



Reproductive success of stream fish species in relation to high and low flow patterns: The role of life history strategies and species traits

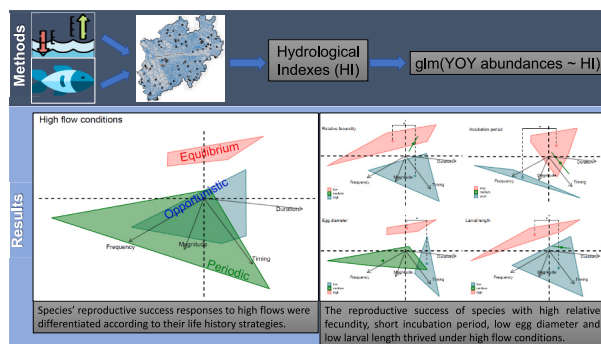
Lucas Mignien^{*}, Stefan Stoll

University of Applied Sciences Trier, Environmental Campus Birkenfeld, Campusallee, 55768 Hoppstädten-Weiersbach, Germany
University of Duisburg-Essen, Faculty of Biology, Universitätsstraße 5, 45141 Essen, Germany

HIGHLIGHTS

- Hydrological variability explained on average 64% of the variance in species' reproductive success responses.
- Species' reproductive success responses to high flow were differentiated according to their life history strategies.
- Four reproductive traits mediated these differences between life history strategies in response to high flow.
- Using life history strategies and ecological traits related to flow regime components can improve conservation approaches.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:
Ecohydraulics
Discharge regime
Young-of-the-year
Recruitment
Year class strength

ABSTRACT

Hydrological variability is a key factor in structuring biotic and abiotic processes in river ecosystems and is of particular importance to fish populations. We used 171 hydrological indices (HI) and young-of-the-year (YOY) fish abundances as indicators of reproductive success to compare species' response patterns to high and low flows on short-, intermediate-, and long-term scales. Our study included 13 common fish species in headwater streams of North Rhine-Westphalia, Germany. Generalized linear models using YOY abundances and HI on high- and low-flow patterns explained on average 64 % of the variability. HI calculated from long time series worked better than HI describing short- and intermediate-term high- and low flows. Species' reproductive success response to low flow HI depended on specific ecological traits whereas high flow HI differentially affected species according to their life history strategies. Equilibrium strategists responded negatively to high frequency and magnitude along with late timing of high flow, while periodic and opportunistic species mostly thrived under these conditions. We identified four species traits that mediated these differences between life history strategies. The reproductive success of species with low relative fecundity, large eggs and larvae, and long incubation periods was negatively impacted by the high frequency, high magnitude, and late timing of high flows. Conversely, the reproductive success of species with high relative fecundity, short incubation periods and small eggs and larvae was fostered by strong, frequent, and late high flows. The consideration of the relationship between reproductive success, life history, and fish species traits over several years under a range of flows is a novel step towards the

^{*} Corresponding author at: University of Applied Sciences Trier, Environmental Campus Birkenfeld, Campusallee, 55768 Hoppstädten-Weiersbach, Germany.
E-mail address: L.Mignien@umwelt-campus.de (L. Mignien).

<https://doi.org/10.1016/j.scitotenv.2024.174366>

Received 26 February 2024; Received in revised form 2 June 2024; Accepted 27 June 2024

Available online 2 July 2024

0048-9697/© 2024 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

implementation of measures to mitigate negative impacts and enhance conditions for successful fish reproduction.

1. Introduction

Hydrological variability plays a critical role in shaping riverine ecosystems and exerts a profound influence on the dynamics and biodiversity of aquatic communities, particularly on fish species (Poff et al., 1997). Changes in flow patterns shape diverse microhabitats and influence resource availability, thus affecting spawning, migration, recruitment, and food availability, ultimately defining the composition and distribution of fish communities (Tonkin et al., 2017).

Fish species exhibit life history strategies that are co-evolved reproductive traits that allow them to cope with varying hydrological conditions across river systems (Rose and Mueller, 1993). The eco-evolutionary success of the bearers of traits such as spawning behaviour, larval and juvenile survival, and maturation is driven by the interplay of environmental factors, including flow patterns, temperature fluctuations, and resource availability (Humphries et al., 1999; Lytle and Poff, 2004). Because the success of spawning and survival in the early stages greatly determines the strength of subsequent cohorts of fish, a better understanding of how flow drives the early life of fish is crucial for managing populations in rivers with altered flow (Balcombe et al., 2006; Chambers and Trippel, 1997; King et al., 2003). Alterations in the flow regime can result either from direct human intervention or hydrological changes due to climate change.

In a variety of biogeographic regions, trait-based analyses have shown that stream-fish assemblages converge along hydrological gradients. Therefore, ecological insights can be readily transferred and applied to understand how fish populations react to flow variability (Blanck and Lamouroux, 2006; Logez et al., 2010; Olden and Kennard, 2010). The impact of altered flow patterns on fish communities and the adaptive capacity of certain traits to mitigate these effects have been further emphasized by Freeman et al. (2022), reinforcing the value of trait-based analyses in guiding conservation and management strategies when dealing with flow variability.

To further understand the intricate relationships between species traits and environmental conditions, Winemiller and Rose (1992) developed a triangular life history model, elaborating on Pianka's r- and K-selection continuum (Pianka, 1970). It seeks to explain how traits such as longevity, age at maturity, fecundity, and offspring size interact with environmental templates, such as flow regimes, to ensure the best reproductive success. Within this trichotomy, opportunistic strategists (O) are species with high fecundity, small eggs, and low juvenile survival due to limited parental care. They mature early, have a small body size, and are typically associated with habitats characterized by frequent and extreme disturbances. Periodic strategists (P) are characterized by high fecundity, medium-sized eggs, and low juvenile survival owing to the absence of parental care. They mature late, reach a large body size, and are typically favoured by regularly occurring hydrological fluctuations. The larvae of opportunistic and periodic species typically have low amounts of yolk (consumed within hours to days), are small, undeveloped, and tend to swim poorly when first feeding exogenously (Wolter and Sukhodolov, 2008). Equilibrium strategists (E) have low fecundity, large eggs, small clutch sizes and high juvenile survivorship because of high parental care. They have intermediate to late periods to maturity, small to medium body size, and are expected to thrive in more stable environments with less flow variability (Mims and Olden, 2012). The larvae of the equilibrium species typically have substantial amounts of yolk, which they consume over several days. They are large, well-developed, and swim well when fed exogenously (Humphries et al., 2020).

The impact of hydrological variability in the context of reproduction under different flow conditions has been investigated in a variety of

studies. For example, high flows have been shown to initiate bed-material turnover, flush fine sediments from gravel, which refines spawning grounds, promotes juvenile recruitment, improves oxygenation for incubated eggs, and creates interstices for emergence (Zeh and Dönni, 1994). However, high flows can pose risks to young-of-the-year fish because of their low swimming ability, resulting in displacement-related mortality, soft tissue damage from suspended particles, and destruction of incubating eggs by streambed scouring (Montgomery et al., 1996). On the other hand, during low flows, young-of-the-year fish face increased mortality due to habitat reduction, higher intraspecific competition, predation (Hakala and Hartman, 2004; Penha et al., 2015), as well as physiological constraints such as temperature increases and oxygen concentration deficits (White et al., 2016; Winne et al., 2010). Nonetheless, the low-flow recruitment hypothesis suggests that periods of low flow, characterized by high water temperatures and prey densities, can benefit small-bodied fish that produce multiple clutches (Humphries et al., 1999).

Most studies have examined individual correlations between fish traits and flow events (Freeman et al., 2022). However, traits are combined in non-random ways, and hydrological patterns are complex and consist of sequences of longer and shorter, stronger, and weaker high and low flow sequences (Poff and Ward, 1989). Decomposing the flow regime into different components such as magnitude, duration, and frequency thus provides a nuanced understanding of hydrological variability and its ecological implications for fish reproduction (Tonkin et al., 2011). Identifying the impact of high-flow and low-flow components can improve the implementation measures to enhance conditions for fish reproduction (Chambers and Trippel, 1997). That being said, the relative importance of different ecological effects of hydrological variability on the reproductive success of fish assemblages remains poorly understood, making such studies desperately needed (Humphries et al., 2020).

Indeed, studies focusing on the reproductive success of freshwater fish species under various flow conditions remain mainly conceptual as illustrated by the Riverscape Recruitment Synthesis Model (RRSM) (Humphries et al., 2020). This model integrates factors such as temperature, physical complexity, movement, predation, and species traits to understand the drivers of fish reproductive success in rivers. Under low-flow conditions, due to higher concentrations of nutrients leading to increased food availability for fish larvae, moderate recruitment strength for equilibrium and opportunistic species is expected. On the other hand, under high-flow conditions, recruitment strength for equilibrium species may be lower due to the greater risk of predation and high current speeds in the main channel. Opportunistic species are also predicted to have relatively high recruitment strength due to the dispersal of larvae among floodplains. Even though the RRSM provides a conceptual basis for generating relevant predictions for fish reproductive success, such hypotheses yet remain to be tested with in-field observations.

