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Long-Term Fish Assemblage Responses to Instream Restoration in Boreal Streams: Insights From a 24-Year BACI Study

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ABSTRACT

1. Freshwater ecosystems are increasingly threatened by human activities and climate change, emphasizing the need for effective habitat restoration supported by long-term monitoring.
2. We examined fish species responses to instream restoration in six boreal streams in northern Finland over a 24-year period (1999–2022) using a Before–After–Control–Impact (BACI) design, including 3 years before and 21 years after restoration. Each stream contained three reaches: one restored with large woody debris and stones (LWD + s), one with added stones only and one left as a control. Using generalized linear mixed models, we assessed the effects of restoration type, water temperature and discharge on total fish density and biomass as well as on key species, brown trout (*Salmo trutta*), burbot (*Lota lota*) and European bullhead (*Cottus gobio*).
3. Overall fish abundance and biomass declined over time, including in control reaches, suggesting a shifting baseline of ecological conditions. However, LWD + s-restored reaches showed weaker long-term declines in fish density and biomass than control reaches, indicating that wood additions buffered fish populations against long-term environmental deterioration. Brown trout showed more positive long-term responses in reaches containing LWD + s, whereas burbot responses were more strongly associated with stone additions, reflecting species-specific habitat preferences. European bullhead was not affected by restoration. Rising water temperatures and variable flows were associated with reduced fish densities, consistent with regional climatic trends.
4. Our results demonstrate that while local restoration can mitigate habitat degradation, its success is constrained by broader hydrological and thermal variability. Effective river management in boreal regions may require integrating catchment-level water retention measures with instream habitat enhancement, supported by sustained long-term BACI-based monitoring to capture delayed ecological responses.

1 | Introduction

The United Nations Decade for Ecosystem Restoration (2021–2030) underscores that ecological restoration is essential for mitigating ecosystem degradation. Historically, river restoration has primarily focused on enhancing habitats by improving the

structural characteristics of river channels. While instream habitat restoration remains a crucial component, the scope of restoration has expanded from form-based habitat enhancement towards process-based restoration that seeks to restore key physical and ecological processes both within river channels and across catchments (Beechie et al. 2010; Wohl et al. 2015).

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For example, stream flows shape ecosystem processes and influence the composition and structure of aquatic communities. A comprehensive understanding of the impacts of flow regimes on biota is essential for successful river restoration at both local and regional scales (Liang et al. 2015; Palmer and Ruhi 2019; Theodoropoulos et al. 2020).

A significant number of boreal forest rivers were dredged to facilitate log floating during the early 20th century (Iversen et al. 2000; Nilsson et al. 2005). Dredging simplified the morphological complexity of streambeds and altered hydrological patterns important for aquatic organisms (Jutila 1985; Muotka and Syrjänen 2007). The latter half of the century witnessed restoration efforts targeting thousands of kilometres of modified streams, with a focus on enhancing habitat conditions for economically valuable salmonid species (Nilsson et al. 2005; Vehanen et al. 2010). Previously removed boulders were returned to the streams to construct flow-modifying structures such as deflectors and boulder dams, and lateral channels were reopened and gravel beds were created (Yrjänä 2003). This approach was based on the premise that restoring habitat heterogeneity through physical modifications will encourage the recolonization of diverse organisms, thereby linking physical habitat restoration with biological recovery and biodiversity enhancement (Palmer et al. 2007).

Despite the significant resources allocated to restoration of degraded river ecosystems, there are relatively few comprehensive assessments of the ecological effectiveness of these projects (Skinner et al. 2023). Some evidence indicates that biological communities respond weakly to stream habitat restoration (Palmer et al. 2010; Theodoropoulos et al. 2020), and the overall benefits of in-stream restoration structures can be unclear or non-existent (Thompson 2006; Stewart et al. 2009; Brettschneider et al. 2023). Some recent syntheses from intensively monitored catchment studies have further highlighted the challenges of detecting population-level restoration responses in salmonid systems (Bilby et al. 2024; Bisson et al. 2024). These difficulties may partly arise from incomplete understanding of the processes regulating fish abundance and production, which can lead to restoration efforts being implemented at insufficient spatial scales relative to the extent of habitat degradation. In addition, ecological recovery following habitat restoration may take decades, meaning that restoration responses can remain undetected without prolonged monitoring. Long-term datasets are therefore essential for distinguishing restoration effects from natural environmental variability and broader directional environmental change.

However, there are several instances of positive responses, particularly among salmonid fishes, suggesting specific ecological gains (Whiteway et al. 2010; Marttila et al. 2019). While in-stream restoration has been successful in enhancing habitat heterogeneity in boreal streams, evidenced by decreased flow velocities and increased bed complexity (Muotka and Syrjänen 2007; Gardeström et al. 2013), biotic responses appear weak or difficult to detect for many species (Nilsson et al. 2015). This juxtaposition underscores the complex and varied nature of ecological responses to restoration efforts, highlighting the need for more targeted restoration strategies.

Long-term restoration outcomes are increasingly influenced by directional environmental change, including climate-driven shifts in temperature and hydrological regimes. Reduced discharge, altered flow variability and increasing temperatures may modify habitat quality, fish performance, and the persistence of restoration effects through time (Woodward et al. 2010; Palmer and Ruhi 2019; Theodoropoulos et al. 2020). Consequently, restoration responses observed shortly after implementation may weaken, strengthen or change direction over decadal timescales as regional environmental conditions continue to shift. This highlights the importance of long-term monitoring for distinguishing restoration effects from broader climatic and hydrological trends (Heino et al. 2009; Carpenter et al. 2011).

The evaluation of ecological restoration projects is pivotal for justifying their application in the management of natural resources (Wortley et al. 2013). A lack of thorough or sufficiently long-term assessment poses the risk of persistently employing inefficient methodologies, thus diminishing restoration efficiency (Nilsson et al. 2015). Robust monitoring and evaluation of restoration outcomes remain challenging and are still inconsistently implemented (Wortley et al. 2013; Tickner et al. 2020). Additionally, while numerous studies have delved into the potential impacts of climate change on freshwater environments, the majority have concentrated on individual organisms or single-species populations, rather than on community-level or broader ecological impacts (Woodward et al. 2010).

We investigated long-term impacts (3 years pre-restoration and 21 years post-restoration) of in-stream habitat restoration on fish community density and biomass across six forest streams in northern Finland. Channelized in the 1950s and 1960s for timber transport, these streams underwent restoration in 2001 through the addition of logs and boulders. We evaluated the comparative benefits of two habitat enhancement approaches: the large woody debris versus stone-based structures. We posited that large wood, by altering stream flow, increasing pool volume and enhancing organic matter retention, offers distinct advantages over adding only boulders (Wohl et al. 2015; Swanson et al. 2021). Consequently, we anticipated that the combined introduction of large wood and boulders would yield long-term fish population benefits compared to the addition of boulders only.

Building on our previous investigations (Vehanen et al. 2010; Louhi et al. 2016), to examine short-term restoration effects on brown trout (*Salmo trutta*) densities and growth, this study extends the analysis to a 21-year post-restoration recovery period, focusing on changes in overall fish density, biomass and species-specific densities. We incorporate environmental data (stream flows, water temperatures) covering the 24-year study duration to elucidate fish density fluctuations. We hypothesized that over this extended period, environmental factors, particularly low-flow conditions, would predominantly influence fish populations. However, these effects were expected to be less pronounced in sections restored with large wood, as wood structures may provide refuges and buffer fish against drought conditions (Vehanen et al. 2010).

2 | Material and Methods

2.1 | Study Streams, Study Design and Restoration

This study was conducted in six boreal forest streams located in northeastern Finland within the upper River Oulujoki catchment (Figure 1). The streams were selected randomly from previously channelized forest streams in the region and are representative of boreal Fennoscandian headwater systems. Stream widths ranged from 2 to 5.5 m, and channels were characterized by boulder-, cobble- and gravel-dominated substrates. Additional background information on the study streams and restoration design is provided in Vehanen et al. (2010) and Louhi et al. (2016).

