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Research article

Contrasting long-term trends in juvenile abundance of a widespread cold-water salmonid along a latitudinal gradient: effects of climate, stream size and migration strategy

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A changing climate reshapes the range distribution of many organisms, and species with relatively low thermal optima, like many salmonids, are increasingly expected to face local population extinctions at lower latitudes. Understanding where and how fast these changes are happening is of pivotal importance for successful mitigation and conservation efforts.

We used an extensive electrofishing database to explore temporal trends of juveniles of brown trout *Salmo trutta* in 218 locations from 174 Swedish streams, over the last 30 years (1991–2020). We hypothesized that 1) declines in abundance have occurred predominantly in the warmer, southern regions, while increases have occurred in the colder, northern regions, 2) larger stream sizes may partly offset negative effects of climate, and 3) migrating and resident populations are affected differently by a warming climate.

We found that abundance of brown trout juveniles generally declined in warmer regions especially in smaller streams (≤ 6 m wide), while the abundance increased in colder regions. In larger streams, negative effects of higher temperatures were seemingly buffered, as we found lower rates of decline or even positive trends. The rate of change (i.e. the slopes of the trends in abundance) was more pronounced towards the climate extremes, and was on average zero in regions with a normal annual air temperature (average temperature over 30 year period) around 5–6 °C. Warmer climate had stronger effects on migrating compared to resident populations, suggesting that climate-induced loss of stream connectivity could be an additional factor that hinders recruitment in anadromous populations in a changing climate.

Considering predictions of increasing temperatures and frequency of summer droughts, management of cold-water salmonid populations should focus on conserving and restoring riparian vegetation, wetlands, climate and thermal refugia, and habitat integrity overall. Such measures may, however, not suffice for small streams at lower latitudes, unless hydrological connectivity is maintained.

Keywords: anadromous species, brown trout, climate, hydrological connectivity, temperature, temporal trends

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Introduction

A warming climate causes restructuring of natural ecosystems globally. Continued temperature increases are predicted to cause shifts in species distribution patterns and increase the risk of local extinctions (Perry et al. 2005, Lassalle and Rochard 2009, Comte and Grenouillet 2013, Urban 2015). Freshwater habitats are especially threatened by human activities and environmental change (Strayer and Dudgeon 2010, Best and Darby 2020, Tickner et al. 2020), which compromise the ability of these ecosystems to provide essential ecosystem functions and services (e.g. water provision, biodiversity, fish production, etc.). Recent evidence suggests that declines in freshwater species populations outpace declines in the marine and terrestrial realms (Reid et al. 2019). As a consequence of the apparent dire situation in freshwater ecosystems, there is a strong need for better knowledge into human impacts on these environments (including effects of a warming climate) to support management actions (Maasri et al. 2021).

Freshwater fish species are especially vulnerable to a warming climate (Barbarossa et al. 2021) and their vulnerability is projected to be higher in the northern hemisphere, due to greater predicted magnitude of climatic change (Comte and Olden 2017). Increasing air temperatures may cause water temperatures to periodically exceed the maximum thermal tolerance of many species (van Vliet et al. 2013). Altered flow regimes caused by deviation in precipitation patterns can result in dramatic changes in habitat conditions and hydrological and ecological connectivity (Dai 2013, Truchy et al. 2020). Even extended periods of temperatures below lethal thresholds but exceeding the optimal thermal range of species can cause severe effects by decreasing activity and growth rates (Ficke et al. 2007). Local and regional environmental conditions, such as stream size and hydrological connectivity, can influence the resilience of riverine communities to increasing temperatures. Larger streams have lower probability of drying, and are less affected by fluctuations in air temperature (Caissie 2006). They can also be more productive, offer higher connectivity within the river network, and contain more diverse habitats, some of which may provide (cold) thermal refugia during high temperature periods (Pracheil et al. 2013, Doretto et al. 2020). Where the integrity and connectivity within, or among, river networks are maintained, some species can make compensatory movements to cooler locations (e.g. tributaries), and establishment of persistent populations can occur if habitat conditions are suitable (Troia et al. 2019, Barret and Armstrong 2022). However, anthropogenic barriers (e.g. dams and road culverts), as well as drought-induced changes in the riverine habitat, may severely hamper species dispersal and longitudinal migration (Markovic et al. 2017). Furthermore, while climate-driven range shifts may save certain populations from extinction, the immigrating population may also affect the original ecosystem constituents and cause shifts in ecosystem structure and function (Wallingford et al. 2020).

Brown trout *Salmo trutta* is a cold-water species broadly distributed in boreal streams and of high ecological and economical value (Lobón-Cerviá 2017). Declines in suitable habitat for brown trout are occurring or are predicted to occur in many places as the consequence of altered river discharge and increased water temperatures (Keleher and Rahel 1996, Jonsson and Jonsson 2009, Filipe et al. 2013). Fall-spawning species like brown trout and some other salmonids are especially vulnerable to high winter flows, which can scour eggs from gravel nests (Wenger et al. 2011). Growth of young stream-living brown trout occurs in the interval of circa 3–19 °C, with an optimum of around 13–14 °C for trout feeding on invertebrates and 16–17 °C for trout feeding on fish or fish-based food pellets (Forseth and Jonsson 1994, Elliott and Hurley 2000, Elliott and Elliott 2010). Behavioral experiments suggest a preferred water temperature for juveniles between 15 and 16.5 °C (Larsson 2005), although it can be increased by prior acclimation at higher temperatures (Cherry et al. 1977). Incipient critical lethal temperatures for brown trout juveniles are between 22 and 25 °C (Elliott and Elliott 2010), which corresponds to a drastic decline in feeding rate and activity (Ojanguren et al. 2001), although juvenile brown trout can withstand slightly higher temperatures for brief periods of time (i.e. a few hours) (Elliott and Elliott 1995). Because of the relatively low tolerance to high temperatures, brown trout is particularly vulnerable to climate warming and extreme low-flow conditions (Burkhardt-Holm et al. 2002, Nicola et al. 2009, Warren et al. 2015), in particular where shading from riparian vegetation is absent (Broadmeadow et al. 2011). Furthermore, while some populations reside their whole life in running waters, other populations host individuals that migrate to the sea or to lakes (Armstrong et al. 2003). Migratory behavior occurs when individual fitness increases by exploiting feeding grounds further from the natal habitat, so that the cost of migration is less than the increased growth and fecundity (Gross et al. 1988, Bohlin et al. 2001). Suboptimal conditions for growth (e.g. high competition pressure or limited food availability) maintain a strong selective pressure for moving away from nursery habitats (Gross et al. 1988). However, increased potential fitness stemming from a migratory strategy is part of a trade-off with a migration associated increase in mortality-risk (Jensen et al. 2019), which may be exacerbated by lowered swimming capacity and aerobic scope at temperatures above the thermal optimum (Baisez et al. 2011, Verberk et al. 2011, Meyer and Schill 2021). Low water levels may cause spawning habitats to become unavailable for anadromous spawners, and warmer temperature may hasten reproduction events (Jonsson and Jonsson 2009, Kaeding and Mogen 2022). Low water levels can also lead to the loss of hydrological spatial connectivity in the river network and to a temporal mismatch between the spawning period and the availability of habitats and resources (Larsson et al. 2015, Rytwinski et al. 2017, Nack et al. 2019). In addition, increased water temperatures may increase the activity

