

Research Paper

Fluctuating densities of juvenile brown trout (*Salmo trutta*) and Alpine bullhead (*Cottus poecilopus*) over a 25-year period in the Atna River, Norway

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Long term monitoring data from pristine or relatively unimpacted watersheds represents a valuable ecological baseline in the 21st century. Here, we present a 25-year time series of brown trout (*Salmo trutta*) and Alpine bullhead (*Cottus poecilopus*) densities in the boreal-subalpine Atna River in Norway (62 °N) and investigate their relationships with discharge and water temperatures. There was an overall negative trend in densities of Alpine bullhead, a declining trend in densities of age 0 brown trout, and no clear trend for age ≥1+ brown trout across the study sites. There were substantial fluctuations in densities for both species, and the majority of the variance originated from year-to-year variation. For older brown trout, approximately 33 % of the variance could be attributed to site-level factors, i.e. systematic differences in densities between sites. Concurrently, there were changes in some of the discharge and temperature-related metrics. The lowest flow of the year became gradually higher throughout the period whereas mean discharge in spring decreased. The best supported models showed a negative relationship between fish densities and mean annual discharge (Alpine bullhead and older brown trout) and a negative relationship between density and minimum annual discharge for age-0 brown trout. The models explained only modest amounts of overall variance in the dataset (range 0 to 12 %) but did document a potentially limiting effect on fish densities on an annual basis. We discuss the likely mechanisms by which discharge and water temperature can influence the abundance of brown trout and Alpine bullhead in river systems and highlight the value of long-term monitoring as a baseline when investigating broad-scale shifts in abundance.

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INTRODUCTION

Long-term ecological monitoring is imperative for conservation and management, yet time series that span decades remain surprisingly scarce on a global scale (Revenga *et al.* 2005; Lindenmayer *et al.* 2012). In a rapidly changing world, datasets from largely pristine environments provide necessary blueprints to establish conservation targets and quantifiable goals for restoration efforts in impacted watersheds (Friberg *et al.* 2011; Radinger *et al.* 2019; Lindenmayer 2020). Importantly, separating natural variation from anthropogenic pressures is inherently challenging and may be contested when setting goals for restoration measures (Warren *et al.* 2015). Knowing the range of natural states is therefore necessary when setting goals for

management, and long-term monitoring in reference sites provide a valuable context (Lindenmayer *et al.* 2012; Ramos-Merchante *et al.* 2021).

The Atna River watershed in southern Norway is a mainly undeveloped and intact river system that has been monitored since 1985. Studies were initially precipitated by public objection to proposed hydropower developments in the river in the 1960s. The river was issued an initial 10-year termed protection status in 1973 to ensure proper environmental impact assessments. The findings from that assessment led to the permanent protection of the river in 1985 and prompted the establishment of a monitoring and research program in late 1984 (Sandlund & Aagaard 2004). As a result, the watershed

remains one of the best studied in Norway, with numerous journal articles, special issues, books, and reports published during the first 20 years of the program (Tvede & Halvorsen 2004; Aagaard *et al.* 2004; Jensen *et al.* 2021).

Since the initial assessments, ecological monitoring in the Atna River has continued in various forms. First, together with the Vikedal watershed in southwestern Norway, Atna is monitored annually for the purpose of continuity in the data sets. It is now one of the longest running time series on fish, invertebrates, and algae in running waters in Norway and provides an important reference condition for rivers in Southern Norway (Jensen *et al.* 2021). Second, the Atna River was included in the national monitoring program *Reference Rivers* in 2017 (Moe *et al.* 2018). The Reference River program includes 75 rivers across the entire country that are largely unaltered from their natural condition. The Reference Rivers monitoring sites includes two of the long-term monitoring sites in Atna (sites 3 and 4; Figure 1), in addition to another seven study sites located upstream towards the headwaters. Because the Atna River exhibits virtually a natural flow regime, it is a suitable study system for natural population dynamics and long-term trends. Due to many competing demands over water in modern society, the relationship between riverine fishes and flow is thoroughly studied – and one where context, scale and duration proves to be of particular significance (Warren *et al.* 2015). Riverine fishes are adapted to a life in running water, but different species have requirements during stages of their ontogeny. Thus, the impacts of the various components of the natural flow regime can manifest differently between rivers and regions depending on the physical settings (Nislow & Armstrong 2012).

The objective of this article is to provide an up-to-date assessment of the densities of juvenile brown trout *Salmo trutta* (Linnaeus, 1758)

and Alpine bullhead *Cottus poecilopus* (Heckel, 1836) in the Atna River. We present the estimates of fish densities from the four long-term monitoring sites and estimate population trends within and across sites between 1998 and 2024. We present concurrent trends in discharge and water temperature; relate these variables to fish densities; and discuss potential mechanisms by which fish densities respond to these abiotic factors. Finally, we discuss the need for further analysis in the watershed and point to potential synergies with other ongoing research programs.

MATERIAL AND METHODS

Study site

The Atna River watershed has been introduced thoroughly by a number of publications (Sandlund & Aagaard 2004 eds. and references therein: Tvede & Halvorsen 2004; Hesthagen *et al.* 2004a, b; Aagaard *et al.* 2004) and will be briefly discussed here. The watershed is located east of the main divide on the Scandinavian peninsula and drains eastward to River Glomma, the longest river and the largest drainage basin in Norway (Figure 1). The Atna watershed drains the eastern parts of Rondane National Park at over 2200 meters and empties in River Glomma at 338 meters above sea level. The area of the watershed is 1319 km² (generated from <http://www.nevina.nve.no>) with a hypsographic mean elevation of 1064 m, which corresponds roughly with the tree line (Tvede & Halvorsen 2004). The primary vegetation zone is boreal but due to the substantial topographic relief, local vegetation spans boreal, subalpine, and alpine zones. Coniferous forests (Norwegian spruce and Scots pine) dominate elevations up to