In each stream, three reaches were selected for the experiment (Table 1). Reaches were separated by at least 300 m of slow-flowing habitat and represented independent experimental units. Fish monitoring was conducted within standardized sections of approximately 350 m² within each reach. Pre-restoration monitoring was carried out during 1999–2001, after which one reach per stream was restored using stones only, one using stones combined with large woody debris (LWD + s), and one was left untreated as a control. Treatments were assigned in randomized order within each stream, following a randomized block BACI design.

The two restoration treatments were designed to represent alternative restoration strategies rather than different levels of restoration intensity. In the LWD + s treatment, large wood

replaced part of the boulder placement used in the stone-only treatment, although boulders and spawning gravel were still added. Consequently, the LWD + s treatment did not simply involve a greater quantity of restoration material but a different combination of structural elements.

Restoration was conducted in autumn 2001 along the full length of each restored reach (Table 1). Restoration measures aimed to increase habitat heterogeneity, flow diversity and refuge availability by returning dredged boulders and cobbles to the channel and by adding large woody debris and spawning gravel. More detailed descriptions of the restoration methods are provided in Vehanen et al. (2010).

A habitat survey, conducted in all study sections both before and immediately after restoration, revealed that restoration led to the formation of deeper sections with slower water flow and increased habitat heterogeneity, particularly where wood was added (Vehanen et al. 2010). Most drastic change was the loss of aquatic vegetation (mainly mosses) in the boulder-restored sites. In a new habitat survey 12 years post-restoration, mosses had recovered in the boulder-restored sites but remained low in the LWD + s-restored sites (Louhi et al. 2016). LWD + s sites were characterized by significantly more wood and deeper stream pools, whereas channelized sections featured a high presence of aquatic macrophytes and a near absence of wood. Boulder-restored sections displayed moderate characteristics in most aspects (Louhi et al. 2016). Visual assessments of the restoration structures indicated partial deterioration over time (Louhi et al. 2016).

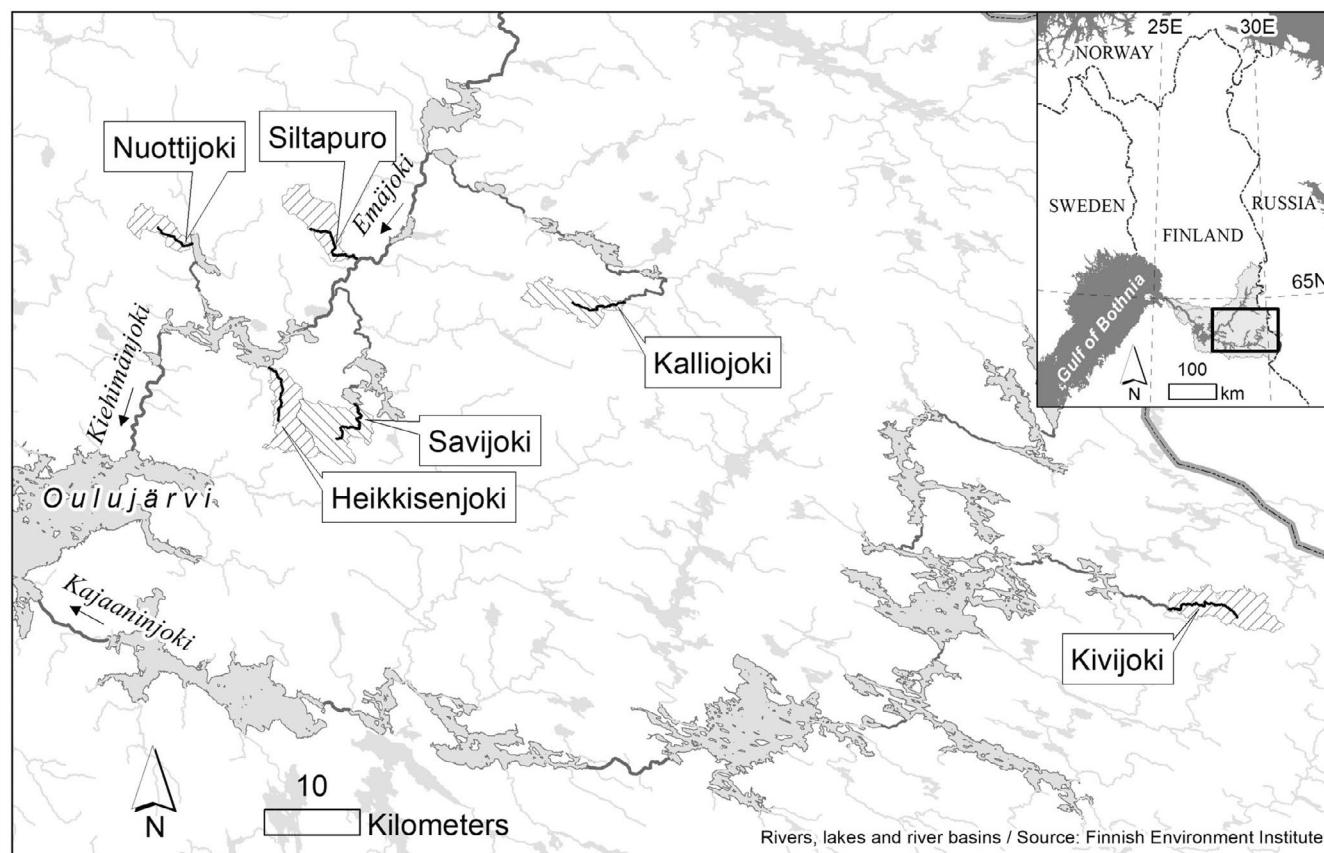


FIGURE 1 | The location of the six study streams in Finland. The hatched areas indicate the catchment area for each stream.

TABLE 1 | Characteristics of the six study streams and restored reaches.

Stream	Reach position and treatment	Reach length (m)	Mean width (m)
Kivijoki	Stone	630	4.0
	LWD + s	190	3.0
	Control	250	2.0
Kalliojoki	Stone	160	3.5
	Control	200	5.0
	LWD + s	180	4.0
Savijoki	Control	220	3.5
	LWD + s	540	3.5
	Stone	100	3.0
Heikkisenjoki	Control	280	4.5
	LWD + s	600	3.5
	Stone	130	2.5
Siltapuro	Control	1040	5.5
	LWD + s	1100	4.5
	Stone	460	5.0
Nuottijoki	Stone	300	3.5
	LWD + s	720	3.4
	Control	320	3.5

Note: LWD + s indicates reaches restored using large woody debris and stones, whereas stone reaches were restored using stones only. Reaches are presented in upstream-to-downstream order within each stream.

For each stream under study, the catchment area was delineated and land use within each catchment was characterized using data derived from the CORINE Land Cover database (European Environment Agency 2018). The catchments of the six study streams ranged from 14.1 to 34.4 km² (Figure 1, Table S1). Drainage of peatlands for forestry was the major modification to natural hydrological systems in the catchments of the study streams. No major new peatland drainage activities were recorded in the catchments during the monitoring period. However, routine forest management activities, including local logging operations, continued within the catchments.

2.2 | Fish Monitoring

Fish densities and biomass were monitored annually from 1999 to 2022, covering a 24-year period. Sampling was conducted each August to minimize potential seasonal shifts in fish assemblages and associated assessment bias, using standardized electrofishing techniques (Vehanen et al. 2010; Sutela et al. 2017). In each case, a three-pass removal method was used to enhance accuracy. The Zippin maximum-likelihood method for three catches (Zippin 1958) was used for estimating population size (N) and biomass (g). Species-specific catchability coefficients were also calculated for each identified species.