and number of warm-water predators such as pikeperch *Sander lucioperca* and pike *Esox lucius*) (Nyberg et al. 2001, Winfield et al. 2008), thus increasing the encounter rate of predators for migrating trout (Degerman and Sers 1993, Jepsen et al. 2000, Winfield et al. 2008). However, migrating populations could also be less affected by a warming climate than freshwater residents due to a greater ability to reach climate refugia, and colonize suitable habitats (Schtickzelle and Quinn 2007, Isaak et al. 2022). Whether resident or anadromous trout populations are more resilient to climate change is still an open question.

In the boreal hemisphere brown trout is expected to face a decline in southern populations accompanied by northwards migration, or range shifts to higher altitudes (Jonsson and Jonsson 2009, Kovach et al. 2016, Kärcher et al. 2021). Such predictions are supported by increasing evidence of negative populations trends for brown trout in Switzerland, Wales and New Zeeland (Scott and Poynter 1991, Burkhardt-Holm et al. 2002, Clews et al. 2010), and positive trends in Iceland and northern Norway (Svenning et al. 2021). Despite the amount of data collected in many countries by long-term monitoring efforts targeting salmonids, there is an overall scarcity of studies that used temporal data to quantify climate-induced changes in trout ecology (Kovach et al. 2016, but see Eby et al. 2014, LeMoine et al. 2020). Sweden has developed a long-standing, spatially broad, and standardized monitoring of salmonids via electrofishing surveys, which offers an excellent basis for investigating climate-driven trends of brown trout extending over several decades and a large latitudinal and climatic gradient. While the amount of lake-migrating trout populations has decreased considerably in the last decades, mainly due to man-made migration obstacles (Ros 1981), a thorough and more recent assessment of long-term temporal trends of resident and migrating trout populations across this gradient is missing. Investigating long-term changes in abundance across space and in relation to different environmental conditions is of pivotal importance to implement management and conservation actions (Muhlfeld et al. 2018).

This study aimed to explore temporal trends of brown trout in the last 30 years, from 1991 to 2020, across Sweden. We formulated three hypotheses:

1. Declines in abundance have occurred in the warmer, southern regions, while increases in abundance have occurred in the colder, northern regions.
2. Larger stream sizes can partly offset negative effects of a warmer climate.
3. Migrating and resident populations are affected differently by a warming climate.

The analyses were based on electrofishing data on juvenile abundances, which can be considered indicative of population trends given the relatively strong stock-recruitment relationship in brown trout (Cattanéo et al. 2002, Jonsson and Jonsson 2011, Cauvy-Frauníe et al. 2020).

Methods

Electrofishing data

Data on brown trout abundance and stream size (i.e. width and average depth) were extracted from the Swedish Electrofishing RegiSter ('SERS'; SERS, 2021) and included time series collected between 1991 and 2020 from 218 locations spread across 174 streams in Sweden (Fig. 1), for a total of 4691 electrofishing sampling occasions. Data in SERS are quality assured by using a strict sampling protocol (Bergquist et al. 2014), including posterior quality checks. We used the following criteria for data selection:

1. we included sites with moderate flow velocity (> 0.1 and < 0.8 m s^{-1}) and dominated by a coarse substrate (gravel, stones and boulders), representing typical brown trout streams in the region (Pedersen et al. 2017);
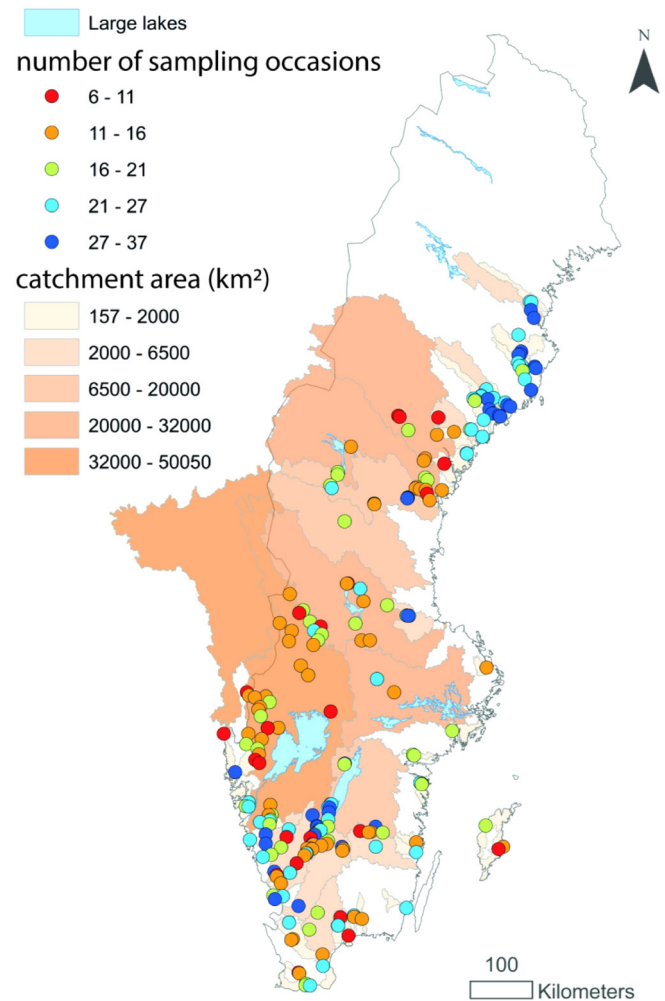

Figure 1. Map of Sweden showing the spatial distribution of the electrofishing sampling locations included in the analyses. The color of the dots indicates the number of sampling occasions (expressed in classes) for each location. Orange polygons indicate the main catchments containing the sampling locations, with the color scale indicating the catchment areal extent (km^2).

