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Hanieh Seyedhashemi, Hilaire Drouineau, Elorri Arevalo, Marion Legrand, Florentina Moatar, et al.. Climate-Induced Changes in River Hydrological and Thermal Conditions in a Large Basin: Implications for Diadromous Fish Migration. Canadian Journal of Fisheries and Aquatic Sciences, 2025, 10.1139/cjfas-2024-0208 . hal-04905434

**HAL Id: hal-04905434**

**<https://edf.hal.science/hal-04905434v1>**

Submitted on 22 Jan 2025

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# Climate-Induced Changes in River Hydrological and Thermal Conditions in a Large Basin: Implications for Diadromous Fish Migration

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## Abstract

Climate-induced changes in river conditions, such as water temperature and current velocity, can disrupt species migration patterns by altering the conditions encountered during migration. We assessed these impacts across the Loire River basin in Europe by compiling long-term fish passage data for three diadromous fish species at fishways, alongside reconstructed time series of water temperature and current velocity. We considered both water temperature and current velocity on days when migration was observed as "suitable conditions" for the species' upstream migration. Our findings for the 1963–2019 period revealed that trends in the frequency of suitable conditions for upstream migration were species-specific. For Atlantic salmon, particularly fall migrants, the frequency of suitable conditions has declined over time in certain areas. In contrast, the frequency of suitable migration conditions for both allis shad and sea lamprey has shown an overall increase across the basin. This study offers policy-makers and environmental managers valuable insights for developing effective, spatially explicit strategies to preserve diadromous fish populations amid ongoing climate change.

**Keywords:** global change, fish migration, connectivity, long-term, large scale, Loire basin

# 1 Introduction

Many animal species synchronize their key life events with river conditions as an adaptive strategy to maximize their fitness and that of their offspring (Pau et al. 2011; Thackeray et al. 2016). Photoperiod, water temperature ( $T_w$ ), and discharge (Q) serve as fundamental triggers for migration initiation and control, foraging (for mates, shelter, or food), and reproductive movements of aquatic organisms (Acolas et al. 2006; García-Vega, Sanz-Ronda, and Fuentes-Pérez 2017; N. Jonsson 1991; Milner, Solomon, and Smith 2012). Temperature critically affects fish metabolism and survival of early life stages (Brown et al. 2004; Jatteau et al. 2017). Discharge and associated current velocity (V) directly influence the energy costs and pace of fish migration (Eyto et al. 2022; B. Jonsson and N. Jonsson 2009; Tetzlaff et al. 2008), as well as egg survival (Louhi, Mäki-Petäys, and Erkinaro 2008). As such, species phenology often results in local adaptations to those environmental factors to optimise their fitness and that of their offspring (Villeneuve, Komoroske, and B. S. Cheng 2021). However, climate change significantly affects these environmental cues, which in turn jeopardize the ecological processes that depend on them (Arevalo, Maire, et al. 2021; Crozier, Siegel, et al. 2020).

In European areas, large-scale studies have shown increases in river temperatures over the last few decades, which are expected to continue in the coming decades (Michel et al. 2020; Wilby and M. Johnson 2020), potentially at higher rates than air temperature (H. Seyedhashemi, Vidal, et al. 2022). The intensity and frequency of droughts (Giuntoli et al. 2013) and floods (Blöschl et al. 2019) are also on the rise due to alterations in rainfall patterns, water withdrawals, and flow regulation from anthropogenic activities (Habets et al. 2014).

Water warming can alter the timing of spawning events (B. Jonsson and N. Jonsson 2009; Pankhurst and Munday 2011), the energy costs of migration, and the swimming performance of fish (Fenkes et al. 2016; Lennox, Eliason, et al. 2018). The rapid rate of climate change is expected to bring significant changes to the availability and quality of aquatic habitats over a short period (Lennox, Crook, et al. 2019; Reid et al. 2019), affecting species' phenology by shifting migration or reproduction periods (Eyto et al. 2022; L. Hughes 2000; Legrand, Briand, Laëtitia Buisson, Besse, et al. 2021; Manhard, Joyce, and Gharrett 2017; Perkin and Wilson 2021; Tillotson et al. 2021). However, rapid changes in river conditions may not always allow organisms to adapt (Bryant 2009; Crozier and Hutchings 2014; Sandblom et al. 2016). Moreover, modifications in thermal and hydrological conditions can also occur simultaneously and in opposing directions (Maire, Thierry, et al. 2019; H. Seyedhashemi, Vidal, et al. 2022). This can modify the occurrence of temperature-discharge associations suitable for ecological processes and exacerbate the impact of climate change on species migration and reproduction (Arevalo, Géraldine Lassalle, et al. 2020; Crozier and Hutchings 2014). For instance, Arevalo, Géraldine Lassalle, et al. 2020 identified a significant increase in the number of days presenting both high water temperature and low river discharge in several large rivers across France, which could have an impact on the migration and spawning behaviors of diadromous fish. Therefore, there is a need to further explore the joint evolution of water temperature and river discharge and its impact on migratory species.

