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# No support for using brown trout as an indicator species for ecological impacts of low flow in Swedish rivers

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ABSTRACT

The impact of low flows on riverine ecology in Sweden is not fully understood. Recent summer droughts, along with their regionally projected increase, together demonstrate the need for a more solid foundation guiding ecologically responsible planning. Impact assessments can be made via indicator species sensitive to low flow, if their response to the flow conditions can be clearly understood, using for example historical data on species abundance and flow. In Swedish rivers, there are extensive electrofishing data with a special focus on salmonids, predominantly brown trout *Salmo trutta*, which are previously reported to be sensitive to low flow. There are also available national data on river flows, largely based on simulations. We processed and used these data sets, along with information on additional environmental factors. We tested if sites had less than their median trout abundance during the year of the minimum winter or summer low-flow. Adverse impacts of low flow could be shown only for young-of-the-year trout. The impact was small with at most 57 % of remaining sites having lower than median trout abundance (compared to 44 % overall) during the year of the lowest winter flow. The insubstantial effect means that using trout as a low-flow indicator species in Sweden cannot be supported by the currently available data. We believe the main causes of the small effects are limitations in the time resolution of trout data and spatial resolution of the flow data, followed by the ability of trout to escape low flows by seeking deeper habitats.

## 1. Introduction

River ecology is largely dependent on the flow regime, which shapes habitats and provides possibilities for longitudinal migration and nutrient transport (Allan and Castillo, 2007). However, the natural flow regime of many rivers has deteriorated due to the impact of different flow management practices, including the redistribution of water by hydropower regulations, abstractions for irrigation purposes, and runoff from urbanized areas (Vörösmarty et al., 2010; Arheimer and Lindström, 2019). Additional changes to the hydrological regime are caused by the impacts of climate change (van Oorschot et al., 2018; Arheimer and Lindström, 2019). In Sweden, the ecological status of rivers is evaluated partly based on the hydrological regime and its deviation from the natural flow regime (SwAM, 2019), following the European Water Framework Directive (European Commission, 2000). Severe summer droughts in southern Sweden over the past decade such as in 2018, along with their projected increased frequency and severity in the future due to climate change (e.g. Teutschbein et al., 2023) highlight the need to specifically consider low-flow impacts on ecological functions. Potential ecological problems related to low flow, in the form of reduced water quality, reduced habitat, low water volume and depth, and dry river sections have been identified by the Swedish Agency for Marine and Water Management (SwAM, 2023).

Ecological impacts associated with altered flow regimes can be evaluated based on species' past responses to change, using indicator species sensitive to flow. Often, salmonids (Salmonidae) are considered indicators for river quality assessment (Nielsen, 1997; Smialek et al., 2021). Their sensitivity to the flow regime (Cunjak et al., 1998; Poff and Zimmerman, 2010; Kovach et al., 2016), along with their high recreational and economical value, has prompted a large body of information

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on their depth and flow requirements (e.g. Bjornn and Reiser 1991; Warren et al., 2015) and this information is applied for river management decisions. For instance, in the United Kingdom, water abstraction is restricted if the discharge falls below a threshold relative to the natural flow regime in spawning areas of Atlantic salmon (*Salmo salar*) (Acreman and Ferguson, 2010).

In Sweden, the fish fauna can be grouped into several biogeographic regions with partially different species communities (Degerman and Sers, 1992) and the communities are often species poor (e.g. Näslund et al., 2023a), making it difficult to apply a country-wide multi-species approach for assessments. However, one particular salmonid species, the brown trout (*Salmo trutta*), is typically seen as a good candidate indicator species for the quality of riverine environments, as it inhabits streams and rivers throughout the majority of the country, sometimes without any other fish species present (Degerman and Sers, 1992). While widespread, the brown trout (like many of the species in the salmonid family) also have demands on its habitat and alterations in depth, current velocity, habitat complexity, water chemistry, temperature and other environmental parameters affects its residence in terms of both presence and numbers (Armstrong et al., 2003; Jonsson and Jonsson, 2011). Over the past several decades, country-wide electrofishing monitoring has been conducted in thousands of shallow (depth typically <50 cm) river sections suitable for juvenile trout, making large amounts of historical brown trout data available for investigation through the Swedish Electrofishing Register ("SERS"; SERS, 2021). Hence, the brown trout is a promising candidate species for evaluating effects of low flow on shallow river ecosystems.

Adult brown trout prefer water depths greater than 50 cm (i.e. greater than what is typically in the electrofishing monitoring), but they can reside and spawn in shallower habitats, particularly in smaller streams (Shirvell and Dungey, 1983; Hayes and Jowett, 1994; Smialek et al., 2019). Bell (1986) noted that trout require at least 15 cm water depth to pass an in-stream obstruction, which is relevant for both in-stream dispersal and spawning migrations. Juvenile brown trout use shallower habitats than adults; the youngest fry stages occupy areas with depths ranging from only a few centimeters to approximately 35 cm and depth preference increases with body size (Greenberg et al., 1996; Mäki-Petäys et al., 1997). It is therefore expected that the impact of flow and/or water depth on salmonids and other fish would vary depending on the size and life stage of the fish (Tallaksen and van Lanen, 2004), but also in relation to season and other environmental conditions such as migration barriers, temperature, predation pressure, and habitat complexity (Bjornn and Reiser, 1991; Degerman, 2001). Göthe et al. (2019) developed a regression model for fish biodiversity in Swedish rivers that includes flow indicators, focusing on "dry furrows" downstream of hydropower regulation dams (i.e. natural river channel spillways with bypassed water flow, typically with relatively steep slopes). Based on data from the SERS database, they showed that the magnitude of flow reduction was negatively related to the presence of a species community characterized by brown trout, Atlantic salmon and European eel (Göthe et al., 2019). While the cause of the low flow is artificial in the bypassed sections, the results suggest that flow could be a key variable determining the abundance of trout. To date, the sensitivity of trout to low flow in more natural Swedish rivers is poorly detailed, although there are many recent news reports on droughts being observed as problematic for trout populations (e.g. TT, 2013, 2018; SR, 2023). Considerable negative effects, albeit substantially variable, of summer droughts have been indicated in a long-term study on trout densities in a small British stream (Elliott et al., 1997). An investigation with a similar objective, based on data from the Swedish west coast (period: 1983–1994), suggested that salmonids may primarily be more negatively affected by competition during such events, so that less competitive species or age classes do relatively worse compared to stronger ones (Degerman et al., 1997). A recent study suggested negative trends in brown trout abundance in smaller streams (≤6 m wet width) in southern Sweden over the past three decades (Donadi et al., 2023). Southern Sweden has been identified as an area with a drying hydrological trend (Teutschbein et al., 2023) and the lack of water as well as high water temperatures have been identified as candidate impact factors driving the observed decline in trout populations (Donadi et al., 2023). A few brown trout populations, in regions particularly affected by droughts, are locally adapted to cope with this risk by adopting early age migration out of stream systems (Titus and Mosegaard, 1989; Landergren, 2004), indicating that low flow conditions can be a strong force of natural selection on migratory behavior, when it is predictable over time frames relevant for evolutionary processes.

Given that several reports have indicated salmonid sensitivity to low flows, and that large amounts of data in SERS to date are relatively unexplored for the support of generic conclusions of trout sensitivity to low flow, **the aim of this work is to investigate if brown trout can be used as a national-scale indicator species for the impact of low flows in Sweden, specifically to help with assessments of ecological quality to better fulfill Sweden's obligations in accordance with the Water Framework Directive.** We use a logistic regression procedure to identify whether indicators for low flow have a negative impact on brown trout. We also use machine learning techniques to attempt to falsify our initial conclusions.

## 2. Materials and methods

We related young-of-the-year (henceforth "0+") and older (age ≥1 year; predominantly older juvenile parr, but also some adult stream resident fish included; henceforth "≥1+") trout abundance from the SERS database to simulated and observed daily flow from the Swedish Meteorological and Hydrological Institute (SMHI). We only used electrofishing data from multi-pass fishing and only data that are representative of locations with flow data (i.e. excluding data from small tributaries, which do not have modeled flow data). River flow was analyzed in terms of indicators developed in the context of the trout life cycle. We primarily used logistic regression to investigate whether lower than average trout densities could be associated with low flow events, which would indicate impacts of low flow on trout. We also used a machine learning model in an attempt to defeat our tentative conclusions by generating confounders. After processing the data, as further explained below, we arrived at a dataset with 20 831 rows, each representing one electrofishing survey from one location, and these originated from 2374 sites in total. (The filtering of data and targeted evaluation of data quality for our purposes is presented in Section 3.)

All analyses were run in R (R Core Team, 2022). The 'tidyverse' suite of R-packages (Wickham et al., 2019) were used for data wrangling/-housekeeping, and Figs. 1–4 (along with the package 'sf' for reading map input; Pebesma, 2018). Hydrological data were analyzed and plotted using 'HYPEtools' (Capell and Brendel, 2023). The package 'robustbase' (Maechler et al., 2023) was used for outlier resistant statistical modeling and 'rpart' (Therneau and Atkinson, 2022) was used for recursive partitioning.

### 2.1. Flow indicator development

Suitable indicators for low flow were developed with consideration to the natural and altered hydrological regimes in combination with the typical trout life cycle in Sweden. The natural hydrological regime and its alterations due to hydropower regulation varies across Sweden. In much of northern Sweden, the highest natural flows occur during spring snowmelt and the lowest flows occur in winter when water is stored as snow (Gottschalk et al., 1979). Here, hydropower regulations act to reduce flow seasonality, which means that winter flows are typically increased (Arheimer and Lindström, 2019). However, introduced variability at short time scales (Elenius and Lindström, 2022) can reduce low flows temporarily. On the other hand, parts of southern Sweden typically face minimum flows during summer due to higher evapotranspiration and/or lower precipitation (Gottschalk et al., 1979). These flows

