al. 2015). In our study, the pit mining ponds function as fragmented habitats, largely disconnected from the river system. Such habitat fragmentation in riverine environments can reduce genetic diversity in fish populations, weakening their resilience and capacity to adapt to environmental changes (Van Leeuwen et al. 2017; Brauer et al. 2018), with isolated populations exhibiting reduced diversity and diminished potential for long-term persistence (Brauer and Beheregaray 2020). Eutrophication, by increasing algal production and resource availability, elevates densities of key intermediate hosts such as snails, thereby increasing the abundance and transmission rate of parasites (Johnson et al. 2007). The POND treatment is characterised by habitat fragmentation, stagnant conditions, elevated nutrient levels, and expected higher temperatures, all of which can increase vulnerability to parasite infection. In terms of the river treatments, the more environmentally complex RES sites are expected to support a higher diversity of microhabitats than UNRES sites, leading to greater spatial variability in parasite abundance and correspondingly lower overall parasite densities. Thus, we predicted that fish in the RES treatment would have lower parasite loads than those in both the POND and UNRES sites.

Fish growth rate—a measure of size change over time (Jobling 2002)—is a valuable indicator of environmental conditions (Sogard 1997; Lewis et al. 2021), with growth increasing in response to greater resource availability (Rahman et al. 2008; Vesterinen et al. 2022) but generally limited by high population density (Holm et al. 1990; Lorenz et al. 2012; Matthias et al. 2018). Although environmental complexity, such as that intended through the RES treatment, can enhance resource availability (Soukup et al. 2022), greater food intake promotes faster growth only when the energy gained exceeds the metabolic costs of a more active lifestyle. Increased swimming effort required to cope with higher flow velocities, navigate complex habitats and avoid predators, as observed in river-dwelling fish (Goodrich and Clark 2023), means that the heterogeneity of the RES sites would not be expected to promote faster growth. In higher temperatures, fish may feed more frequently and digest their food more quickly, leading to accelerated growth, until thermal limits are reached (Matthias et al. 2018; Lewis et al. 2021). Warmer habitats, with prolonged spring and summer climates and delayed onset of stressful autumn and winter conditions, can promote faster growth rates (Mann 1991). In terms of nutrient enrichment, nitrogen and phosphorus are key nutrients affecting freshwater food webs, shaping resource availability, and directly influencing growth (Elser et al. 1990; Rahman et al. 2008). Higher temperatures and nutrient levels were expected in ponds; therefore, we hypothesised that fish in the RES and UNRES treatments would have slower growth rates compared to those in the POND treatment.

4 | Methods

4.1 | Study Species

This study focused on populations of the upland bully (*Gobiomorphus breviceps*), a small, non-diadromous native fish species with a conservation status of 'Not Threatened' (Dunn et al. 2018). As a generalist species, upland bullies have broad environmental tolerances and are abundant in all treatments, occurring at every sampling site despite differences in environmental characteristics amongst treatments. They are opportunistic and generalist carnivores (Staples 1975a; McDowall 1990), and it was anticipated that their dietary preferences would largely mirror the availability of macroinvertebrate prey in different treatments. As consumers of lower trophic level prey, and as prey for larger fish and bird species (Griffiths 1976; Ryan 1986; Jellyman 1989; Hamilton 1998), upland bullies are important components of terrestrial and aquatic food webs.

4.2 | Study Design

Environmental variables and fish communities were surveyed at 10 sites along the Aparima River (Figure 3). Sites where the experimental gravel and overburden skimming method was applied were juxtaposed with degraded stretches of river and pit-mined ponds. RES, UNRES, and POND sites were located within a 12-km reach. The survey was repeated three times in February, March and April 2023. All four POND sites were sampled monthly. On the February sampling trip, two UNRES and two RES sites were sampled due to time constraints. All three UNRES and all three RES sites were sampled during the March and April surveys.