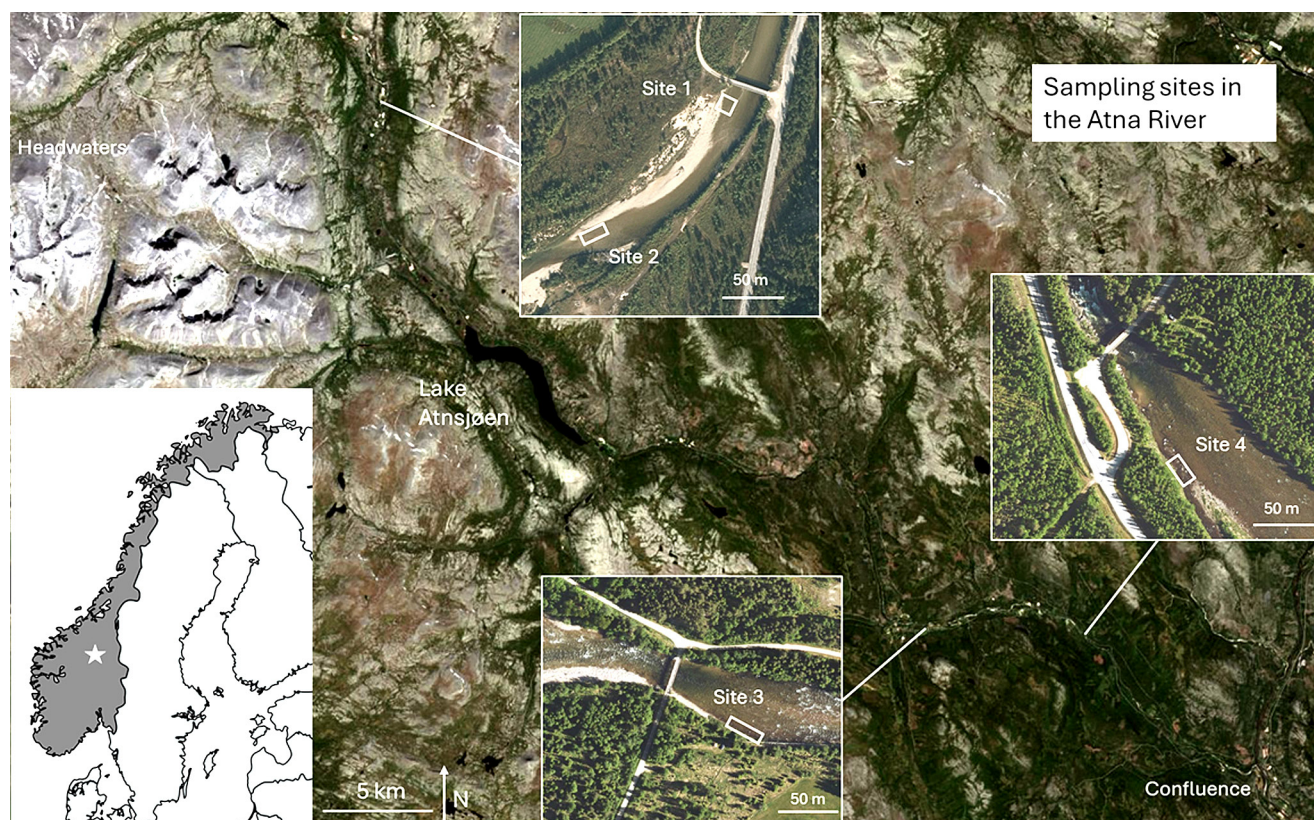


Figure 1. Aerial image showing the main part of the Atna river watershed and its location in southern Norway (left inset). The river originates in Rondane (top left, denoted headwaters) and enters River Glomma in the bottom right corner (denoted confluence). Study sites are shown as rectangles in the insets – note, however, that exact study sites can vary slightly from year to year depending on flow conditions. Aerial imagery provided by the Norwegian Mapping Authority under CC BY 4.0 © 2024 Kartverket. Map created with mapchart.net under CC BY-SA 4.0 DEED.



Figure 2. Aerial view from study site no. 3. The tributary Setninga enters the Atna River approximately 200 m upstream of the island. Photo: KM Myrvold.

750 meters; birch dominates elevations up to 1150 m; and willows, small shrubs, moss and lichen dominate the zone between the tree line and barren peaks (Tvede & Halvorsen 2004).

Lake Atnsjøen (61.9 °N, 10.2 °E; elevation 701 m) is the only lake on the mainstem. Our dataset includes two sites upstream of the lake and two sites downstream of the lake (Figure 2). There is no upstream passage from sites 3 and 4 due to impassable waterfalls. The gradient between sites 1 and 2 and the lake is low and passable for fish. The substrate is dominated by sand and pebbles upstream of the lake, and cobble and boulders downstream of the lake (Bogen 2004). The majority of brown trout that use the lake for foraging and overwintering likely spawn in the upstream sections of River Atna, wherein the juveniles spend a few years in the river before migrating to the lake; however, there is probably substantial variation in life histories in terms of spawning, rearing, foraging, and overwintering locations. River-resident life-history types of brown trout likely dominate the sections downstream of the lake, but it is likely that the juveniles sampled in this study could originate from parents with variable life histories and migration patterns. Alpine bullhead are assumed to have relatively small home ranges once they reach adult stages. The water is clear and nutrient poor, with low electrical conductivity (typical range between 3 and 10 μ S; Eriksen *et al.* 2024).

Hydrographical and temperature data

Several stream gauges and air and water temperature monitoring stations exist in the watershed. Discharge data from the outlet of lake

Atnsjøen are displayed below (Figure 3). Due to the volume of the lake, the hydrograph is relatively buffered compared with the sections upstream of the lake. The hydrograph is snowmelt dominated with low flows from October through April; snowmelt in May and June; and rain-driven spates throughout summer and early autumn.

We extracted six variables pertaining to river discharge in the years corresponding to fish sampling (1998 – 2024; Table 1). *Annual discharge values* (Q) reflect the entire year, whereas *springtime discharge values* (SQ) reflect the conditions during the months of May and June. All calculations were based on the daily average values to smooth out outlier values. There was no correlation between Qmean and Qmin (Pearson $r = 0.02$, $t = -0.09$, $d.f. = 24$, $P = 0.93$).

Data on water temperature were collected at the same location as the discharge data at the outlet of Lake Atnsjøen. We derived 3 variables with relevance to hatching and summer rearing (Table 1). All calculations were based on the daily average values to smooth out outlier values. Data from 1999 were missing 5 measurements; however, we deem this acceptable as it does not influence the four-month mean, minimum and maximum values appreciably. Mean temperature averaged 9.29 °C (range 7.97 – 11.66 °C); minimum temperature averaged 2.66 °C (range 1.24 – 4.14 °C), and maximum temperature averaged 15.59 °C (range 12.85 – 18.63 °C).

We performed simple linear regressions to identify monotonic trends in the explanatory variables over the course of the study (Table 2). Two variables, Qmin and SQmean, showed statistically significant trends in the period. Qmin had a positive trend, implying