In this study, we assessed the reproductive success of common central European freshwater fish species to high and low flow components across different time scales and related these patterns to their life history strategies and individual ecological traits. To investigate this, we first characterized the hydrological variability in the streams using Hydrological Indexes (HI). We assessed hydrological conditions according to three time windows before the respective fishing date, differentiating the response of fish to short-term (1 year), intermediate-term (5 years), and long-term (10 years) hydrological variations, and analysed the species' reproductive success responses to the flow components of duration, magnitude, frequency, rate of change and timing. Then, according to our analyses, we grouped species' reproductive success

responses to high and low flow, which act on aquatic species as “ecological bottlenecks” (Poff et al., 1997), and we discussed the response patterns in the context of ecological species traits and life history strategies.

Based on the predictions of the life history theory (Mims and Olden, 2012), we first hypothesize the reproductive success of opportunistic species to depend more on short-term flow variability whereas the reproductive success of equilibrium strategists would show the lowest response to flow variability on short time scales. Conversely, equilibrium strategists, which are adapted to more stable environments, will exhibit the highest sensitivity to the magnitude and frequency of flow events, over both short and long-term scales. For periodic strategists, we hypothesize that their reproductive success will be predominantly driven by the duration and predictability of flow, particularly over medium to long-term periods. Then, based on the hypothesis formulated by Humphries et al. (2020), we hypothesize the reproductive success of opportunistic and periodic species to be favoured under high flow conditions due to their ability to thrive outside the main river channels, reducing their susceptibility to disturbances. In contrast, equilibrium species, which tend to breed and inhabit the main channels, will experience lower reproductive success due to increased washout. However, under low flow conditions, we hypothesize more complex reproductive success patterns, less related to life history strategies because of the influence of density-dependent competition, predation, and water quality, that are more likely to drive reproductive success than sheer hydrological variability (Humphries et al., 2020). Specifically, we expect reduced reproductive success in salmonid species towards frequent and early low flows, heightening vulnerability during their critical life stages. Conversely, smaller-bodied species are expected to thrive in low-flow conditions by utilizing refuges while highly fecund species will benefit from late and frequent low flows. Finally, species with short larval stages are expected to thrive under prolonged low flows by minimizing predation and starvation risks.

Our study used an integrative approach combining multiple fish species, their ecological traits and life history strategies towards the different components of the flow regime over an extensive timeframe. Based on in-field data, we aim to shed light on the relative importance of hydrological variability on fish reproductive success in Central

European headwater streams. By discerning the risks and benefits associated with high- and low-flow components, targeted measures can be implemented to mitigate negative impacts and enhance conditions for successful fish reproduction.

2. Material and methods

2.1. Study area and fish data

The study was performed on rivers in the German federal state of North Rhine-Westphalia, in the Western part of Germany (Fig. 1). North Rhine-Westphalia is part of three ecoregions: The Northern German lowlands (Ecoregion 14 ‘Central lowlands’) and the lower mountainous areas (Ecoregions 8 and 9 ‘Western sub-alpine mountains’ and ‘Central sub-alpine mountains’, Illies and Greiner, 1978). North Rhine-Westphalia serves as an exemplary region for central European river systems due to its characteristic small to medium-sized streams, moderate population densities, and a representative mix of agricultural, forested, and urban land uses (Kufeld et al., 2010). These features mirror the typical conditions found in low-mountain central European streams (Wolf et al., 2021), allowing for the transferability of our results to large parts of Central Europe. Furthermore, North Rhineland Westphalia has a long history of environmental monitoring and research, supported by robust institutional frameworks and comprehensive data collection efforts (Ehlert et al., 2002) which makes it an ideal study area for investigating hydrological variability and its impacts.

To limit the ecological heterogeneity in the dataset, this study focused on headwater streams with a width of up to approx. 10 m, i.e., the upper and lower parts of the trout zone stream type located in low mountainous areas and the loach-stickleback zone in the lowland areas of North Rhine-Westphalia. Headwater streams are crucial components of river networks due to their small size, diverse habitats, and sensitivity to environmental changes (Richardson, 2020). They serve as early indicators of ecosystem health, as alterations can quickly impact fish populations and their reproductive success (Lowe and Likens, 2005). Furthermore, because headwater streams are interconnected with downstream reaches, understanding their ecological dynamics is essential for effectively managing and conserving entire river networks

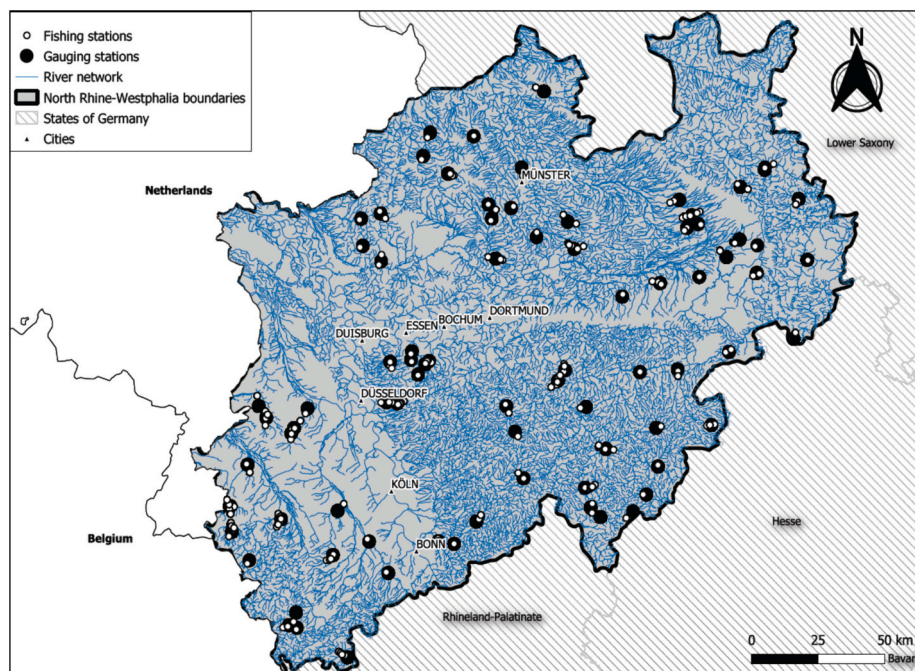


Fig. 1. Map of the locations of the selected fishing and gauging stations in North Rhineland Westphalia, Germany.

(Freeman et al., 2007).

Access to an extensive dataset spanning several decades was essential to undertake long-term assessments of fish reproductive success. We were thus granted access to the electrofishing database at the state's Environmental Agency LANUV, containing datasets of full fish community samples of stream reaches from 1982 to 2019. Electrofishing was done according to Diekmann et al. (2005), which is the German, EU Water Framework Directive-compliant standard method for electrofishing, to ensure the comparability of fish community data. In wadeable streams, a reach length of approximately 40× the stream width was sampled. In non-wadeable streams, reaches of approximately 100× the stream width were sampled by boat. The sections were never shorter than 100 m and contained all habitat types that were available in a reach in representative proportions. Electrofishing was executed as single passes with generator-powered DC electric fishing gear along the riverbanks to a water depth of 1.5 m and against the current. To avoid the confounding effects of seasonality, fishing was conducted in late summer or early autumn. At this time of the year, the migration activity of fish in Central Europe is low, and the young of the year are large enough to be identified at the species level. The fishing was conducted under stable low-flow conditions, and extreme flow or other adverse conditions were avoided. All the stunned fish were placed in flow-through containers until the end of fishing, counted, measured, and released. Based on the local length-frequency distribution in each species, electrofishermen classified individuals as young-of-the-year (YOY) or older. Only YOY were considered for this study and YOY fish abundances were standardized for each species according to the length of the fished stream reach.

A total of 35 species were fished. Only species with a minimum of 15 replicate samples and >170 individuals were considered to guarantee the good performance of the models. Thirteen species fulfilled these criteria (Appendix A, Table A.1).

2.2. Life history strategies and ecological species traits

Life history strategies of the fish species (Table 1) were assigned using 22 categories of seven biological trait classes, which are instructive for the opportunistic-periodic-equilibrium trichotomy of life-history strategies (Winemiller, 1989; Winemiller and Rose, 1992; Appendix A, Table A.2). A similar approach was used by Olden and Kennard (2010) and Manfrin et al. (2019). Additionally, 13 other ecological traits were used to investigate detailed specific responses to flow variability

Table 1

Life history strategies and ecological traits of the selected YOY fish species. Life history strategies were assigned by Manfrin et al. (2019) based on trait information from "the freshwater.info" database (Schmidt-Kloiber and Hering, 2015).