2. we selected sites where electrofishing had included the whole stream width, to avoid sampling artefacts;
3. to minimize potential variation caused by competitive interactions between brown trout and Atlantic salmon *Salmo salar*, which is usual most pronounced between trout 1+ and salmon 0+ (Kennedy and Strange 1986, Armstrong et al. 2003, Milner et al. 2007), we selected sites where the occurrence of Atlantic salmon was detected in < 10% of the fishing occasions and where the overall mean salmon abundance was estimated to be < 5 individuals per 100 m²; the number of excluded sites was < 5% of the total amount included in the final dataset, as Atlantic salmon usually prefer larger rivers than those included in this study.
4. to ensure inclusion of time series of similar length, and collected within the same time interval across locations, we chose sites sampled at least five times in different years, and where the first fishing occasion was performed not later than 1995, and the last one not before 2016;
5. based on information provided by county boards and experts' judgment, locations with fish stocking, intense flow regulation, construction of fishways, in-stream restoration, or strongly affected by acidification or liming were excluded;
6. only locations where the migration strategy of local brown trout populations (i.e. resident, migratory to sea or migratory to lakes) was known with confidence by experts were selected.

Electrofishing was always performed by wading, mostly between mid-July and October, predominantly using bank-side DC-equipment from Lug AB (Luleå, Sweden). All fish were handled according to ethical approvals, following Swedish law (each sampling event being associated to a specific license; a prerequisite for receiving permission to electrofish in Sweden) and the fish were returned to the streams alive (Bergquist et al. 2014). The brown trout caught by electrofishing were mostly juveniles (fry and parr), as most of the adults either reside in a deeper section of the river, or move away from the fished area during electrofishing, since the larger bodied fish react to the electric field from a farther distance compared to smaller bodied fish (Nordwall 1999). The smallest individuals observed in each location had an average size of 58 mm ± 33 (mean ± standard deviation), and the largest 0+ individuals had an average size of 67 ± 17 mm (mean ± standard deviation). The abundance was estimated through successive removals, usually including three electrofishing passes over the survey area (Bohlin et al. 1989), or, when this was not possible (i.e. < 10% of the sampling occasions), from average catch probability based on one pass (Bergquist et al. 2014). Both the assessment of what constitutes a juvenile and the abundance estimation are done during data registration into SERS. Sampled streams included between one to five electrofishing locations. Locations were sampled mostly irregularly, mainly due to budget limitations, except for a few sites belonging to the national monitoring program, where electrofishing was conducted every year throughout the whole study period. Our selected dataset

included locations that were sampled a minimum of 6 and a maximum of 37 times (on average 20 times), mostly in different years (Fig. 1, Supporting information). Stream wetted width (from here onwards 'stream width') and average depth were measured at each sampling occasion. Minimum and maximum stream width were 0.5 and 20.3 m, respectively, and the average was 4.4 ± 2.9 m (mean ± SD). Minimum and maximum stream depth were 0.1 m and 1.2 m, respectively, and the average was 0.20 ± 0.07 m (mean ± SD). The length of the sampled area was 47 ± 17 m (mean ± SD). Information on migration strategies of the local trout population was classified into three categories: stream resident trout, trout migrating to sea (anadromous populations), and trout migrating to lakes (potadromous populations). Most migratory populations of brown trout have a fraction of fish remaining as stream residents (Klemetsen et al. 2003; Nevoux et al. 2019), so the classification is based on whether there is a migratory fraction or not in a given population.

Climate data

We used a space-for-time approach, whereby the spatial variation in climatic conditions throughout Sweden was used to explain the direction and magnitude of site-specific temporal trends in brown trout juvenile abundance. To capture climatic variation at a country-wide scale, we used 'climate normals', which according to recommendations from the World Meteorological Organization (WMO 2018) are average temperatures calculated over 30 year time periods to reduce year-to-year variability, and that are used as descriptors of the temperature climate. The normal period considered was 1991–2020, and the variable considered was mean annual air temperature (hereafter called 'normal annual temperature'), which was calculated by the Swedish Meteorological and Hydrological Institute (SMHI; www.smhi.se/data/meteorologi/temperatur) using estimates from the meteorological stations closest to each sampling location.

We investigated the variation in ecologically relevant climate variables along the climate gradient represented by our dataset. Specifically, we calculated the average annual number of days with low flow (< 5 L • s⁻¹) for the period 2004–2020 (flow data were not available before this period in time) for 60 randomly selected streams where electrofishing was performed. These streams spanned the full latitudinal and climatic gradient of our dataset. Flow estimates were based on the S-HYPE model (Bergstrand et al. 2014) and provided by SMHI (https://vattenwebb.smhi.se/modelarea/). We also used data from 28 weather stations located far from large cities (with the exception of Stockholm, that was included for comparison) and spread all over Sweden to calculate the average number of days per year with an air temperature >25 °C at noon (when the hottest periods typically occur in the dataset). Both the average annual numbers of days with low flow and days with an air temperature > 25 °C at noon were plotted against normal annual temperatures.

Finally, we explored temporal trends of climate variables over the time period relevant for our study, to gain insights

into potential mechanisms behind changes in brown trout abundance. To explore trends in temperature variables, the number of hot days and the average annual air temperature from each of the 28 weather stations were plotted against year for the period 1990–2020, except for few cases where data were available only until 2018 or 2019. To explore changes in stream flow the average winter (December, January, February) and summer (June, July, August) flow for each of the 60 randomly selected streams were plotted against year for the period 2004–2020.

Data analysis

To explore whether temporal trends in brown trout abundance across Sweden were related to different climatic conditions, stream size, and migration strategies, we performed a two-step analysis. In the first step we analyzed site-specific trends using regression models of estimated juvenile abundance (number of individuals per 100 m^2) for each sampling location against the explanatory variable YEAR. Our aim was not to find the best model fit but rather to use a standardized method to investigate and compare the direction and extent of temporal changes in trout abundance. For this first step, we used generalized least squares models, which extend linear regression by modelling temporal correlation with dependent data (Zuur et al. 2009). We modeled the temporal correlation using an auto-regressive correlation structure of order 1 (AR-1), which models the residual at time s as a function of the residual of time $s - 1$ together with noise, so that the further away two residuals are separated in time, the lower their correlation. The models also included the covariate DATE OF ELECTROFISHING expressed as Julian day to account for the variation introduced by sampling the same location at different dates across years. In the few cases (0.8% of observations) where sampling was performed more than once in the same year at a given location, we calculated the average year abundance and the average Julian day before analysis.