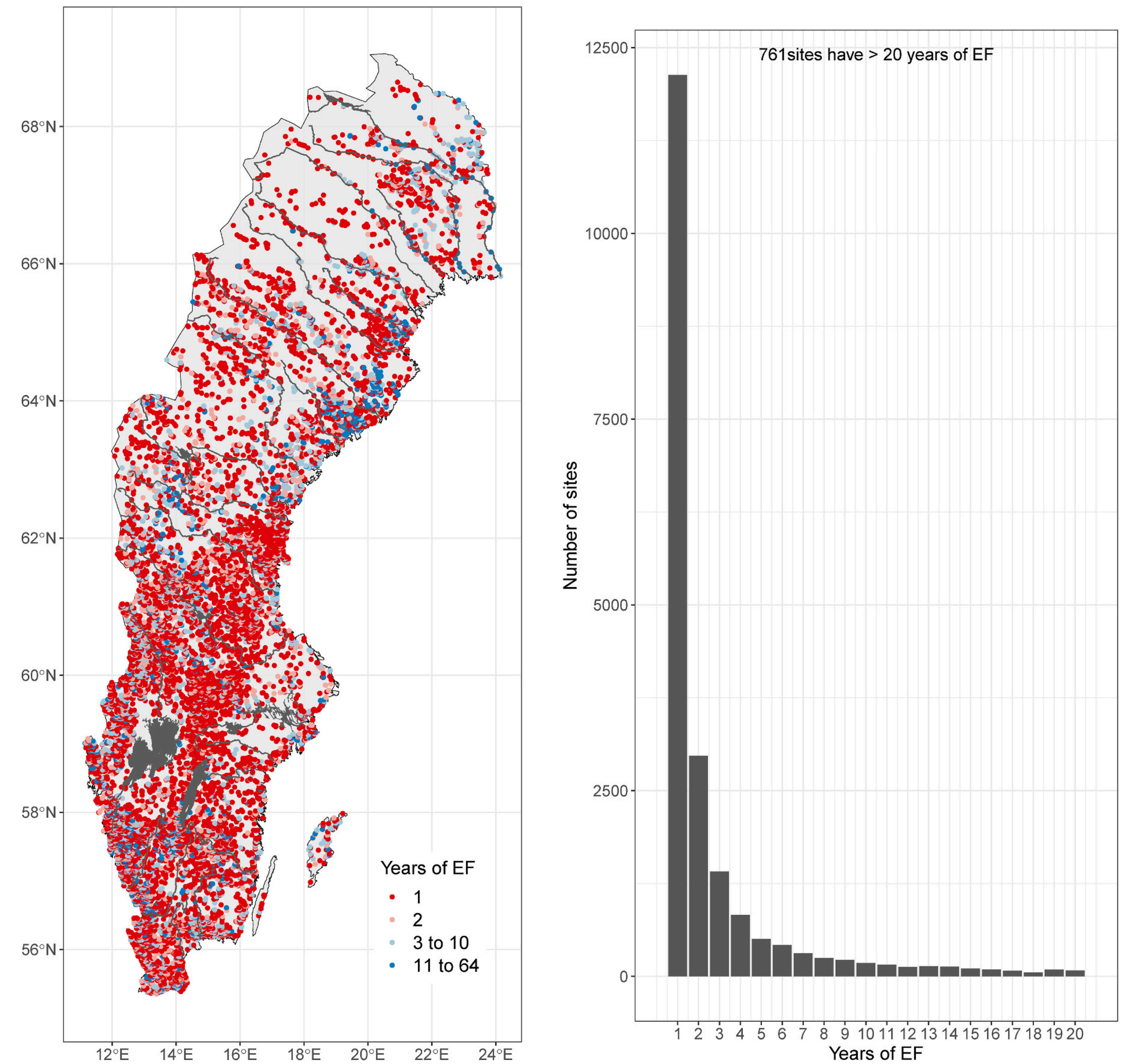


**Fig. 1.** Map and histogram of the number of years with electrofishing trout data per site. The histogram is cut at 20 years, with 761 sites having more years of data. A subset of these sites were selected for the analysis and this is described below, e.g. in Fig. 3.

can be further reduced by hydropower regulations and other water management practices such as irrigation, in addition to the impacts of climate change resulting in drier conditions in the south (Arheimer and Lindström, 2014).

Trout spawning in Sweden typically occurs in the period October to November (and rarely in December), earlier in northern rivers than in southern ones (Degerman 2001). During the spawning and egg incubation period, low-flow impacts can be expected related to siltation that covers the eggs, impeded migration, loss of spawning habitat and redd superimposition, redd dewatering, abnormally high temperatures or freezing affecting energy expenditure and survival of embryos and juvenile fish, and increased predation risk (Barlaup et al., 1994; Bradford and Heinonen, 2008; Freeman et al., 2022). Low flows in the summer could impact young-of-the-year (0+) as well as older trout parr and adults (≥1+) by e.g. crowding, resource limitation, rapid warming leading to lethal temperatures or low oxygen levels, and stranding (Bradford and Heinonen, 2008; Freeman et al., 2022). In smaller streams, 0+ can be particularly vulnerable to stranding during the first months of life in late spring and summer, as they tend to remain on shallow spawning grounds for some time and have limited ability to escape when locked into shallow pools as water levels drop (Titus and Mosegaard, 1992; Halleraker et al., 2003).

Investigations of the impact of low flow on trout should therefore focus on the spawning period in October to December and on the summer period when low flows are caused by summer droughts. Thus, these two periods were included as the target periods for our analyses. We here define the summer period as May to July (i.e. when trout 0+ are still residing in shallow spawning areas), preceding the trout observation data included in the analysis, which is from August and September. Yearly data for the winter period October to December refers to the year predating the autumn electrofishing. Within the two chosen periods, we use hydrological simulations and observations to calculate common flow indicators presented in Table 1. These indicators give combined information on extreme low flows (LQ) and on low flows of somewhat longer duration (Q95).

### 2.2. River flow data

The flow indicators were developed based on daily river flow data from SMHI's hydrological rainfall-runoff model HYPE (Lindström et al., 2010) with the Swedish parameter set S-HYPE (Strömqvist et al., 2012) version 2016g. We used simulation period 1971–2020, with a 10-year

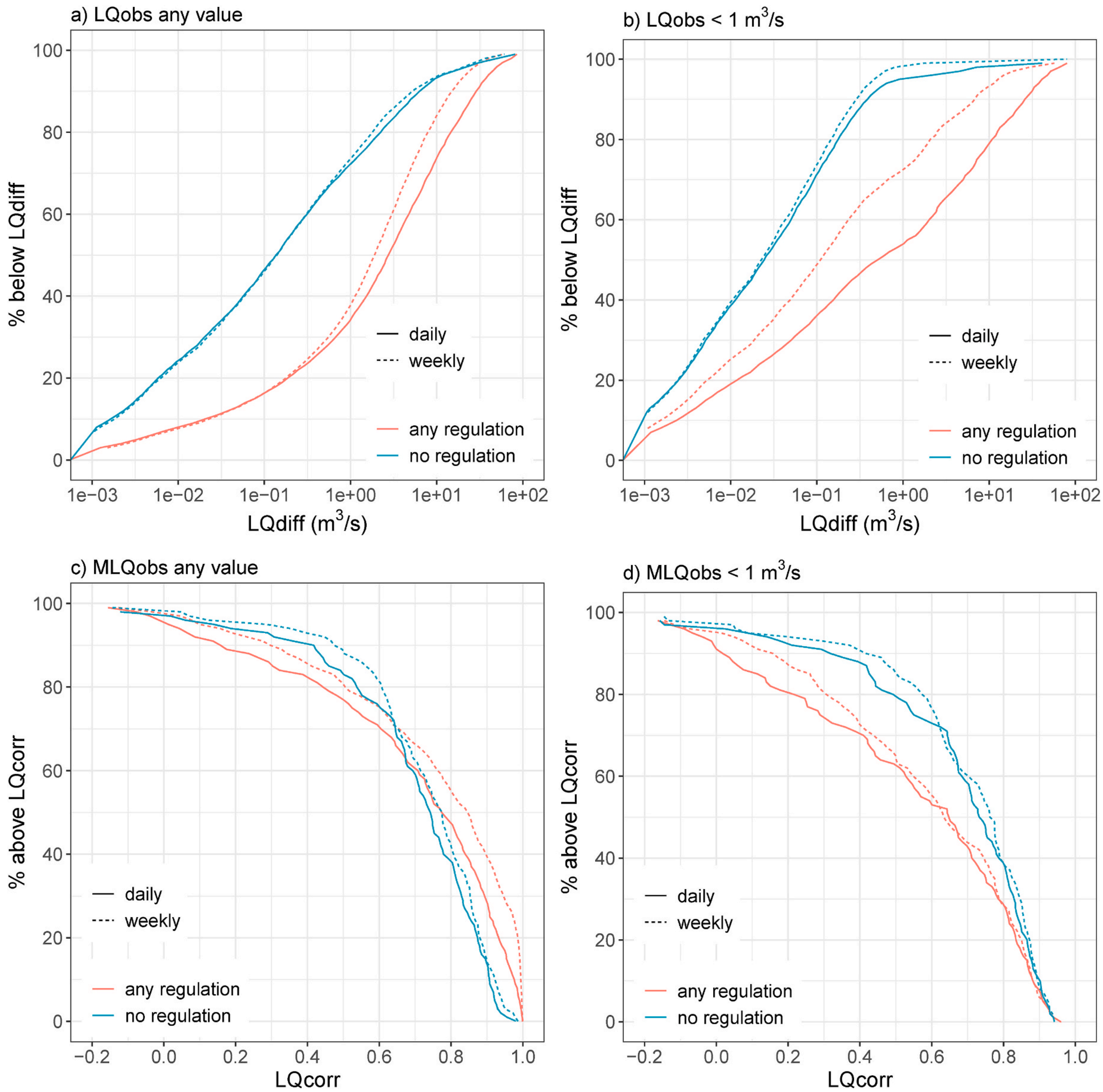


**Fig. 2.** Percent of samples below values of absolute differences in yearly LQ (LQw and LQs) between simulation and observation given on the x-axis, considering a) all flow conditions, and b) observed LQ $< 1$ m$^3$/s. The figure also presents percent of samples above values of LQcorr relating to the Pearson correlation coefficient between simulated and observed yearly LQ considering c) all flow conditions, and d) stations with mean observed LQ $< 1$ m$^3$/s.

initialization period from 1961. In S-HYPE, Sweden's hydrology is simulated with an average resolution of approximately 10 km$^2$, corresponding to about 40 000 sub-catchments, each having a combination of various land use and soil classes. Prior to this work calibration was performed, predominantly in terms of parameter values tied to the soil and land use classes which makes it possible to use the model in ungauged basins, however sometimes with local adjustments to further improve agreement with observations. Observations from SMHI's database were used in the calibration process, which mainly focused on the period 2009–2018. The objective of the calibration was to use the model as the official SMHI tool for advisories and warnings of high and low flow and for the evaluation of scenarios related to land use and climate change.

In the model, each sub-catchment has a main river that is fed by local runoff and inflow from upstream sub-catchments. The simulated flow represents the flow in this river at the sub-catchment outlet. At 579 of these outlets, the simulated flow was replaced by available observed flow on a daily basis, to improve performance. Flow in tributaries, which enter the main river in the sub-catchment, is treated in a lumped way as total contribution (i.e. tributaries are not explicitly modeled). Sweden has many lakes, and lake-specific rating curve parameters can be given for a lake that is located at the sub-catchment outlet. Lake regulation is also included in the model (e.g. Arheimer and Lindström, 2014; Elenius and Lindström, 2022), but does not play a large role here because most of the filtered fish data is from unregulated sites.