Species	Life history strategy	Maximum life span (years)	Maximum body length (cm)	Female maturity (years)	Spawning time	Fecundity (no. oocytes)	Egg diameter (mm)	Parental care
Atlantic salmon	E	8–15	>39	2–3	1 per year	55,000-60,000	>2	No protection with nest or hiding eggs
Brook lamprey	P	<8	<20	>5	1 per year	< 55,000	<1.35	No parental care
Brown trout	E	8–15	>39	4–5	1 per year	< 55,000	>2	No protection with nest or hiding eggs
Bullhead	E	<8	<20	3–4	1 per year	< 55,000	>2	Protection with nest or hiding eggs
Common dace	P	8–15	<20	2–3	1 per year	55,000-60,000	1.35–2	No parental care
European chub	P	8–15	20–39	3–4	> 1 per year	55,000-60,000	1.35–2	No parental care
European grayling	E	8–15	20–39	2–3	1 per year	55,000-60,000	>2	Protection with nest or hiding eggs
European perch	P	>15	20–39	4–5	1 per year	> 60,000	1.35–2	No parental care
Gudgeon	O	<8 years	<20	<2	> 1 per year	< 55,000	<1.35	No parental care
Minnnow	O	<8	<20	2–3	> 1 per year	< 55,000	1.35–2	No parental care
Ninespine stickleback	O	<8	<20	<2	1 per year	< 55,000	<1.35	Protection with nest or hiding eggs
Stone loach	O	<8	<20	<2	1 per year	55,000-60,000	<1.35	No parental care
Three-spined stickleback	O	<8	<20	<2	> 1 per year	< 55,000	1.35–2	Protection with nest or hiding eggs

(Appendix A, Table A.3). Information on ecological species traits was retrieved from the database "freshwater ecology.info" (Schmidt-Kloiber and Hering, 2015), and missing data were supplemented from Manfrin et al. (2019). Each category was related to a single or a mix of opportunistic, periodic, and equilibrium life strategies (Olden and Kennard, 2010; Winemiller, 1989; Winemiller and Rose, 1992) (Appendix A, Table A.2).

2.3. Flow data and calculation of hydrological indices (HI)

Discharge data were obtained from 167 gauging stations operated by seven different water agencies in North Rhineland Westphalia. All datasets spanned from 2000 to 2019. The mean daily discharge was calculated based on hourly data for each station. Gaps were filled using linear interpolation and data records with >5 % missing values were excluded from the analysis. To match the fished reaches and the gauging stations, a buffer zone of four kilometers was drawn around each gauging station. Fish sampling sites inside the buffer zone were matched to their corresponding gauging stations if they were part of the same stream and did not have a major tributary between them. This consolidated dataset for analyses comprised data from 82 gauging stations, and 567 electrofishing events distributed over 207 fishing locations spanning from 2001 to 2019.

The 171 HI based on the daily mean discharge records were calculated for all gauging stations using the EflowStats package (Mills and Blodgett, 2017). According to Poff et al. (1997) and Richter et al. (1996), these 171 HI fall into five categories. These included the magnitude ($n = 94$), frequency ($n = 14$), duration ($n = 44$), timing ($n = 10$) and rate of change ($n = 9$) of flow. HI on flow magnitude were subsequently divided into groups that inform about average, low and high flow ($n = 45, 22, 27$ respectively), frequency into low and high flow ($n = 3, 11$ respectively), duration into low and high flow ($n = 20, 24$ respectively), timing into average, low and high flow ($n = 3, 4, 3$ respectively) and rate of change into average flow only ($n = 9$). In total, nine subcategories of HI refer to the dimensions of the flow regime.

As we were interested in comparing the effects of short-, medium- and long-term hydrological variation on species' reproductive success, we calculated three separate sets of 171 HI for each fishing event based on the matching one-, five-, and ten-year series of hydrological data from the period preceding the fishing from the respective gauge station. Here, to reduce the number of explanatory variables, we used LASSO regression (Least Absolute Shrinkage and Selection Operator; Tibshirani,

1996). Models were calculated for each time frame, resulting in a total of three sets of 20 HI eligible for the next part of the analysis (Appendix A, Table A.5).

2.4. Hydrological models of fish species

As in Mignien and Stoll (2023), we opted for simple GLM models without random effects. We compared models with and without random factors, accounting for the spatial and temporal structure in the dataset for the 13 most common species with sufficient replicates. These analyses showed that 85 % of the individual HI and 88 % of the HI classes identified as significant in the GLMM models were also significant in the respective GLM models. Additionally, PCA of the effect sizes of the significant HI of the GLMM and GLM results showed very similar patterns for this subset of species. Therefore, to develop a uniform approach for all species, including rarer species and species of conservation concern for which the amount of data would not have been sufficient for more complex models, random spatial and temporal effects were not utilized in the final models.

Before the GLM analysis, YOY abundances were normalized according to an ordered quantile transformation (Peterson and Cavanaugh, 2020). This transformation was the most accurate based on the estimated normality statistics. Models were then run for the abundance of each species and followed a Gaussian-type family with an identity link function. Stepwise regression was implemented to determine the subset of variables in the dataset, resulting in the best-performing model. A comparison of the models fitted by the maximum likelihood was made using Akaike information (Akaike, 1974) using forward selection. The normality of the distribution of residuals was assessed using a QQ-plot. To assess if the share of explained variability of certain HI classes significantly differed within and across time periods or life history strategies, Kruskal-Wallis tests and GLMM were applied to the percentage of explained variance of indexes per HI class in each species' model, with the period or life history strategy as an independent factor.

2.5. Comparison of the species responses to high and low flow

We adapted the workflow developed by Mignien and Stoll (2023) to disentangle species' reproductive success in relation to the different components of the flow regimes (Fig. 2). A PCA was run on estimate values of the significant models previously calculated. Before the PCA, estimates were normalized and the number of principal component axes was selected according to the Kaiser-Guttman criterion (Yeomans and Golder, 1982). In the first step, reproductive success was related to the life history strategies of the species; subsequently, reproductive success was related to 20 individual ecological traits (including those used to assign species life history strategies). PCA was used to explore the relationships among reproductive success, species traits, and flow components. By transforming the original variables into a smaller set of

uncorrelated variables, PCA allowed us to visualize the main axes of variation and identify the most influential flow components driving variation in reproductive success according to high and low flow conditions.

Then, clusters of periodic, opportunistic, and equilibrium strategists or species with similar traits were used to identify ecological pattern responses to high- and low-flow conditions. Significant differences between the clusters were assessed using Analysis of similarities (ANOSIM). ANOSIM aims to evaluate the dissimilarity between two or more groups of samples based on a resemblance matrix. In our study, ANOSIM tested whether there were significant differences in species composition and ecological traits between clusters identified in the PCA analysis under different flow conditions. It therefore provided a robust statistical framework for detecting significant ecological responses to different flow components. Only significant results were reported in the PCA plots. All statistical analyses were performed in R (version 4.0.2) and all the geometrical processing was performed in QGIS (version 3.16.0).

3. Results

3.1. Model results

For the 13 Central European fish species, GLMs were fitted to explain species' reproductive success using sets of short- intermediate- and long-term HIs as predictors. All GLMs selected between one and ten HI (Appendix A, Table A.8), with R^2 of the models ranging between 0.26 and 0.99 (mean \pm SD: 0.66 ± 0.26 ; Fig. 3a). Only in one combination of a species and a time period, namely, the common dace (*Leuciscus leuciscus*) and intermediate-term HIs, the model did not pick up any HI. Species' reproductive success responded more to long-term than short-term HI (Fig. 3b), as the mean R^2 of the GLM increased with the length of the hydrological time series used to calculate the set of HI in all but two species, common dace and ninespine stickleback (*Pungitius pungitius*). The relative importance of the flow components differed between the GLMs with short- intermediate-, and long-term HIs. In the short-term, HIs relating to the magnitude of flow dominated, explaining $>50\%$ of the variability in the models (Fig. 3b). In the intermediate-term GLMs, HIs relating to the magnitude and duration of flow were the most important and explained 60 % of the variability. Finally, in the long-term GLMs, HIs relating to the duration of flow contributed the most to the models and timing HIs have the highest proportional change to other models (Fig. 3b).

Opportunistic and equilibrium strategists showed similar levels of response to hydrological patterns (with 57 % and 61 % of explained variance, respectively) whereas periodic strategists displayed a higher share of explained variability response to HI (79 %) (Fig. 3c). For opportunistic species models, the magnitude was the dominant flow component and explained approximately 30 % of the total variability, followed by the duration (23 %) and the rate of change (20 %) (Fig. 3c).