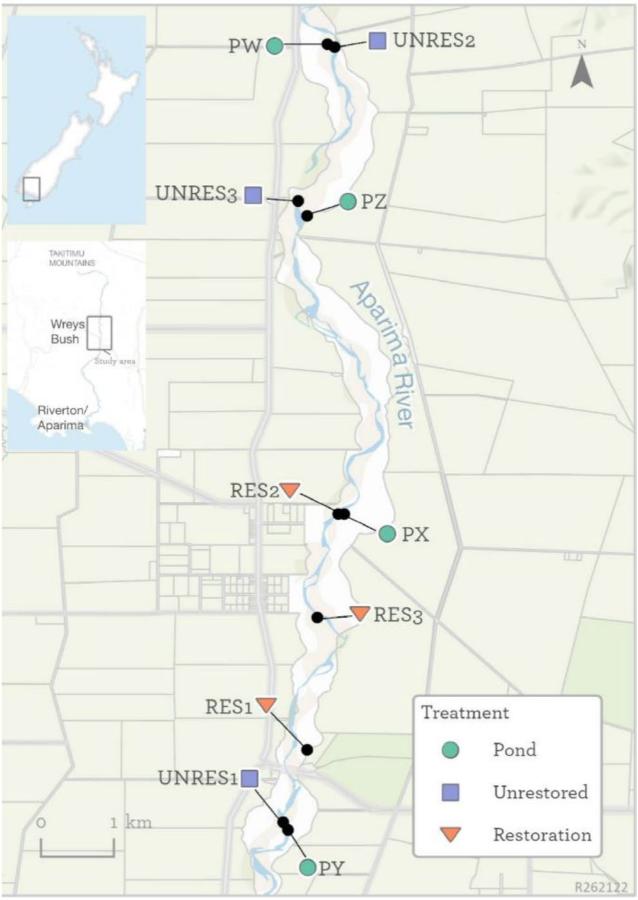

FIGURE 3 | Location of study area and study sites on the Aparima River, Southland, New Zealand. *Map source:* The Department of Conservation and licensed by the Department of Conservation for reuse under a Creative Commons Attribution 4.0 International License, contains data sourced from the LINZ Data Service licensed for reuse under https://creativecommons.org/licenses/by/4.0/. [Color figure can be viewed at wileyonlinelibrary.com]

4.3 | Sampling Procedures

Environmental variables were recorded to characterise the habitat conditions of each treatment, as these can influence the presence, distribution and fitness of freshwater species. Velocity (m/s) (measured with a portable Flo-Mate 2000 flowmeter), wetted width (m) and depth (m), were used to calculate discharge (m^3/s) at river sites. Water samples for nutrient analysis were taken at ½ the depth of the sampling point and frozen at −20°C until analyses. Total nitrogen (TN) and total phosphorus (TP) were quantified in the laboratory on a Skalar Sans plus segmented flow autoanalyzer (Skalar Analytical B.V., Breda, the Netherlands) following standard methodology (Valderrama 1981; Ebina et al. 1983). Dissolved oxygen (mg/L) and temperature (°C) were measured with a YSI Pro 2030 field metre but could not be recorded at the same time of day at all sites, and as their values fluctuate throughout the day, they were excluded from analysis.

Fish sampling techniques were chosen for each habitat type to capture an unbiased sample of species and size classes (Joy et al. 2013; Mehdi et al. 2021). River sites (UNRES/RES treatments) had high velocity, hard bottoms, and were generally wadable (water depths of less than 65 cm), so electrofishing was used to sample these sites. A 40-m reach of the river was treated as one replicate site, and when multiple channels were present all channels were surveyed in this reach. Single-pass upstream electrofishing was conducted using a Kainga EFM300 backpack electrofishing machine (NIWA Instrument Systems, New Zealand). In contrast, POND sites had no flow, deeper and more turbid water and a soft bottom, making electrofishing unsuitable. Thus, POND sites were sampled using unbaited fyke nets (fine mesh 5-m wing, 60 cm drop) and Gee's minnow traps (3 mm mesh size). Each POND site had six sampling stations, located approximately 20 m apart, with each sampling station containing one fyke net and two Gee's minnow traps. Traps were left overnight, and fish were identified and measured the following morning. All procedures involving animal capture, handling and euthanasia were approved by the University of Otago Animal Ethics Committee (AUP-22-98).

A total of 280 upland bullies (10 per site per sampling month) were euthanised by immersion in AQUI-S (175 mg/L), then frozen at −20°C until dissections. Care was taken to select upland bullies of a range of sizes and from multiple locations within the sampling site to obtain an accurate representation of the population. In the laboratory, upland bullies were thawed before being measured (total length in mm) and weighed (total weight in grams). They were then dissected under a dissecting microscope (Olympus SZ51).

4.4 | Diet Analysis

The digestive tract of all 280 upland bullies was dissected to determine macroinvertebrate prey diversity. Twenty-five digestive tracts were empty (20 of these were in POND fish, likely due to some fish not feeding while in traps), and thus the gut contents of 255 upland bullies were considered for analysis. Aquatic macroinvertebrates were identified to the lowest practical taxonomic level (Winterbourn et al. 2006; NIWA 2007) and then aggregated into taxonomic groups (taxa) as per the New Zealand Freshwater Macroinvertebrate Trait Database (NIWA 2018). This database groups taxa into families for insects and molluscs, and higher orders for crustaceans and other groups. Terrestrial macroinvertebrates (adult Diptera) were identified to order. Rare taxonomic groups (occurring once as one or two individuals in a single digestive tract) were excluded from the analysis.

4.5 | Parasite Infection

The preserved condition of 30 upland bullies was poor and deemed unsuitable for parasite examination. Thus, 250 upland bullies were inspected for parasite infection. All fish tissues were dissected, and the species, location and number of parasites were recorded. More than 85% of upland bullies were infected with *Apatemon jamiesoni*, and, given its disproportionately high prevalence and abundance compared to other parasite species, only *A. jamiesoni* was used for statistical analysis. *A. jamiesoni* is a recently described trematode that infects upland bullies in abundance (Blasco-Costa et al. 2016). It emerges as a cercaria (larva) from the New Zealand freshwater mud snail (*Potamopyrgus antipodarum*), and enters upland bullies, forming a metacercarial cyst within the fish (Blasco-Costa et al. 2016; Presswell 2022). When birds consume infected fish, *A. jamiesoni* completes its lifecycle in their digestive tract; eggs are then released into the environment with bird faeces (Blasco-Costa et al. 2016), and the cycle proceeds accordingly. Parasite load was calculated as the number of *A. jamiesoni* per gram of fish to avoid any bias that could arise from comparing parasite load in fish of different sizes. The weight of all parasites within each fish, estimated following Lagrue and Poulin (2015), was subtracted from the mass of each individual upland bully when determining parasite load per gram.