Here, we are interested in the physical implications of flow, as opposed to indirect impacts relating to e.g. temperature, which we treat separately (Section 2.4). Previous investigations on the physical implications of low flow have focused more on depth than flow itself, as habitat availability in a river section is largely determined by depth of the water. A full model of the temporal and spatial variability in water depth at cross sections of all investigated sites would require substantially more data and computing resources compared with estimates of flow. However, for an overall sense of the depths, we used SMHI's previously calibrated expression for average water depth $y_0$ (m) as a function of flow $q$ (m$^3$/s)

$$y_0 = c\, q^f, \qquad (1)$$

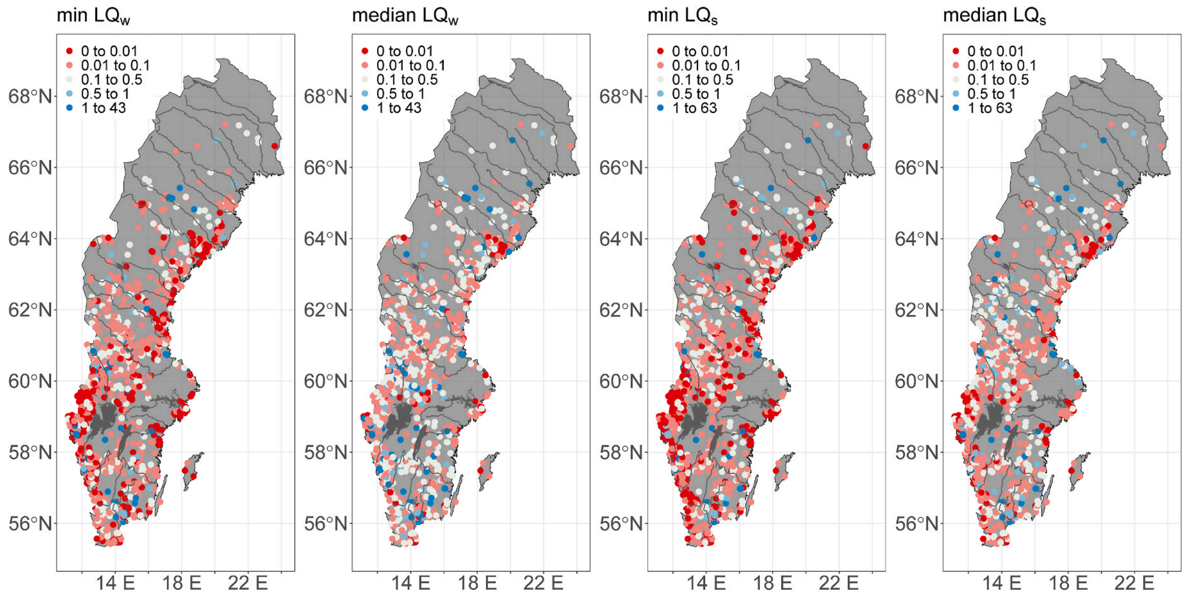


**Fig. 3.** Minimum and median winter (LQw) and summer (LQs) low flow ($m^3/s$) in sub-catchments with filtered electrofishing data (for selection of sites shown, see Section 3.2 below). Large rivers and lakes of Sweden are marked for geographical context.

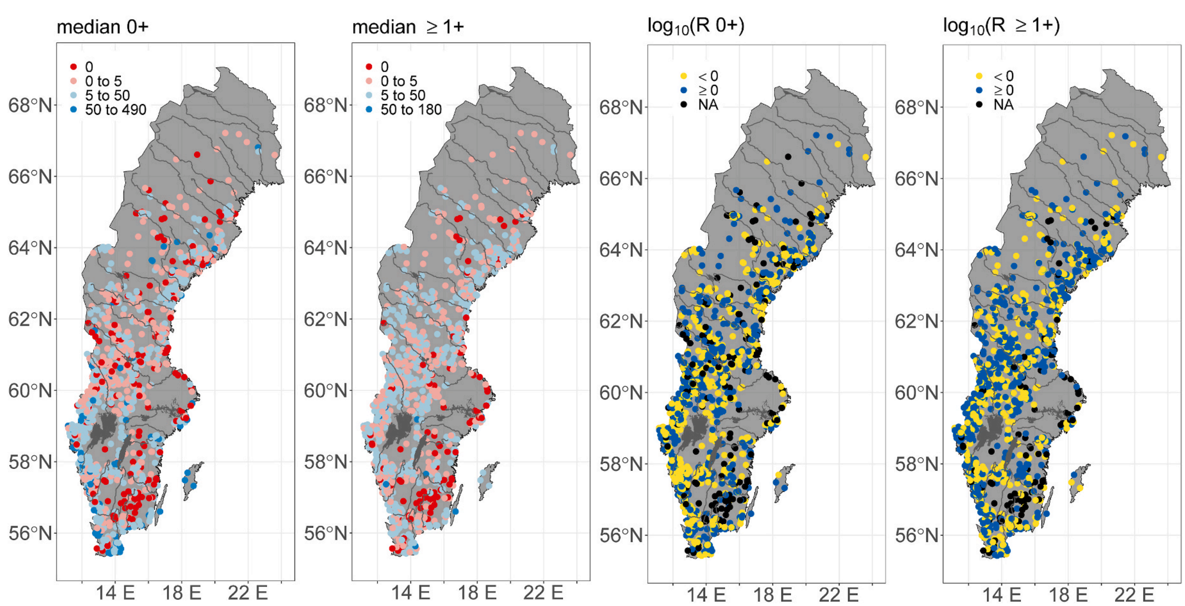


**Fig. 4.** Median 0+ and ≥1+ trout abundance per filtered site (number per 100 $m^2$), and $\log_{10}$ of the ratio $R$ between trout abundance at the year of the lowest winter low-flow divided by the median trout abundance. Apart from filters described in the Materials and Methods, only sites with at least three years of electrofishing observations were kept here; only one site per sub-catchment is shown in the figure.

**Table 1**
Flow indicators, serving as input for the hypothesis tests and machine learning. The period is the winter (w), respectively the summer (s), preceding the electrofishing record. The unit of flow is $m^3/s$.

| Indicator | Description | Indicator | Description |
|---|---|---|---|
| LQw | Lowest winter flow in the year | LQs | Lowest summer flow in the year |
| Q95w | Flow exceeded 95 % of days in the winter | Q95s | Flow exceeded 95 % of days in the summer |

where $c = 0.56\ (m^3/s)^{1-f}$ and $f = 0.3405\ (-)$ are the calibrated coefficient and exponent of the expression (Lindström et al., 2017). This was based on 2778 observations of average depth and flow in Swedish rivers.

For example, average depths of 0.1 m, 0.3 m and 0.5 m would be estimated from flow rates 0.01 $m^3/s$, 0.2 $m^3/s$ and 0.7 $m^3/s$ respectively. The maximum depth is of course larger than the average depth, and may be more indicative of the short-term trout survival, as the fish can move to deeper areas at low flow (Stradmeyer et al., 2008). Therefore, we tentatively expect that impacts of low flow on trout should primarily occur at flows less than the order 1 $m^3/s$ (see Section 1), and to decipher impacts of varying low-flow magnitude below this value, we would need to describe low-flows with higher accuracy, say 0.1 $m^3/s$.

### 2.3. Trout data

Observations on trout abundance were taken from SERS (20210602-version; SERS, 2021), where all electrofishing surveys in Sweden are registered. The abundance (or density) is presented as the number of 0+ and ≥1+ trout per 100 $m^2$. Electrofishing is an efficient method in wadable areas and consists of using electrodes that create an electric field which attracts the fish to the anode and stuns it for capture. By running multiple ($k$) such removal passes over the same area (so-called multi-pass electrofishing), the fish abundance can be estimated statistically, using a maximum likelihood estimator for $k$ removals (Bohlin et al., 1989). Density estimation based on consecutive removal takes into account variable catchability of individual trout in different conditions (e.g. habitat complexity and water temperature.

The analyzed version of SERS included a total of 74 867 electrofishing surveys (rows) and 265 descriptors (columns describing catches, environmental and geographical parameters), representing over 21 000 unique electrofishing sites. The surveys were conducted all over Sweden (Fig. 1), with the oldest dating back to the 1950's, but with a majority performed from the 1990's and onwards. Most sites are represented by only one record, and the dataset is much better distributed spatially than it is temporally.

The most common species caught in the surveys is brown trout *Salmo trutta* L., including all migratory forms of the species (i.e. sea-migrating, lake-migrating, and stream resident populations). The great abundance of trout data in SERS is a consequence of targeting Swedish electrofishing monitoring to typical salmonid fish habitats (Näslund et al., 2023b). For the same reason, other common species represented in SERS are generally biased towards other rheophilic species like Atlantic salmon (*Salmo salar*) and bullheads (*Cottus* spp.). The survey period is standardized in the national monitoring to allow for capture of salmonid 0+ individuals, with a clear majority of the sites sampled in August and September. Swedish populations of brown trout vary in their life-history strategy, both in terms of migratory behavior (migrating or resident; with generally migratory populations also containing a resident fraction) and migration (smolt) age (smoltification occurring at lower average age in southern populations, as compared to northern populations) (Degerman, 2001). However, since this study compare population densities among years within electrofishing sites (see 2.5 Analysis), these population differences are not expected to affect the results.

### 2.4. Other environmental data

Effects of water stress in general are dependent on other environmental and geographical factors (Sabater et al., 2018). SERS contains information on many such factors and Table 2 shows factors selected to be assessed in our analysis, describing conditions such as geography and characteristics of the river. Parameters with a strong link to flow were not included here because flow is accounted for by simulations as described in Section 2.2, with the idea of being able to assess flow conditions for trout also when and where electrofishing was not performed.

In addition to the descriptors from SERS, descriptor data from the hydrological model (first presented in Strömqvist et al., 2012) and the SMHI dam register (SMHI, 2013) were used (Table 3). The existence of a lake at the outlet of the sub-catchment representing an electrofishing observation was included because it is expected to increase resilience to low flow. On the other hand, more farmland or urban areas upstream of the electrofishing location can impact trout negatively, as would dams in the up- or downstream direction (Donadi et al., 2021). Low flows in the summer can also be related to high temperatures that can directly impact fish, and in an attempt to distinguish this impact from the direct impact of flow, indicators were developed for the mean and maximum seasonal temperature.

### 2.5. Analysis

The initial objective of our study was to find a broadly applicable model using trout as an indicator species for the adverse ecological effects of flow. We had initially explored various ways to model the response of trout abundance to structural and flow related factors. It included both traditional regression and machine learning based approaches (e.g. random forest, xgboost etc). We noted that tree methods worked best because the data is laden with special conditions, but that overall we could not find a model which had significant predictive power. As a result, we narrowed the focus of our study to investigate whether the data exhibits an ecologically significant effect of low flow on trout at all.

We designed a test statistic which would be sensitive to where effects would be most detectable if they existed: at the extremes of distributions. Our test statistic groups trout abundance and flow by site, wherein we note whether the lowest flow resulted in a lower trout abundance than the median for the site: a binary outcome. We treat sites as exchangeable, and intentionally confound time, location and structural factors in order to focus our search on a general effect of low flow. We factor this search by the magnitude of the lowest flow as represented by the quantiles of all sites – these are the factor levels in our analysis – in order to consider whether a detectable effect behaves sensibly (e.g. increases with lower flows). We therefore frame the data for each site as a contrast between trout median density and the density at the lowest flow (0+ and ≥1+ trout analyzed separately), as follows:

For each site, at each year for which we have electrofishing data on trout in the filtered dataset (Table 4 below) in August or September, we calculated the lowest flow during that year's summer period. We then compared the trout densities, in the year of the lowest flow, to the median trout densities for that site over all years in August/September. The same procedure was repeated by choosing the lowest flow of the previous winter instead.