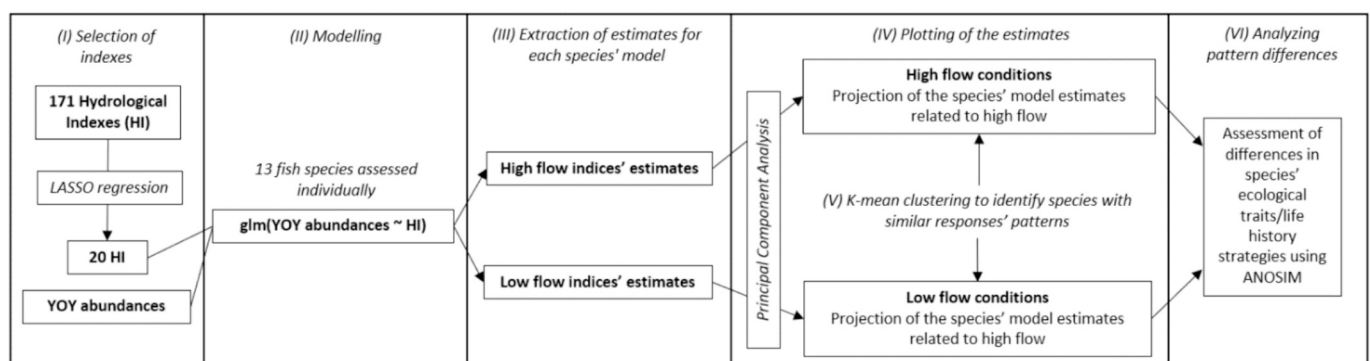


Fig. 2. Concept diagram of the workflow to assess fish species responses to low- and high-flow conditions. The workflow was developed by Mignien and Stoll (2023).

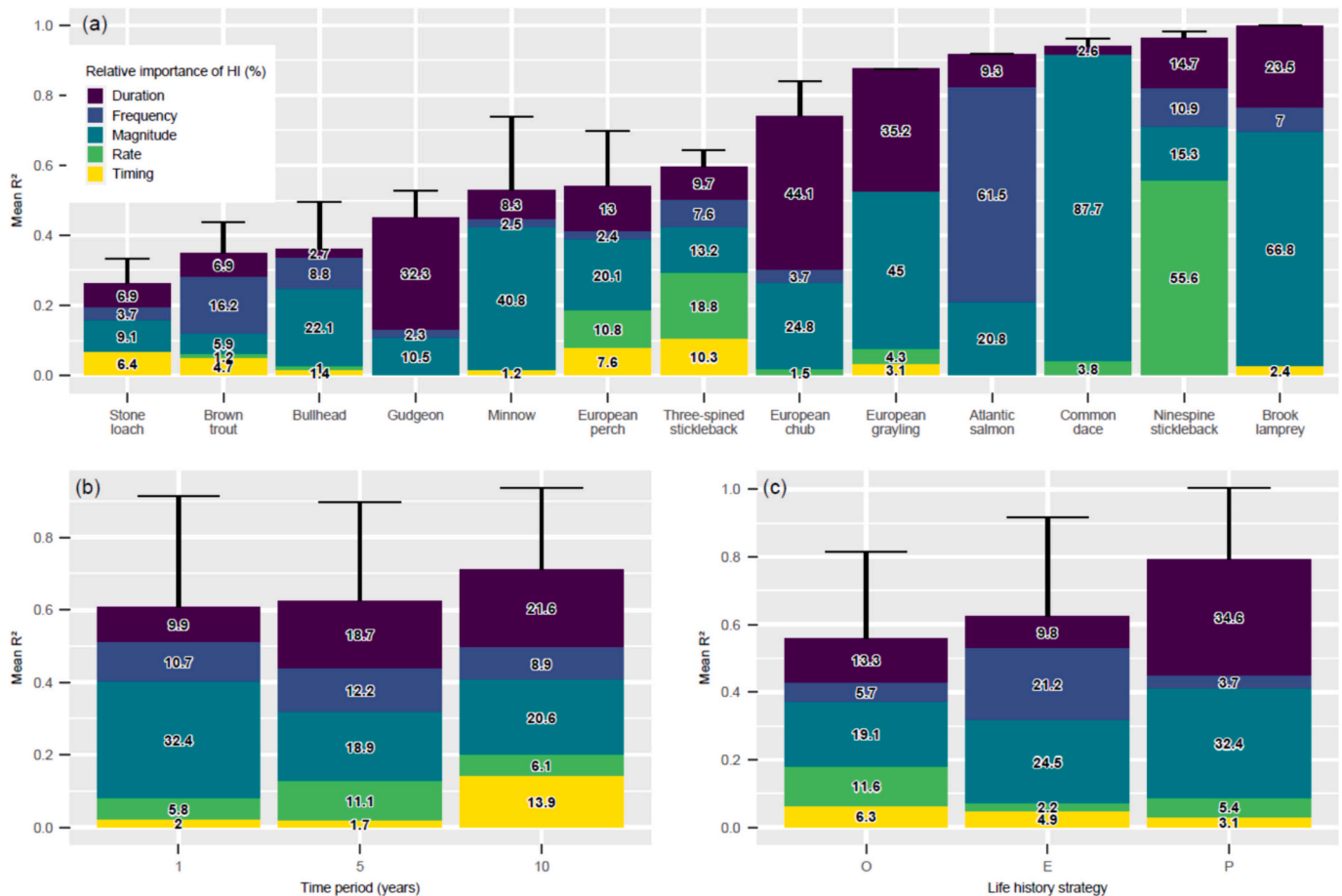


Fig. 3. (a) Mean explained variability for each species GLMs for the three time periods, error bars depict SD. (b) Mean explained variability of the GLM models explaining species abundances using short-term (1 year), intermediate-term (5 years) and long-term (10 years) hydrological data to calculate indices of hydrological alteration (HI), error bars depict SD. (c) Mean explained variability for groups of species with opportunistic (O), equilibrium (E) and periodic (P), life-history strategies in the three time periods. In (a), (b) and (c) the stacked bars represent the percentage of explained variability relating to the five components of the flow regime. Error bars depict SD.

Concerning the equilibrium species models, magnitude and frequency were the most dominant flow components and accounted for 75 % of the total variability (40 % and 35 %, respectively) (Fig. 3c). Regarding periodic species' models, the flow components duration, and magnitude were the most important and explained 43 % and 40 % of the total variance, respectively (Fig. 3 c).

Ten of the 13 species (all except common dace, ninespined stickleback and stone loach) and 12 of 13 species (all except common dace) showed significant reactions to low flow and high flow HIs, respectively. For high flow conditions, species' reproductive success was found to be negatively impacted (Kruskal-Wallis; $\chi^2 = 7.750$; $df = 2$; $p = 0.021$) on the long-term time scales 1–10 years (Dunn test; $z = -2.160$; $p = 0.031$) and 5–10 years (Dunn test; $z = -2.580$; $p = 0.010$) (Fig. 4a). Across all species, we observed a positive mean effect of low flows on species' reproductive success at the short-term time scale, whereas, at longer time scales, the positive and negative effects of low flow conditions cancelled each other out (Fig. 4b).

3.2. Species reproductive success responses to high and low flows

3.2.1. Comparison of species' reproductive success based on their life histories in relation to high flows

A share of 59.5 % of the variance in the reproductive success response of the species to high flow conditions was covered in the first two PCA axes (Fig. 5). Species grouping according to their life history traits resulted in the first cluster being composed of equilibrium species,

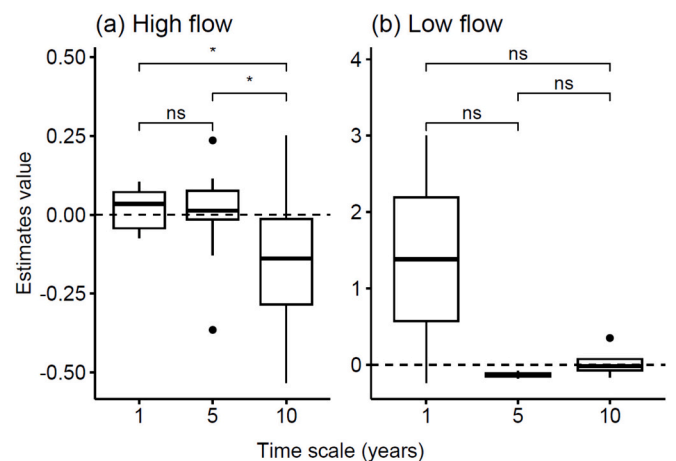


Fig. 4. Boxplot of the estimates extracted from significant generalized linear models between fish species and hydrological indicators over a three-time period scale for (a) high flow conditions and (b) low flow.

including European grayling (*Thymallus thymallus*), bullhead (*Cottus gobio*), Atlantic salmon (*Salmo salar*), and brown trout (*Salmo trutta*). The reproductive success of these species responded negatively to the high frequency, large magnitude, and late timing of high flows. The