4.6 | Otolith Analysis

The growth of upland bullies in their second year (1+) was estimated to test the effect of treatment on fish growth. Second-year growth rates were chosen instead of first-year growth rates as there is no definite spawning period for upland bullies and they can lay several times per season (Hamilton et al. 1997; McDowall and Eldon 1997). Analysing 1+ growth rates eliminated the uncertainty associated with spawning and hatch times. Sagittal otoliths from 40 upland bullies (four per site, all captured in March 2023) were dissected and air-dried. One otolith from each fish was mounted on a microscope slide with Crystal Bond thermoplastic resin in the sagittal plane. Each otolith was sanded to reveal the core and then polished by a range of 3M Lapping Film Sheets. Annual growth increments (annuli) were independently counted by two observers on an Olympus CH-2 compound microscope (magnification: 40–100×). If a consensus was not attained for an age estimate, the two observers analysed the otolith together and came to a joint conclusion. Nine upland bullies (three from each treatment) had not reached their second year of growth, so were removed from the statistical analysis. Photographs of otoliths were taken using an AmScope Microscope Digital Camera (model number MU1003) attached to an Olympus CH-2 compound microscope (magnification: 40×). The clearest transect from edge to core was taken, avoiding the flat edge, and measurements of annuli were made along this line using calibrated AmScope software. All measurements were made until the end of the second winter (the third summer of growth was not included, and no measurements were taken at the otolith edge).

4.7 | Statistical Analysis

All statistical analysis was conducted in R (version 4.2.3) (R Core Team 2022) with $\alpha = 0.05$. Effect sizes, measured using partial eta-squared values (partial η^2), which range from 0 to 1, were calculated using the 'etasq' function from the 'heplots' package (Friendly et al. 2022). The biological relevance of effect sizes was determined using standardised effect size categories: 'trivial' < 0.1, 'small' > 0.1, 'medium' > 0.3 and 'large' > 0.5 (Cohen 1998; Nakagawa 2004; Nakagawa and Cuthill 2007). Graphs of the results were produced using the ggplot2 package (Wickham 2016) and the RColorBrewer package (Neuwirth 2022). Treatment was a categorical predictor variable in analyses, with three levels (RES, UNRES and POND).

Response variables were diet diversity, parasite load and growth. The Shannon diversity index (Shannon 1948), calculated using the 'vegan' package (Oksanen et al. 2022), was used to determine the diet diversity of each individual fish. The mean diet diversity of fish from each site was calculated and used for statistical analysis. Parasite load was determined by calculating the number of *A. jamiesoni* cysts per gram of fish (with the weight of all parasites removed). The parasite load of each individual fish was log-transformed to reduce skewness. The mean parasite load of fish from each site was calculated from their log-transformed values and used for statistical analysis. Growth was the interval (mm) between the first- and second-year annuli in upland bully otoliths. Although not a response variable, invertebrate sensitivity (based on invertebrates in the diet) was examined. The percentage abundance by number (%*N*) of EPT taxa in each treatment was determined by calculating the %*N* of each EPT taxon for each treatment and month ((number of each EPT taxon per treatment per month/total number of taxa per treatment per month) × 100). These values were averaged across sampling months, followed by summing all taxa per EPT order.

Repeated measures ANOVAs were run on diet diversity and parasite load using the 'car' package and the 'plyr' package (Wickham 2011). Shannon diversity index values and parasite load were the dependent response variables of interest, while treatment was an independent predictor variable, and time was a within-subjects factor. When results were significant, post hoc tests were used to compare overall treatment differences averaged across time using the 'TukeyHSD' function. An ANOVA was carried out to test the effect of treatment on growth using the R functions 'lm' and 'Anova' from the 'car' package (Fox and Weisburg 2019). A post hoc pairwise comparison was run using the 'emmeans' function from the 'emmeans' package (Lenth 2024).

5 | Results

POND sites had no surface water flow, greater depth, and high levels of total nitrogen and total phosphorus, representing hydrologically, morphologically, and chemically distinct ecosystems compared to the more dynamic and continuously flowing RES and UNRES sites (Table 1), which experienced increasing discharge across the sampling months. Of the 280 upland bullies analysed—sampled from across each site and treatment area to ensure a representative population and selected to include a range of sizes—37.5% were female, 32.5% were male, and the sex of 30% could not be determined. 72% of fish identified as females were found to be gravid. The mean length of upland bullies was 46.7 mm, and their mean weight was 1.9 g.