Given the null hypothesis that low flows do not affect trout densities, we would expect site trout densities at flow minima to be above the site median as often as they are below it. The aim of our analysis is to investigate whether this null hypothesis can be rejected and under what conditions. We framed the analysis as a logistic regression wherein the endogenous variable is a Boolean indicating whether the density at the lowest flow is below the median (true) or not (false). We want to examine if the magnitude of the lowest flow is a significant indicator, so our exogenous variable is "lowest flow" quantized into decile bins (0–10 %, 10–20 %, 20–30 %, …) of the all-site lowest flow distribution. That is, if a site is in the 0–10 % bin, then its lowest flow is within the 0–10

**Table 2**
The selected descriptors from SERS, serving as input for the machine learning approach.

| Data | Description |
|---|---|
| alt | Elevation (m) |
| lat | Latitude (WGS84 decimal) |
| long | Longitude (WGS84 decimal) |
| length | Sampled l ength of stream at the electrofishing site (m) |
| wwidth | Stream wet width at the electrofishing site, here full width by Table 4 (m) |
| area | Estimated electrofished area ($m^2$) |
| oveg | Vegetation cover above water level (multi-category choice) |
| uveg | Vegetation below water level (multi-category choice) |
| uveg_type | Dominating vegetation type below water level (multi-category choice) |
| env | Surrounding environment type (multi-category choice) |
| domtree1 | Dominating tree species in surrounding environment (multi-category choice) |
| shadow | Degree of shading at noon (%, rounded to one significant figure) |
| wood | Number of dead wood pieces in the water (at least 10 cm ⌀ and 50 cm long) |
| bottomtop | Bottom topography (multi-category choice) |
| substr1 | Dominating bottom substrate (multi-category choice) |
| liming | Affected by liming (yes/no) |
| impact1 | Other source of large impact (multi-category choice) |
| watertemp | Observed water temperature (°C) |
| distlake_us | Estimated distance to upstream lake (km) |
| distlake_ds | Estimated distance to downstream lake (km) |
| maxdepth | Maximum depth at measurement location (m) |

**Table 3**
The selected descriptors from other sources, serving as input for the machine learning. The unit of temperature is °C.

| Data | Description | Source |
|---|---|---|
| slc1_bin | Binary indicator of existence of lake in sub-catchment | S-HYPE input |
| farmland | Proportion of farmland in upstream catchment area | S-HYPE input |
| urban | Proportion of urban area in upstream catchment area | S-HYPE input |
| maxTs | Highest simulated yearly summer water temperature | S-HYPE input |
| meanTs | Mean simulated yearly summer water temperature | S-HYPE input |
| maxTw | Highest simulated yearly winter water temperature | S-HYPE input |
| meanTw | Mean simulated yearly winter water temperature | S-HYPE input |
| upstr_dams | Number of dams in the upstream catchment | SMHI register |
| downstr_dams | Number of dams in the downstream catchments | SMHI register |

percentile compared to the lowest flows at all other sites. We utilize sum/deviance contrasts to code "lowest flow" such that the intercept in the model can be interpreted as the grand mean of the log-odds and the coefficients of the quantile bins can be interpreted as contributions deviating from it. This enables us both to study in which direction a quantile bin contributes and whether it is statistically significant given the model. Our alternative hypothesis is that low flows do affect trout densities. If it is true, we would expect the following:

1. The lowest quantile bin should contribute to the odds of an affirmative response most.
2. The affirmative contribution of each level should decrease monotonically.

Since there are many quantile bins, the probability of false discovery may be significant. We therefore adjust the statistically significant threshold using the Bonferroni correction (Bonferroni, 1936) to account for implicit multiple hypothesis testing. Further, if the null hypothesis is successfully rejected we will attempt to defeat the alternative hypothesis by adding factors to the logistic regression unrelated to flow which may confound the results and render them insignificant. Since we both have a number of other variables to consider and significant reason to believe that their effect may be non-linear and/or interactive, we trained a recursive partitioning algorithm (Therneau and Atkinson, 1997) on all non-flow variables (similar to a decision tree), and treat the predictions as an additional exogenous variable in our logistic regression. We used this method because the data exhibits both correlation between variables and heterogeneity dependent on thresholds within variables; this is complicated to represent using traditional methods such as linear regression. Tree methods (amongst which random forests and adaptive boosting would be other examples) enable us to both take correlations and thresholding into account in a simple way. If the results from the "lowest flow" quantile bins are confounded, we would expect that the additional variable will render them statistically insignificant and/or make the distribution of coefficients incoherent due to the effects of collinearity.

The analysis was repeated using Q95 instead of the lowest flow, to investigate if trout would respond differently in relation to an indicator representing low flows of somewhat longer duration than the minimum daily flow. (Note that Q95 is the flow that is exceeded 95 % of the time for a given site, in accordance with common notation in low-flow literature, whereas the limits of the quantile bins are framed as the percent of sites with flow indicator below this value.)

## 3. Results and discussion

Here we evaluate and discuss the quality and indicators of the flow and trout data used for the analysis, before we proceed to describe the results of the analysis of possible trout impacts of low flow.

### 3.1. Flow data quality and indicators

The assessment of flow data quality is based on a comparison between simulated and observed flow in selected stations. Out of 523 stations that have more than 10 years of observed flow in the period 1971–2020, we base the comparison on 45 % of the stations that were not used for local calibration. However, lake parameters were locally adjusted also in this subset, as needed, since S-HYPE as the official SMHI tool requires optimal performance. This means that the generic agreement between simulations and observations in ungauged rivers could be slightly lower than at evaluated stations. This agreement is not a direct measure of performance, because both simulations and observations have inherent uncertainties in especially the low-flow regime. However, larger overall agreement would indicate more robust results.

Different sources contribute to uncertainties in the observed flow (Di Baldassarre and Montanari, 2009) and several challenges are linked particularly to the low-flow regime. First, the presented "observed flow" is usually calculated from an observed water level together with a rating curve, which is a calibrated function relating water level to flow. Uncertainties are introduced when this curve is extrapolated to lower flows than those used for its calibration, when cross sections change over time, or if vegetation growth causes damming. Second, the observed flow in

**Table 4**
Criteria to filter out sites from the Swedish electrofishing register (SERS) sites and surveys that do not fulfill criteria for this study.

| Filter | Source | Description | Reason |
|---|---|---|---|
| tributary | WHIST | Exclude sites in tributaries, here defined as having a catchment area that is not larger than the catchment area of the upstream sub-catchment(s) of the hydrological model, if any. | Tributaries are not represented by the simulated flow. |
| bypassed | S-HYPE | Exclude sites at river stretches that are bypassed by hydropower production flow, here defined as sites having less than 20 % of natural average flow. | Bypassed rivers were already studied (Göthe et al., 2019). They represent different behavior than other parts of rivers. |
| trout_tot | SERS | Exclude sites with no observed trout | Assess trout where it was ever present |
| trout_years | SERS | Exclude sites with less than 3 years of observed trout | The median trout is used as part of the analysis |
| method | SERS | Exclude sites with 1-pass surveys, leaving mostly 2–3 pass surveys. | Quality increase. |
| wwidth | SERS | Exclude surveys where the full stream width was not used. | Quality increase. |
| month | SERS | Only include surveys from August and September | Increase consistency between surveys and use months that are non-overlapping with periods used for flow indicators. |
| period (year) | SERS | Only include surveys from year 1972 and onwards | Most electrofishing sites are later than this time, and comparison to simulated flow including the previous winter can be made from here. |

the SMHI database is routinely given with three decimals in unit $m^3$/s, meaning that zero flow could represent any flow below 0.005 $m^3$/s. Third, during ice damming in the winter, observations are not possible, and instead estimates are made which can be very uncertain. Last, when hydropower is neither producing or spilling water, the observed flow is often presented as 0 $m^3$/s, although in reality there is always some leakage. However, this last aspect does not play a large role here as most of the flow data used in this work is from unregulated sites. Simulations of low flow come with uncertainties as well and are generally expected to be more uncertain than observations. These uncertainties represent difficulties in balancing calibration performance in all flow regimes as well as having incomplete information on abstractions. Therefore, ideally the analysis of how low flows impact brown trout populations would include empirical flow data. However, only a few sites ($n = 33$) in the filtered electrofishing dataset were located where flow observation data exists, rendering our use of modeled streamflow data.

In the evaluation of differences between simulated and observed flow we consider the degree of regulation, i.e. the percentage of the annual flow that can be stored in upstream reservoirs by regulation. 92 % of the fish data that is used in our analysis was obtained at unregulated sites (as described in the model). Therefore, compliance between simulations and observations will be discussed for unregulated conditions only, although figures also present results of the full evaluation dataset. Apart from comparisons based directly on the daily time series, we also present comparisons based on daily time series that were obtained by taking rolling averages with a window of 7 days from the original data (using the 'rollmean' function in the zoo R-package; Zeileis and Grothendieck, 2005). These are presented in figures (called "weekly") but the discussed performance indicators refer to indicators based on the original daily time series, which is very similar.

Fig. 2a shows the percentage of samples below values of absolute differences between simulated and observed LQw and LQs, i.e. the lowest yearly flow in the defined winter and summer periods. 47 % of the evaluation data has differences smaller than 0.1 $m^3$/s if all low-flow conditions are evaluated, but the more interesting regime of observed LQ less than 1 $m^3$/s (Fig. 2b) has 71 % of differences being smaller than 0.1 $m^3$/s. The errors are further reduced with smaller values of LQ, see Appendix 5 of the Supplementary information. Very similar results are obtained if Q95 is analyzed or results are analyzed separately for the winter and summer seasons, between 44-47 % and 71–73 % respectively.

For the trout analysis, the aspect of low-flow that was employed was not low-flow indicators in absolute terms, but rather a comparison of the increase or reduction of low-flow and trout between years, for the winter and summer seasons. Therefore, the correlation of LQ (and Q95) between simulation and observation is assessed here for the winter and summer periods. Fig. 2c shows the percentage of samples above thresholds of the Pearson correlation coefficient between yearly simulated and observed LQw and LQs. A correlation coefficient above 0.6 is obtained in 75 % of the stations (73 % in summer and 78 % in winter when the analysis is separated), and slightly less at 73 % (66 % in summer and 80 % in winter) if only considering stations that have mean observed LQ less than 1 $m^3$/s (Fig. 2d). This means that unfortunately, it is the correlation of summer low-flows in the low-flow regime that has the lowest correlation between simulated and observed yearly minimum flows. The percentage of stations with higher correlation than 0.6 is quickly reduced. Results are slightly better for Q95 with correlation coefficient above 0.6 in 81 % of the stations (81 % in summer and 80 % in winter), and for the low-flow regime in 77 % of stations (74 % in summer and 80 % in winter). Overall these results indicate that the flow data quality seems to be sufficient in the relevant low-flow regime.

Fig. 3 shows the spatial distribution of the simulated lowest and median winter and summer flows. These statistics were based on a spatial and temporal sub-selection according to the electrofishing data that was chosen for the analysis (cf. Section 3.2). Almost all of these sites have minimum low-flow below 1 $m^3$/s; and in many cases the median low-flow is also below this value. There is no obvious geographical pattern of the lowest flows, perhaps because electrofishing sites were everywhere chosen in rivers small enough for wading. In the southern part of the country, there is a small indication of lower low-flows in the summer season, and seasonal differences are even smaller in the north. Further description of the distribution of low flows is presented in Appendix 5 of the Supplementary information.

### 3.2. Trout data quality and statistics

The main advantages of electrofishing as opposed to other capture methods is the generally high capture efficiency and low mortality rate when conducted correctly, which allows for accurate density estimates and a possibility to release fish alive back into the stream (Bergquist et al., 2014). However, there are also limitations to this method, because the stream depth cannot exceed wading depth and there is a capture bias against large fish and certain fish species, as well as decreasing efficiency with increasing stream width (Kennedy and Strange 1981; Nordwall 1999; Bergquist et al., 2014).