High flow conditions

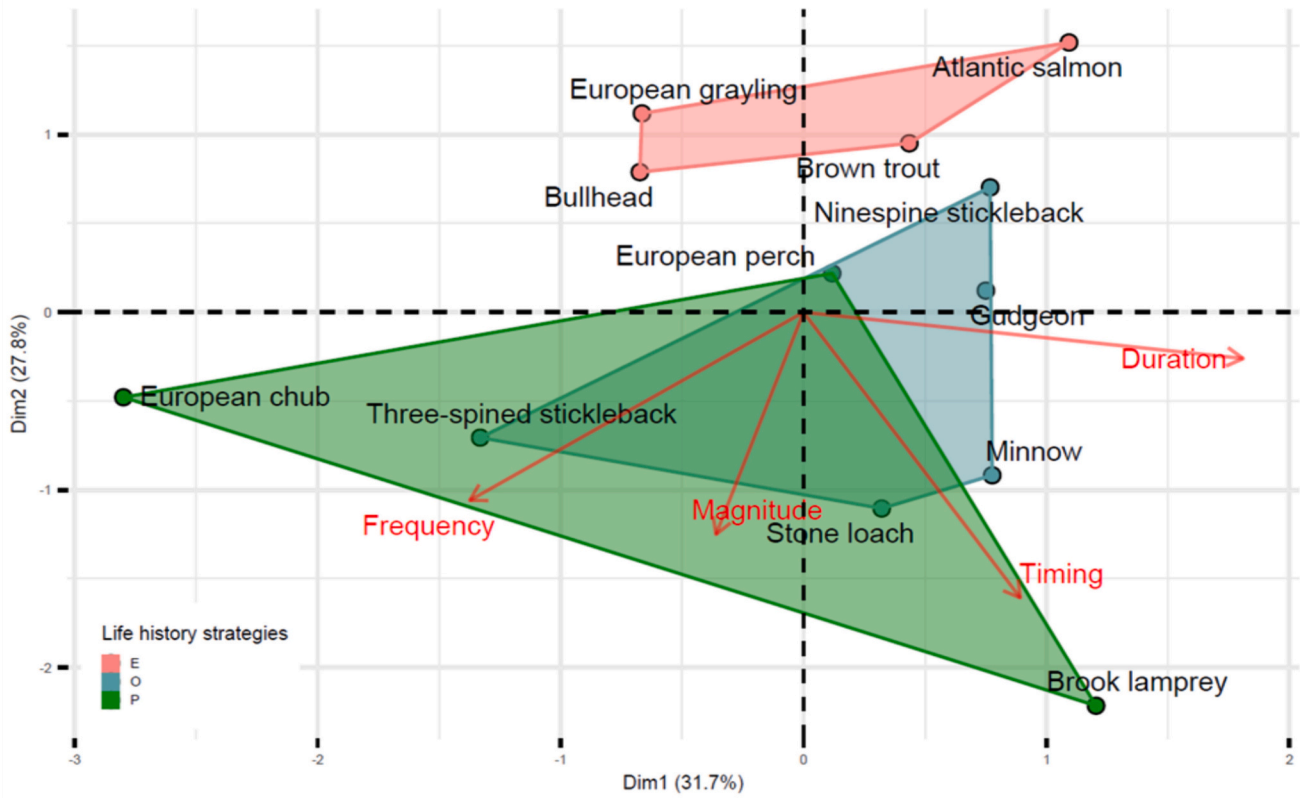


Fig. 5. PCA biplot of estimates extracted from significant generalized linear models between fish species and hydrological indicators of high flow conditions. Variables are composite indexes of hydrological indicators grouped by flow component. The full list of HI contributing to the individual species models is presented in Appendix A Table A.6.

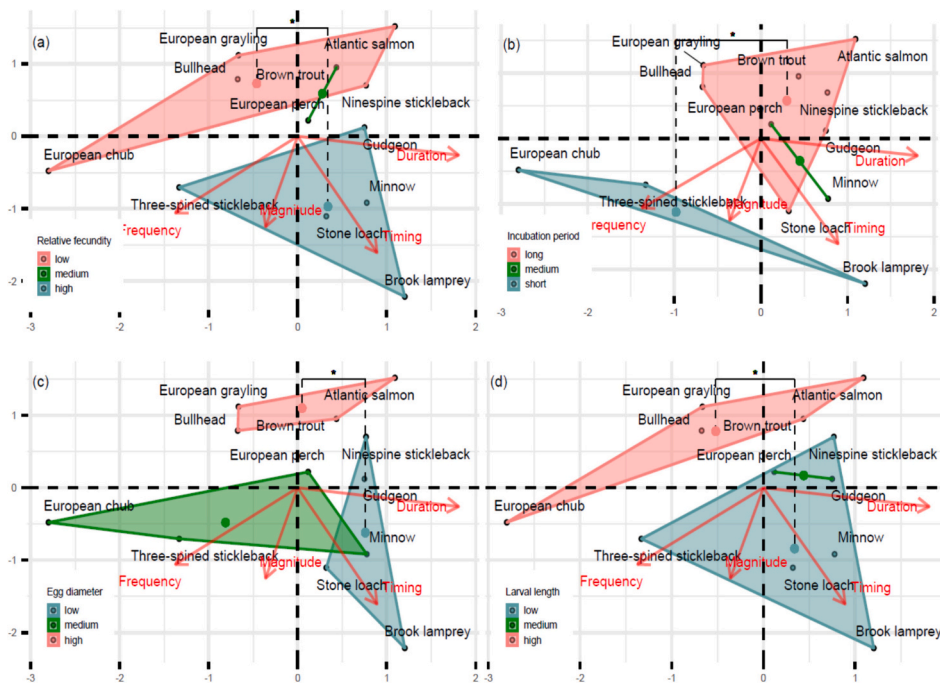


Fig. 6. PCA biplot of estimates extracted from significant generalized linear models between fish species and hydrological indicators of high flow conditions. Variables are composite indexes of the same hydrological indicators as Fig. 5. Species' reproductive success responses were clustered according to four ecological traits: (a) relative fecundity (b) incubation period (c) egg diameter and (d) larval length. Details about the modalities of these traits can be found in Table A.4 of Appendix A.

reproductive success of periodic species was, on average, positively affected by the high magnitude and frequency of high flows, except for the European perch (*Perca fluviatilis*). Stone loach (*Barbatula barbatula*) and brook lamprey (*Lampetra fluviatilis*) were positively affected by the large duration and the late timing whereas three-spined stickleback (*Gasterosteus aculeatus*) and chub (*Squalius cephalus*) reproductive success mainly responded negatively to large duration. The reproductive success of opportunistic species such as the minnow (*Phoxinus phoxinus*), gudgeon (*Gobio gobio*), and ninespine stickleback (*Pungitius pungitius*) was least affected by high flow patterns. Even though the reproductive success of these species responded to individual HI (see Fig. 3a and Appendix A, Table A.6), it showed a mostly positive reaction to the frequency of high flow (except for perch).

3.2.2. Comparison of species' reproductive success based on their reproductive traits in relation to high flows

Among the individual ecological species traits that contributed to the characterization of life history strategies, we identified four that were particularly indicative of the differential reaction of fish species to flow components: relative fecundity, incubation period, egg diameter, and larval length. The reproductive success of species with low fecundity was affected differently by the flow components than that of species with high fecundity (Fig. 6a; ANOSIM: $R = 0.244$; $p = 0.023$). Species with low relative fecundity, including chub, bullhead, grayling, salmon, perch, and ninespine stickleback, were mainly negatively affected by the late timing and high magnitude of high flow, whereas the reproductive success of species with high relative fecundity, including stickleback, gudgeon, stone loach, minnow, and brook lamprey thrived under high frequency, high magnitude, and late timing of high flow. Species with medium relative fecundity, brown trout, and perch, showed intermediate patterns. They were impaired by the high frequency and magnitude of the high flow.

Flow components influenced reproductive success differently in species with short incubation periods compared to species with long incubation periods (Fig. 6b; ANOSIM: $R = 0.599$; $p = 0.025$). Species with a short incubation period comprising chub, three-spined stickleback, and brook lamprey benefited from the high frequency, magnitude, and late timing of high flow, whereas the reproductive success of species with long to medium incubation periods, including bullhead, grayling, brown trout, salmon, ninespine stickleback, gudgeon, and perch, responded negatively under high frequency, magnitude, and late timing of high flow. Stone loaches and minnows were mostly driven by the long duration and late timing of the high flow.

Furthermore, the effect of the flow component on the reproductive success of species with small egg diameters differed from its effect on species with large egg diameters. (Fig. 6c; ANOSIM, $R = 0.333$; $p = 0.027$). Species with low to medium egg diameters, such as the gudgeon, stone loach, and brook lamprey, were fostered by the long duration and late timing of flow, whereas the reproductive success of species with large egg diameters, such as the bullhead, Atlantic salmon, brown trout, and grayling, was negatively affected by the high frequency, high magnitude, and late timing of high flow. Species such as ninespine stickleback, gudgeon, and perch showed an intermediate pattern and were mostly favoured by a long duration of high flow.

Finally, the reproductive success of species with low larval lengths was affected differently by the flow component than by species with high larval lengths (Fig. 6d; ANOSIM, $R = 0.204$; $p = 0.048$). Species with high larval length, including chub, bullhead, grayling, salmon, perch, and ninespine stickleback, were mainly negatively impacted by the late timing and high magnitude of high flow. In contrast, the reproductive success of species with high relative fecundity, including three-spined stickleback, stone loach, minnow, and brook lamprey thrived under high frequency, high magnitude, and late timing of high flow. Species with medium larval length, perches, and gudgeons showed intermediate patterns. They were impaired by the high frequency and magnitude of high flow.