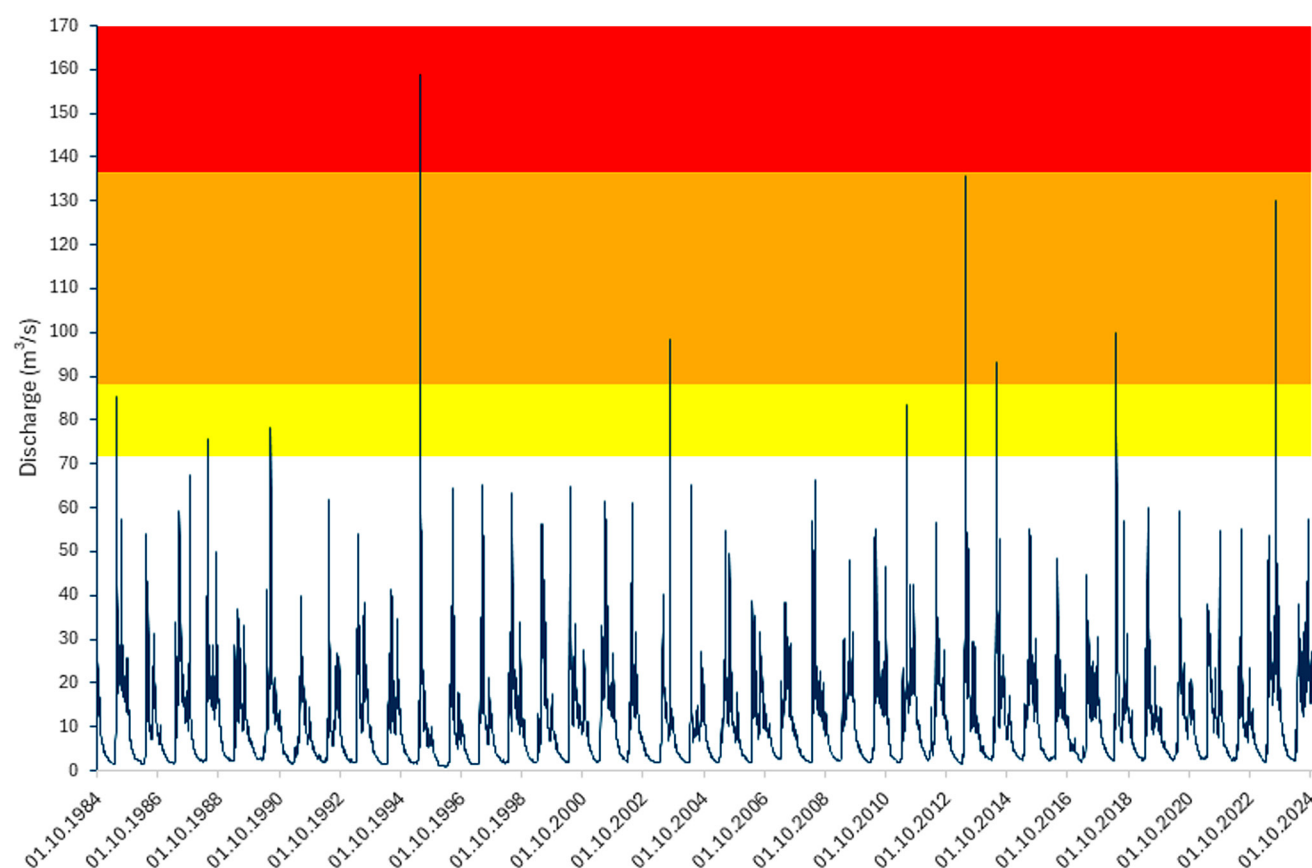


Figure 3. Daily mean discharge (m^3s^{-1}) downstream of Lake Atnsjøen from 01. October 1984 through 31. October 2024. The colors in the background reflect flood recurrence intervals. Yellow level (mean annual flood) is reached when the discharge exceeds $72.4 \text{ m}^3\text{s}^{-1}$, orange level (5-year flood) at $89.0 \text{ m}^3\text{s}^{-1}$, and red level (50-year flood) at $137.4 \text{ m}^3\text{s}^{-1}$. All floods that reached at least the yellow level were associated with snowmelt in the months of May and June, with two exceptions: 15. August 2003 and 9. August 2023, which were both rain-driven floods. No fish sampling was conducted in 2003 due to the flood. Data provided by the Norwegian Water and Energy Directorate NVE, stream gauge no. 2.32.0 Atnasjø (61.852°N , 10.222°E).

Table 1. Variables pertaining to river discharge and water temperature used in the modeling of densities of Alpine bullhead and brown trout in the Atna River. Values were extracted from daily averages measured at the NVE stream gauge station 2.32.0 Atnasjø.

Variable	Explanation and biological rationale
Qmean	Annual mean discharge (m^3s^{-1}): Gives an indication of the average hydrological conditions each year
Qmax	Maximum discharge of the year (m^3s^{-1}): The highest flow conditions each year
Qmin	Minimum discharge of the year (m^3s^{-1}): The lowest flow conditions each year
SQmean	Mean spring discharge (m^3s^{-1}): Gives an indication of the hydrological conditions in the months of May and June each year when snowmelt is typically at its peak and brown trout fry are emerging from the gravel
SQmax	Maximum spring discharge of the year (m^3s^{-1}): The highest flow conditions in May and June
SQmin	Minimum spring discharge (m^3s^{-1}): The lowest flow conditions in May and June
Tmean	Mean summer temperature ($^\circ\text{C}$): Gives an indication of the thermal regime in the months of May through August each year when fish often achieve their highest growth rates
Tmax	Maximum summer temperature ($^\circ\text{C}$): The highest temperature from May to August
Tmin	Minimum summer temperature ($^\circ\text{C}$): The lowest temperature from May to August

that the lowest flow of the year became gradually higher throughout the period. SQmean displayed a negative trend, which means that the mean discharge in spring decreased over the period (Table 2).

Fish sampling

Data on the fish community was obtained using three-pass depletion electrofishing following principles summarized by Forseth & Forsgren (2008). The fish community in Norway is dominated by salmonids (Klemetsen *et al.* 2003) and consequently, most of the sampling methods have been developed to target juvenile salmonids in streams (Bohlin *et al.* 1989; Forseth & Forsgren 2008). Surveys were conducted using a pulsed direct current backpack electrofisher from early August to mid-September depending on flow conditions. An area of approximately 100 m^2 was fished, and we targeted habitats suitable for rearing by young-of-the-year (age-0 brown trout) and older juvenile brown trout (i.e. ≥ 1 year old, denoted $\geq 1+$). Sites were chosen where channel hydrogeomorphology permitted effective electrofishing. Fish were kept in separate buckets between passes, but we did not set block nets. Fish were identified to species, measured to total length (millimeters), and released back into the stream after the survey was done. Age classes of brown trout were assigned primarily based on the length frequency distribution. Alpine bullhead (Figure 4; also known as Siberian sculpin) occupies similar habitats, and we only included individuals in catchable sizes in the analyses, i.e. longer than 35 mm and ages ranging from 1 to 5 years; Hesthagen *et al.* 2004a).

Population estimates for each sampling occasion were calculated using the removal function in package FSA (Ogle *et al.* 2023)

Table 2. Monotonic trends in the explanatory variables over the course of this study (1998 – 2024). Asterisk denotes statistically significant trends at the $\alpha = 0.05$ -level for a linear regression model.