From the large amount of data in SERS, there are some issues with quality that the user should be aware of and mitigate as possible. There is sparse and missing data in many places because some of the descriptors are not mandatory for all survey purposes. Inconsistencies such as errors in records, for example typos or use of non-existing categories, do occur. It can also be assumed that the large spread in time and space could lead to temporal inconsistencies, e.g. due to progress in electrofishing equipment construction and function. However, SERS is the only available register with sufficient data to build nation-wide statistical inferences about trout, and wading electrofishing is known to be particularly suitable for estimating brown trout population densities (Bohlin et al., 1989). In addition, many of the shortcomings can be mitigated by choosing a suitable subset of the data, which is done here. For the analysis, subsets of the survey data and descriptors were selected based on quality, completeness and consistency of the records, in addition to expected relevance for trout abundance, added value compared with flow data obtained from simulations, and proximity to locations where flow was calculated.

While Tables 1–3 above have described parameters that were included in the analysis, what remains is to filter out electrofishing sites and surveys that do not have sufficient quality for the purpose of this study, see Table 4. The first criterion in the table deserves special attention. The removal of sites in tributaries as defined here, which is necessary to be able to compare with flow data, implies that sites with the lowest flows might have been removed as well, which might impact the analysis of trout dependence on low flow. The catchment area of each electrofishing site was used in defining tributaries and it was obtained using SMHI's GIS-tool WHIST (Strömqvist et al., 2009). The second criterion of excluding river stretches bypassed by hydropower production is also likely removing sites with low-flows at the lower end of the spectrum, however this choice was performed to avoid duplicating the previous investigation of Göthe et al. (2019). In addition to these criteria, each electrofishing site was matched to the sub-catchment with the closest outlet, which is where the flow data are obtained. We do not expect large differences in the flow between the sub-catchment outlet and the matched trout location.

In summary, the filters applied are expected to render the data of higher quality while also by necessity likely removing some trout sites at the lowest flows. The analysis is therefore not representative of all sites with trout populations, but rather for wadable sites in rivers that are not tributaries and not bypassed, i.e. where electrofishing can be performed, flow data exists and where previous studies are missing.

Fig. 4 shows the median abundance of 0+ and ≥1+ trout in remaining sites, based on all available years. The highest abundance is typically observed in coastal rivers, with sea-migrating trout populations and high production potential, in the southwestern part of the country (Degerman, 2001). Further description of the distribution of trout densities is shown in Appendix 5 of the Supplementary information. The figure also shows the 10-logarithm of the ratio $R$, where $R$ is trout abundance at the year of the minimum winter low-flow (LQw) divided by the median abundance. Points in yellow show where the abundance was reduced during the year of minimum LQw. From the figure, there is no obvious pattern of where trout is impacted. Here, $R$ for all sites with zero median trout abundance is set to NA, shown in black. This figure is shown for the summer season in Appendix 2 of the Supplementary information, also with no clear patterns of trout impacts.

### 3.3. Environmental descriptor quality and statistics

The quality of environmental descriptors that were applied from the SERS register (Table 2) is considered quite high, as this sub-selection was partly made based on quality. The upstream land use (Table 3) and water temperature is also well described. SMHI's dam register (Table 3) was last updated in 2013 and is not a complete description of dams in Sweden. For comparison, some of the electrofishing sites that have regulations upstream have no dams upstream in this registry. This means that the number of dams upstream and downstream is only an indication of the true number of dams. Distributions of environmental data is shown in Appendix 5 of the Supplementary information.

### 3.4. Analysis results

For all analyses the intercept is significantly negative (that is, there is a bias towards assigning a low probability to an affirmative response) because the data contains a large number of zero trout densities which skews the median toward zero. We begin with the analysis of the summer flows.

#### 3.4.1. Impacts of summer minimum flow

Table 5a shows the logistic regression of affirmative responses using age ≥1+ trout densities (lowest flow trout density below median for site) as explained by factored summer "lowest flows". Reference to the corresponding flow ranges is provided in Appendix 3. The "lowest flow" factor for age ≥1+ trout is mostly statistically insignificant at a significance threshold of 0.05. It is statistically significant (Bonferroni corrected) at quantile range 10–20 % but not at 0–10 % which seems incoherent. Further, none of the individual quantile bins have a coefficient large enough to create an affirmative prediction (i.e. probability larger than 50 % for a density lower than median) given the intercept, resulting in a constant negative prediction.

We repeat the analysis for age 0+ trout densities in Table 5b. Only the 0–10 % bin is statistically significant (after Bonferroni correction). Its coefficient is positive and large enough to result in an affirmative prediction. The higher quantile ranges are not statistically significant; they are also not monotonic, with the 40–50 % and 50–60 % bin varying contributing affirmatively whilst bins to either side contribute negatively.

#### 3.4.2. Impacts of winter minimum flow

We now repeat the analysis in the section above using the winter flows, see Table 5c for age ≥1+ trout densities. The only significant quantile bin (after Bonferroni correction) is 50–60%. Further, the direction of the coefficients varies throughout the range making the results incoherent.

We repeat the analysis for age 0+ trout densities, as shown in Table 5d. Quantile ranges 0–10 %, 10–20 % and 20–30 % are all positive and statistically significant after Bonferroni correction. Additionally, quantile 80–90 % is negative and statistically significant. Whilst all coefficients are not significant, there is a clear trend from positive to negative in lower to higher quantile bins, with maximal magnitudes at the extremes of the range.

The plot in Fig. 5 shows the quantile bins and the corresponding fraction of low flows with 0+ trout densities lower than the site median. The slope has $p$-value $\ll 0.05$, and shows a clear trend. That is, as the lowest flow for any given site increases relative to all sites, the fraction of 0+ trout density below the median at the year of the lowest winter flow decreases linearly.

In the case of age 0+ trout densities and winter flows, we can reject our null hypothesis that low flows have no effect. We therefore continue to try to defeat our alternative hypothesis by fitting a recursive partitioning algorithm to the non-flow related fields in an attempt to predict

**Table 5**
Results from logistic regressions of affirmative responses using age ≥1+ (a, c) or age 0+ (b, d) trout densities (lowest flow trout density below median for site) as explained by factored summer (a, b) and winter (c, d) lowest flows. The table shows the estimated coefficients, standard error, $z$-value and $p$-value for all fitted parameters of the logistic regressions; $p$-values <0.005 (i.e. significant after Bonferroni correction) are marked in bold font. Reference to flow ranges corresponding to the quantiles is provided in Appendix 3.

| | a) Summer: ≥1+ trout | | | | b) Summer: 0+ trout | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | SE | $z$ | $p$ | Estimate | SE | $z$ | $p$ |
| intercept | −0.45 | 0.04 | −10.5 | < **0.001** | −0.37 | 0.04 | −8.73 | <**0.001** |
| 0–10% | 0.23 | 0.13 | 1.7 | 0.091 | 0.40 | 0.13 | 3.04 | **0.002** |
| 10–20% | 0.44 | 0.12 | 3.6 | < **0.001** | 0.27 | 0.12 | 2.25 | 0.02 |
| 20–30% | −0.02 | 0.13 | −0.20 | 0.84 | −0.12 | 0.13 | −0.97 | 0.33 |
| 30–40% | 0.05 | 0.13 | 0.39 | 0.69 | −0.16 | 0.13 | −1.24 | 0.22 |
| 40–50% | 0.30 | 0.12 | 2.5 | 0.01 | 0.23 | 0.12 | 1.83 | 0.07 |
| 50–60% | −0.02 | 0.13 | −0.19 | 0.85 | 0.09 | 0.13 | 0.72 | 0.47 |
| 60–70% | −0.25 | 0.13 | −1.91 | 0.06 | −0.03 | 0.13 | −0.25 | 0.80 |
| 70–80% | −0.06 | 0.13 | −0.47 | 0.64 | −0.03 | 0.13 | −0.25 | 0.80 |
| 80–90% | −0.24 | 0.13 | −1.82 | 0.07 | −0.18 | 0.13 | −1.44 | 0.15 |
| | c) Winter: ≥1+ trout | | | | d) Winter: 0+ trout | | | |
| | Estimate | SE | $z$ | $p$ | Estimate | SE | $z$ | $p$ |
| intercept | −0.39 | 0.04 | −9.18 | < **0.001** | −0.24 | 0.04 | −5.66 | <**0.001** |
| 0–10% | 0.25 | 0.13 | 2.01 | 0.04 | 0.49 | 0.13 | 3.85 | <**0.001** |
| 10–20% | 0.06 | 0.13 | 0.42 | 0.68 | 0.38 | 0.13 | 2.85 | **0.004** |
| 20–30% | −0.003 | 0.12 | −0.03 | 0.98 | 0.31 | 0.12 | 2.59 | 0.009 |
| 30–40% | −0.14 | 0.13 | −1.02 | 0.30 | 0.10 | 0.13 | 0.77 | 0.44 |
| 40–50% | 0.37 | 0.12 | 3.04 | **0.002** | −0.03 | 0.12 | −0.21 | 0.83 |
| 50–60% | −0.19 | 0.13 | −1.51 | 0.13 | −0.11 | 0.13 | −0.89 | 0.37 |
| 60–70% | −0.08 | 0.13 | −0.59 | 0.55 | −0.23 | 0.13 | −1.91 | 0.06 |
| 70–80% | 0.02 | 0.13 | 0.15 | 0.88 | −0.10 | 0.13 | −0.75 | 0.45 |
| 80–90% | −0.13 | 0.13 | −0.98 | 0.33 | −0.37 | 0.13 | −2.85 | **0.004** |

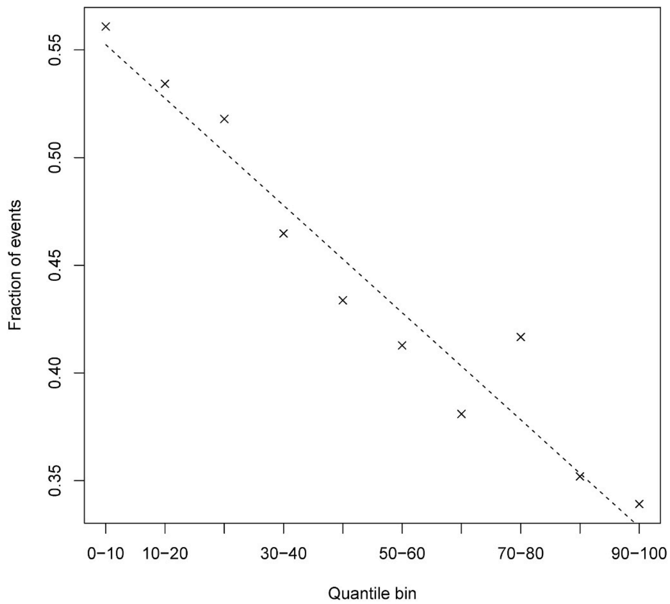


**Fig. 5.** Quantile bins and the corresponding fraction of sites within each quantile bin where the age 0+ trout density at the lowest winter flow is below the median.

observations where the age 0+ trout density is below the site median. We use just data where the lowest flow is in the <30 % quantile because it is where the signal is concentrated. The tree diagram in Fig. 6 shows the decision tree resulting from the fitting process. The conjunctions indicate inequalities which decide whether the left or right branch should be taken (true or false, respectively). The lead notes indicate the number of FALSE/TRUE labels within the branch.