Upland bullies in river RES and UNRES sites consumed considerably more sensitive Ephemeroptera, Plectoptera and Trichoptera (EPT) taxa than those in POND sites, whose diets were dominated by cladocerans, copepods, and ostracods (Table 2). The difference in diet diversity, based on Shannon diversity index values (where higher values indicate greater diversity), was not significant among treatments (Table 3; Figure 4). The mean diet diversity was highest in the RES treatment (0.69 ± 0.14 standard deviation [SD]), followed by the POND (0.58 ± 0.19 SD), and UNRES (0.55 ± 0.16 SD) treatments.

There was a difference in parasite load between treatments (Table 3 and Figure 5). Post hoc tests confirmed that the POND treatment had significantly higher parasite loads than RES ($p = 0.01$*) and UNRES treatments ($p = 0.04$*), whereas there was no significant difference between UNRES and RES treatments ($p = 0.52$). The mean (log-transformed) parasite load was 4.94 (±0.27 SD) in POND sites, considerably higher than the river sites: 2.72 (±1.12 SD) in RES sites and 3.35 (±1.0 SD) in UNRES sites. The mean parasite load values (before log-transformation) were 10.99 (±11.47 SD) in RES sites, 18.69 (±18.09 SD) in UNRES sites and 68 (±79.26 SD) in POND sites.

An ANOVA testing the influence of treatment on upland bully growth (mm per year), revealed a significant difference in growth across treatments ($p = 0.0002$***, $F = 11.63$, partial $\eta^2 = 0.45$, df = 2, df (residual) = 28; Figure 6). Post hoc tests showed that growth rates were significantly higher in POND fish than in RES fish ($p = 0.0002$***) and UNRES fish ($p = 0.03$*), with no difference between RES and UNRES fish ($p = 0.18$).

TABLE 1 | Mean and standard deviation (SD) of environmental variables per treatment across sampling months, displayed as mean (±SD).

	RES	UNRES	POND
Depth (m)	0.29 (±0.09)	0.41 (±0.14)	0.92 (±0.4)
Total nitrogen (μg/L)	266.29 (±84.28)	292.57 (±157.67)	418.79 (±227.03)
Total phosphorus (μg/L)	7.95 (±2.89)	19.54 (±13.73)	33.21 (±30.06)
Velocity (m/s)	0.34 (±0.1)	0.38 (±0.32)	0
Discharge (m^3/s)	3.91 (±1.96)	5.97 (±7.19)	0

Note: All variables were sampled monthly in February, March, and April, except POND depth which was sampled in February and April only.

TABLE 2 | Mean and standard deviation (SD) of percentage abundance by number (%*N*) of EPT taxa in fish diet per treatment across sampling months, displayed as mean (±SD).

Order	%*N* POND	%*N* RES	%*N* UNRES
Ephemeroptera	0	25.97 (±13.76)	33.27 (±20.71)
Plecoptera	0	1.1 (±0.36)	0
Trichoptera	0.23 (±0.25)	27.13 (±9.3)	12.57 (±6.15)
Total %*N* EPT taxa	0.23 (±0.25)	54.2 (±16.61)	45.84 (±21.6)

TABLE 3 | Results of repeated measures ANOVA testing the influence of treatment (RES vs. UNRES vs. POND) and time on mean diet diversity and mean parasite load per site per sampling occasion.

		df	*F*	*p*	Partial η^2
Diet diversity	Treatment	2	1.69	0.27	0.4
	Time	2	2.01	0.18	0.31
	Treatment:time	4	1.41	0.3	0.47
Parasite load	*Treatment*	*2*	*7.46*	*0.03**	*0.75*
	Time	2	0.32	0.74	0.19
	Treatment:time	4	1.22	0.36	0.24

Note: Degrees of freedom (df), *F* value (*F*), *p* value (*p*), and partial eta-squared values (partial η^2) are shown. Significant effects are in italics.