Variable	Slope	SE(slope)	t-value	P-value	r ²
Qmean	0.0544	0.0364	1.49	0.148	0.085
Qmax	0.7119	0.6072	1.17	0.253	0.054
Qmin	0.0221	0.0055	4.00	0.001*	0.400
SQmean	-0.0288	0.1112	-0.26	0.798	0.003
SQmax	-0.1396	0.5860	-0.24	0.814	0.002
SQmin	-0.1581	0.0620	-2.55	0.018*	0.213
Tmean	0.0393	0.0215	1.83	0.080	0.122
Tmax	0.0079	0.0484	0.16	0.872	0.001
Tmin	0.0302	0.0168	1.80	0.084	0.119

with the Zippin estimator (Zippin 1958). Densities were expressed as the number of individuals per 100 m². The abundance of fish decreased throughout the period of the study. Consequently, single-pass electrofishing surveys were conducted when fewer than 10 fish were caught on the 1st pass. When single pass electrofishing was conducted, we borrowed the capture probability from other sites the same year, separately for brown trout and Alpine bullhead, and divided the single pass catch with the borrowed capture probability value. We estimated the standard error of the new estimate (y) where $k = 1$ passes were made based on borrowed values of capture probability (p) and its reciprocal ($q = 1 - p$) from the three-pass site as follows (Bohlin *et al.* 1989):

$$SE(y) = \sqrt{\frac{yq^k}{1-q^k} + var(p) \left(\frac{ykq^{(k-1)}}{1-q^k} \right)^2}$$

Arctic Grayling *Thymallus thymallus* (Linnaeus, 1758) and common minnow *Phoxinus phoxinus* (Linnaeus, 1758) were caught only occasionally in sites 3 and 4. These species were far outnumbered by brown trout and Alpine bullhead and were consequently not included in the analysis. Arctic char *Salvelinus alpinus* (Linnaeus, 1758) exists in Lake Atnsjøen but was not encountered in the sampling sites. The analysis hence focuses on Alpine bullhead and brown trout, where brown trout was separated into young of the year (0+) and older ($\geq 1+$) in most of the analyses, with one sampling occasion per year. Finally, no fish sampling was conducted in 2003 due to flooding.

Statistical analyses

We tested for autocorrelation of densities in each study site by calculating the Ljung-Box statistic in the *forecast* package in R (Hyndman *et al.* 2024) with a maximum lag of 10 years. Except for Alpine bullhead in site 3 there was no significant autocorrelation at the $\alpha = 0.05$ -level in the density data (supplementary material S.1). We therefore proceeded with the trend analyses without prewhitening the data (Bayazit & Önöz, 2007). We conducted both a monotonic trend test for the entire period and a nonlinear trend analysis.

We evaluated monotonic temporal trends in densities using the Mann-Kendall test in package *Kendall* (McLeod 2022). The test is non-parametric and does not assume normally distributed errors. Trend analyses were conducted within and across study sites. To quantify the covariation between different groups (Alpine bullhead, age-0 brown trout, and older brown trout) within sites and to quantify the synchronicity of groups across sites we calculated Pearson's correlation coefficient for all combinations.

To assess nonlinear trends, we performed a trend analysis with generalized additive models (GAMs). Models were specified in the *mgcv* package (Wood 2011), with density of each species and age group in each site as the normal Gaussian response variable. *Year* was defined as the smoother function with an identity link function, and we used restricted maximum likelihood (REML) as the estimator. For the 25-year time series we allowed 5 nodes, hence defining $k = 5$.

To partition the variance in densities between site-level differences and year-to-year variation we conducted a variance decomposition analysis by specifying an empty, two-level mixed model with site as a random effect in the *lme4* package in R (Bates *et al.* 2015). We view site as a random effect because the sites were initially chosen from a larger population of potential study sites. This is the same as a one-way ANOVA with random effects and can be written as

$$\text{Eq. 1: } \text{Density}_{ij} = \beta_{0j} + r_{ij},$$

where the site-specific intercepts around the grand mean can be introduced as

$$\text{Eq. 2: } \beta_{0j} = \gamma_{00} + u_{0j}$$

Substituting the site-level intercepts into the level 1 equation we obtain

$$\text{Eq. 3: } \text{Density}_{ij} = \gamma_{00} + u_{0j} + r_{ij},$$



Figure 4. An adult Alpine bullhead (*Cottus poecilopus*) in the tributary Setninga, just upstream from its confluence with the Atna River. Photo: KM Myrvold.

where γ_{00} is the grand mean intercept, u_{0j} is the site-level deviation from the grand mean intercept, and r_{ij} is the residual-level, year-to-year variance. Finally, to explain the variation in density, we added explanatory variables pertaining to discharge and temperature (defined in Table 1) while allowing for site-specific intercepts as follows:

$$\text{Eq. 4: } \text{Density}_{ij} = \gamma_{00} + \gamma_{10}\text{predictor}_{ij} + u_{0j} + r_{ij}$$

Here, γ_{00} is the grand mean density, γ_{10} is the average slope across all sites, u_{0j} is the unique increment to the intercept associated with site j . Models were ranked using AIC (Akaike 1973) and a single best approximating model was chosen if its delta AIC value exceeded 2.0. We used full maximum-likelihood estimation to permit model comparison for each species or age class. All analyses were conducted in R v. 4.4.2 (R Core Team 2024). Plots were generated using package *ggplot2* (Wickham 2016).

RESULTS

Trends in densities from 1998 through 2024

Densities of Alpine bullhead, age 0 brown trout, and older brown trout fluctuated considerably over the 25-year period (Figure 5). Densities were higher overall in the first few years, and overall lower since the year 2020. Densities of Alpine bullhead exceeded 150 individuals per 100 m² in the most abundant years in sites 1 and 2 upstream of the lake. Densities of 0+ brown trout were predominantly below 50 individuals 100 m² whereas densities of older juvenile brown trout only exceeded 15 individuals per 100 m² three times in site 3 and once in site 4.

All the statistically significant trends had a negative trajectory, with seven out of 16 trends displaying a significant downward trend in density over the period (Table 3). Alpine bullhead declined in sites 1, 2, and 4, whereas young of the year brown trout declined in sites 3 and 4. Sites 3 and 4 also saw declines in overall densities of brown trout. Fluctuations in densities were evident throughout the 25-year period and low densities over the last three years of the study likely contributed to the overall negative trends.

The monotonic declines were largely corroborated by the results from the nonlinear trend analysis using GAMs. Significant nonlinear trends were found for Alpine bullhead in all sites; age-0 brown trout in sites 3 and 4; and for older brown trout at site 3 (supplementary material S.2). Differences between the Mann-Kendall and GAM analyses were found for Alpine bullhead at site 3 and older brown trout in site 3, where the GAM detected significant trends, and the Mann-Kendall monotonic trend analysis did not (Table 3; supplementary material S.2).

The declines were evident across all sites for Alpine bullhead. With the exception of sites 2 and 3, each pair of sites displayed a significant correlation in Alpine bullhead densities (supplementary material S.3). This implies some level of synchronicity in the abundance of Alpine bullhead in the Atna River. Densities of age 0 brown trout correlated in sites 1 and 2, whereas densities of older brown trout correlated in sites 3 and 4.

We also assessed synchronicity for pairs of species within each site. Relatively few pairs of species displayed any covariation. Alpine bullhead and age 0 brown trout displayed positive significant correlation in sites 3 and 4, and age 0 brown trout and older brown trout correlated significantly in site 4 (supplementary material S.4).