We use the prediction from our fitting as an additional exogenous variable in the previous logistic regression (summary results in Table 6). The new predictor variable is statistically significant but it does not affect either the statistical significance or the coefficient distribution of the "lowest flow" factor. Thus, both remain coherent with the alternative hypothesis of low flows in winter affecting 0+ brown trout negatively.

**Table 6**
Logistic regression of affirmative responses using age 0+ trout densities (lowest flow trout densities below median for site) as explained by factored winter lowest flows and an additional predictor from the recursive partitioning algorithm fitted on non-flow variables. The table shows the estimated coefficients, standard error, *z*-value and *p*-value for all fitted parameters of a logistic regression. Bold *p*-values indicate significance after Bonferroni correction.

| | Winter: 0+ trout | | | |
|---|---|---|---|---|
| | Estimate | SE | *z* | *p* |
| intercept | −0.36 | 0.04 | −7.37 | < **0.001** |
| predictor | 0.66 | 0.11 | 6.22 | < **0.001** |
| 0–10% | 0.55 | 0.13 | 4.18 | < **0.001** |
| 10–20% | 0.38 | 0.13 | 2.84 | **0.004** |
| 20–30% | 0.32 | 0.12 | 2.64 | 0.008 |
| 30–40% | 0.10 | 0.13 | 0.78 | 0.44 |
| 40–50% | −0.02 | 0.12 | −0.19 | 0.85 |
| 50–60% | −0.07 | 0.13 | −0.52 | 0.60 |
| 60–70% | −0.25 | 0.13 | −1.94 | 0.05 |
| 70–80% | −0.05 | 0.13 | −0.41 | 0.68 |
| 80–90% | −0.42 | 0.13 | −3.22 | **0.001** |

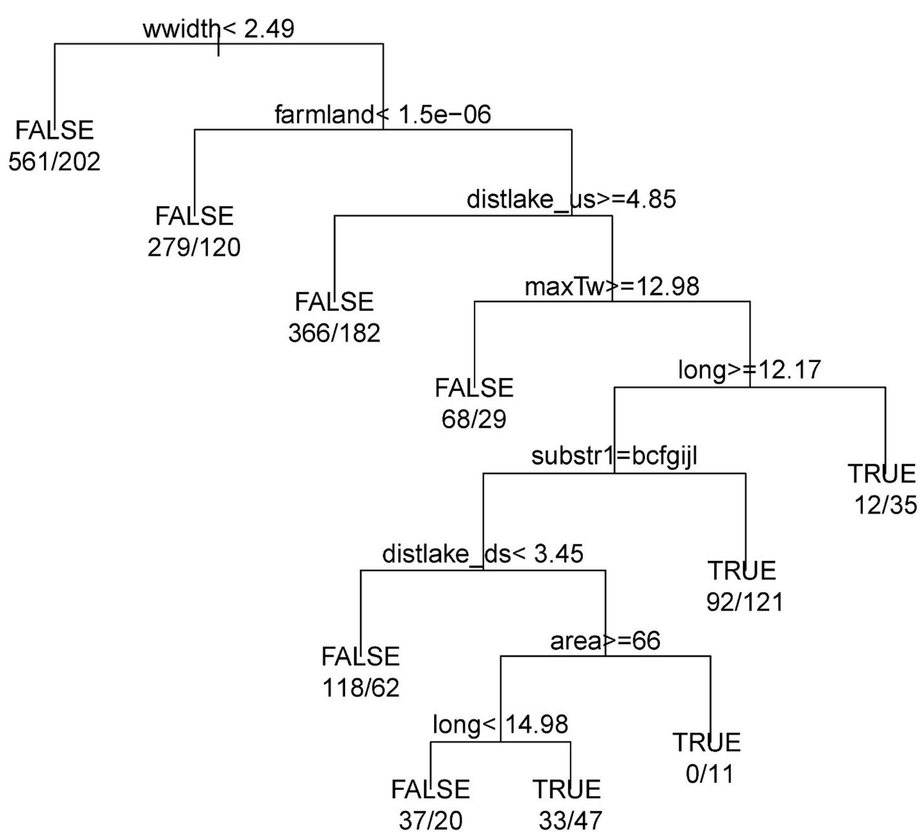


**Fig. 6.** A decision tree fitted using a recursive partitioning algorithm trained to identify whether the trout density after the lowest winter flow is smaller than the median density across all years for any given site. The conjunctions indicate inequalities which decide whether the left or right branch should be taken (TRUE or FALSE respectively). The lead notes indicate the number of FALSE/TRUE labels within the branch.

#### 3.4.3. Summary of results

In summary, the data indicates a reason to reject the null hypothesis that winter low flows have no effect on 0+ brown trout in favor of the alternative hypothesis, i.e. that winter low flows indeed do affect 0+ brown trout. The impact was small with at most 57 % of remaining sites having lower than median trout abundance at the year of the lowest flow, compared to 44 % overall. We could not defeat the alternative hypothesis by considering other environmental factors. For other combinations of trout age and season, the null hypothesis could not be convincingly rejected.

#### 3.4.4. Summer and winter impacts of 95th percentile flow

In Appendix 4 of the Supplementary information, the analysis performed above is repeated using the 95th percentile lowest flow instead of the minimum flows. The findings are similar but weaker when compared to those based on the minimum seasonal flow.

### 3.5. Notes on sensitivity of 0+ trout to low flow in winter

While summer droughts are often receiving much concern, low winter flows are possibly paid less attention to by environmental and fisheries managers. Older trout (i.e. age ≥1+, in the summer after the winter in question) seem to generally cope with low winter flows, likely due to a general avoidance of shallow water in winter, as well as adaptive movement behavior responses (e.g. Bremset, 2000; Brown et al., 2001). However, the age 0+ trout are negatively affected in a small, but statistically significant, majority of our cases (Table 5d, Table 6). The trout that are age 0+ at the time of electrofishing would be early-stage embryos during the investigated winter low flows (October–December) (October–December), meaning that they have no ability to move to cope with low flow. Hence, nest stranding is one candidate factor which may affect this age class negatively, a phenomenon which has been observed downstream of hydropower plants in Norway (Skoglund et al., 2023). Temperature may also be problematic during low flow. Low temperatures and ice formation in the nest could possibly kill the eggs (Huusko et al., 2007), and relatively high temperatures in warmer winters may accelerate development so that the eggs hatch too early in the season (Elliott and Elliott, 2010). Another candidate factor affecting recruitment of trout is that low flow in late fall/early winter may restrict the spawning migration of adult trout, as well as available spawning habitats, leaving some areas with no or only few new recruits (Smialek et al., 2021).

### 3.6. Notes on small low-flow impacts overall and future strategies

It was surprising to us that the data did not show any substantial impact of low flow on brown trout, given the previous literature on the sensitivity of salmonids to low flow. However, challenges relating to the establishment of fish response to flow conditions have also been indicated before by several review papers (Poff and Zimmerman, 2010; Warren et al., 2015; Freeman et al., 2022). Freeman et al. (2022) noted that fish populations may be affected by hydrological events and conditions at other sites in a river network than the specific site where they are momentarily observed, as well as by the flow at other times of the year than during an often-sparse annual sampling. For instance, if fish are not sampled specifically during extremely low flows, the impact of these conditions would be difficult to assess from monitoring data. The fish may have sought temporary refuge in deeper pools under extreme conditions (Elliott, 2000), after which they returned to their original habitat. Furthermore, they mention that even in cases where fish were sampled during extreme low-flow conditions, the flow data to which comparisons should be made could be uncertain, e.g. if it is derived from flow models. Another complicating factor mentioned is that the sensitivity of fish to low flow may be non-monotonic. Hypothetically, depending on the depth and current velocity under normal flow, and body size of the fish, conditions may first improve with a reduced water level (e.g. by reducing predation risk from in-stream predators, or reducing energy costs for swimming), but worsen dramatically at very low flow when the river starts to dry out. (However, the possibility of non-monotonic response was considered in our analysis by separation into quantile bins.) Lastly, uncertainties in the fish sampling procedure is mentioned as a potential difficulty where flow conditions could affect the capture efficiency (Bohlin et al., 1989). Below, we explore how these and other factors might have impacted the results.

Overall, the flow data quality in our study seems to be sufficient in the relevant regime (see Section 3.2), although it cannot be excluded that higher quality would have impacted the results. The time resolution is also sufficient, using daily flow. A larger challenge with flow data is probably the limitations in spatial resolution, which prompted exclusion of many electrofishing sites for the analysis. The trout density data is also estimated to be of sufficient quality after questionable data was filtered out. Here, the time resolution with yearly or less frequent sampling may be a larger issue. Another factor might be that electrofishing is typically not performed when there is only stagnant water or if zero occurrence of fish is expected due to very low water levels (information that is communicated by fisheries managers and electrofishing practitioners, but not noted in SERS).

The lack of significant trout dependence on low flows may be attributed to various factors and we made an attempt to rank them in Table 7, starting with the limitations in electrofishing time resolution and flow spatial resolution. These are predominantly linked to the ability of trout to escape low flows, giving it a lower sensitivity to low flows, at least when analyzed based on annual sampling. It is well known that brown trout show behaviors that either indicate or directly demonstrate movement strategies adapted to cope with both low and high flow (e.g. Elliott, 2000; Stradmeyer et al., 2008; Bunt et al., 1999). Lack of flow simulations for smaller streams may have reduced the chance of detecting negative effects of low flow, given that there are reports of severe, albeit variable, effects from small streams (e.g. Elliott et al., 1997). Additional flow simulations could possibly contribute to development of a trout-based indicator, but given the results in this study such a hypothetical indicator would likely be restricted to generally work only for smaller streams. As shown in the decision tree in Fig. 6, other environmental factors play potentially interactive roles in whether the low winter flow leads to reduced 0+ trout densities. Possibly, regional or river type specific indices of low flow impacts may be developed based on trout as an indicator species, but this requires further investigation. We think that issues relating to data quality contributed less to our results than these factors. The table also suggests possible future mitigation strategies. Each of these strategies may of course come with its own challenges. We think it may be worthwhile to first evaluate if other species can serve as ecological status indicators for low-flow impacts in Swedish rivers, preferably starting with species with low movement ability and demonstrated responses to flow modifications (e.g. algae or invertebrates; Sabater et al., 2018). Also, the aspect of biological diversity should ideally be considered, requiring a movement towards assessment of multiple species (e.g. using eDNA metabarcoding; Blancher et al., 2022).