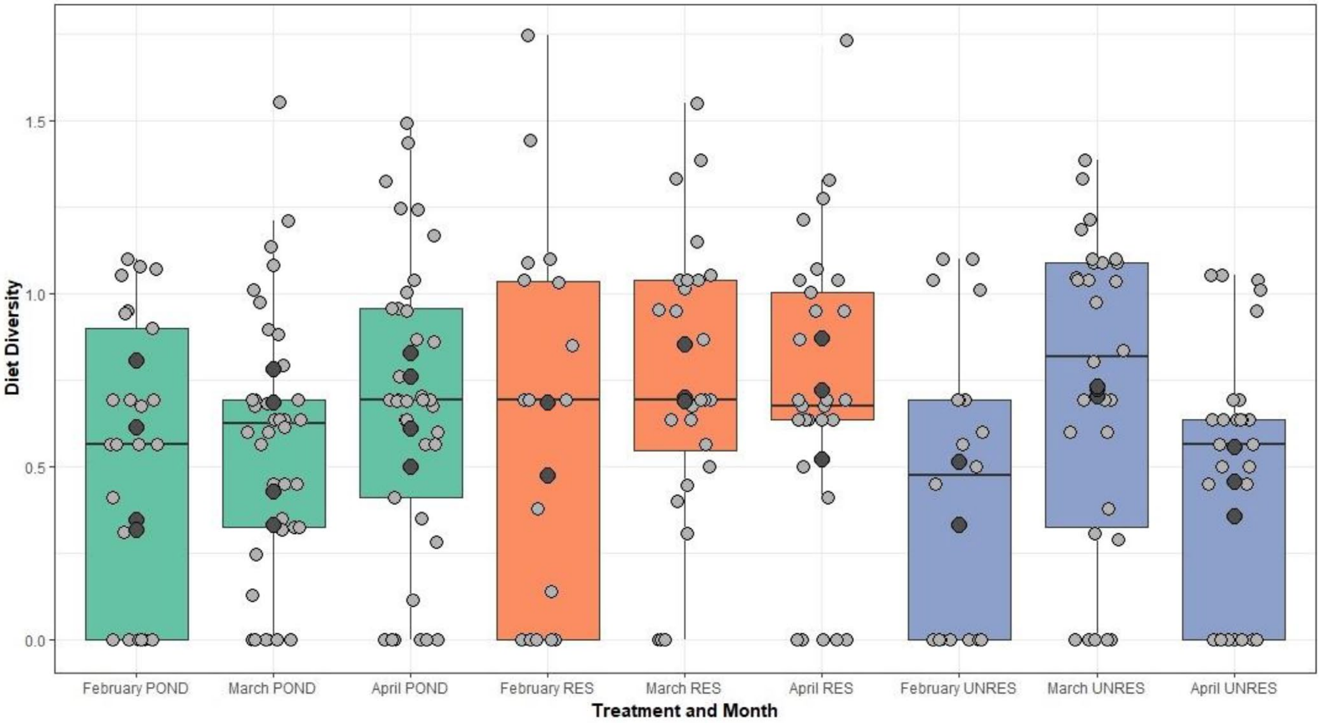

FIGURE 4 | Diversity (based on Shannon diversity index) of diet contents across treatments and months. Boxplots show the ranges and the distribution (median, 25th and 75th percentiles) of the data. Black dots represent the mean diet diversity value per site, and grey dots show the diet diversity per individual fish. Dots have been jittered slightly to account for overlap. [Color figure can be viewed at wileyonlinelibrary.com]