2.3 | Stream Flows

We used the national-scale model VEMALA (Huttunen et al. 2016) to compute stream-specific daily flow data for our study streams. VEMALA is a national-scale hydrological model that simulates water flow dynamics by incorporating spatially distributed representations of key hydrological processes, accounting for the effects of climate, topography, land cover and land use practices (Vehviläinen and Huttunen 2001; Vehviläinen et al. 2005). By incorporating daily precipitation and temperature data, VEMALA employs various submodels to predict daily flow dynamics, encompassing precipitation patterns, snow accumulation and melting processes, surface water dynamics, as well as storage components such as soil moisture and groundwater, alongside a comprehensive lake and river routing scheme. Notably, the model undergoes continual calibration against a substantial national gauging network for accuracy and reliability.

We analysed stream flow data over an extended period (1990–2022), beyond the primary study period, to assess long-term trends in discharge and to determine whether flow conditions during the study period differed from the longer-term hydrological baseline. Initially we computed the standardized daily anomalies (mean = 0, standard deviation = 1) from the daily flow time series for each stream during these years. We then summed the standardized daily anomalies sequentially, and the resultant time-series was plotted to determine stream-specific cumulative curves of standardized daily anomalies for the flow time series (Jacobeit et al. 2001). Turning points in the accumulated deviation curve (peaks and troughs) indicate shifts between periods of below- and above-average stream flow relative to the long-term mean.

2.4 | Water Temperature

Automatic temperature loggers (StowAway TidbiT, Onset Computer Corporation, Bourne, MA, U.S.A.) were used to monitor water temperature during the early study years 1999–2003 to reveal the annual cycle in water temperatures (Vehanen et al. 2010).

Surface water temperature was measured each year (1999–2022) and at the study site in August during the fish sampling using a digital water thermometer. This value was used to represent temperature changes during the study in the analysis of fish population dynamics. Like stream discharge, we used temperatures from the previous autumn to explain next year's fish abundance.

2.5 | Water Chemistry and Catchment Characteristics

Water chemistry was monitored in all streams during nine subsequent years (1999–2007, 1–7 samples per year) during the open water period. In one of the streams, River Nuottijoki, sampling was continued annually until 2021 to detect possible long-term trends in water quality. Total phosphorus (µg/L), total nitrogen (µg/L), water colour (mgPt/L), total iron (µg/L), alkalinity (mmol/L), and pH were analysed in the laboratory.

Water chemistry data were obtained from national environmental monitoring databases maintained by Finnish environmental authorities. Analyses were conducted using standardized and accredited laboratory methods routinely applied in Finnish environmental monitoring programmes (Finnish Environment Institute 2025).

2.6 | Data Analysis

The post-restoration period was divided into three periods, each 7 years long: early post-restoration (2002–2008), mid-term (2009–2015) and long-term (2016–2022). Fish abundance was analysed against the 1999–2001 pre-restoration period. This temporal subdivision enabled evaluation of how restoration responses changed over time (Smokorowski et al. 2015; Bylak et al. 2023) and facilitated interpretation of temporal changes across comparable post-restoration intervals. The division was ecologically justified because hydrological conditions differed markedly among the three phases of the study, as indicated by the long-term discharge analyses.

A previous mark–recapture study by Vehanen et al. (2010) indicated minimal brown trout migration between study sections. Consequently, each study reach was treated as an independent experimental unit. We applied generalized linear mixed models (GLMMs) to assess how restoration efforts, either the addition of stones alone or in combination with large woody debris (LWD + s), affected fish abundance and biomass. In statistical analyses, Zippin-estimated counts were modelled with sampled area included as a log-transformed offset. For visualization, figures illustrate area-standardized fish densities (individuals per 100 m²) to facilitate comparison among sites.

The total abundance of all fish species combined was analysed assuming a negative binomial distribution with a log link. The total biomass of all fish species combined was analysed assuming a Gamma distribution with a log link. Species-specific abundances for the most common wild species occurring in all streams and study reaches—brown trout, European bullhead (*Cottus gobio*) and burbot (*Lota lota*)—were analysed using the same negative binomial GLMM framework as for total abundance, including sampled area as a log-transformed offset.

The models accounted for temporal variation by including monitoring period (pre-restoration and three post-restoration periods) and restoration treatment (control, stone, LWD + s), as well as their interaction, as fixed effects. Stream and year were included as random intercepts to account for spatial structure and repeated measurements over time. The primary focus was on detecting treatment-specific responses over time, particularly differences between restored and control reaches across monitoring periods.

The primary analyses consisted of BACI-based GLMMs fitted to the observed fish abundance and biomass data. Fish abundance was analysed using Zippin-estimated counts with sampled area included as a log-transformed offset, whereas biomass was analysed as biomass per unit area. These BACI models tested whether restored reaches differed from control reaches over time without baseline adjustment.

In addition, complementary baseline-adjusted analyses were conducted to evaluate how strongly individual reaches changed relative to their own pre-restoration conditions through time. For each reach, the mean value during the pre-restoration years (Period 0) was used as a baseline, and post-restoration responses were expressed as deviations from this reach-specific baseline ($\Delta = \text{value} - \text{baseline}$). These annual Δ values were analysed using Gaussian mixed models. Thus, the two analytical approaches addressed different but complementary ecological questions: the BACI analyses evaluated whether restored reaches differed from control reaches over time, whereas the baseline-adjusted analyses described the magnitude and direction of change relative to each reach's own baseline conditions under long-term environmental variability. Water temperature and minimum autumn stream discharge (September–November) from year $n - 1$ were included as covariates to characterize the effects of thermal and hydrological variability on fish abundance and biomass in year n .

All analyses were conducted in R (version 4.4.3). Model fitting was performed using the glmmTMB package, with hypothesis testing based on Type III Wald χ^2 tests. Estimated marginal means and pairwise contrasts were calculated using the emmeans package and are presented to illustrate patterns among treatments and periods. Model assumptions were evaluated using residual diagnostics, including checks for overdispersion and influential observations. No major deviations from model assumptions were detected.

3 | Results

3.1 | Water Chemistry

While there was annual variability in water quality, no clear directional changes were evident in the available monitoring data (Figure S1). Predominantly, the streams were slightly acidic alongside a notably high total Fe (iron) concentration and diminished alkalinity (Table S2), aligning with the typical chemical profile of boreal rivers that flow through peatland areas. The minimum observed pH ranged from 4.8 to 5.7 (Table S2).

3.2 | Water Temperature

The maximum summer temperatures, reaching around 20°C, were observed typically in mid-July (Figure S3). As winter approaches, water temperatures drop to near 0°C towards the end of October and the beginning of November. Signs of warming started appearing from the beginning of March, but temperatures rose above 5°C typically only at the start of May. Continuous logger measurements from the early study years further indicated clear stream-specific differences in seasonal thermal dynamics among the study streams (Figure S2).