## 4. Conclusions

Currently available data does not support the use of trout as a general indicator species for low-flow impacts in Sweden. The analyses show no general impact of low flow on adult trout and only a very small general impact on young-of-the-year trout (but impacts in specific cases may still be large). We believe the main causes are limitations in the time resolution of trout data and spatial resolution of the flow data, followed by the ability of trout to escape low flows, and possibly also limitations in data quality. Some of these challenges might be overcome by improvements in data collection/production and alternative data sources such as filming fish in rivers or by using drones and satellite imagery. However, because of the large effort this would require, and given the trout ability

**Table 7**
Factors possibly contributing to lack of substantial observed trout impact of low flow, in stipulated order of importance (most important at the top). Possible mitigation strategies are also mentioned.

| Factor | Description | Potential mitigation strategies |
|---|---|---|
| Limitations in electrofishing time resolution | Limitations in time resolution of trout data in relation to its movement behavior, such as escape to refugia during low flows. Trout densities may have been impacted during the time of the lowest flows also if no impact was observed in the fall surveys. | - Additional electrofishing with higher time resolution.<br>- Targeted surveys during low flow.<br>- Conduct tagging experiments on trout to see if they die after low flow events.<br>- Perform controlled experiments with reduced release from regulated dams to investigate movement behavior and low-flow mortality. |
| Limitations in flow spatial resolution | Absence of flow data in smaller tributaries, resulting in removal of sites that could experience the lowest flows. | - Higher spatial resolution of the hydrological model<br>- Development of methods to provide sub-scale flow data of high enough quality.<br>- Other methods to obtain hydrological data, e.g. drones or satellite |
| Limited trout sensitivity to low flow | Although trout have reported sensitivity to low flows, they might be sensitive only at very low flows, perhaps below the requirements of other species. | - Increase randomness of results, e.g. not limiting surveys in periods when no trout is expected.<br>- Study other species that may be more sensitive to low flows and have lower movement capacity, or assembly of species e.g. from eDNA metabarcoding. |
| Limitations in flow data quality | Limitations in flow data quality (observations and simulations) and perhaps a non-sufficient link to the water depth in the center of the river, which is what ultimately limits migration and survival. | - Improved observation data including more calibration data for rating curves from low flows.<br>- Further model development such as inclusion of more abstractions, updated process descriptions, and recalibration.<br>- Combination with hydraulic methods to describe water depth. |
| Limitations in electrofishing data quality | Difficulties inherent to electrofishing and the non-randomness of records. | - Include reports on when electrofishing was not deemed suitable or possible due to very low flow in the electrofishing database.<br>- Implement national monitoring with a high degree of randomness in both spatial and temporal dimensions.<br>- Supplement electrofishing with quantitative eDNA monitoring for trout, with better coverage in time and space. |

to escape low flows and potentially tolerate quite low flows, we think a better strategy would be to first evaluate other candidate low-flow indicator species, and combinations thereof.

## CRediT authorship contribution statement

**Maria Elenius:** Writing – original draft, Validation, Methodology, Data curation, Conceptualization. **Emir Uzeirbegovic:** Writing – review & editing, Methodology, Formal analysis. **Joacim Näslund:** Writing – review & editing, Conceptualization. **Axel Lavenius:** Writing – review & editing, Methodology, Investigation, Data curation.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

We have shared the link to our data/code in the Attach File step https://doi.org/10.6084/m9.figshare.24080637 (Figshare)

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.indic.2024.100414.

## References


Acreman, M.C., Ferguson, A.J.D., 2010. Environmental flows and the European water framework directive: environmental flows and WFD. Freshw. Biol. 55, 32–48. https://doi.org/10.1111/j.1365-2427.2009.02181.x.

Allan, J.D., Castillo, M.M., 2007. Stream Ecology - Structure and Function of Running Waters, second ed. Springer, Dordrecht.

Arheimer, B., Lindström, G., 2014. Electricity vs Ecosystems - understanding and predicting hydropower impact on Swedish river flow. Presented at the in: Evolving Water Resources Systems: Understanding, Predicting and Managing Water-Society Interactions. Proceedings of ICWRS2014, Bologna, Italy, pp. 313–319. https://doi.org/10.5194/PIAHS-364-313-2014.

Arheimer, B., Lindström, G., 2019. Detecting changes in river flow caused by wildfires, storms, urbanization, regulation, and climate across Sweden. Water Resour. Res. 55, 8990–9005. https://doi.org/10.1029/2019WR024759.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., Milner, N.J., 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. 62, 143–170. https://doi.org/10.1016/S0165-7836(02)00160-1.

Barlaup, B.T., Lura, H., Sægrov, H., Sundt, R.C., 1994. Inter-and intra-specific variability in female salmonid spawning behaviour. Can. J. Zool. 72, 636–642. https://doi.org/10.1139/z94-086.

Bell, M.C., 1986. Fisheries Handbook of Engineering Requirements and Biological Criteria. US Army Corps of Engineers, Portland.

Bergquist, B., Degerman, E., Petersson, E., Sers, B., Stridsman, S., Winberg, S., 2014. Standardiserat elfiske i vattendrag – en manual med praktiska råd. Aqua Rep. 15 (2014), 165. Drottningholm: Swedish University of Agricultural Sciences, Department of Aquatic Resources. https://pub.epsilon.slu.se/12124/.

Bjornn, T.C., Reiser, D.W., 1991. Habitat Requirements of Salmonids in Streams, vol. 19. American Fisheries Society Special Publication, pp. 83–138.

Blancher, P., Lefrançois, E., Rimet, F., Vasselon, V., Argillier, C., Arle, J., Beja, P., Boets, P., Boughaba, J., Chauvin, C., Deacon, M., Duncan, W., Ejdung, G., Erba, S., Ferrari, B., Fischer, H., Hänfling, B., Haldin, M., Hering, D., Hette-Tronquart, N., Hiley, A., Järvinen, M., Jeannot, B., Kahlert, M., Kelly, M., Kleinteich, J., Koyuncuoğlu, S., Krenek, S., Langhein-Winther, S., Leese, F., Mann, D., Marcel, R., Marcheggiani, S., Meissner, K., Mergen, P., Monnier, O., Narendja, F., Neu, D., Pinto, V.O., Pawlowska, A., Pawlowski, J., Petersen, M., Poikane, S., Pont, D., Renevier, M.-S., Sandoy, S., Svensson, J., Trobajo, R., Zagyva, A.T., Tziortzis, I., van der Hoorn, B., Vasquez, M.I., Walsh, K., Weigand, A., Bouchez, A., 2022. A strategy for successful integration of DNA-based methods in aquatic monitoring. Metabarcoding and Metagenomics 6, 215–226. https://doi.org/10.3897/mbmg.6.85652.

Bohlin, T., Hamrin, S., Heggberget, T.G., Rasmussen, G., Saltveit, S.J., 1989. Electrofishing — theory and practice with special emphasis on salmonids. Hydrobiologia 173, 9–43. https://doi.org/10.1007/BF00008596.

Bonferroni, C., 1936. Teoria statistica delle classi e calcolo delle probabilita. Istituto Superiore di Scienze Economiche e Commericiali di Firenze 8, 3–62.

Bradford, M.J., Heinonen, J.S., 2008. Low flows, instream flow needs and fish ecology in small streams. Can. Water Resour. J. 33, 165–180. https://doi.org/10.4296/cwrj3302165.

Bremset, G., 2000. Seasonal and diel changes in behaviour, microhabitat use and preferences by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. Environ. Biol. Fish. 59, 163–179. https://doi.org/10.1023/A:1007691316864.

Brown, R.S., Power, G., Beltaoa, S., 2001. Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. J. Fish. Biol. 59, 1126–1141. https://doi.org/10.1111/j.1095-8649.2001.tb00180.x.

Bunt, C.M., Cooke, S.J., Katopodis, C., Mckinley, R.S., 1999. Movement and summer habitat of brown trout (*Salmo trutta*) below a pulsed discharge hydroelectric generating station. Regul. Rivers Res. Manag. 15, 395–403. https://doi.org/10.1002/(SICI)1099-1646(199909/10)15:5<395::AID-RRR556>3.0.CO;2-1.

Capell, R., Brendel, C., 2023. HYPEtools: Tools for Processing and Analyzing Files from the Hydrological Catchment Model HYPE. CRAN. https://CRAN.R-project.org/package=HYPEtools.

Cunjak, R.A., Prowse, T.D., Parrish, D.L., 1998. Atlantic salmon (Salmo salar) in winter: "the season of parr discontent". Can. J. Fish. Aquat. Sci. 55 (Suppl. 1), 161–180. https://doi.org/10.1139/d98-008.

Degerman, E., 2001. Havsöringens ekologi. Fiskeriverket informerar 2001:10. Gothenburg: Swed. Board Fish. 1–122. ISSN 1404-8590.

Degerman, E., Sers, B., 1992. Fish assemblages in Swedish streams. Nord. J. Freshw. Res. 67, 61–71.

Degerman, E., Niskakoski, K., Sers, B., 1997. Betydelsen av minimivattenföring sommartid för lax (Salmo salar) och öring (Salmo trutta) på västkusten. (English summary: the effects of summer drought on salmonid populations in streams on the Swedish west coast). Information från Sötvattenslaboratoriet. Drottningholm 1, 41–54.

Di Baldassarre, G., Montanari, A., 2009. Uncertainty in river discharge observations: a quantitative analysis. Hydrol. Earth Syst. Sci. 13, 913–921. https://doi.org/10.5194/hess-13-913-2009.

Donadi, S., Degerman, E., McKie, B.G., Jones, D., Holmgren, K., Sandin, L., 2021. Interactive effects of land use, river regulation, and climate on a key recreational fishing species in temperate and boreal streams. Freshw. Biol. 66, 1901–1914. https://doi.org/10.1111/fwb.13799.

Donadi, S., Näslund, J., Sandin, L., Sers, B., Vasemägi, A., Degerman, E., 2023. 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. Ecography 5, e06522. https://doi.org/10.1111/ecog.06522.

Elenius, M., Lindström, G., 2022. Introduced flow variability and its propagation downstream of hydropower stations in Sweden. Nord. Hydrol 53 (11), 1321. https://doi.org/10.2166/nh.2022.138.

Elliott, J.M., 2000. Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress. J. Fish. Biol. 56, 938–948. https://doi.org/10.1111/j.1095-8649.2000.tb00883.x.

Elliott, J.M., Hurley, M.A., Elliott, J.A., 1997. Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. J. Appl. Ecol. 34, 1229–1238. https://doi.org/10.2307/2405234.

Elliott, J., Elliott, J.A., 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. J. Fish. Biol. 77, 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x.

European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. Official Journal of the European Communities 43:L 327/1,22 December 2000. http://data.europa.eu/eli/dir/2000/60/oj.

Freeman, M.C., Bestgen, K.R., Carlisle, D., Frimpong, E.A., Franssen, N.R., Gido, K.B., Irwin, E., Kanno, Y., Luce, C., Kyle McKay, S., Mims, M.C., Olden, J.D., LeRoy Poff, N., Propst, D.L., Rack, L., Roy, A.H., Stowe, E.S., Walters, A., Wenger, S.J., 2022. Toward improved understanding of streamflow effects on freshwater fishes. Fisheries 47, 290–298. https://doi.org/10.1002/fsh.10731.

Göthe, E., Degerman, E., Sandin, L., Segersten, J., Tamario, C., McKie, B.G., 2019. Flow restoration and the impacts of multiple stressors on fish communities in regulated rivers. J. Appl. Ecol. 56, 1687–1702. https://doi.org/10.1111/1365-2664.13413.

Gottschalk, L., Jensen, J.L., Lundquist, D., Solantie, R., Tollan, A., 1979. Hydrologic regions in the Nordic countries. Nord. Hydrol 10, 273–286. https://doi.org/10.2166/nh.1979.0010.

Greenberg, L., Svendsen, P., Harby, A., 1996. Availability of microhabitats and their use by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in the River Vojmån, Sweden. Regul. Rivers Res. Manag. 12, 287–303. https://doi.org/10.1002/(SICI)1099-1646(199603)12:2/3<287::AID-RRR396>3.0.CO;2-3.