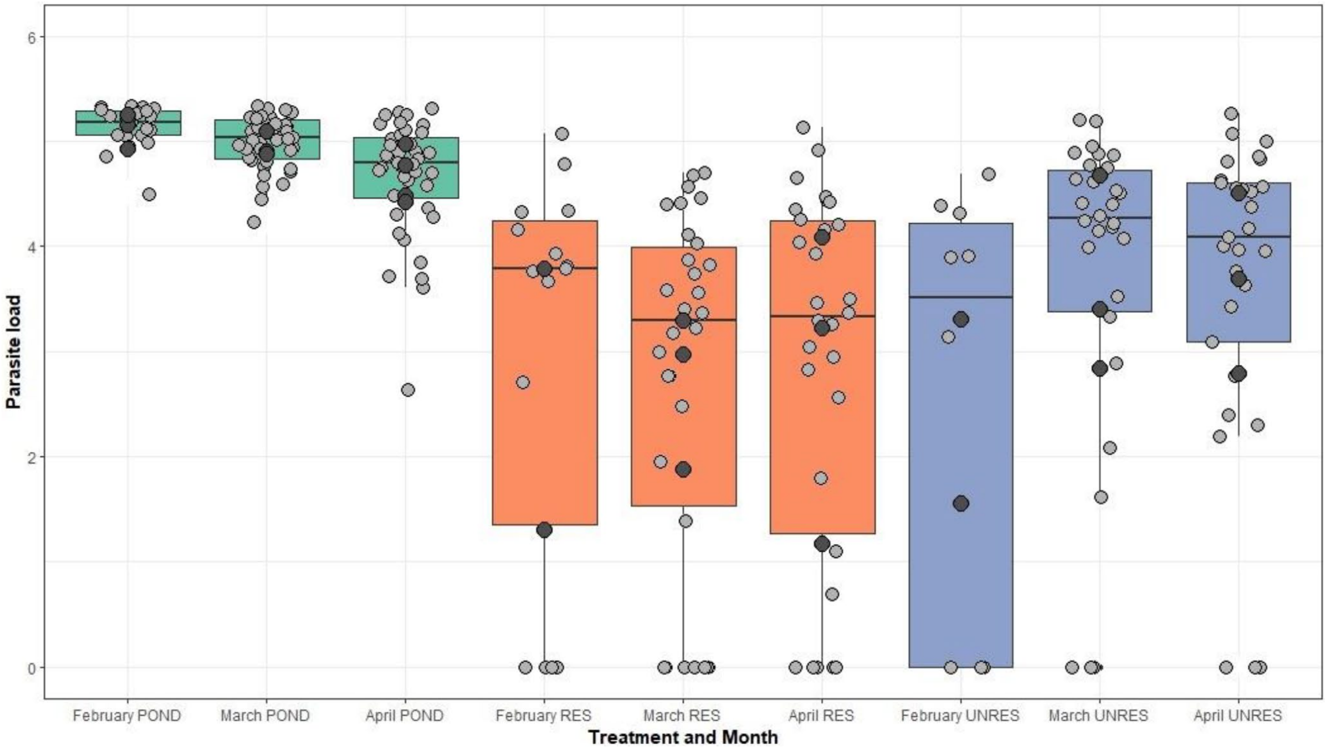

FIGURE 5 | Parasite load (*Apatemon jamiesoni* cysts per gram of fish, log-transformed to reduce skewness) across treatments and months. Boxplots show the ranges and the distribution (median, 25th and 75th percentiles) of the data. Black dots represent the mean parasite load per site, and grey dots show the parasite load per individual fish. Dots have been jittered slightly to account for overlap. [Color figure can be viewed at wileyonlinelibrary.com]

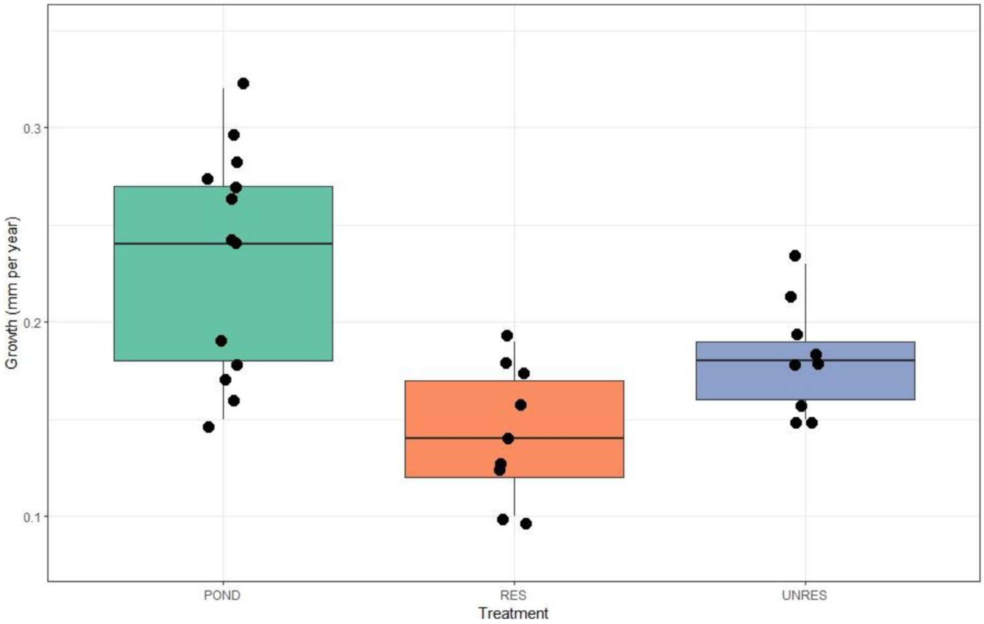

FIGURE 6 | Growth (mm per year) of second-year (1+) upland bully otoliths. Boxplots show the ranges and the distribution (median, 25th and 75th percentiles) of the data. Dots have been jittered slightly to account for overlap. [Color figure can be viewed at wileyonlinelibrary.com]

6 | Discussion

Our study of upland bully populations in treatments with distinct histories of gravel extraction revealed large differences in fish population health between pond and river sites. As predicted, parasite infection and growth rates in ponds were greater than in the other treatments, indicative of higher temperatures and nutrient levels. However, river sites where experimental gravel and overburden skimming had been undertaken (RES) did not significantly differ from degraded control sites (UNRES) in any of the measured population health indicators. Although this result indicates that gravel can be extracted in a way that does not impact the fish population health variables assessed, it does not support the predicted benefits of increased heterogeneity resulting from the intended restorative effects of the gravel and overburden skimming technique. Specifically, the anticipated outcomes of greater diet diversity and lower parasite densities were not observed. The similarities in population health between RES and UNRES sites could be attributed to several factors, including the possibility that the distance between these treatments was not large enough relative to the scale of the catchment. This proximity may have allowed fish populations to remain well connected, making it difficult to detect potential differences between treatments. Diet data, which reflects recent prey consumption, likely corresponds to the spatial scale of each treatment; however, longer-term data from growth rates and parasite loads within river sites may include fish that have not remained in specific treatments for their entire lives. Future research could apply the gravel and overburden skimming method at larger spatial scales with greater distances between sites, incorporating pre- and post- extraction monitoring and regular assessments thereafter. This approach would reduce connections between fish populations and their resources and provide clearer insights into the restorative potential of the gravel and overburden skimming technique.

Variation in the diet diversity of upland bullies, opportunistic and generalist species, may reflect environmental differences that influence the diversity of their macroinvertebrate prey. A more diverse prey selection typically indicates a more complex and resilient food web, contributing to healthier fish populations. Although our macroinvertebrate analysis focused solely on prey items, accurately assessing macroinvertebrate diversity and composition across treatments would require comprehensive sampling directly from the ecosystem. However, as generalist feeders, upland bullies' diet choices should largely mirror the most abundant prey available. Contrary to our hypothesis, diet diversity was similar amongst treatments. POND sites sustained a diversity of macroinvertebrate prey that was comparable to the riverine sites, despite the relative isolation and high nutrient levels of ponds.