The average August water temperature based on field measurements conducted during annual sampling was 12.3°C across years and study reaches. The lowest average temperature across the six streams was observed in the initial year of the study (1999) at 8.9°C, whereas the highest average occurred in the most recent study year (2022), reaching 15.5°C. A correlation

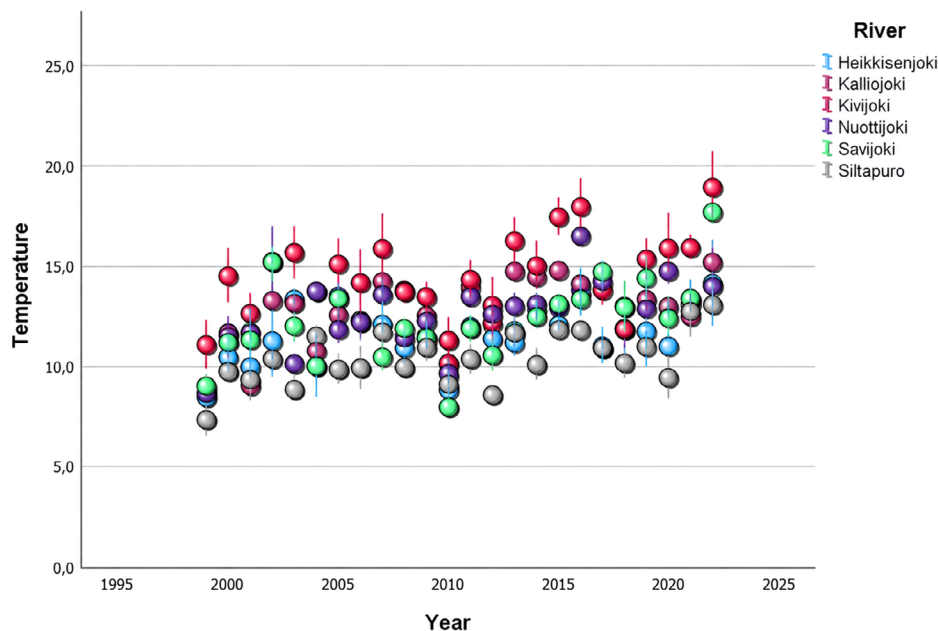


FIGURE 2 | Mean August surface water temperatures ($\pm$ SE, °C) in the six study streams during annual fish sampling. For each stream and year, values were calculated from temperature measurements taken at the three study reaches.

analysis revealed a relatively strong relationship between the rise in mean water temperature and time, yielding a correlation coefficient of 0.618 ($p < 0.001$, $df = 24$). Notably, the increase in water temperature was not consistent; for instance, in 2010, the average temperature decreased to 9.5°C and in 2018, it dropped to 11.9°C (Figure 2).

3.3 | Stream Flows

The yearly mean (SD) and median flows in the study streams 1990–2022 were (m^3/s): Heikkisenjoki: 0.50 (0.82), 0.19, Kalliojoki: 0.37 (0.73), 0.11, Kivijoki: 0.44 (0.73), 0.21, Nuottijoki: 0.17 (0.22) 0.09, Savijoki: 0.42 (0.89), 0.13 and Siltapuro: 0.42 (0.69), 0.16. There was large variability in the annual mean flows and a weak significant correlation (partial Pearson correlation controlling for streams) between median annual flow and year ($r = 0.285$, $N = 195$, $p < 0.001$) (Figure S3). Typically, the highest flows in these streams were observed in May, due to snowmelt and lowest during wintertime in February–March.

The cumulative plots of standardized anomalies in the stream flows relative to the average flow (1990–2022) indicated a down-trend in flows shortly after the restoration in 2001, with noticeable decreases occurring in 2003 and a further reduction in 2011. Average stream flows began an upward trend from 2014 onward (Figure 3).

3.4 | Fish Species Caught

Altogether 12 fish species were caught during the study: brown trout (11,588 individuals), European bullhead (3464 ind.), minnow (*Phoxinus phoxinus*, 2470 ind.), ide (*Leuciscus leuciscus*, 1091 ind.), burbot (947 ind.), pike (*Esox lucius*, 447 ind.), perch (*Perca fluviatilis*, 423 ind.), grayling (*Thymallus thymallus*, 395

ind.), roach (*Rutilus rutilus*, 241 ind.), brook lamprey (*Lampetra planeri*, 68 ind.), bleak (*Alburnus alburnus*, 2 ind.) and stone loach (*Barbatula barbatula*, 1 ind.). Three species were recorded in all streams and reaches (brown trout, European bullhead and burbot). Five species occurred in all streams (brown trout, European bullhead, burbot, perch and roach) and three species (pike, grayling and minnow) were found in five of the six study streams.

3.5 | Total Fish Density and Biomass

Total fish abundance and biomass exhibited substantial interannual variability and clear temporal trends over the study period (Figures S4 and S5). In the BACI models, restoration treatment had no significant effect on either total fish abundance or biomass and treatment $\times$ period interactions were also non-significant (Table 2; Tables S3–S5 and S8–S10). In contrast, period had a strong effect on both responses, indicating pronounced temporal variation irrespective of restoration treatment. Water temperature was negatively associated with total fish abundance, whereas minimum autumn discharge had no significant effect in the models (Table 2; Tables S3 and S4).

In the baseline-adjusted analyses, control reaches showed a consistent decline in total fish abundance across all three post-restoration periods (Figure 4; Table 2). Treatment had a significant effect on baseline-adjusted abundance, while the overall treatment $\times$ period interaction remained non-significant (Table 2). Reaches restored with large woody debris (LWD + s) exhibited a significantly more positive change in abundance relative to baseline compared with control reaches: abundance increased following restoration, subsequently declined, but remained significantly higher than in control reaches throughout the post-restoration period (Figure 4; Table 3, Tables S6 and S7). Although abundance in stone-restored reaches also increased

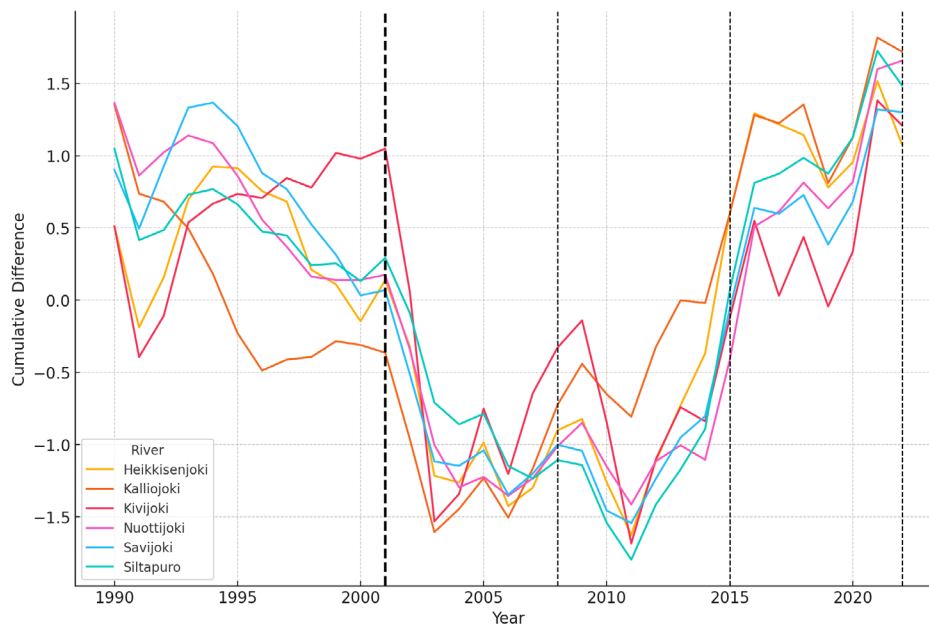


FIGURE 3 | Cumulative difference in flows compared to the mean flow from 1990 to 2022. The study began in 1999, with restoration carried out in 2001 (thick dashed line). The post-restoration period was analysed in three seven-year intervals (narrow dashed lines).

TABLE 2 | Summary of fixed effects from generalized linear mixed models analysing total fish abundance and total fish biomass from unadjusted and baseline-adjusted analyses.