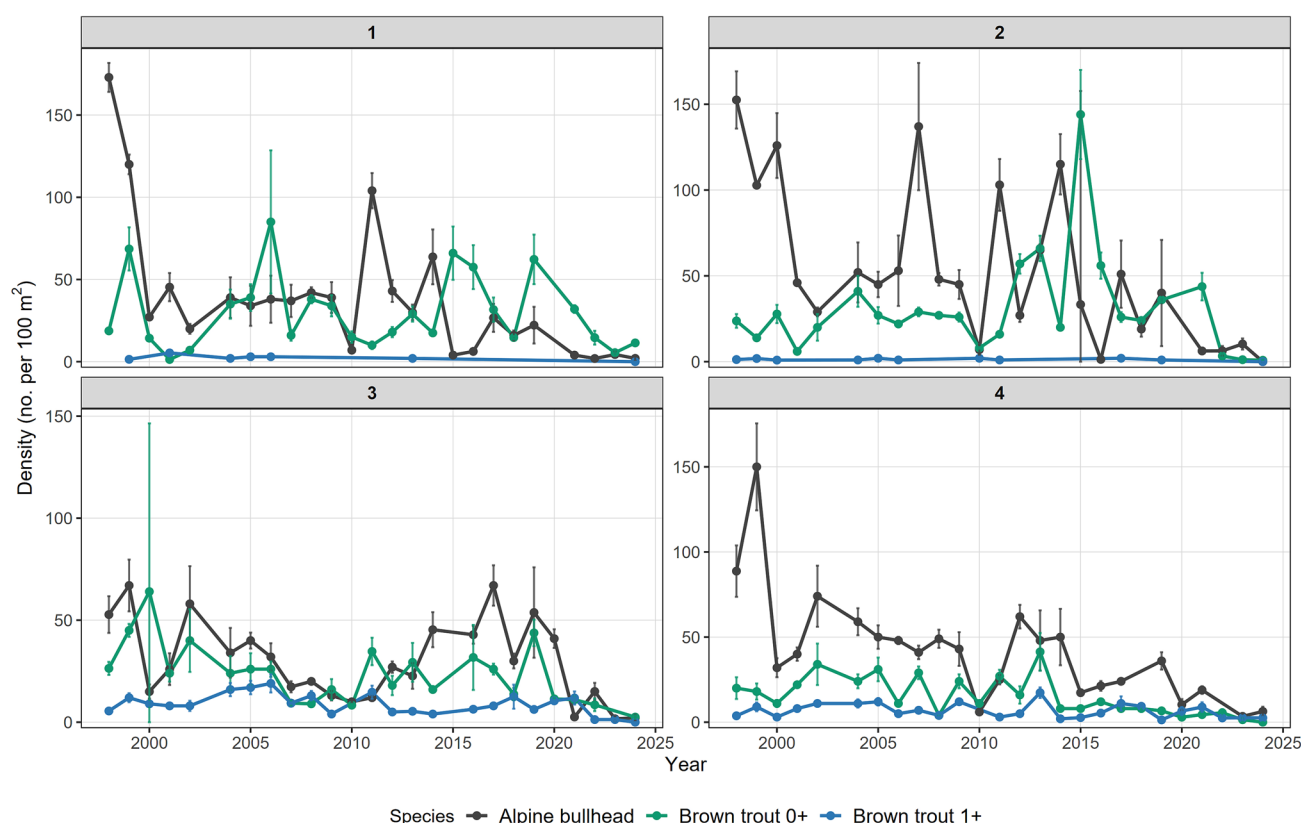


Figure 5. Densities of each species and age class in each site (sites 1 – 4) from 1998 through 2024. Densities are expressed as the number of individuals per 100 m², and error bars for the estimates (SE) are displayed as vertical lines around the point estimate.

Table 3. Monotonic trends for each species and age group in the respective study sites from 1998 through 2024. The table displays the nonparametric correlation coefficient Kendall's tau; the P value testing the hypothesis of no trend; the Mann-Kendall statistic (S) and its variance (varS); and the Sen's slope. A positive Sen's slope indicates an increasing trend over time and a negative Sen's slope indicates a decreasing trend in densities over time. Significant trends are denoted by*.

Site	Species	Kendall's tau	P (tau)	Mann-Kendall S	varS	Sen's slope
1	Alpine bullhead	-0.508	0.0004*	-152	1831	-2.110
	Brown trout 0+	-0.087	0.5593	-26	1833	-0.194
	Brown trout $\geq 1+$	-0.250	0.5387	-5	42	-0.500
	Brown trout all	-0.093	0.5283	-28	1833	-0.258
2	Alpine bullhead	-0.484	0.0008*	-145	1832	-3.134
	Brown trout 0+	-0.017	0.9255	-5	1830	-0.097
	Brown trout $\geq 1+$	-0.119	0.6857	-6	153	0
	Brown trout all	-0.013	0.9441	-4	1831	-0.048
3	Alpine bullhead	-0.244	0.0926	-73	1832	-1
	Brown trout 0+	-0.377	0.0113*	-103	1620	-0.969
	Brown trout $\geq 1+$	-0.289	0.0526	-79	1620	-0.347
	Brown trout all	-0.384	0.0077*	-115	1832	-1.472
4	Alpine bullhead	-0.538	0.0003*	-148	1623	-2.734
	Brown trout 0+	-0.534	0.0002*	-171	2045	-0.875
	Brown trout $\geq 1+$	-0.222	0.1283	-66	1827	-0.128
	Brown trout all	-0.449	0.0015*	-145	2054	-1

Variance decomposition

The overall average densities for Alpine bullhead, age 0 brown trout, and older brown trout were 41, 25, and 5 individuals per 100 m², respectively (Table 4). The variation in densities of Alpine bullhead and brown trout was largely driven by year-to-year fluctuations; however, for older brown trout there was an effect of site indicating systematic differences in densities between sites.

For Alpine bullhead and age 0 brown trout, the influence of site-level factors had minimal influence on the overall density variation over the course of the study, which can be observed in the plot where the site-level means lie close to the grand mean density (supplementary material 5). This implies that factors that operate on an annual time scale were more influential for these two groups, and that adding explanatory variables that vary on a yearly basis are necessary to explain this variation. For older brown trout there was an effect of site, most likely due to low densities in sites 1 and 2 relative to 3 and 4. Site-level means deviated farther from the grand mean density for this age class. Explaining variation in densities over time could be improved by including site-level predictors for this age group; however, with only four sites included in the long-term monitoring program the statistical power will be limited.

Relationships between river discharge, water temperature and fish densities

Finally, we assessed the relationships between the discharge and temperature metrics and the densities of the respective species / age classes. Each group had one single-best supported model among the candidate models that were assessed in this study (i.e. with a delta AIC < 2.00), and all groups displayed a negative relationship between the discharge metrics and densities for this best supported model (Table 5). Alpine bullhead and older brown trout related negatively to the lowest discharge of the year (Qmin; Figure 6), whereas age 0 brown trout related negatively to the annual mean discharge (Qmean; Figure 6). Maximum temperature Tmax was within 2 AIC points of the best approximating model for older brown trout and will be discussed.