While the UNRES treatment displayed fluctuations in diet diversity over time (Figure 4), the diversity of prey in the RES sites remained stable, suggesting sufficient environmental heterogeneity to support prey populations and consistent fish foraging behaviour, regardless of hydrological and morphological conditions. Such stability arising from habitat complexity is an important trait for the temporal resilience of freshwater communities, particularly in the face of climate change. These findings align with those of Soukup et al. (2022), who found that habitat complexity exerts bottom-up effects on community structure and energy flow within food webs, enhancing foraging opportunities and promoting overall food web stability. The diet of upland bullies in POND sites was dominated by cladocerans, copepods and ostracods, taxa typical of lentic habitats and tolerant of environmental stressors (Gilippa et al. 2018; White et al. 2021). In contrast, upland bullies in RES and UNRES sites consumed more EPT taxa, known to be sensitive to stressors like eutrophication, pollution and sediment accumulation, and to prefer cold, well-oxygenated environments with elevated flows and riffle habitats (Jowett and Richardson 1990; Chanut et al. 2019; Burgazzi et al. 2021; Barrett et al. 2022; Sabha et al. 2022). However, EPT taxa are typically stream-associated, so their low frequency would be expected even in a healthy pond.

Although RES sites had the lowest mean parasite density, there was no significant difference compared to UNRES sites, whereas parasite loads were significantly higher in POND sites. Parasites serve as indicators of species within a system, with their presence implying the presence of their various hosts (Shea et al. 2012) and offering insights into the ecosystem's health and habitat conditions. Although not reflected in the diet of upland bullies, with similar percentage relative abundances of *Potamopyrgus antipodarum* snails across all treatments (POND = 1.4%, RES = 0.6% and UNRES = 1.7%), the significantly greater number of parasites in the POND treatment suggests that ponds support elevated densities of *P. antipodarum*, the first intermediate host of *A. jamiesoni*. The absence of higher *P. antipodarum* densities in diet analysis was likely a reflection of diet preference rather than relative abundance. The density of *P. antipodarum* can substantially increase in low velocity zones, and its abundance shows a rapid decline at high velocities (Holomuzki and Biggs 2007), highlighting the lentic nature of the POND treatment. A consumer of algae, *P. antipodarum* has faster development in environments conducive to algal growth, which are typically characterised by warm temperatures and elevated nutrient levels (Elser et al. 1990; Rahman et al. 2008; McKenzie et al. 2013). This further confirms the nutrient-rich nature of the POND sites which are eutrophic based on nitrogen and phosphorus concentrations, as per Burns et al. (1999). Our findings are consistent with a study in which eutrophication in lentic systems enhanced the intensity of parasite infection and transmission in amphibians by increasing nutrient availability, algal production, and snail host densities, ultimately amplifying per-snail parasite output (Johnson et al. 2007). Higher temperatures enhance embryonic development of *P. antipodarum* (Gust et al. 2011), supporting population growth, and hence their ability to act as hosts to *A. jamiesoni* in large numbers. This suggests that conditions in the POND treatment may be warmer compared to the riverine treatments, which would positively influence parasite presence and reproduction rates.

The presence, abundance and diversity of parasites in fish can serve as indicators of ecosystem function (Sures et al. 2017; Morales-Serna et al. 2019) and provide insights into the environmental conditions of the treatments in this study. The prevalence of parasites has been linked to eutrophication (Johnson et al. 2007; Okamura et al. 2011), and elevated levels of both parasites and nutrients were found in the POND treatment. Lower parasite numbers, as found in the RES and UNRES treatments, are more common in higher water velocity conditions, as flow can influence the ability of parasites to attach to their hosts (Samsing et al. 2015). Higher flows reduce contact time between parasites and their hosts, thereby reducing attachment and settlement success (Samsing et al. 2015). In our study, the relatively small overall size of *A. jamiesoni* (Blasco-Costa et al. 2016) could result in difficulties resisting flowing water; thus the lower levels of *A. jamiesoni* infection in the RES and UNRES sites are consistent with their lotic nature, which may help to protect fish against *A. jamiesoni* infection. Additionally, warmer temperatures can enhance parasite transmission and increase their growth, life cycle progression and prevalence (Poulin 2006; Macnab and Barber 2012), and the greater parasite density in pond fish is an indicator of warmer temperatures in ponds. High parasite densities, such as the significantly higher parasite loads in fish from the POND treatment, may negatively impact their host's body condition, reproduction, energetic state, behaviour, growth and survival (Lemly and Esch 1984; Houde and Torio 1992; Poulin 1994; Ferguson et al. 2011; Hammond-Tooke et al. 2012). Although POND fish had high parasite densities, they also exhibited fast growth rates, which may be explained by the energy gained from consuming abundant infected prey contributing to increased growth, and offsetting the physiological costs of parasitism, as per Henriksen et al. (2019).