Response	Model type	Treatment	Period	Treatment × Period	Key covariates
Total abundance	BACI	ns	***	ns	Temperature (−)*
Total abundance	Baseline-adjusted	**	*	ns	Min. discharge (+)*
Total biomass	BACI	ns	***	ns	Ns
Total biomass	Baseline-adjusted	***	*	ns	Min. discharge (+)*

Note: Significance refers to Type III Wald χ^2 tests of fixed effects.
Abbreviation: ns, not significant.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

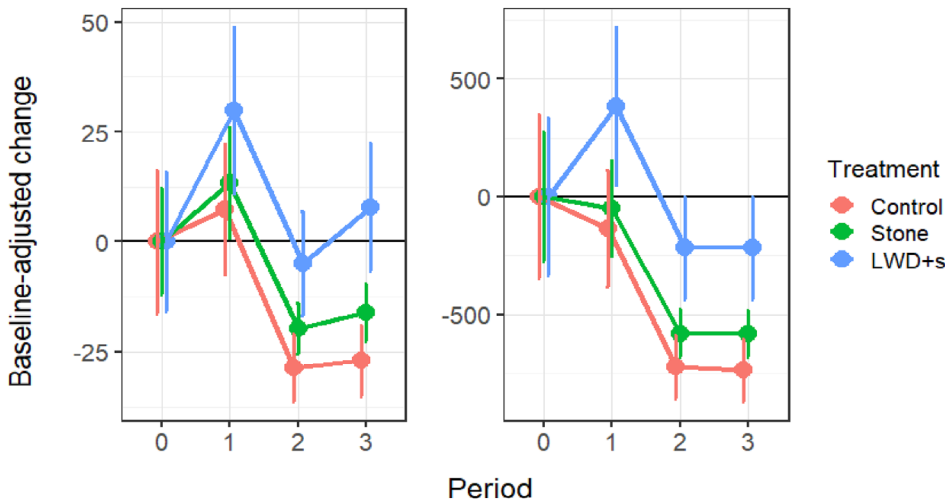


FIGURE 4 | Baseline-adjusted changes in (left panel) total fish abundance (ind. per 100 m²) and (right panel) total fish biomass (g per 100 m²) across restoration treatments and periods. For each treatment, changes were calculated as differences in model-predicted values (estimated marginal means) relative to the pre-restoration baseline (Period 0). Points represent predicted means and error bars indicate $\pm$ SE.

after restoration, these changes did not differ significantly from controls (Figure 4; Table 3).

Baseline-adjusted biomass showed an even stronger response to LWD+s restoration. Wood-restored reaches exhibited a pronounced positive change in biomass relative to baseline, whereas stone-restored reaches again did not differ from control reaches (Figure 4; Table 3, Tables S11 and S12). Period also influenced baseline-adjusted biomass, with lower values in later post-restoration periods (Figure 4; Table 2, Table S9). Higher minimum autumn discharge was associated with greater baseline-adjusted abundance and biomass (Table 2, Tables S4 and S9).

3.6 | Individual Species Responses

Brown trout abundance showed a significant effect of period and a significant Treatment $\times$ Period interaction, whereas the main effect of treatment was not significant (Table 4; Tables S13 and S14). Abundance declined markedly over time in control reaches, indicating a shifting baseline (Figure 5; Table S15). In contrast, declines were less pronounced in LWD+s-restored reaches than in control reaches. This pattern was confirmed by within-treatment contrasts, which showed a significant decline from the baseline in control reaches but no corresponding decline in LWD+s-restored reaches during Period 3 (Table S16). In stone-restored reaches, temporal changes did not differ

significantly from those in control reaches. Similarly, treatment contrasts indicated that during the latest post-restoration phase, brown trout abundance was higher in LWD+s-restored reaches than in control reaches, whereas no significant differences were detected between stone-restored and control reaches (Table S17). Thus, LWD+s restoration buffered against the long-term decline in brown trout abundance rather than inducing an immediate post-restoration increase. Baseline-adjusted responses were consistent with these findings (Figure 6). Although mean baseline-adjusted abundance in LWD+s-restored reaches tended to exceed that in control reaches, this difference did not reach statistical significance when averaged across post-restoration periods (Table 5). The primary effect of LWD+s restoration on brown trout was expressed as a delayed divergence from declining control trajectories rather than as a uniform increase in abundance.

Burbot abundance exhibited strong temporal variation and treatment-specific responses, with significant effects of treatment, period and their interaction (Figure 5; Table 4; Tables S18 and S19). As in brown trout, burbot abundance declined over time in control reaches (Figure 6). Predicted marginal means illustrated contrasting post-restoration patterns among treatments (Figure 6; Table S19). Stone-restored reaches exhibited higher model-predicted abundances than both control and LWD+s-restored reaches during post-restoration periods, whereas no corresponding increase was apparent in LWD+s-restored reaches (Tables S20 and S22). Within-treatment contrasts relative to the

TABLE 3 | Key treatment contrasts from baseline-adjusted models for total fish abundance and biomass.

Response	Contrast	Estimate	95% CI	p
Abundance (Δ)	LWD + s – Control	+27.3 ind/100 m ²	10.2 to 44.1	0.0029
Abundance (Δ)	Stone – Control	+4.1 ind/100 m ²	–9.8 to 17.6	0.62
Biomass (Δ)	LWD + s – Control	+478 g/100 m ²	215 to 741	0.0007
Biomass (Δ)	Stone – Control	+36 g/100 m ²	–180 to 252	0.74

Note: Estimates represent differences relative to control reaches, averaged across post-restoration periods (Periods 1–3). Abbreviation: CI, 95% confidence interval.

TABLE 4 | Summary of fixed effects from species-specific generalized linear mixed models analysing fish abundance.

Species	Model type	Treatment	Period	Treatment $\times$ Period	Key covariates
Brown trout	BACI	ns	**	**	ns
Brown trout	Baseline-adjusted	ns	**	**	ns
Burbot	BACI	**	**	*	Min. discharge (+)*
Burbot	Baseline-adjusted	**	**	*	Min. discharge (+)*
European bullhead	BACI	ns	ns	ns	Temperature (–)***; Min. discharge (+)***
European bullhead	Baseline-adjusted	ns	ns	ns	Temperature (–)***; Min. discharge (+)***

Note: Significance refers to Type III Wald χ^2 tests of fixed effects.