In the second step we extracted the slope coefficients of the explanatory variable YEAR for each location, and their standard errors. We used linear mixed-modeling to run a weighted linear regression, where the response variable was the slope coefficients weighted by the associated standard errors. We accounted in this way for the uncertainty on the temporal trends estimates, so that temporal trends with a lower standard error were considered more informative than those with a larger standard error. The fixed part of the model (i.e. the explanatory factors) were CLIMATE, as represented by the normal annual temperature, the quadratic effect of CLIMATE, to account for potential non linearities, STREAM WIDTH (continuous variable), and TROUT MIGRATION STRATEGY (categorical variable with three levels: resident, lake migrating and sea migrating). STREAM WIDTH was collinear with stream depth (Spearman's rank correlation: $\rho = 0.49$; $p < 0.001$), and was used as a proxy for stream size. The two-way interactions CLIMATE × STREAM WIDTH and CLIMATE × TROUT MIGRATION STRATEGY were also included to explore whether larger stream sizes could

partly offset negative effects of warmer climates (hypothesis 1), and whether migrating trout population were more or less vulnerable to warmer climates compared to resident populations (hypothesis 2). For this purpose, we ensured that we had a good representation of locations with different trout migration strategies and stream widths along the climatic gradient (Supporting information). Even though Atlantic salmon was observed only in 21 out of the 218 sites of our dataset and showed an average abundance > 1 individual per m^2 only in six locations, we included as covariate the average abundance of Atlantic salmon observed over the sampling occasions in each site, to account for potential variation caused by competitive interactions between Atlantic salmon and brown trout. The optimal fixed structure of the model was determined using comparison of Akaike Information Criterion (AIC) scores and F-statistic, and only significant factors were retained in the final model (Zuur et al. 2009). Factors were considered statistically significant at $p \leq 0.05$. In the random part of the model we included the random factor STREAM (174 levels) nested within CATCHMENT (65 levels, Fig. 1), and a residual variance structure to account for heterogeneity of residual variance. Alternative variance structures allowing residual spread to vary with either CLIMATE, STREAM WIDTH, TROUT MIGRATION STRATEGY or a combination of CLIMATE and TROUT MIGRATION STRATEGY were compared using AIC (Zuur et al. 2009). Collinearity between predictors was assessed by calculating the variance inflation factor (VIF) for each predictor, using a threshold value of 2, and Spearman's rank correlation coefficients. Marginal and conditional R^2 values were estimated following Nakagawa and Schielzeth (2013). Factors were considered statistically significant at $p \leq 0.05$. Independence, normality and homogeneity of variance of residuals were confirmed by plotting relationships between residuals vs fitted values and observed vs theoretical quantiles (QQ-plots). Moreover, to explore whether our results were robust against variance induced by the inclusion of locations with limited sampling, we tested our model on a subset of data including locations with at least 10 sampling occasions, performed in different years. All analyses were conducted in R ver. 4.0.5 (www.r-project.org). When interactions between two explanatory factors were statistically significant, we used the R package (www.r-project.org) 'ggeffects' ver. 1.0.1 (Lüdecke 2018) to visualize marginal effects, i.e. the effect of one predictor variable on the response variable when the other predictors were held constant. Maps to visualize the spatial distribution of the slopes of temporal trends and of climate normal variables were built with the R package (www.r-project.org) 'maps' ver. 3.3.0 (Becker 2020).

Results

Trends in brown trout juvenile abundance

Declines in juvenile brown trout abundance in the last thirty years (1991–2020) were observed in a total of 106

locations (spread across 94 different streams), while increases were observed at 112 locations (spread across 102 different streams; see Supporting information for an example). Despite substantial geographic variation, a clear latitudinal pattern emerged, with moderate to strong declines (slope < −1) occurring more frequently in the southern part of Sweden (82% at latitudes below 59 degree), where normal annual temperatures were higher (Fig. 2). In contrast, moderate to strong increases (slope > 1) were more frequent in the northern regions (71% at latitudes above 59 degree), where normal annual temperatures were lower (Fig. 2).

Our best (final) model explaining variation in the slopes of the temporal trends (using a linear mixed model accounting for the uncertainty in the estimates) included the interactive effects of CLIMATE × STREAM WIDTH and CLIMATE × TROUT MIGRATION STRATEGY, while the quadratic effect of CLIMATE and the average abundance of Atlantic salmon were not statistically significant ($F = 1.030$, $p = 0.320$, and $F = 15.291$, $p = 0.404$, respectively) and their inclusion did not improve the model fit (Supporting information). The slopes of the temporal trends were significantly explained by climate, here represented by normal annual temperature, but the direction and magnitude of the effects varied for streams of different sizes (i.e. interactive effect of normal annual temperature and stream width, Table 1 and Fig. 3A). For smaller streams (≤ 6 m wide), declines were more likely to occur in

warmer regions (normal annual temperature above 5–6 °C), and the magnitude of the decline increased with the normal annual temperature, so that the warmer the area over the last 30 years, the steeper the decline (Fig. 3A). In colder regions (normal annual temperature below 5–6 °C) increases in trout abundances occurred instead in smaller streams. Larger streams showed an opposite trend, with increases in abundance of trout juveniles over time in the southern rivers and declines in the northern rivers (Fig. 3A). Our dataset included only few streams of width > 10 m (Supporting information), which explains the large confidence intervals around predictions for such stream sizes.

Furthermore, we found evidence that air temperatures had a stronger effect size, i.e. produced steeper changes in trout abundance, in particular stronger declines, for migrating trout populations, especially those migrating to sea, compared to resident populations (Table 1, Fig. 3B). Also, the cut-off value of normal annual temperature that separate increases and declines (i.e. where the estimated average slopes equal zero) for sea migrating trout occurred in colder regions compared to resident trout (Fig. 3B).