3.2.3. Comparison of species' reproductive success based on their life histories in relation to low flows

We were not able to identify differences in the reproductive success of fish species in connection with low flow components based on life history strategies (Fig. 7; ANOSIM: $R = 0.005$; $p = 0.472$).

Nevertheless, individual species responded differently to low flow components. The reproductive success of the brown trout and salmon was negatively impacted by the late timing, high frequency, long duration, and high magnitude of low flows. In bullhead, gudgeon and three-spined stickleback, reproductive success was favoured by high magnitudes of low flow. Grayling, brook lamprey, minnow and European perch primarily benefited from the long duration but low magnitudes of low flow. The reproductive success of European chub responded positively to high frequency and late timing of low flow.

4. Discussion

4.1. Ecohydrological models

The five components of the flow regime – magnitude, frequency, duration, timing, and rate of change – play crucial roles in shaping the reproductive success of fish species, albeit with differing degrees of influence across temporal scales and according to high and low flows.

In the short term (one year), the magnitude of flows had the greatest influence on reproductive success. High-magnitude flow events have an immediate effect on YOY and their habitats, where sudden increases in water volume can swiftly alter the physical characteristics of the environment, affecting the availability of shelter, spawning and nesting areas, and food sources (Freeman et al., 2001). The frequency of flows had the second-highest relative influence on fish reproductive success. Frequent flow disturbances cause short-term alterations such as reduced extent and diversity of habitat for YOY, shifts in reproduction periods, and disruption of migration patterns that impact reproductive success (Bowen et al., 2003; McAdam et al., 1999).

Studies focusing on flow conditions over multiple timescales are rare (Beesley et al., 2014), particularly those that emphasize medium-term flow conditions. This timeframe corresponds to the adult life span and represents a transition phase between short-term events and long-term flow regimes. The results were largely intermediate between short- and long-term, with a higher similarity to short-term patterns along with a higher importance of duration and rate of change at the expense of the magnitude.

In the long term (10 years), among all the components of the flow regime, the timing of the flow events displayed the highest relative change over time and their effects became more evident when viewed over longer periods. Shifts in flow timing cause severe disruptions in cues for spawning and egg hatching thus leading to reduced reproductive success and diminished recruitment of juvenile fish (Benke et al., 2000; Fausch and Bestgen, 1997).

Differentiating between life history strategies, the reproductive success of opportunistic species was largely influenced by the magnitude, duration, and rate of change in flow conditions, while that of the equilibrium species was largely driven by the magnitude and frequency of the flow. Equilibrium strategists have been predicted to be associated with stable environments (Olden and Kennard, 2010; Tedesco et al., 2008), and the importance of the magnitude and frequency of flows was found to be particularly high for species that do not normally tolerate frequent and intense disturbances. This implies that these two components have a strong negative influence on their reproductive success. Concerning periodic strategists, their reproductive success was largely shaped by the duration and magnitude of high flows. Studies have found a strong positive relationship between the prevalence of periodic strategists and high flow frequencies (Tedesco et al., 2008), emphasizing the importance of predictable flow conditions, which was not the case here. However, our results highlighted the importance of prolonged flow events which are crucial for periodic strategists because they act as

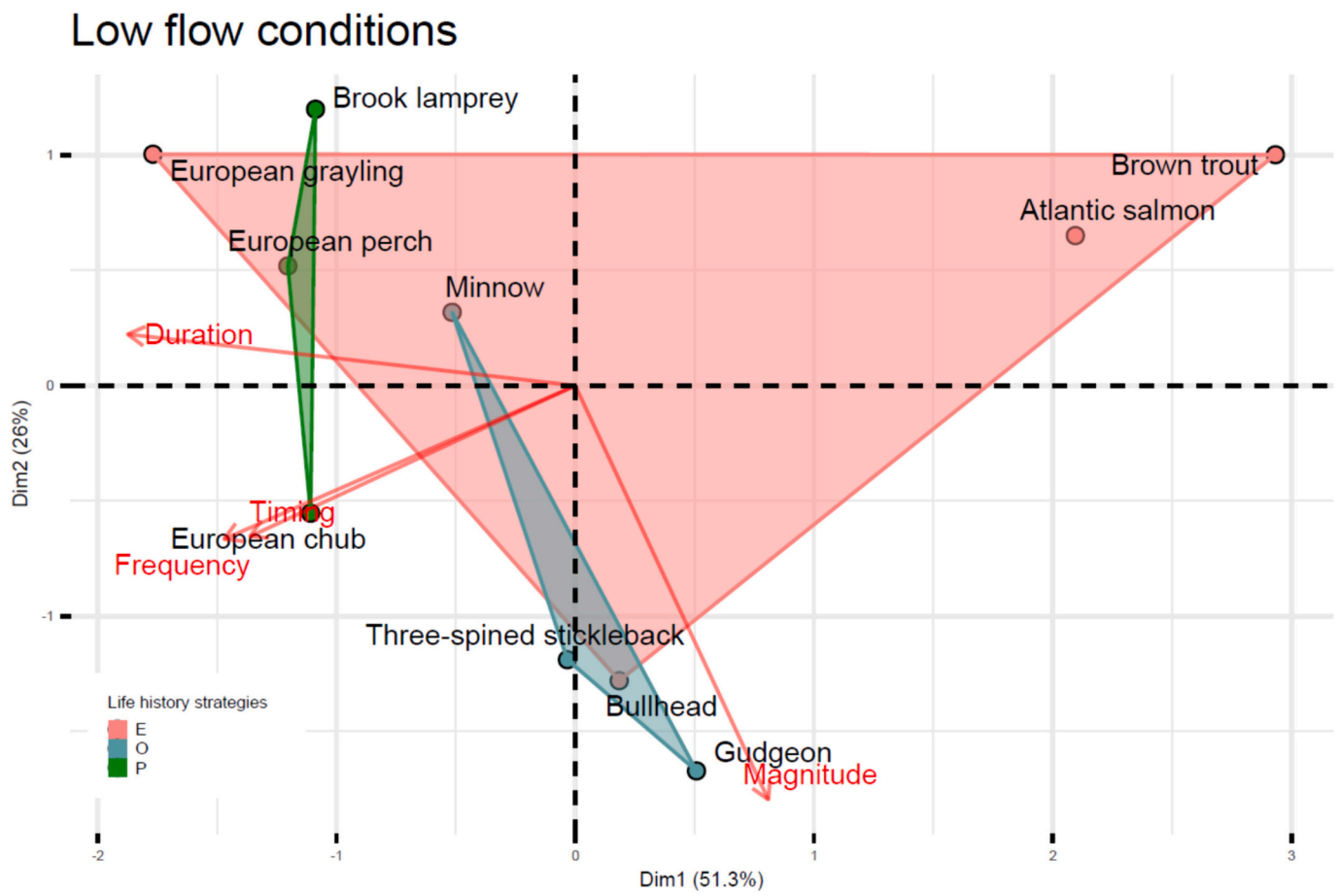


Fig. 7. PCA biplot of estimates extracted from significant generalized linear models between fish species and hydrological indicators of high flow conditions. Variables are composite indexes of hydrological indicators grouped by flow component. The full list of HI contributing to the individual species models is presented in Appendix A Table A.7.

spawning and locomotive cues (Winemiller and Rose, 1992) and facilitate access to floodplain habitats and resources (Benke et al., 2000; Tockner et al., 2000).

4.2. Low flow

We examined species' reproductive success under low flow conditions but found no clear relationship in their responses to their life-history strategies. With the increasing importance of biotic interactions during low flow (Lake, 2003), species must develop individual strategies to be ecologically successful, leading to individual specialization. If abiotic conditions are essential for the reproductive success of species, they can increase their ecological success with convergent adaptation strategies (Lytle, 2001). Hence, by investigating response patterns at the species level, we found common ecological features likely to structure species reproductive success in the face of the different components of the flow regime.

The reproductive success of brown trout and Atlantic salmon, two salmonid species, is adversely impacted by high frequency and the early timing of low flows. Low flow stands out as the primary cause behind the significant decline in the number of young-of-the-year (YOY) salmonids, as supported by Bell et al. (2000) and Lobón-Cerviá (2009). This impact is particularly pronounced when these low flow conditions coincide with the emergence period. During such times, the vulnerability of the young stages towards stranding, hypoxia, and restricted food availability is evident due to their limited adaptive capacity (Wootton, 1989). Elliott et al. (1997) noted increased mortality among YOY brown trout during frequent drought periods, a phenomenon closely linked to

reduced densities of returning females. The significance of water flow extends to its role as the primary determinant of salmonid entry into rivers, and variations in river flow, play a pivotal role in the timing of their upstream migration (Jonsson and Jonsson, 2009). The early timing of low river flow has been shown to delay the migration of Atlantic salmon, and low flow conditions during or just after emergence can diminish the survival rates of young fish (Elliott, 1985; Potter, 1988). Moreover, elevated water temperatures exacerbate the hypoxic consequences arising from low flows, while insufficient winter flows heighten the risk of fish mortality due to freezing (Huusko et al., 2007). Since salmonid populations hold both commercial and conservation significance, the timing and frequency of low flows should be closely monitored to ensure their sustainability.