Upland bully growth rates between RES and UNRES sites were not significantly different, while the POND treatment displayed significantly faster growth. The contrast in growth rates between river and pond treatments may be related to environmental factors such as velocity, discharge and temperature. Fish require less energy for swimming or maintaining their position against slower velocities in lentic habitats, while higher velocities are typically associated with increased energy demands (East and Magnan 1987; Matthews et al. 1996; Sethi et al. 2022). The reduced flow in ponds could mean that upland bullies have lower energy requirements for swimming, and thus, more energy available for growth. Temperature can impact prey abundance and availability and can alter rates of predator digestion and food assimilation (Mann 1991) and may have had a regulating effect on growth in this study. The faster growth rates in the POND sites indicate that this treatment may have higher temperatures that promote growth.

Resource and prey availability can impact the growth rates of fish (Mann 1991; Sogard 1997; Rose et al. 2015). Nitrogen and phosphorus, which were found in greater concentrations in ponds, exert a considerable influence over freshwater food webs and resource abundance, as they promote the growth of algal phytoplankton (Elser et al. 1990; Rahman et al. 2008). Algae are a vital food source for zooplankton and macroinvertebrates (Rahman et al. 2008; Vesterinen et al. 2022), and the enhanced fish growth within the POND sites aligns with their higher nutrient levels which support a plentiful food supply. The increased growth rate in ponds also suggests that macrophytes, which expand the surface area available for algal colonisation (Yofukuji et al. 2021), may occur in higher numbers in ponds.

The faster growth of upland bullies in ponds may be linked to higher macroinvertebrate abundance, which would provide more prey and foraging opportunities for fish. This supports the idea that lentic environments often sustain high macroinvertebrate densities, especially during winter (Sethi et al. 2022). The greater foraging opportunities could lead to reduced energy expenditure for fish, allowing more energy to be allocated towards growth. Faster growth rates of fish may lead to earlier sexual maturity and faster reproduction (Jobling 2002; Pauliny et al. 2015), reduce predation risk and enhance survival (Goodrich and Clark 2023), and increase prey size, capture efficiency, and foraging ability (Sogard 1997; Fernandez-Jover and Sanchez-Jerez 2015). However, trade-offs among life-history traits mean that rapid growth in fish is often associated with accelerated aging and a shortened lifespan (Lee et al. 2013; Pauliny et al. 2015), higher biomass of parasites (Barber 2005), and smaller adult size (Stearns 1989). In addition, the underlying factors of faster growth in the POND fish, such as eutrophication and elevated temperatures, are unlikely to be beneficial for fish populations in the long term.

Upland bullies demonstrated high catch rates in ponds, and it is likely that they were more abundant in ponds than in riverine treatments, although the different sampling techniques mean that this cannot be quantified. Various investigations demonstrate that as population density increases, individual growth rates tend to decrease due to competition for resources (Holm et al. 1990; Lorenzen and Enberg 2002; Lorenz et al. 2012; Matthias et al. 2018). In a study specifically focusing on a lake population of upland bullies, it was observed that their growth was density-dependent (Staples 1975b). In the present study, despite the likely higher densities of bullies in ponds, they exhibited faster growth rates, which suggests that nutrient levels, temperatures and other environmental conditions in pit-mined ponds outweigh any density-dependent limitations of the population.

7 | Conclusions and Recommendations

Restoration and gravel extraction can considerably alter the surrounding environment, and the diet, growth and parasite load of resident fish populations can provide insights into these changes. Our study indicates that the two gravel extraction methods assessed create habitats with distinct biological, hydrological, morphological and physicochemical characteristics, as reflected in the health of generalist freshwater fish populations. The greater growth of fish in pit-mined ponds could be due to elevated nutrient levels, lack of flow and potential higher temperatures prevailing in these unnatural environments. Furthermore, the significantly higher rate of parasite infection documented in the ponds may be caused by conditions within these habitats that are favourable to parasites and their hosts, potentially leading to adverse impacts on fish population health. Our findings indicate that pit mining creates lentic, homogenous ponds that support fish populations experiencing distinct stressors and displaying different health characteristics compared to those in lotic river environments. The diet, parasite load and growth of generalist fish captured at RES sites, designed for restoration, were similar to those of the control UNRES sites, making the restorative effects of gravel and overburden skimming uncertain. However, habitats at RES sites resemble natural conditions more closely than those formed by pit mining, where higher growth rates and parasite loads in fish reflect a stagnant and eutrophic environment. Based on the variables assessed, the gravel and overburden skimming technique is a less environmentally disruptive gravel extraction option compared to pit mining. Restoring ecosystem functioning and native biodiversity in river ecosystems is crucial. Therefore, further regulation, monitoring and development of integrative gravel extraction and restoration techniques, designed to support these restoration goals, are recommended.

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Ethics Statement

All procedures involving animal capture, handling and euthanasia were approved by the University of Otago Animal Ethics Committee (AUP-22-98).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.28692383.v1.

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