The comparison of models with different variance structures indicates that the best model was the one that allowed for an exponential increase in the spread of residuals for warmer regions and for migrating trout populations, especially those migrating to the sea (Supporting information). This was also
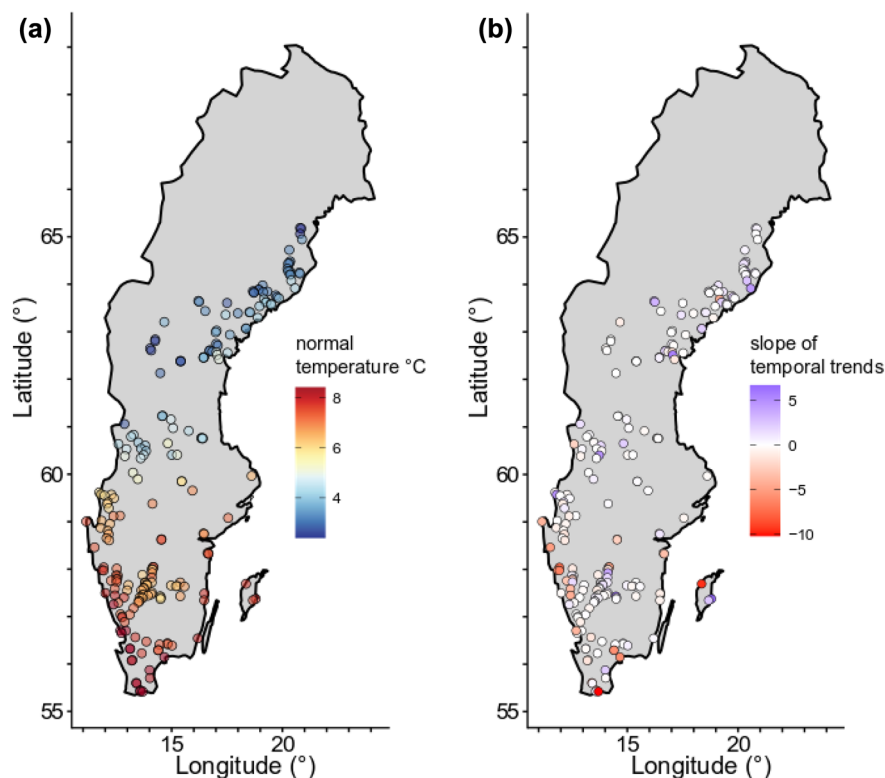

Figure 2. Map of Sweden showing the (a) normal annual air temperature, estimated using the averages for the period 1991–2020 from the Swedish Meteorological and Hydrological Institute's weather stations, and (b) slope of the temporal trends in brown trout juvenile abundance (colored points) based on electrofishing data collected between 1991 and 2020, as estimated by generalized least squares models with AR-1 correlation structure.

Table 1. Estimates of the effects (and interactions) of normal annual temperature, stream width and migration strategy, on the slopes of the temporal trends of brown trout *Salmo trutta* abundance. Significant p-values (p <0.05) are indicated in bold.

Explanatory factors	df_{num}	df_{den}	F-value	p-value	coeff	SE
Intercept	1	124	24.539	**<0.001**	3.316	0.669
Normal annual temperature	1	27	26.046	**<0.001**	-0.586	0.115
Migration strategy	2	27	3.552	**0.043**		
Lake migrating vs sea migrating					-0.653	0.932
Resident vs sea migrating					-1.535	0.611
Stream width	1	27	11.441	**0.002**	-0.259	0.077
Normal annual temperature × migration strategy	2	27	3.733	**0.037**		
Lake migrating vs sea migrating					0.144	0.163
Resident vs sea migrating					0.285	0.107
Normal annual temperature × stream width	1	27	10.338	**0.003**	0.045	0.014

supported by the different spread in the response variable (i.e. the slopes of the temporal trends) for different values of normal annual temperature (Supporting information) and types of migration strategies (Supporting information). This may be partly explained by higher average juvenile trout abundances (often associated to higher variation) in locations with warmer climate (Supporting information) and with populations of migrating trout (Supporting information). Our model had a marginal R^2 of 0.23, and a conditional R^2 of 0.26, i.e. there was a low intra-class correlation, indicating relatively high variation in trout abundance between sites within the same stream and catchment. Results from the analysis performed on a subset of data excluding the sites with limited temporal replication (i.e. with < 10 sampling occasions performed in different years) were similar to the results obtained using the full dataset (Supporting information).

Spatial and temporal patterns of climate-related variables

Low flows and high temperatures were more frequent in the southern regions compared to the northern regions. In fact, there was a positive correlation between the normal annual temperature and the number of days with low flows, which increased exponentially above a normal annual temperature of 7.5 °C (Fig. 4A). Also, the normal annual temperature was positively correlated with the average number of hot days per year, i.e. days with temperature at noon > 25 °C (Fig. 4B).

Changes in the thermal and flow regime in the last decade were in general faster in the last decade. The number of hot days per year and the average annual air temperature showed a moderate to steep increase at many stations (Supporting information). Temporal trends of average winter and summer flow showed large between-river variation, however there was evidence for a stronger increase over time in winter flow in colder regions (Supporting information), and a stronger decrease over time in summer flow in warmer regions (Supporting information).

Discussion

Overall, our results point out the varying effect of climate on Swedish brown trout during the last three decades,