The reproductive success of the three-spined stickleback, gudgeon, and bullhead was fostered by the strong magnitude of low flows. They are mainly late spawners (except gudgeons) and small-bodied species. Their rapid maturation and short generation times allow them to reproduce more frequently, which can help offset potential losses during challenging droughts (Lennox et al., 2019). Furthermore, their small body sizes allow them to find refuges or microhabitats with more favourable flow conditions by diving down into interstices where larger-bodied individuals would struggle to do so during high-magnitude droughts (Roussel and Bardonnet, 2002).

Chub's reproductive success was fostered by the high frequency and late timing of high flow. Because of its high fecundity, chub maximizes the odds of offspring survival in the face of frequent droughts, and because this species has a relatively long spawning period (from May to September) along with a multiple batch spawning strategy, spawning

events are ensured to occur under favourable environmental conditions (Nunn et al., 2002). This species tolerates high temperatures and low oxygen concentrations (Kupren et al., 2010), which are typically associated with low flow conditions. In addition, high temperatures are an important factor in the rapid growth of chub during the first year of life; therefore, it can adapt its spawning timing and location based on environmental cues, such as water temperature, to optimize reproductive success (Bouchard et al., 1998). Finally, the reproductive success of brook lamprey, grayling, perch, and minnow was mainly fostered under the extended duration of low flow. These species all share a short larval stage duration, which appears to be advantageous during prolonged low flow conditions because it reduces the time spent in this vulnerable stage, where individuals are prone to starvation because of their high dependency on external food sources (Houde, 2006). Moreover, larvae of these species are more susceptible to predation because of their small size and limited mobility, and a shorter larval stage reduces the exposure time to predators, increasing their chances of survival during low-flow conditions when predator-prey interactions might be heightened due to confined habitats (Paradis et al., 1996).

4.3. High flow

Our results based on in-field observations confirmed the theoretical predictions from the Riverscape Recruitment Synthesis Model (RRSM) from Humphries et al. (2020) predicting that under high flow conditions, due to favourable conditions, opportunistic and periodic species' reproductive success would be relatively high, in contrast to equilibrium species. Additionally, we found that the dissimilar responses of species to high flows were primarily determined by their relative fecundity, egg diameter, incubation period, and larval length.

Based on their life history traits, reproductive success differs in response to high flow, partly because of spawning behaviour. Indeed, many equilibrium species breed in the main channels of rivers, where their eggs and YOY are at risk of washout from high-flow events (Humphries et al., 2002). Conversely, because opportunistic and periodic species do not necessarily breed in the main channel, their reproductive success is relatively high compared to that of equilibrium species because they are less likely to be affected by high-flow events. Additionally, many small eggs and larvae are dispersed in diverse environments, providing ideal conditions for survival and growth (Winemiller and Rose, 1993).

These assumptions were further supported by the fact that the reproductive success of species with intermediate to low egg diameter and intermediate to high relative fecundity (traits related to periodic and opportunistic strategies) benefited from high-flow conditions. In contrast, the reproductive success of species with a high egg diameter and low relative fecundity (equilibrium strategists) was negatively impacted under the same flow conditions. These findings were consistent with life-history models predicting that a single optimal offspring size should be produced, conditional on environmental cues (Einum and Fleming, 2004; McGinley et al., 1987; Smith and Fretwell, 1974). For freshwater fish, offspring size is expected to decrease, whereas the number of offspring is expected to increase with increasing environmental variability, which is primarily driven by differences in hydrological regimes (Lake, 2000; Poff et al., 1997). Here, we found that the differences in offspring size and number were driven by different components of the flow regime. Even though all species displaying high relative fecundity (except perch and ninespine stickleback) thrived under harsh high-flow conditions, the responses of species' reproductive success according to their egg diameter traits were more nuanced. Indeed, species such as minnow, stone loach, gudgeon, and brook lamprey that produce smaller eggs were particularly fostered under extended and late flow events, whereas species such as chub and three-spined stickleback, which have medium eggs, thrived better under frequent and strong flow events.

In the light of the finding that fish employ various reproductive

strategies to mitigate the risks of unpredictable environmental changes, the term bet-hedging has been coined (Cohen, 1967; Roff, 2001). This theory has been further expanded when a variety of offspring characteristics, not just size or number, can be favoured in harsh environments (Rees et al., 2010). For example, shorter incubation periods are advantageous during harsh flow events because they reduce the risk of scouring or egg burial (Korman et al., 2011). Here, we observed that the reproductive success of species with different incubation periods diverged in response to high flow, whereas the reproductive success of species with a short incubation period was fostered during frequent, high-magnitude events, in contrast to that of species with medium to long incubation periods.

The reproductive success of species with small larvae, typical of opportunistic strategists, showed positive responses to all components of the flow regime during high flow conditions, whereas the reproductive success of species with large larvae, tied with equilibrium strategists, was negatively affected by the same flow conditions. The larvae of periodic and opportunistic species often live in shallow habitats, rely on zooplankton or meiofauna to achieve their transition phase, and are often found in backwaters rather than in floodplains (King et al., 2003). Because the larvae of opportunistic and periodic species can find refuge along with the necessary food outside the main channel, they can better cope with harsh flow events. Conversely, larvae at equilibrium, predictably found in the floodplain, are more exposed to extreme hydrological events despite having better swimming abilities (Humphries et al., 2020).

4.4. Towards an integrative approach to fish reproductive success

Very few studies investigated the relationship between reproductive success, life history strategies, and other ecological traits in the context of different components of the flow regime (Zeug and Winemiller, 2008; Falke et al., 2010). The functional relationships between the components of the flow regime and species traits remain understudied; however, they are critical for a mechanistic understanding of the effects of hydrological variation on fish species and communities (Humphries et al., 2020). Such studies are crucial for improving our understanding of the reproductive success of riverine fish and for making adequate conservation and restoration decisions, as high and low flows are projected to occur more frequently in the future (Huang et al., 2015).

It is important to understand that the flow regime alone is not sufficient to ensure successful reproductive outcomes (Humphries et al., 2020). Other factors, such as habitat structure and trophic status, also play important roles in influencing the reproductive success of freshwater fish in riverine ecosystems. These features, which are closely tied to the physical structure and flow patterns of rivers, significantly impact the availability of suitable spawning grounds and food sources under varying high- and low-flow conditions (Schlosser, 1991; Wolter et al., 2016). When water levels rise, habitats, such as deep pools, submerged logs, and undercut banks, provide essential refuges that offer protection from swift currents and facilitate successful spawning (Hafs et al., 2014; Snelder and Lamouroux, 2010). Conversely, during low-flow periods, microhabitats such as gravel beds, riffles, and side channels are crucial for fish reproduction by providing safe spaces for egg deposition and protecting developing embryos from thermal stress (Elliott, 2000; Magoulick and Kobza, 2003). Therefore, the natural habitat structures and connectivity that ensure that fish can reach these structures are key to the long-term thriving of populations (Schwartz and Herricks, 2008). Given the influence of habitat structure and flow patterns on fish reproductive success, it is imperative for management strategies to prioritize the preservation and restoration of diverse riverine habitats (Bunn and Arthington, 2002). This includes protecting deep pools, submerged logs, and undercut banks during high-flow periods, as well as maintaining and creating suitable microhabitats such as gravel beds, riffles, and side channels during low-flow periods.

Fish species coexist in intricate systems and their interactions with

other biotic components can significantly affect their responses to low flow (Humphries et al., 1999). Decreasing water volume leads to reduced habitat size, restricting fish mobility and increasing the concentration of all aquatic organisms, resulting in moderate to high predation and competition (Bunn and Arthington, 2002). Therefore, the presence of predators and density-dependent competition are crucial parameters influencing the reproductive success of species during low flows (Humphries et al., 2020). Due to the heightened predation pressure during low-flow periods, targeted predator management strategies may be necessary to mitigate negative impacts on fish reproductive success. This could include habitat modifications to create predator refugia such as submerged vegetation and woody debris offering crucial shelter for fish by creating barriers that prevent predators from hunting effectively (Everett and Ruiz, 1993).

Finally, water quality needs to be considered, especially during low flows, as dissolved oxygen levels in pools could drop to lethal levels due to discharge declines and increased temperatures, which is particularly detrimental to young individuals (Humphries et al., 1999). Furthermore, pollutants become concentrated during low flow, and their combination with constrained habitat availability can result in stressed and weakened fish, making them more susceptible to diseases and reducing their overall survival rates (Demeke and Tassew, 2015). Efforts to improve and maintain water quality, particularly during low-flow events, are essential for safeguarding fish reproductive success. Implementing measures to reduce nutrient runoff, pollutants, and sedimentation can help mitigate the adverse effects of poor water quality on fish populations (Zhao et al., 2018).