The discharge-related metrics explained some of the overall variance in fish densities (Table 6); however, for older brown trout there was no overall improvement over the empty model. In all cases, the variance on the site level increased when introducing the predictor variable because the residual level accounted for most of the variance in the data. Therefore, the overall variance decreased for Alpine bullhead and age 0 brown trout after inclusion of the covariate (Table 6; Figure 6).

Table 4. Intercept estimates and variance decomposition for Alpine bullhead, age 0 brown trout, and older brown trout. Model specification is given in Equation 3.

Species / age class	Intercept γ_{00}	SE Intercept	Site-level variance u_{0j}	Residual variance r_{ij}	% Site-level variance	% Residual-level variance
Alpine bullhead	40.6	4.15	17.9	1264.9	1.4	98.6
Brown trout 0+	24.7	3.16	23.1	420.4	5.2	94.8
Brown trout $\geq 1+$	4.9	1.52	8.0	16.4	32.7	67.3

Table 5. Parameter estimates and model selection results for the candidate models for each species. Model specification is given in equation 4 and the variables are defined in Table 1. The best approximating models for each species / age class are highlighted in bold, and models within 2.0 AIC points of the best model are in *italics*.

Species	Predictor variable	Intercept	Intercept SE	Intercept t-value	Slope	Slope SE	Slope t-value	Site-level variance	Residual variance	AIC
Alpine bullhead	Qmean	87.63	26.63	3.29	-4.28	2.39	-1.79	19.62	1223.71	994.14
	Qmax	45.19	10.59	4.27	-0.07	0.15	-0.47	17.88	1262.07	997.06
	Qmin	132.18	25.34	5.22	-45.14	12.33	-3.66	23.08	1109.09	984.73
	SQmean	17.52	18.62	0.94	1.06	0.84	1.27	19.89	1242.85	995.68
	SQmax	23.83	10.28	2.32	0.28	0.16	1.79	21.33	1222.38	994.13
	SQmin	15.61	8.78	1.78	4.08	1.26	3.23	22.57	1139.71	987.36
	Tmean	139.77	37.87	3.69	-10.73	4.08	-2.63	17.28	1181.71	990.58
	Tmax	44.33	30.49	1.45	-0.24	1.95	-0.12	17.66	1264.86	997.27
	Tmin	62.32	14.44	4.32	-8.21	5.23	-1.57	19.63	1232.60	994.85
Brown trout 0+	Qmean	61.88	15.44	4.01	-3.40	1.38	-2.46	24.21	395.37	893.48
	Qmax	29.38	6.54	4.49	-0.07	0.09	-0.83	23.40	417.36	898.69
	Qmin	34.21	15.65	2.19	-4.70	7.55	-0.62	22.82	418.86	898.98
	SQmean	29.94	10.84	2.76	-0.24	0.48	-0.51	23.15	419.26	899.11
	SQmax	24.76	6.30	3.93	0.00	0.09	-0.02	23.09	420.40	899.36
	SQmin	26.75	5.66	4.72	-0.34	0.76	-0.45	23.26	419.47	899.17
	Tmean	59.86	21.56	2.78	-3.80	2.30	-1.65	23.16	408.97	896.68
	Tmax	28.46	17.51	1.63	-0.24	1.11	-0.22	23.02	420.22	899.32
	Tmin	20.91	8.57	2.44	1.41	3.00	0.47	23.17	419.42	899.14
Brown trout ≥ 1+	<i>Qmean</i>	11.38	3.75	3.03	-0.59	0.31	-1.88	7.90	15.55	390.57
	Qmax	5.67	2.05	2.76	-0.01	0.02	-0.55	8.14	16.31	393.71
	Qmin	13.15	3.92	3.36	-4.23	1.80	-2.34	10.31	14.92	388.90
	SQmean	4.72	2.92	1.61	0.01	0.11	0.08	7.97	16.40	394.01
	SQmax	3.64	2.01	1.81	0.02	0.02	0.96	7.92	16.17	393.09
	SQmin	5.04	1.91	2.63	-0.02	0.20	-0.10	8.01	16.40	394.00
	Tmean	0.53	5.59	0.09	0.48	0.58	0.82	7.76	16.26	393.35
	<i>Tmax</i>	<i>-4.19</i>	<i>4.33</i>	<i>-0.97</i>	<i>0.58</i>	<i>0.26</i>	<i>2.24</i>	<i>7.82</i>	<i>15.22</i>	<i>389.17</i>
	Tmin	6.62	2.48	2.67	-0.65	0.75	-0.87	7.99	16.21	393.26

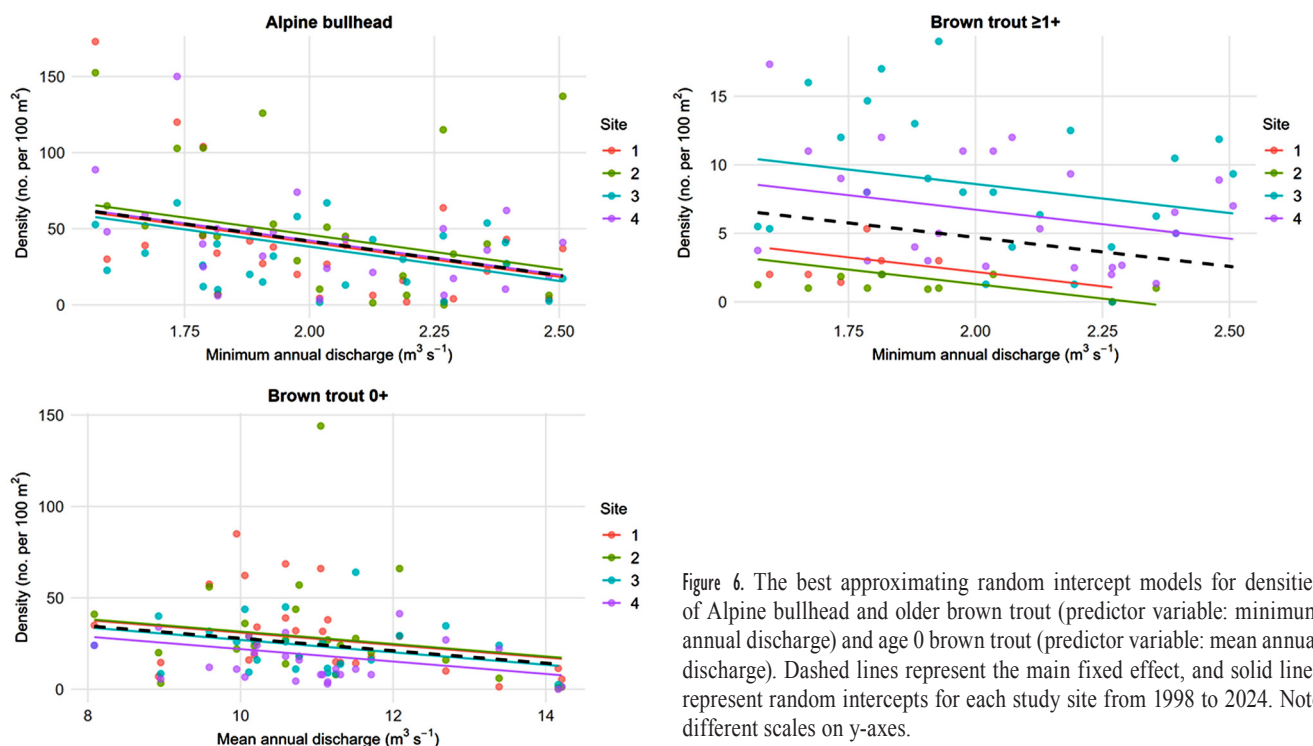


Figure 6. The best approximating random intercept models for densities of Alpine bullhead and older brown trout (predictor variable: minimum annual discharge) and age 0 brown trout (predictor variable: mean annual discharge). Dashed lines represent the main fixed effect, and solid lines represent random intercepts for each study site from 1998 to 2024. Note different scales on y-axes.