Abbreviation: ns, not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

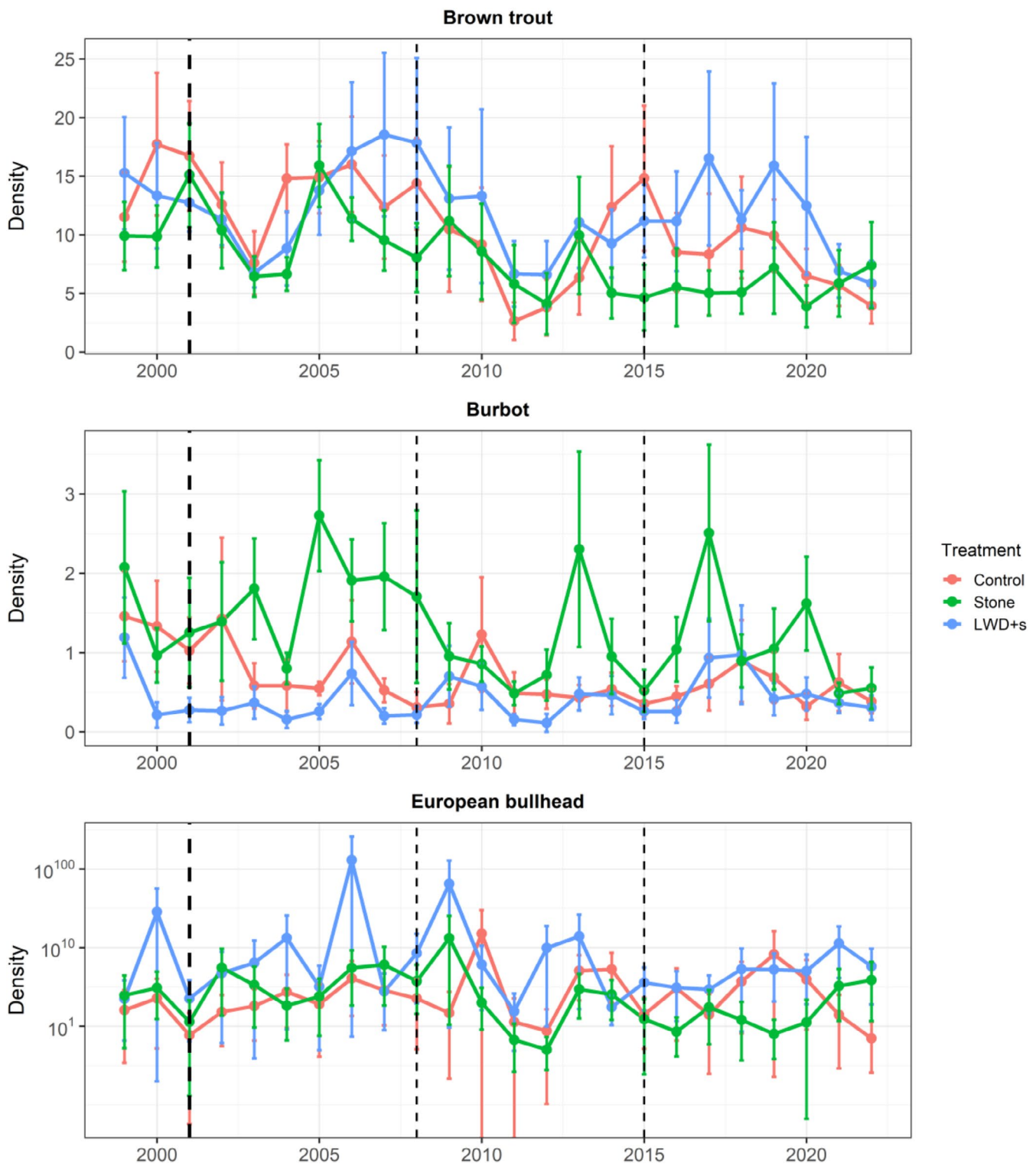


FIGURE 5 | Densities (ind./100 m² ± SE) of brown trout, burbot and European bullhead across restoration treatments from 1999 to 2022 in the six study streams in northeastern Finland. The thick vertical dashed line indicates the timing of restoration (2001), while the narrow vertical dashed lines separate the three seven-year monitoring periods. Note that the y-axis scales vary between species and a logarithmic scale is used for bullhead.

pre-restoration period indicated significant changes from the baseline also in control reaches (Table S21), demonstrating that baseline conditions were not stable over time. Consequently, changes relative to baseline within individual treatments alone did not explain the observed treatment-specific temporal patterns. Minimum autumn discharge was positively associated

with burbot abundance (Table 4; Table S19), highlighting the importance of hydrological conditions in shaping burbot population dynamics alongside restoration effects.

European bullhead abundance showed no consistent response to restoration treatment or monitoring period (Figure 5). No

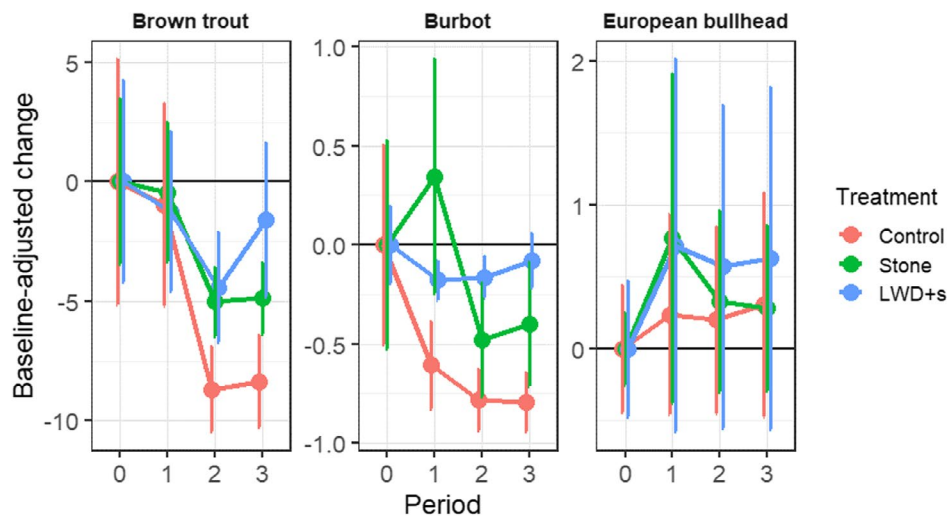


FIGURE 6 | Species-specific baseline-adjusted changes in brown trout, burbot and European bullhead densities following stream restoration. Changes are shown as differences in model-predicted fish density (estimated marginal means; Δ ind. per 100 m²) relative to the pre-restoration period (Period 0), which is set to zero for all treatments. Points represent estimated marginal means and error bars indicate $\pm$ SE.

TABLE 5 | Key treatment contrasts from baseline-adjusted models for total fish abundance.

Species	Contrast	Estimate (ind/100 m ²)	95% CI	<i>p</i>
Brown trout	LWD + s— Control	+12.6	−0.7 to 25.9	0.067
Brown trout	Stone— Control	−4.0	−11.5 to 3.5	0.41
Burbot	LWD + s— Control	−0.10	−0.72 to 0.53	0.92
Burbot	Stone— Control	+1.36	−0.08 to 2.79	0.067
European bullhead	LWD + s— Control	+1.07	−2.63 to 4.77	0.77
European bullhead	Stone— Control	−0.51	−2.85 to 1.83	0.86

Note: Estimates represent model-based differences in baseline-adjusted abundance (individuals per 100 m²) relative to control reaches, averaged across post-restoration periods (Periods 1–3). *p*-values are Sidak-adjusted. Abbreviation: CI, 95% confidence interval.

significant effects of treatment, period or their interaction were detected in either the BACI or baseline-adjusted analyses (Table 4; Tables S23 and S24). Model-predicted abundances across treatment $\times$ period combinations are presented in Tables S25 and S26, and treatment contrasts within periods are presented in Table S27. No significant differences were observed between restored and control reaches during post-restoration periods (Table S27). European bullhead abundance was strongly associated with water temperature and minimum autumn discharge. Water temperature was negatively related to abundance, whereas minimum autumn discharge had a positive effect (Table 4; Table S24). These effects were consistent across treatments and periods, indicating that large-scale environmental

conditions rather than local habitat restoration primarily governed bullhead population dynamics.

4 | Discussion

Our 24-year study demonstrated that instream restoration influenced long-term fish assemblage dynamics, but the effects depended on restoration method and species. Fish abundance and biomass declined over time even in control reaches, indicating a shifting ecological baseline. Nevertheless, reaches restored with large woody debris and stones (LWD + s) showed less pronounced long-term declines than control reaches, indicating that wood additions buffered fish communities against long-term environmental deterioration. Brown trout benefited most from LWD + s restoration, whereas burbot responded more positively to stone restoration, reflecting species-specific habitat preferences. European bullhead showed no consistent response to restoration. Although restoration improved habitat conditions, water temperature and minimum autumn discharge were also associated with fish abundance, indicating that long-term restoration outcomes were influenced by broader climatic and hydrological variability.

Water temperature and minimum autumn discharge were associated with variation in fish abundance and biomass, although the effects differed among species. Higher autumnal water temperature was generally associated with lower total fish abundance, whereas higher minimum discharge was linked to more favourable post-restoration responses. At the species level, burbot responded primarily to discharge, while European bullhead was influenced by both temperature and discharge. These results indicate that regional conditions shaped the significance of local responses to restoration in small boreal streams.

Water temperature increased during the 24-year study, whereas stream flow exhibited substantial interannual variability and long-term hydrological shifts. Although causality cannot be directly established, the combined effects of rising temperatures

and altered flow regimes likely contributed to the observed long-term patterns in fish abundance. Similar relationships between climate-driven warming, hydrological variability and reductions in cold-water fish species have been documented in other northern and boreal rivers (Marsh et al. 2021; Donadi et al. 2023). Global assessments further indicate that climate change alters water temperature and discharge patterns in northern rivers, with consequences for fish growth, reproduction and habitat stability (Prowse et al. 2006; Wrona et al. 2016). The observed long-term hydrological variability and gradual warming in our study streams are consistent with these broader climatic trends.