This study underscores the critical need to understand the interplay between reproductive success, life history strategies, and ecological traits in relation to various components of the flow regime. Such knowledge is essential for informed conservation and restoration efforts, especially with the increasing frequency of extreme flow events. Successful fish reproduction relies not only on flow regimes but also on habitat structure and water quality. Diverse habitats, like deep pools and gravel beds, provide essential spawning and refuge areas under different flow conditions. Additionally, factors like predation, competition, and water quality during low flows significantly impact reproductive success. Effective management must therefore prioritize habitat preservation, predator control, and water quality improvement to support thriving fish populations in riverine ecosystems.

CRedit authorship contribution statement

Lucas Mignien: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Stefan Stoll:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

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

The authors do not have permission to share data.

Acknowledgements

We would like to thank the following federal water agencies for providing the discharge data: Ruhrverband, Niersverband, Entwässerungs-Genossenschaft (LINEG), and the State Office for Nature, Environment and Consumer Protection North Rhine-Westphalia (LANUV) which, in addition to discharge data, also provided the fish sampling data set.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.174366>.

References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Autom. Control* 19, 716–723. <https://doi.org/10.1109/TAC.1974.1100705>.
- Balcombe, S.R., Arthington, A.H., Foster, N.D., Thoms, M.C., Wilson, G.G., Bunn, S.E., 2006. Fish assemblages of an Australian dryland river: abundance, assemblage structure and recruitment patterns in the Warrego River, Murray - Darling Basin. *Mar. Freshw. Res.* 57, 619. <https://doi.org/10.1071/MF06025>.
- Beesley, L.S., Gwinn, D.C., Price, A., King, A.J., Gawne, B., Koehn, J.D., et al., 2014. Juvenile fish response to wetland inundation: how antecedent conditions can inform environmental flow policies for native fish. *J. Appl. Ecol.* 51, 1613–1621. <https://doi.org/10.1111/1365-2664.12342>.
- Bell, V.A., Elliott, J.M., Moore, R.J., 2000. Modelling the effects of drought on the population of brown trout in black brows Beck. *Ecol. Model.* 127, 141–159. [https://doi.org/10.1016/S0304-3800\(99\)00209-4](https://doi.org/10.1016/S0304-3800(99)00209-4).
- Benke, A.C., Chaubey, I., Ward, G.M., Dunn, E.L., 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. *Ecology* 81, 2730–2741. [https://doi.org/10.1890/0012-9658\(2000\)081\[2730:FPDOAU\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2730:FPDOAU]2.0.CO;2).
- Blanck, A., Lamouroux, N., 2006. Large-scale intraspecific variation in life-history traits of European freshwater fish: traits variation in freshwater fish. *J. Biogeogr.* 34, 862–875. <https://doi.org/10.1111/j.1365-2699.2006.01654.x>.
- Bouchard, P., Chappaz, R., Cavalli, L., Brun, G., 1998. Influence of environmental variables on the growth of *Leuciscus cephalus* (Linnaeus 1766), in the river durance, south-East France. *Ann. Limnol. Int. J. Limnol.* 34, 193–200. <https://doi.org/10.1051/limn/1998018>.
- Bowen, Z.H., Bovee, K.D., Waddle, T.J., 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Trans. Am. Fish. Soc.* 132, 809–823. <https://doi.org/10.1577/T02-079>.
- Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ. Manag.* 30, 492–507. <https://doi.org/10.1007/s00267-002-2737-0>.
- Chambers, R.C., Trippel, E.A., 1997. Early life history and recruitment: legacy and challenges. In: Chambers RC, Trippel EA, editors. *Early Life Hist. Recruit. Fish Popul.*, Dordrecht: Springer Netherlands, pp. 515–549. https://doi.org/10.1007/978-94-009-1439-1_19.
- Cohen, D., 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *J. Theor. Biol.* 16, 1–14. [https://doi.org/10.1016/0022-5193\(67\)90050-1](https://doi.org/10.1016/0022-5193(67)90050-1).
- Demeke, A., Tassew, A., 2015. *A Review on Water Quality and its Impact on Fish Health*. Diekmann, M., Brämick, U., Lemcke, R., Mehner, T., 2005. Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities: Indicator fish species in German lowland lakes. *J. Appl. Ecol.* 42, 901–909. <https://doi.org/10.1111/j.1365-2664.2005.01068.x>.
- Ehler, T., Hering, D., Koenzen, U., Pottgiesser, T., Schuhmacher, H., Friedrich, G., 2002. Typology and type specific reference conditions for medium-sized and large Rivers in North Rhine-Westphalia: methodical and biological aspects. *Int. Rev. Hydrobiol.* 87, 151–163. [https://doi.org/10.1002/1522-2632\(200205\)87:2/3<151::AID-IRH151>3.0.CO;2-A](https://doi.org/10.1002/1522-2632(200205)87:2/3<151::AID-IRH151>3.0.CO;2-A).
- Einum, S., Fleming, I.A., 2004. *Environmental Unpredictability and Offspring Size: Conservative Versus Diversified Bet-Hedging*.
- Elliott, J.M., 1985. Population dynamics of migratory trout, *Salmo trutta*, in a Lake District stream, 1966–83, and their implications for fisheries management. *J. Fish Biol.* 27, 35–43. <https://doi.org/10.1111/j.1095-8649.1985.tb03230.x>.
- 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. <https://doi.org/10.2307/2405234>.
- Everett, R.A., Ruiz, G.M., 1993. Coarse woody debris as a refuge from predation in aquatic communities: an experimental test. *Oecologia* 93, 475–486. <https://doi.org/10.1007/BF00328954>.
- Falke, J.A., Bestgen, K.R., Fausch, K.D., 2010. Streamflow reductions and habitat drying affect growth, survival, and recruitment of brassy minnow across a Great Plains Riverscape. *Trans. Am. Fish. Soc.* 139, 1566–1583. <https://doi.org/10.1577/T09-143.1>.
- Fausch, K.D., Bestgen, K.R., 1997. Ecology of Fishes Indigenous to the Central and Southwestern Great Plains. In: Knopf FL, Samson FB, editors. *Ecol. Conserv. Gt. Plains Vertebr.*, vol. 125, New York, NY: Springer New York, pp. 131–166. https://doi.org/10.1007/978-1-4757-2703-6_6.
- Freeman, M.C., Bowen, Z.H., Bovee, K.D., Irwin, E.R., 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. *Ecol. Appl.* 11, 179–190. [https://doi.org/10.1890/1051-0761\(2001\)011\[0179:FAHEOJ\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0179:FAHEOJ]2.0.CO;2).
- Freeman, M.C., Pringle, C.M., Jackson, C.R., 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *JAWRA J. Am. Water Resour. Assoc.* 43, 5–14. <https://doi.org/10.1111/j.1752-1688.2007.00002.x>.

- Winemiller, K.O., Rose, K.A., 1993. Why do Most fish produce so many tiny offspring? *Am. Nat.* 142, 585–603. <https://doi.org/10.1086/285559>.
- Winne, C.T., Willson, J.D., Whitfield, Gibbons J., 2010. Drought survival and reproduction impose contrasting selection pressures on maximum body size and sexual size dimorphism in a snake. *Seminatrix pygaea. Oecologia* 162, 913–922. <https://doi.org/10.1007/s00442-009-1513-8>.
- Wolf, S., Esser, V., Schüttrumpf, H., Lehmkühl, F., 2021. Influence of 200 years of water resource management on a typical central European river. Does industrialization straighten a river? *Environ. Sci. Eur.* 33, 15. <https://doi.org/10.1186/s12302-021-00460-8>.
- Wolter, C., Sukhodolov, A., 2008. Random displacement versus habitat choice of fish larvae in rivers. *River Res. Appl.* 24, 661–672. <https://doi.org/10.1002/rra.1146>.
- Wolter, C., Buijse, A.D., Parasiewicz, P., 2016. Temporal and spatial patterns of fish response to Hydromorphological processes: fishes response to Hydromorphology. *River Res. Appl.* 32, 190–201. <https://doi.org/10.1002/rra.2980>.
- Wootton, R.J., 1989. *Ecology of teleost fishes*. Dordrecht: Springer Netherlands. <https://doi.org/10.1007/978-94-009-0829-1>.
- Yeomans, K.A., Golder, P.A., 1982. The guttmann-kaiser criterion as a predictor of the number of common factors. *The Statistician* 31, 221. <https://doi.org/10.2307/2987988>.
- Zeh, M., Dönni, W., 1994. Restoration of spawning grounds for trout and grayling in the river high-Rhine. *Aquat. Sci.* 56, 59–69. <https://doi.org/10.1007/BF00877435>.
- Zeug, S.C., Winemiller, K.O., 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Res. Appl.* 24, 90–102. <https://doi.org/10.1002/rra.1061>.
- Zhao, C., Yang, S., Liu, J., Liu, C., Hao, F., Wang, Z., et al., 2018. Linking fish tolerance to water quality criteria for the assessment of environmental flows: a practical method for streamflow regulation and pollution control. *Water Res.* 141, 96–108. <https://doi.org/10.1016/j.watres.2018.05.025>.