Table 6. Variance in density explained by inclusion of predictor variables for Alpine bullhead and brown trout. The variables increased the variance at the site level but decreased the overall variance.

Species / age class	Statistic	Empty model	AIC-best model	% of explainable variation
Alpine bullhead	Site-level variance	17.9	23.1	
	Residual-level variance	1264.9	1109.1	
	Total variance	1282.8	1132.2	
	Site-level of total %	1.4	2.0	-29.2
	Residual-level of total %	98.6	98.0	12.3
	Improvement overall			11.7
Brown trout 0+	Site-level variance	23.1	24.3	
	Residual-level variance	420.4	393.0	
	Total variance	443.5	417.3	
	Site-level of total %	5.2	5.8	-5.3
	Residual-level of total %	94.8	94.2	6.5
	Improvement overall			5.9
Brown trout $\geq 1+$	Site-level variance	8.0	10.3	
	Residual-level variance	16.4	14.9	
	Total variance	24.4	25.2	
	Site-level of total %	32.7	40.9	-29.3
	Residual-level of total %	67.3	59.1	9.0
	Improvement overall			-3.5

DISCUSSION

Overall trends in brown trout, Alpine bullhead, and environmental factors

Twenty-five years of monitoring fish populations in the Atna River revealed an overall negative trend in densities of adult Alpine bullhead (3 out of 4 sites), a declining trend in densities of age 0 brown trout (2 of 4 sites), and an inconclusive trend for older juvenile brown trout (negative trend in 1 of 4 sites). There were substantial fluctuations in densities for both species over the duration of the monitoring program, and the majority of the variance originated from year-to-year variation in the densities of Alpine bullhead and age 0 brown trout (more than 94 % of the total variance). For older juvenile brown trout, approximately 33 % of the variance could be attributed to site-level factors, i.e. systematic differences in densities between sites, which presumably owed to very low densities in sites 1 and 2 compared to sites 3 and 4. With limited numbers of older brown trout in sites 1 and 2 we will be cautious when interpreting these results.

Concurrently, there were changes in the discharge and water temperature-related metrics over the time period. Q_{min} (the minimum daily discharge) increased significantly, whereas Q_{mean} (annual mean discharge) increased although not significantly ($P = 0.15$). The best approximating models for densities of Alpine bullhead and older brown trout included minimum annual discharge as the predictor variable and mean annual discharge for age 0 brown trout, all showing a negative relationship with fish densities. Because the study sites are within the same river with no river-level replication, caution needs to be exerted before assuming causality and attributing the changes in fish densities to these variables. Detecting coherent signals of climate change is best achieved by conducting spatially expansive, long-term studies with clear hypothesis of the ecological mechanisms able to produce a shift in the abundance or distribution of organisms (Lawlor *et al.* 2024). In the following we discuss the likely mechanisms by which discharge and temperature can impact

the abundance of brown trout and Alpine bullhead in river systems.

Main effects

Due to the long duration of this study, we were limited to discharge and temperature as explanatory variables as they were the only factors with an unbroken record. The best supported models showed a negative relationship between fish densities and mean annual discharge (Alpine bullhead and older brown trout) and a negative relationship between density and minimum annual discharge for age 0 brown trout. The models explained only modest amounts of overall variance in the dataset (range 0 to 12 %), but did document a potentially limiting effect on fish densities on an annual basis. A high mean annual discharge indicates prolonged periods of high discharge events relative to dry periods over the course of a year. Q_{min} was unrelated to the mean annual discharge, presumably because low-flow conditions occur in winter irrespective of the total amount of precipitation that year. Temperature-related metrics produced a less clear response relative to discharge, with none of the best approximating models in the candidate set. However, T_{max} was within one AIC unit of the best approximating model for older brown trout, which will be discussed below.

Clearly, a suite of abiotic and biotic factors interacts to affect fish population sizes on various time scales and only addressing one or a few of these factors can limit or bias the identification of the ecological mechanisms at act (Nislow & Armstrong 2012; Warren *et al.* 2015). However, discharge is the key abiotic factor in river ecosystems, affecting virtually all aspects of stream biota through its pervasive controls over channel morphology, sediment transportation, the thermal landscape, and fluxes of organic material (Poff *et al.* 1997; Allan *et al.* 2021). By focusing on annual means, maxima, and minima and those of the early critical period (May-June) we believe the selected variables covered an important aspect of juvenile brown trout hatching and rearing and adult Alpine bullhead ecology (Poff & Zimmerman 2010; Nislow & Armstrong 2012; Blum *et al.*

2018). The temporal resolution of the fish data did not permit us to mechanistically separate out the differential effects of the various components of the flow regime in terms of direct impacts on fish densities, nor its indirect impacts through changes to the physical habitat, food resources, or other unobserved processes (Power *et al.* 2008; Poff & Zimmerman 2010). As Warren *et al.* (2015) noted, “*The direct and indirect effects of river flow will affect different fish life-stages in distinct ways but responses appear to be highly variable and attempts to generalize among salmonid species and hydrological regimes has proven problematic.*”

Potential mechanisms influencing fish densities

Some of the mechanisms by which high discharge events impact fish in rivers include scouring and mobilization of stream bed substrate (Unfer *et al.* 2011; Goode *et al.* 2013), deposition of fine materials and changes to shelter and interstitial space (Osmundson *et al.* 2002), displacement of individuals and direct mortality (Jensen & Johnsen 1999), and through changes to the invertebrate community (Warren *et al.* 2015). However, the scale, context, and duration largely influence the direction and extent to which the population is impacted (Power *et al.* 2008; Unfer *et al.* 2011; Warren *et al.* 2015). Whereas flooding can cause increased displacement and mortality of individuals on a local scale over short periods of time, it may improve growth and fitness of survivors via compensatory mechanisms (Nislow & Armstrong 2012). The net result on the population is, however, often detrimental. An analysis in brook trout in Massachusetts showed that compensation could modulate, but not revert, changes in density following changes to stream temperature and discharge (Bassar *et al.* 2016). Generalizations may therefore be tentative because they depend on the mechanisms through which individuals and populations are impacted.