Catchment conditions may also have influenced the hydrological conditions of our study sites. The river catchments consisted of forested mineral soils and peatlands, producing humic water typical of boreal systems influenced by peatland hydrology. Peatland drainage, the main anthropogenic pressure in the area, likely shortened water residence time and increased discharge variability. Peatlands play an important role in buffering flow extremes and regulating water quality through delayed runoff and nutrient retention (Finér et al. 2020; Karimi et al. 2021; Gatis et al. 2023). Although no major land-use changes occurred during the study period, earlier modifications may have amplified both high- and low-flow events, intensifying ecological stress on fish communities. As shown in earlier studies, landscape characteristics together with instream habitat and hydrology strongly influence fish populations (Sutela and Vehanen 2009; Beesley and Prince 2010; Sutela et al. 2010). Restoring catchment water retention could therefore help stabilize flow regimes and enhance the effectiveness of instream restoration for sustaining fish populations.

Long-term monitoring revealed declines in total fish abundance and biomass, as well as in brown trout and burbot abundance, even in control reaches where no restoration was undertaken. This suggests that these unmodified sites were changing over time, consistent with the concept of shifting ecological baselines (Pauly 1995). A similar baseline erosion has been documented across multiple ecosystems as environmental change progresses (Su et al. 2020; He et al. 2024; Soga and Gaston 2024). Although our control reaches were not actual reference sites, the observed declines highlight how broader environmental pressures can affect even unmanipulated sections of river systems. Such trends underscore the importance of long-term ecological monitoring with robust before–after and control–impact designs to detect a gradual but significant ecological change. For ecological assessment frameworks that rely on fixed reference conditions, such as the European Water Framework Directive, shifting baselines pose a challenge: periodic recalibration of reference sites risks institutionalizing already degraded conditions as the new ‘normal’ (Bouleau and Pont 2015).

Instream restoration measures influenced baseline-adjusted changes in total fish density and biomass relative to pre-restoration conditions. Restoration increased fish abundance only temporarily, but declines were less pronounced in restored sections than in control reaches. Reductions were smallest in LWD + s-treated reaches, while stone-treated reaches showed intermediate, non-significant effects. These findings indicate that LWD + s restoration buffered against the overall decline in fish density and biomass by increasing structural complexity,

habitat depth and flow heterogeneity. Pools created by LWD are important during low-flow periods and provide critical overwintering habitats for salmonids (Mäki-Petäys et al. 1997; Huusko et al. 2007). Additionally, wood and pools provide refuge from aquatic and terrestrial predators (Cederholm et al. 1997; Vehanen et al. 2022) and trap organic matter that supports invertebrates and algae, thereby enhancing food availability for fish (Fausch and Northcote 1992; Roni et al. 2014). Some restoration structures deteriorated over time and gravel additions were not retained. Such changes are expected in dynamic stream environments and are consistent with process-based restoration principles, which recognize that restored channels continue to evolve through natural geomorphic processes rather than remain static (Beechie et al. 2010). These changes likely reduced the contrast between treatments through time, potentially limiting the detectability of restoration effects. Nevertheless, the observed long-term patterns suggest that LWD + s structures continued to provide ecologically relevant habitat complexity despite this natural adjustment.

Responses to restoration differed among species. Brown trout and burbot densities declined over time, but restoration altered these trends in contrasting ways. Brown trout abundance increased significantly during the final monitoring period, particularly in LWD + s treated reaches, showing that positive effects developed gradually. Burbot densities increased most during the first monitoring period, especially in stone-treated reaches, indicating a more immediate response. These contrasting temporal and treatment-specific patterns demonstrate that restoration effects were species-specific and dependent on habitat modification type.

Species-specific responses were also associated with environmental variability. Higher minimum autumn discharge was linked to more favourable responses in burbot and European bullhead, whereas higher water temperature was negatively associated with European bullhead abundance. Hydrological and thermal conditions are known to strongly influence fish assemblages in boreal rivers (Sutela et al. 2023). These patterns suggest that habitat restoration effects interacted with hydrological and thermal conditions and that species differed in their sensitivity to environmental variability. Our results are also consistent with findings from small coastal streams, where regional factors, particularly low discharge events and water temperature, strongly influenced fish abundance (Mitsuo 2017).

The differing responses of brown trout and burbot are likely related to the combination of the distinct habitats created by the two restoration approaches and species-specific habitat preferences. LWD + s restoration increased habitat heterogeneity by forming deeper pools, variable flow conditions and greater instream cover, features that favour brown trout, which prefer structurally complex habitats and use deep, slow-flowing areas especially during winter (Mäki-Petäys et al. 1997; Heggenes et al. 1999). In contrast, burbot are primarily benthic and associated with coarse substrates, deeper and slower-flowing habitats and interstitial cover (Dixon and Vokoun 2009; Eick 2013; Pearce et al. 2025). Stone additions may therefore have created more favourable near-bed habitats for burbot, explaining their short-term increase after restoration. Burbot is a widespread fish predator in boreal rivers and is not restricted to any specific river

type (Sutela et al. 2023). It is plausible that by adding stones only, we created conditions that favoured burbot, potentially increasing predation pressure and reducing total fish density (Luhta et al. 2012).

Declines in fish density and biomass were less pronounced in reaches restored with LWD + s than in other treatments, indicating that wood additions had a positive and lasting influence on habitat quality. Positive responses to large wood placement have also been reported for juvenile Pacific salmonids in Columbia River tributaries (Clark et al. 2019). Beyond providing shelter for fish, LWD plays a key role in the ecological functioning of streams (Dickson et al. 2025). Wood modifies channel hydraulics by deflecting flow, promoting pool formation and retaining sediments and organic matter (Harmon et al. 1986; Gurnell et al. 2002). These hydraulic changes enhance habitat diversity and stability, creating refuges during floods and droughts (Naiman et al. 2000). In forested headwaters, wood also regulates nutrient and energy flow by retaining organic material and supporting microbial and invertebrate production (Bilby and Likens 1980; Smock et al. 1989). Through these processes, LWD functions as a structural and biological ‘engineering’ element, linking geomorphology, hydrology and ecosystem productivity. By slowing the downstream transport of organic material and nutrients, wood prolongs nutrient cycling within stream reaches and supports higher standing stocks of benthic invertebrates and periphyton (Fausch and Northcote 1992; Roni et al. 2014). In our LWD + s treatments, logs were anchored to streambanks without branches or twigs. Although we did not conduct a new habitat survey, earlier work demonstrated that these habitat changes were long-lasting (Louhi et al. 2016). The volume of wood added averaged 20–30 m³ ha⁻¹, below the recommended 100 m³ ha⁻¹ (Kail et al. 2007) but substantially higher than typical of Finnish forest streams (Muotka and Syrjänen 2007).

We focused the species-level interpretation on the three dominant species common to all study reaches and rivers and on their relationships with habitat modification, temperature and discharge. Although restoration may also influence broader fish assemblage structure and trophic interactions, assemblage-level responses were more difficult to interpret because several species occurred inconsistently among rivers and study reaches. Our long-term study emphasizes that restoration outcomes are shaped by both habitat modification type and species traits and that local restoration effects operate within a broader context of regional hydrological and thermal variability. Impacts of restoration on trophic interactions, such as potentially enhanced predation by burbot in stone-treated reaches, further illustrate the importance of considering community-level processes when evaluating restoration success. While restoration improved habitat conditions, regional factors such as temperature and discharge variability continued to exert strong control over fish communities, highlighting the limits of local actions under changing climatic and catchment conditions. Our findings support a hierarchical approach that integrates local habitat restoration with catchment-scale management to enhance the resilience of boreal stream ecosystems. Continued long-term monitoring using standardized ecological indicators is essential to capture delayed responses and to better link restoration outcomes to ecosystem functioning (Bernhardt et al. 2005; Bylak et al. 2023; Skinner et al. 2023). By combining catchment water

retention measures with instream structural improvements, management efforts can more effectively stabilize flow regimes and sustain fish populations in boreal streams.