Halleraker, J., Saltveit, S., Harby, A., Arnekleiv, J., Fjeldstad, H.P., Kohler, B., 2003. Factors influencing stranding of wild juvenile brown trout (*Salmo trutta*) during rapid and frequent flow decreases in an artificial stream. River Res. Appl. 19, 589–603. https://doi.org/10.1002/rra.752.

Hayes, J.W., Jowett, I.G., 1994. Microhabitat models of large drift-feeding brown trout in three New Zealand rivers. N. Am. J. Fish. Manag. 14, 710–725. https://doi.org/10.1577/1548-8675(1994)014<0710:MMOLDF>2.3.CO;2.

Huusko, A., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., Koljonen, S., Louhi, P., Alfredsen, K., 2007. Life in the ice lane: the winter ecology of stream salmonids. River Res. Appl. 23 (5), 469–491. https://doi.org/10.1002/rra.999.

Jonsson, B., Jonsson, N., 2011. Ecology of Atlantic salmon and brown trout. Habitat as a Template for Life Histories. Springer, Dordrecht.

Kennedy, G.J.A., Strange, C.D., 1981. Efficiency of electric fishing for salmonids in relation to river width. Fish. Manag. 12, 55–60. https://doi.org/10.1111/j.1365-2109.1981.tb00010.x.

Kovach, R.P., Muhlfeld, C.C., Al-Chokhachy, R., Dunham, J.B., Letcher, B.H., Kershner, J. L., 2016. Impacts of climatic variation on trout: a global synthesis and path forward. Rev. Fish Biol. Fish. 26, 135–151. https://doi.org/10.1007/s11160-015-9414-x.

Landergren, P., 2004. Factors affecting early migration of sea trout *Salmo trutta* parr to brackish water. Fish. Res. 67, 283–294. https://doi.org/10.1016/j.fishres.2003.10.005.

Lindström, G., Bartosova, A., Hjerdt, N., Strömqvist, J., 2017. Uppehållstider i ytvatten i relation till vattenkvalitet. NET, ett generellt uppskalningsverktyg (Retention times in surface water in relation to water quality. NET, a generic upscaling tool). Hydrologi, Nr 119. Norrköping: Swed. Meteorol. Hydrol. 1–28. Inst.ISSN 0283-7722. https://urn.kb.se/resolve?urn=urn:nbn:se:smhi:diva-4515.

Lindström, G., Pers, C., Rosberg, J., Strömqvist, J., Arheimer, B., 2010. Development and testing of the HYPE (Hydrological Predictions for the Environment) water quality model for different spatial scales. Nord. Hydrol 41, 295–319. https://doi.org/10.2166/nh.2010.007.

Maechler, M., Rousseeuw, P., Croux, C., Todorov, V., Ruckstuhl, A., Salibian-Barrera, M., Verbeke, T., Koller, M., Conceicao, E.L., Anna di Palma, M., 2023. Robustbase: Basic Robust Statistics. CRAN. https://CRAN.R-project.org/package=robustbase.

Mäki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P., Kreivi, P., 1997. Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. Can. J. Fish. Aquat. Sci. 54, 520–530. https://doi.org/10.1139/f96-31.

Näslund, J., Bowes, R.E., Sandin, L., Bergman, E., Greenberg, L., 2023a. Fish biodiversity in different types of tributary mouths located within impounded sections of Swedish boreal rivers. Ecohydrol. Hydrobiol. 23, 48–65. https://doi.org/10.1016/j.ecohyd.2022.11.004.

Näslund, J., Andersson, M., Bergek, S., Degerman, E., Donadi, S., Duberg, J., Holmgren, K., Kinnerbäck, A., Sers, B., Staveley, T., Strömberg, H., Myrstener, E., 2023b. Considerations needed for analysing data from the Swedish Electrofishing RegiSter (SERS), with special reference to the RivFishTIME database of long-term riverine fish surveys. Fauna Nor. 42, 47–51. https://doi.org/10.5324/fn.v42i0.5647.

Nielsen, J., 1997. Ørreden som miljøindikator. Miljønyt 24. Danish Ministry of Environment, Copenhagen.

Nordwall, F., 1999. Movements of brown trout in a small stream: effects of electrofishing and consequences for population estimates. N. Am. J. Fish. Manag. 19, 462–469. https://doi.org/10.1577/1548-8675(1999)019<0462:MOBTIA>2.0.CO;2.

Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. The R Journal 10, 439–446. https://doi.org/10.32614/RJ-2018-009.

Poff, N.L., Zimmerman, J.K.H., 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshw. Biol. 55, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x.

Sabater, S., Bregoli, F., Acuña, V., Barceló, D., Elosegi, A., Ginebreda, A., Marcé, R., Muñoz, I., Sabater-Liesa, L., Ferreira, V., 2018. Effects of human-driven water stress on river ecosystems: a meta-analysis. Sci. Rep. 8, 11462 https://doi.org/10.1038/s41598-018-29807-7.

SERS (Swedish Electrofishing Register), 2021. Swedish electrofishing RegiSter – SERS, version 20210602. Drottningholm: Swed. Univ. Agric. Sci., Dep. Aquat. Resour. https://www.slu.se/electrofishingdatabase.

Shirvell, C.S., Dungey, R.G., 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Trans. Am. Fish. Soc. 112, 355–367. https://doi.org/10.1577/1548-8659(1983)112<355:MCBBTF>2.0.CO;2.

Skoglund, H., Vollset, K.W., Wiers, T., Barlaup, B.T., 2023. Assessing the occurrence of egg stranding for trout and salmon in a regulated river. River Res. Appl. 39, 768–776. https://doi.org/10.1002/rra.4099.

SMHI, 2013. Dam register online visualization. last updated in 2013. http://vattenwebb.smhi.se/svarwebb/.

Smialek, N., Pander, J., Mueller, M., van Treeck, R., Wolter, C., Geist, J., 2019. Do we know enough to save European riverine fish? - a systematic review on autecological requirements during critical life stages of 10 rheophilic species at risk. Sustainability 11, 5011. https://doi.org/10.3390/su11185011.

Smialek, N., Pander, J., Geist, J., 2021. Environmental threats and conservation implications for Atlantic salmon and brown trout during their critical freshwater phases of spawning, egg development and juvenile emergence. Fish. Manag. Ecol. 28, 437–467. https://doi.org/10.1111/fme.12507.

SR (Swedish Radio), 2023. Låga vattennivåer i länet hotar lax och öring [Low water levels in the county threaten salmon and trout]. Swedish Radio P4 Halland 2023–06–14. https://sverigesradio.se/artikel/laga-vattennivaer-i-lanet-hotar-lax-och-oring.

Stradmeyer, L., Höjesjö, J., Griffiths, S.W., Gilvear, D.J., Armstrong, J.D., 2008. Competition between brown trout and Atlantic salmon parr over pool refuges during rapid dewatering. J. Fish. Biol. 72, 848–860. https://doi.org/10.1111/j.1095-8649.2007.01767.x.

Strömqvist, J., Dahné, J., Donnely, C., Lindström, G., Rosberg, J., Pers, C., Yang, W., Arheimer, B., 2009. Using Recently Developed Global Data Sets for Hydrological Predictions, vol. 333. IAHS Publ, pp. 121–127. https://iahs.info/uploads/dms/14823.19-121-127-333-15-4177-Stromqvist_corr.pdf.

Strömqvist, J., Arheimer, B., Dahné, J., Donnelly, C., Lindström, G., 2012. Water and nutrient predictions in ungauged basins: set-up and evaluation of a model at the national scale. Hydrol. Sci. J. 57, 229–247. https://doi.org/10.1080/02626667.2011.637497.

SwAM (Swedish Agency for Marine and Water Management), 2019. Havs- och vattenmyndighetens föreskrifter om klassificering och miljökvalitetsnormer avseende ytvatten. 1-88. Havs- och vattenmyndighetens författningssamling HVMFS 2019:25. Gothenburg: Swed. Agency Mar. Water Manag. https://www.havochvatten.se/vagledning-foreskrifter-och-lagar/foreskrifter/register-vattenforvaltning/klassificering-och-miljokvalitetsnormer-avseende-ytvatten-hvmfs-201925.html.

SwAM (Swedish Agency for Marine and Water Management), 2023. Vattenbrist och torka - så påverkar det vattenmiljön [Water shortage and drought - how it affects the water environment]. SwAM web portal [accessed: 2023-08-11]. https://www.havochvatten.se/miljopaverkan-och-atgarder/miljopaverkan/vattenbrist/vattenbrist-och-torka—sa-paverkar-det-vattenmiljon.html.

Teutschbein, C., Elise Jonsson, E., Todorović, A., Tootoonchi, F., Stenfors, E., Grabs, T., 2023. Future drought propagation through the water-energy-food-ecosystem nexus – a Nordic perspective. J. Hydrol. 617 (A), 128963 https://doi.org/10.1016/j.jhydrol.2022.128963.

Tallaksen, L., van Lanen, H.A.J., 2004. Hydrological Drought. Processes and Estimation Methods for Streamflow and Groundwater. Elsevier, Amsterdam.

Therneau, T.M., Atkinson, E.J., 1997. An Introduction to Recursive Partitioning Using the RPART Routines, vol. 61. Mayo Foundation. Technical report.

Therneau, T.M., Atkinson, E.J., 2022. Rpart: Recursive Partitioning and Regression Trees. CRAN. https://CRAN.R-project.org/package=rpart.

Titus, R.G., Mosegaard, H., 1989. Smolting at age 1 and its adaptive significance for migratory trout, *Salmo trutta* L., in a small Baltic-coast stream. J. Fish. Biol. 35 (Suppl. A), 351–353. https://doi.org/10.1111/j.1095-8649.1989.tb03084.x.

Titus, R.G., Mosegaard, H., 1992. Fluctuating recruitment and variable life-history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. J. Fish. Biol. 41, 239–255. https://doi.org/10.1111/j.1095-8649.1992.tb02654.x.

TT, 2013. Fisk hotas av lågt vattenstånd [Fish threatened by low water level]. Svenska Dagbladet, online edition, 2013-04-05 [accessed 2023-08-11]. https://www.svd.se/a/f0493111-ef37-3759-ae86-b84d76bbbe3f/fisk-hotas-av-lagt-vattenstand.

TT, 2018. Fiskar hotade av lågt vatten i åarna [Fishes threatened by low water levels in the rivers]. online edition, 2018-07-06 [accessed 2023-08-11] Sven. Dagbl. https://www.svd.se/a/9md1dd/fiskar-hotade-av-lagt-vatten-i-aarna.

van Oorschot, M., Kleinhans, M., Buijse, T., Geerling, G., Middelkoop, H., 2018. Combined effects of climate change and dam construction on riverine ecosystems. Ecol. Eng. 120, 329–344. https://doi.org/10.1016/j.ecoleng.2018.05.037.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Reidy Liermann, C., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561. https://doi.org/10.1038/nature09440.

Warren, M., Dunbar, M.J., Smith, C., 2015. River flow as a determinant of salmonid distribution and abundance: a review. Environ. Biol. Fish. 98, 1695–1717. https://doi.org/10.1007/s10641-015-0376-6.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4, 1686. https://doi.org/10.21105/joss.01686.

Zeileis, A., Grothendieck, G., 2005. zoo: S3 infrastructure for regular and irregular time series. J. Stat. Software 14, 1–27. https://doi.org/10.18637/jss.v014.i06.