Compared to discharge, models relating water temperature to fish densities received less support, but T_{max} had some influence over older brown trout densities. The relationship was positive but uncertain (1.96 x standard error exceeded the parameter estimate), meaning that years with higher maximum summer temperatures were loosely associated with higher densities of older brown trout. There was no trend in T_{max} over the 25-year period. Furthermore, because older brown trout were primarily found in sites 3 and 4, care should be taken when interpreting the results. Water temperature can limit populations both at the upper and lower level. In the Atna drainage, water temperatures rarely exceed the thermal optima for these species for prolonged periods of time. With a median T_{max} of 15.2 °C and a range between 12.9 °C and 18.8 °C over the 25 year-period, the temperatures are within reported tolerance ranges for brown trout (summarized by Elliott & Elliott 2010). Furthermore, salmonids are known to behaviorally thermoregulate, for example by seeking out patches of relatively cooler water during thermally stressful conditions (e.g. Breau *et al.* 2011), which makes them capable of adjusting to periods with less suitable temperatures.

Compensatory mechanisms at the scale of cohorts can be identified through indications of demographic density dependence (Imre *et al.* 2005; Myrvold & Kennedy 2015; Grossman & Simon 2020). With no individual tagging and only one sampling occasion per year, investigating the relationship between average mass and population density could potentially lend insights into food limitation and intraspecific competition. However, the variability in the timing of sampling between years proved problematic for conducting such an analysis. With a relatively short time between hatching (assumed swim up in Mid-May) and sampling (August and September), a difference in timing of only a few weeks accounts for a substantial

portion of an individual's growing season. Consequently, considering density dependent mortality was not possible in this study.

Even though some sampling uncertainty is implicitly included in the standard errors of the density estimates, we cannot completely discount the effect of increased sampling error in years with high discharge (Forseth & Forsgren 2008). Sampling was conducted during roughly the same discharge levels. The direct effect of sampling error is therefore assumed to be less than that of dilution effects in high water years. Presumably, there will be a greater wetted area in high water years which, everything else being equal, could lead to a more diluted concentration of the same number of fish per river meter. Furthermore, fish could be more distributed due to the dispersing effects of flooding on young-of-the-year (Beall *et al.* 1994) and spawning areas might shift over time due to displacement of gravels (Pulg *et al.* 2022). Finally, we did not have sufficiently many sites to introduce site-level explanatory variables. With only four sites we chose to leave out any site-level variables, but we note that channel configurations differ between sites upstream and downstream of the lake.

Comparison with previous studies

An experimental study in the Atna drainage showed that Alpine bullhead and brown trout displayed similar preferences for stream substrate size (Hesthagen & Heggenes 2003). In allopatry, brown trout regulated their habitat preferences with increasing densities by occupying gradually finer substrate sizes, whereas Alpine bullhead displayed a greater tolerance for crowding in their preferred substrate size category. In both species, small individuals were displaced by larger individuals with increasing densities. In sympatry, large Alpine bullhead displaced brown trout which suggests interspecific competition (Hesthagen & Heggenes 2003). In field settings, a considerable habitat and diet overlap was found between the two species in the Atna River, resulting in a negative correlation between densities during the period 1986–1991 (Hesthagen *et al.* 2004b).

Interestingly, we found a positive correlation between densities of Alpine bullhead and age-0 brown trout in some of the sites during the period 1998–2024. A likely explanation is that the densities were overall higher during the former period (1986–1991; Hesthagen *et al.* 2004b) and that sites with densities lower than 30 fish per 100 m² of either species were excluded from that analysis. In some cases, densities of Alpine bullhead older than 1 year reached up to 280 individuals per 100 m². Consequently, the potential ramifications of interspecific competition were more visible in their study, and the exclusion of low-density situations makes comparison with our study largely tentative. However, the previous study highlights how interspecific competition can be an important mechanism during periods of high densities of brown trout and Alpine bullhead where they co-occur (Hesthagen *et al.* 2004b).

Long-term monitoring of aquatic ecosystems

The wide fluctuations and overall low densities of brown trout and Alpine bullhead since 2021 fit a similar trend observed in rivers across southern Norway. A general trend across both impacted and natural systems suggests a broad stressor such as an unusual hydrologic event or temperature anomaly. Whether these depressed densities result from drought or flooding, in combination with direct or unobserved anthropogenic impacts, remains unanswered (Thrane *et al.* 2022; Eriksen *et al.* 2024). In Southern Norway there have been two large-scale events capable of producing shifts in densities of stream fishes across large geographic extents. First, in 2018 there was widespread drought, high temperatures, and low flows in spring and early summer

(Thrane *et al.* 2022). Second, the eastern and central portions of Southern Norway were hit by widespread rain-driven flooding in August 2023 (Granerød *et al.* 2023).

An assessment of the effects of the 2018 drought did not find any general impacts on fish populations in reference rivers but did document regional declines in Trøndelag (Thrane *et al.* 2022). A recent publication from the same rivers pointed to substantial variation in fish densities within rivers over time, but the full effects of the flooding in 2023 may not have been reflected in the data (Eriksen *et al.* 2024). With only one full sampling event in the aftermath of the 2023 flooding, patterns might emerge as reports are being published. Future studies should investigate the extent to which fish populations in rivers impacted by channelization, hydropower, or constrained by infrastructure respond differently than populations inhabiting unconstrained rivers with a natural flow regime.

With a limited number of study sites retained since the beginning of the monitoring program, we acknowledge that the current design might not be representative of the entire watershed. However, maintaining a handful of study sites is preferable to abolishing the program altogether and will provide useful data on the trends in population densities. Long-term data sets provide important insights into the dynamic nature of wild populations; a context for studies of shorter duration; and can help set targets for management and restoration efforts (Revenga *et al.* 2005; Ramos-Merchante *et al.* 2021). Combining long-term monitoring such as this study with mechanistic studies is an effective strategy to ensure continuity and context (Power *et al.* 2008; Warren *et al.* 2015). Maintaining funding for long term monitoring in watersheds with a limited human footprint may therefore be a relatively cheap investment in the face of global change even with limited number of study sites. Coupled with spatially extensive ecological monitoring such as the Reference River program in Norway (Eriksen *et al.* 2024) and the eLTER (Integrated European Long-Term Ecosystem, critical zone and socio-ecological Research), these long-term data sets can help document ecological shifts and elucidate drivers at scale.

Declaration of the use of large language models

Large Language Models were used to debug, develop, and clean scripts for analyses and visualizations in the R programming language.

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Data availability statement

The data are available upon reasonable request to the corresponding author.

SUPPLEMENTARY MATERIAL

- Supplementary material 1: Data diagnostics
- Supplementary material 2: Nonlinear trend analysis using GAMs
- Supplementary material 3: Correlations between densities of each species across sites
- Supplementary material 4: Correlations between densities of different species within each site
- Supplementary material 5: Variance decomposition

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