Author Contributions

Conceptualisation: T.V., A.H., A.M.-P., T.M. Developing methods: T.V., A.H., T.M., P.L. Conducting the research: T.V., A.H., A.M.-P. Data analysis: T.V. Data interpretation: T.V., A.H., T.M., P.L. Preparation of figures and tables: T.V. Writing: T.V., A.H., T.M., P.L., A.M.-P. All authors contributed critically to the drafts, approved the final manuscript and agree to be accountable for all aspects of the work.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Mean annual total phosphorus ($\pm$ SE) concentrations ($\mu\text{g/L}$) in the six study streams from 1999 to 2007 and in River Nuottijoki from 1999 to 2021. **Figure S2:** An example of the seasonal water temperature dynamics recorded by continuous temperature loggers in five study streams during 2002–2003. **Figure S3:** Mean annual flows in six study rivers in Finland from 1999 to 2022. **Figure S4:** Fish density ($\text{Ind./100 m}^2 \pm \text{SE}$) (left y-axis) across different restoration treatments in the six study streams from 1999 to 2022. The thick vertical dashed line indicates the timing of restoration (2001), while the narrow vertical dashed lines separate the three seven-year monitoring periods (right y-axis). The horizontal dashed line represents the mean of cumulative plots of standardized anomalies in stream flows compared to the long-term mean (1990–2022). **Figure S5:** Fish biomass ($\text{g/100 m}^2 \pm \text{SE}$) (left y-axis) across different restoration treatments in the six study streams from 1999 to 2022. The thick vertical dashed line indicates the timing of restoration (2001), while the narrow vertical dashed lines separate the three seven-year monitoring periods. The horizontal dashed line represents the mean of cumulative plots of standardized anomalies in stream flows compared to the long-term mean (1990–2022). **Table S1:** Catchment characteristics of the six study streams in Finland. **Table S2:** Water chemistry parameters in the six study rivers (1999–2022): Mean, maximum and minimum values, standard deviation and sample size (N). **Table S3:** Results from a generalized linear mixed model (GLMM) fitted to total fish abundance. Abundance was estimated using Zippin removal estimates and analysed on the log scale assuming a negative binomial error distribution. The conditional model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S4:** Type III Wald χ^2 tests for overall fixed effects. Analysis of deviance based on Type III Wald chi-square tests for fixed effects in a generalized linear mixed model (GLMM) fitted to total fish abundance. Abundance was estimated using Zippin multiple-pass removal estimates. Models were fitted on the log scale assuming a negative binomial error distribution, included log-transformed fished area as an offset and random intercepts for river and year. **Table S5:** Estimated marginal means (EMMs) and 95% confidence intervals for the Treatment $\times$ Period interaction derived from the conditional component of the GLMM described in **Table S3**. Estimates are back-transformed to the response scale and expressed as fish counts per 100 m^2 . **Table S6:** Pairwise contrasts between periods within each treatment derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m^2), with p -values adjusted for multiple comparisons using Tukey's method. **Table S7:** Pairwise contrasts between treatments within each period derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m^2), with p -values adjusted for multiple comparisons using Tukey's method. **Table S8:** Results from a generalized linear mixed model (GLMM) fitted to total fish biomass. Biomass was calculated as the summed wet mass of fish captured during electrofishing and analysed

assuming a Gamma error distribution with a log link. The conditional model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S9:** Analysis of deviance based on Type III Wald chi-square tests for fixed effects in a generalized linear mixed model fitted to total fish biomass. **Table S10:** Estimated marginal means (EMMs) and 95% confidence intervals for the Treatment $\times$ Period interaction derived from the conditional component of the generalized linear mixed model. Estimates are back-transformed to the response scale and expressed as total biomass (g) per 100 m^2 . **Table S11:** Pairwise contrasts between periods within each treatment derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as biomass ratios on the response scale (g per 100 m^2), with p -values adjusted for multiple comparisons using Tukey's method. **Table S12:** Pairwise contrasts between treatments within each period derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as biomass ratios on the response scale (g per 100 m^2), with p -values adjusted for multiple comparisons using Tukey's method. **Table S13:** Conditional model fixed effects (log scale) for brown trout (*Salmo trutta*) abundance, derived from the generalized linear mixed model. Abundance was estimated using Zippin multiple-pass removal estimates. The model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S14:** Analysis of deviance based on Type III Wald chi-square tests for fixed effects in a generalized linear mixed model fitted to brown trout abundance. Abundance was estimated using Zippin multiple-pass removal estimates and analysed on the log scale assuming a negative binomial error distribution. The model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S15:** Estimated marginal means (EMMs) and 95% confidence intervals for the Treatment $\times$ Period interaction in species-specific abundance, derived from the conditional component of the generalized linear mixed model described in Table X. Estimates are back-transformed to the response scale and expressed as fish counts per 100 m^2 . **Table S16:** Within-treatment period contrasts in brown trout abundance relative to the pre-restoration period (Period 0), derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m^2), with p -values adjusted using Dunnett's method. **Table S17:** Treatment contrasts within periods in brown trout abundance, derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m^2), with p -values adjusted for multiple comparisons using Tukey's method. **Table S18:** Results from a generalized linear mixed model (GLMM) fitted to burbot (*Lota lota*) abundance. Abundance was estimated using Zippin multiple-pass removal estimates and analysed on the log scale assuming a negative binomial error distribution. The conditional model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S19:** Analysis of deviance based on Type III Wald chi-square tests for fixed effects in a generalized linear mixed model fitted to burbot abundance. Abundance was estimated using Zippin multiple-pass removal estimates and analysed on the log scale assuming a negative binomial error distribution. The model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S20:** Estimated marginal means (EMMs) and 95% confidence intervals in burbot for the Treatment $\times$ Period interaction in species-specific abundance, derived from the conditional component of the generalized linear mixed model. Estimates are back-transformed to the response scale and expressed as fish counts per 100 m^2 . **Table S21:** Within-treatment period contrasts in burbot abundance relative to the pre-restoration period (Period 0), derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m^2), with p -values adjusted using Dunnett's method. **Table S22:** Treatment contrasts within periods in burbot abundance, derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m^2), with p -values adjusted for multiple comparisons using Tukey's method. **Table S23:** Results from a generalized linear mixed model (GLMM) fitted to European bullhead abundance. Abundance was estimated using Zippin multiple-pass removal estimates and analysed on the log scale

assuming a negative binomial error distribution. The conditional model includes log-transformed fished area as an offset and random intercepts for river and year. Species-specific biomass was not analysed. **Table S24:** Analysis of deviance based on Type III Wald chi-square tests for fixed effects in a generalized linear mixed model fitted to European bullhead abundance. Abundance was estimated using Zippin multiple-pass removal estimates and analysed on the log scale assuming a negative binomial error distribution. The model includes log-transformed fished area as an offset and random intercepts for river and year. **Table S25:** Estimated marginal means (EMMs) for the Treatment $\times$ Period interaction in European bullhead abundance, derived from the conditional component of the generalized linear mixed model described in Table S23. Estimates are back-transformed to the response scale and expressed as fish counts per 100 m². **Table S26:** Estimated marginal means (EMMs) and 95% confidence intervals for the Treatment $\times$ Period interaction in European bullhead abundance, derived from the conditional component of the generalized linear mixed model described in Table S23. Estimates are back-transformed to the response scale and expressed as fish counts per 100 m². **Table S27:** Treatment contrasts within periods in European bullhead abundance, derived from the conditional component of the generalized linear mixed model. Contrasts are expressed as abundance ratios on the response scale (counts per 100 m²), with *p*-values adjusted for multiple comparisons using Tukey's method.