demonstrating that juvenile abundance is declining in the southern regions of Sweden, where the climate is warmer, while it is increasing in the northern, colder regions. This pattern fits well with growing global evidence of net population declines at lower latitudes and altitudes (Scott and Poynter 1991, Burkhardt-Holm et al. 2002, Clews et al. 2010, Eby et al. 2014, LeMoine et al. 2020, Floury et al. 2021), and increases in colder regions (Svenning et al. 2022). Sweden encompasses a relatively large latitudinal gradient (ca 14°), corresponding to a broad gradient in mean annual temperature, which was a significant driver explaining trends of brown trout juvenile abundance in this study. Time series data of climate variables suggested that high temperatures and decreased summer flow may be limiting factors for trout populations in the southern regions of Sweden. Such findings are also in line with a recent global meta-analyses of 156 studies showing reduced salmonids productivity at low latitudes and elevations, likely caused by increased temperature and drought frequency, and increased productivity at high latitudes and elevations, where cold temperatures generally limit salmonid growth and abundance (Gallagher et al. 2022). Our results point to the importance of considering thermal heterogeneity at regional and national scales when developing local prescriptions for management and conservation of species with broad distributional ranges, such as brown trout. Climate affects salmonids by modulating water temperature and flow regimes, with multiple consequences on the behavior, growth and survival of populations (Taylor 2008, Jonsson and Jonsson 2009). The increases in brown trout juvenile abundance in cold regions in our dataset could be due to more days with favorable growth conditions, whereas the decreases in the warm regions may be partly due to summer water temperatures temporarily exceeding the limit of thermal tolerance (i.e. 22–25 °C; Elliott and Elliott 2010). The number of days per year with air temperatures at noon > 25 °C has increased in the last decade especially in the southern regions (Supporting information), and average values can be several times higher than in the colder, northern regions (Fig. 4B). Although average daily summer temperatures are seldom above 25 °C in Sweden, daytime air temperature during warmer summer periods may, on occasion, reach 30–35 °C (SMHI; http://www.smhi.se/). These episodes occur mainly in southern regions in Sweden and generally
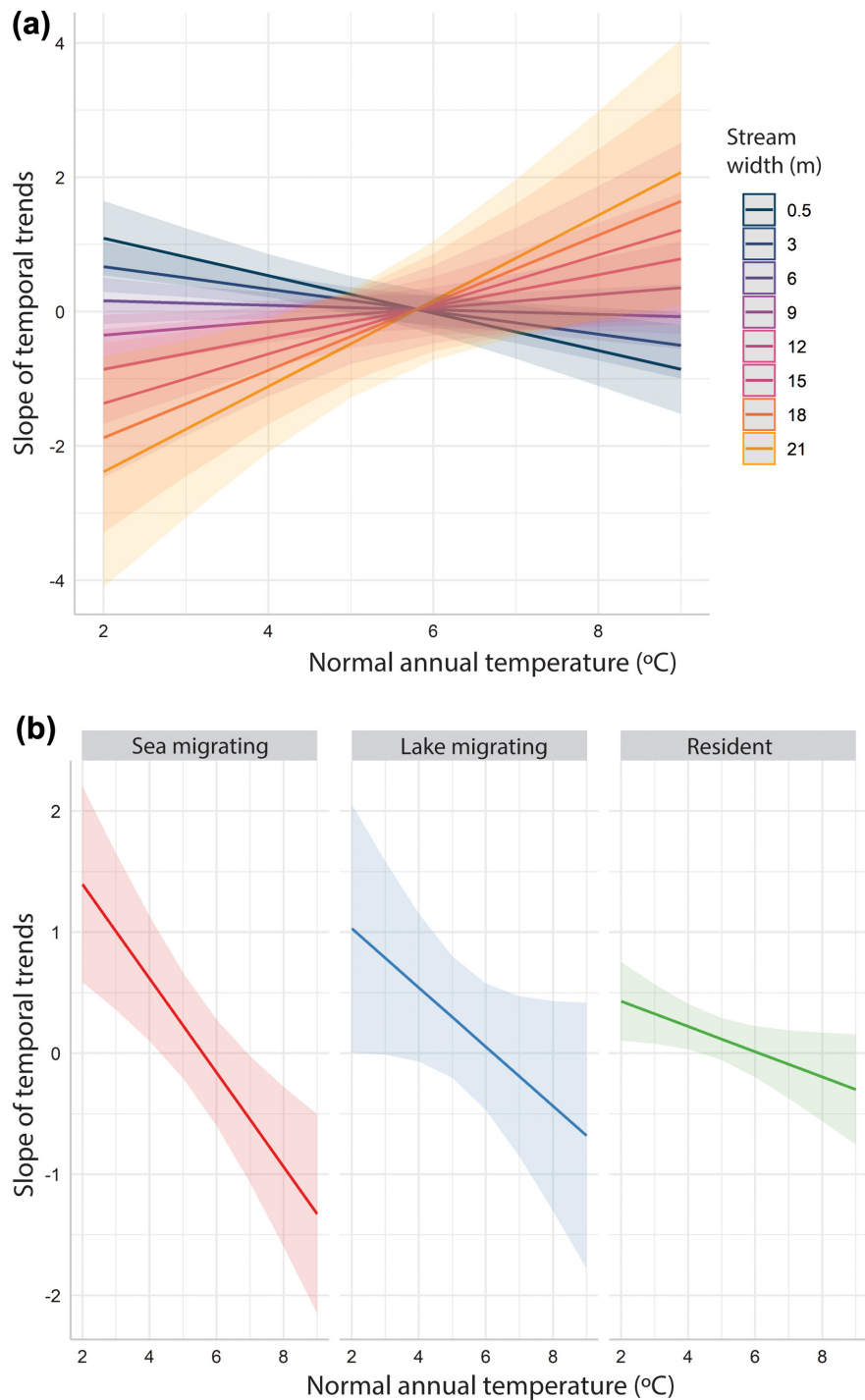
(a)

(b)

Figure 3. Model predictions of the marginal effects of normal annual air temperature on the slope of the temporal trends in brown trout juvenile abundance (a) in streams of different width (m), indicated by different colors, and (b) with different migration strategies. The slopes, expressed as change in the number of individuals per 100 m^2 per year, were weighted by the associated standard errors in a weighted linear regression using linear mixed models – see Methods). Shaded areas show 95% confidence intervals.

last for a few days. Air and stream temperature are generally well correlated, even though linearity is lost at high temperatures (Mohseni and Stefan 1999, Erickson and Stefan 2000). Besides exceptional warm temperatures, which have a critical negative effect on trout survival, even small increases in water temperature, when long lasting, can have substantial effects on salmonid physiology and growth (Elliott and Elliott 2010). Average annual air temperature has increased in the last decade at many locations in Sweden (Supporting information), and could have contributed to the declines
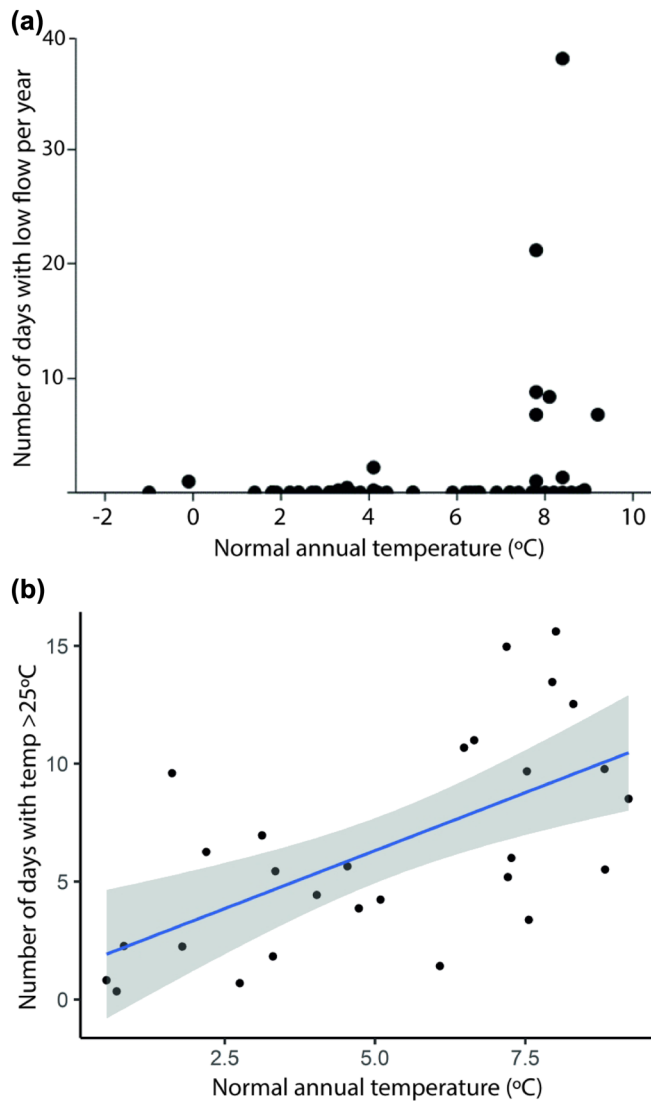
Figure 4. Scatterplots of the (a) number of days with low flows (<5 L • s⁻¹) for the period 2004–2020, and (b) annual number of hot days (with temperature at noon > 25 °C) for the period 1990–2020, plotted versus normal annual air temperature. A linear regression line ($p < 0.05$) was added to aid visualization (panel b).

observed in southern populations via multiple mechanisms acting on different life stages of brown trout. Increased water temperatures in winter enhance the trout egg development rate, which may cause suboptimal timing of the hatching and affects physiological state and behavioral characteristics of the yolk-sac fry and later juvenile stages (Skoglund et al. 2011). In mild compared to cold years salmonids may smoltify earlier in life, hence at smaller sizes, which could negatively affect the survival of individuals migrating to the sea (Jonsson and Jonsson 2011). Higher temperatures may affect food availability at the coast (Beaugrand and Reid 2003). This could cause a mismatch between the smolts' arrival and the occurrence of large but temporally restricted food resources. Furthermore, while trout individuals at sea may find refuge from higher temperature by moving to deeper areas, this may

affect what food they can eat. For stream residents and for migrant adults returning to inland waters, warmer winters could entail on one hand easier access for terrestrial predators caused by reduced ice cover, and on the other hand, increased energy demand due to higher metabolic rate. These two factors may interact in a negative way since foraging is risk associated (Watz et al. 2013, 2016). Finally, increased water temperatures may promote the emergence of various diseases (such as proliferative kidney disease), which further impair aerobic performance and thermal tolerance in infected brown trout (Okamura et al. 2011, Bruneaux et al. 2017). Thus, the combination of extreme temperatures as well as extended periods of higher water temperatures may be a primary cause of declining trout populations in the southern regions.

Another factor that has possibly contributed to reduced abundance of brown trout juveniles in warmer climate regions is the increased frequency of low flow events. Our data showed a decrease over time of summer flow in many rivers in the south (Supporting information), and a large difference in the overall mean number of days with low flow in the warmer regions compared to the colder regions (Fig. 4A). Climate change has been identified as a causal driver of extreme river flows at a global scale (Gudmundsson et al. 2021), yet effects of flow alteration have received far less attention than the effects of temperature changes on trout populations in both the research and management communities (Kovach et al. 2016). In a review of 42 studies from Europe and North America, summer river flow was found to be more consistently related to trout demography and growth than temperature (Kovach et al. 2016). Low flow and droughts can affect brown trout juveniles during summer through several factors, e.g. by altering the composition of drifting invertebrates (Poff and Ward 1991), or by drying the shallow gravel habitats occupied by the newly hatched recruits (Nagrodski et al. 2012, J. Näslund, pers. obs.). In addition, low flow events may cause juveniles and adults to aggregate in pools or move to deeper sections of the rivers, thus increasing the competition for food, especially if the metabolic rate is increased by high temperatures (Audzijonyte et al. 2022). Finally, low flows can also hinder the spawning runs of migrating adults in autumn by decreasing the river network connectivity (Jonsson and Jonsson 2009).

Our results specifically suggest that migrating populations of brown trout are more vulnerable than resident populations to a warming climate. This finding, which should be corroborated by future research, can have large implications for the management and conservation of salmonids. In a global meta-analysis, Gallagher et al. (2022) showed that increased precipitation during the growing season had a significantly higher negative effects on anadromous populations of salmonids compared to freshwater residents. In our study we found that abundance of juveniles of migrating brown trout populations, especially those migrating to the sea, showed sharper and more frequent declines in warmer regions than resident populations. Steeper changes in abundance in migrating trout populations could be partly due to the fact that stream sites hosting migrating populations

had on average higher trout juvenile abundances compared to resident populations (Supporting information), which could amplify the effects of recruitment success and failures. Yet, the combined evidence of stronger declines in migrating trout populations and in smaller streams in the southern regions strongly suggests that low flow events could be a critical limiting factor for trout populations in face of a changing climate. Climate-induced droughts and low flow events can cause the loss of spatial connectivity, and may also increase competition and predation from lentic species as swift running waters becomes slow-flowing (Jonsson and Jonsson 2009, Hasegawa and Yamamoto 2010). A major threat to trout abundance in a climate change scenario are dams for hydropower production and small artificial impoundments, which are the main drivers of water stress and habitat fragmentation (Arthington et al. 2016, Sabater et al. 2018, Morden et al. 2022). In a recent study, we found that trout populations were more negatively affected by intense river regulation from hydropower dams in warmer regions compared to populations in colder regions (Donadi et al. 2021). An alternative explanation to the decreased juvenile abundance in migratory populations could be an increase of the stream resident portion of the population because of temperature-induced improvements in growth and survival. If trout growth and survival is higher in the stream habitats compared to the sea or the lakes into which migration occurs, then a higher proportion of the population is expected to remain in the stream habitat (Gross et al. 1988, Jonsson and Jonsson 2009). This could lead to decreasing number of recruits due to both intercohort competition (Kaspersson et al. 2012) and lower fecundity of stream resident females as compared to migratory females, because of the larger size of the latter (Jonsson and Jonsson 2006). In summary, the integrity as well as the thermal regime of the river network are of fundamental importance for the survival of anadromous species, especially in a changing climate (Markovic et al. 2017), and alterations could potentially select against migratory strategies in facultative anadromous species. Given that migratory fish are typically larger and more fecund than resident fish, a decrease in the proportion of migrating fish could entail large consequences at population level.

Global predictions and long-term data series show poleward trends and expansion to higher altitudes of the distribution and performance of brown trout, but only in scenarios where dispersal is allowed (Flebbe et al. 2006, Hari et al. 2006, Kärcher et al. 2021). In reality, the aquatic landscape is full of man-made migration obstacles (Grill et al. 2017), impeding movement of fish for feeding, colonization of new areas, spawning or seeking shelter from extreme weather conditions. A recent study of brown trout populations in Sweden showed that larger patches of suitable habitat for brown trout led to higher abundances, probably as a response of diminished edge effects driven by predation (Tamario et al. 2021). Also, these authors found that the closer the nearest accessible suitable habitat patch, the higher was the abundance and the lower the between-year variation in trout abundance. Elimination of man-made obstacles and the adoptions of

restoration measures that can ensure the integrity of the river network are therefore essential for the survival of brown trout and other anadromous species, and even more so in face of a warming climate.

Our study also suggests that stream size buffered negative effects of warmer climate on trout juvenile abundance. Larger rivers may be less prone to droughts and temperature fluctuations than small rivers (Caissie 2006), and may contain more thermal refugia or be more connected (Dugdale et al. 2013). Hence, larger rivers could function as refuge from critically low flows and/or high temperatures during warm periods. In warm regions this could explain the slower temporal declines, or even increases, in brown trout juvenile abundance in larger compared to smaller rivers. We should note, however, that the influence of shading by riparian vegetation usually decreases with increasing stream width, and it can happen that water temperature increases significantly in larger rivers in warm days (Doretto et al. 2020, Fuller et al. 2022). Our results also revealed that in the colder climatic regions (normal annual temperature < 5–6 °C) brown trout juvenile abundance has increased in smaller streams and decreased in larger streams (> 6 m wide) in the last 30 years. This is possibly due to more favorable conditions in smaller streams (i.e. higher temperatures and productivity compared to before), and less favorable conditions in larger streams, such as increased competition and predation from warm-water adapted fish species expanding their distribution northwards, e.g. pike (Winfield et al., 2008, Hein et al., 2011), or altered flow regimes. High flows during both winter and summer can cause problems by washing away eggs or fry (Wenger et al. 2011). Unfortunately, we do not have data on the frequency of seasonal high flows to investigate this hypothesis. However, given that the average winter flow has increased in many streams in the north (Supporting information), we cannot exclude the possibility that high flows may be a limiting factor for brown trout populations in large rivers at higher latitudes. From a management perspective, our study highlights the fact that conservation of large rivers may be critically important for the survival of viable brown trout populations in regions at low latitudes in a warming world. At the same time, the preservation of intact riparian zones providing shade can help keep summer stream water temperatures well below the incipient lethal limit for brown trout survival (Broadmeadow et al. 2011, Fuller et al. 2022).

Our study showed a clear latitudinal pattern in trends of juvenile trout abundance, yet we found relatively high remaining variation in the abundance within the same climatic region. Also, the low intra-class correlation of our model indicates that sites within the same stream and catchment did not necessarily show similar temporal trends. This may be caused by several factors that we could not account for, for example, groundwater inputs, which often create patchy distribution of thermally suitable habitats at small spatial scales (Snyder et al. 2015). It could also be due to non-climatic factors such as habitat degradation caused by land-use transformation, e.g. increased sedimentation and algal production, contaminant pollution, and deteriorated oxygen conditions (Allan 2004). Management actions to counteract future

population declines in a warming climate should therefore be planned at a small spatial scale, taking into consideration the local climate context, as well as groundwater influences if possible (Ros et al. 2022). For Sweden, this means that different counties need to approach their freshwater management work in different ways depending on their geographical location. Furthermore, in counties with a range of different climate zones (depending on altitude or latitude), different approaches need to be adapted within the county. The same is likely true for many other countries.

Although we suggest that increasing temperatures and increased frequency of low flow events are significant drivers for decreased recruitment of brown trout in southern Sweden, a warming climate is only one of the emerging threats responsible for the freshwater biodiversity crisis of the last decades (Reid et al. 2019). Multiple, often interrelated, stressors act simultaneously with a changing climate on individual and population levels (Comte et al. 2016, Kovach et al. 2017, Niinemets et al. 2017, Reid et al. 2019, Comte et al. 2021). For example, a shift towards higher altitudes of the brown trout distribution in the Swiss Alps has been attributed to the warming of the water temperature in combination with an increase in the frequency of the temperature-dependent proliferative kidney disease caused by the myxozoan parasite *Tetracapsuloides bryosalmonae* (Burkhardt-Holm et al. 2002, Hari et al. 2006). In North America, a native salmonid species is threatened by invasive hybridization caused by historical stocking and accelerated by decreases in spring precipitation and increases in summer stream temperatures (Muhlfeld et al. 2014, 2017). Finally, species interactions play an important role in a warming climate, and this may be especially true for a cold-water specialists such as brown trout that often thrive in areas with few competitors (Degerman and Sers 1992). An increase of warm-water competitors and predators, e.g. pike and pikeperch (Jepsen et al. 2000, Winfield et al. 2008), could also contribute to declines in trout abundance in progressively warmer regions.

Under a warming climate it is thus important to prevent or decrease any additional stress on trout populations. Restoration of riparian vegetation, especially at the basin-wide scale, can help buffer extreme summer temperatures (Broadmeadow et al. 2011, Johnson and Almlöf 2016, Justice et al. 2017, Turunen et al. 2021, Fuller et al. 2022), and together with the identification and protection of climate and thermal refugia (Keppel et al 2012, Sullivan et al. 2021) should be a priority of climate-smart water management (Elliott 2000, Isaak et al. 2015). Furthermore, the increased incidence of summer droughts in small rivers in the southern (warmer) regions points to the negative effects of large-scale irrigation, channelization and loss of wetlands consequent to human practices to gain arable land in the past centuries. Importantly, conservation policies should adopt a multiple pressures perspective (Craig et al. 2017) and focus not only on climate refugia, but rather on areas where exposure to multiple anthropogenic stressors is low (Rojas et al. 2021). Restoration of river connectivity via barrier removals and construction of nature-like fishways is especially important under a warming climate

to ensure hydrological connectivity and access to colder-water refugia, allowing the passage of migrating trout as well as the wider fish community in the river network (Jones et al. 2021). Also, hydrological restoration of the landscape, e.g. restoring stream channels and wetlands, reducing water abstraction, increasing flows below dams during low flow periods, will increase the resilience of natural populations to habitat changes (Renöfält et al. 2010, Pan et al. 2016, Merriam and Petty 2019). As stated by Martin and Watson (2016) 'Intact ecosystems provide best defense against climate change'.

Author contributions

Serena Donadi: Conceptualization (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Joacim Näslund**: Writing – review and editing (equal). **Leonard Sandin**: Conceptualization-Supporting, Investigation-Supporting, Writing – review and editing-Supporting. **Berit Sers**: Conceptualization (equal); Data curation (equal); Investigation (equal); Writing – original draft-Supporting, Writing – review and editing-Supporting. **Anti Vasemägi**: Writing – review and editing-Supporting. **Erik Degerman**: Conceptualization (lead); Data curation (equal); Formal analysis-Supporting, Investigation (equal); Writing – original draft (equal); Writing – review and editing-Supporting.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5tb2rbp85 (Donadi et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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