However, our ability to explore this question has been impeded by the scarcity of comprehensive and high resolution thermal and hydrological data at a large scale (Michel et al. 2020). Specifically, obtaining long-term time-series data of daily water temperature remains a challenge, resulting in the utilization of air temperature as a proxy for water temperature in numerous large-scale studies e.g., Buisson, Blanc, and Grenouillet 2008; Domisch et al. 2013; Maire, Laffaille, et

al. 2017). However, the relationship between air and water temperature within the context of climate change is complex and can lead to either overestimation or underestimation, depending on circumstances (Kirk and Rahel 2021; van Vliet et al. 2013). Furthermore, it has been determined that water temperature in conjunction with local river hydraulics offers a more comprehensive understanding of the structure of fish and macroinvertebrate communities, as opposed to the utilization of air temperature and discharge, respectively (Picard et al. 2022). Although discharge remains a pertinent measure for water management and is regularly monitored along rivers, discharge-associated variables, including current velocity, water depth, and shear stress, can be more directly related to fish ecology and behavior (Alabaster 1970; Malcolm et al. 2012; Milner, Solomon, and Smith 2012).

In this study, we focused on the potential impact of climate-induced changes in both water temperature and current velocity in the Loire River basin on the migration of three diadromous species: Atlantic salmon (*Salmo salar*), allis shad (*Alosa alosa*), and sea lamprey (*Petromyzon marinus*). Diadromous species are iconic, sharing their life cycle between marine and freshwater environments (Limburg and Waldman 2009). Their long, seasonal upstream migrations (McDowall 1999), sensitivity to climate change (G eraldine Lassalle and Eric Rochard 2009), and alarming population declines (Legrand, Briand, La etitia Buisson, Artur, et al. 2020; Waldman and Quinn 2022) make them ideal subjects for such analysis.

The Loire River basin, one of the largest in Europe, features spatially variable thermal and hydrological regimes, and offers (1) continuous daily time series of water temperature and river discharge, and (2) daily diadromous fish passage data over several decades. This makes it an excellent site to investigate the impacts of climate change on the upstream migration of diadromous species. Furthermore, since the river conditions were reconstructed to reflect natural landscape and basin characteristics, we were able to isolate the potential impacts of climate change from broader global changes (such as water abstractions and withdrawals), focusing specifically on migration-related river conditions. Understanding these climate-driven changes is critical for developing management strategies that could improve fish passage and migration success, for example through targeted improvements to fishways or habitat restoration in areas identified as most affected by altered migration conditions.

## 2 Materials and Methods

### 2.1 Study Area

The Loire River basin, spanning an area of about  $10^5$  km<sup>2</sup>, is one of the largest in Europe and is characterized by diverse land cover, lithology (e.g., texture, grain size, soil composition), and climate conditions (Florentina Moatar and Dupont 2016; H. Seyedhashemi, Vidal, et al. 2022). The study area extends from the headwaters to 110 km upstream of the estuary, thus not covering the most downstream part of the basin under tidal influence. The basin's landscape displays very heterogeneous river conditions over the 1963-2019 period, including mean annual precipitation (from 549 to 2130 mm), mean annual potential evapotranspiration (550–850 mm), mean annual air temperature (6.0–12.5 °C), mean annual water temperature (8–14 °C, mean annual discharge (0.2–850 m<sup>3</sup>/s), and altitude (0–1850 m) across the basin. These variations result in spatially variable thermal and hydrological regimes among different sub-regions (H. Seyedhashemi, Vidal, et al.

2022). The basin is also home to various diadromous fish species: Atlantic salmon, sea lamprey, allis shad, twaite shad, European river lamprey, and European eel (see Arevalo, Géraldine Lassalle, et al. 2020). Given this context, the Loire River basin is an ideal case study to investigate the impact of climate change on the river conditions experienced by diadromous fish during their upstream migration.

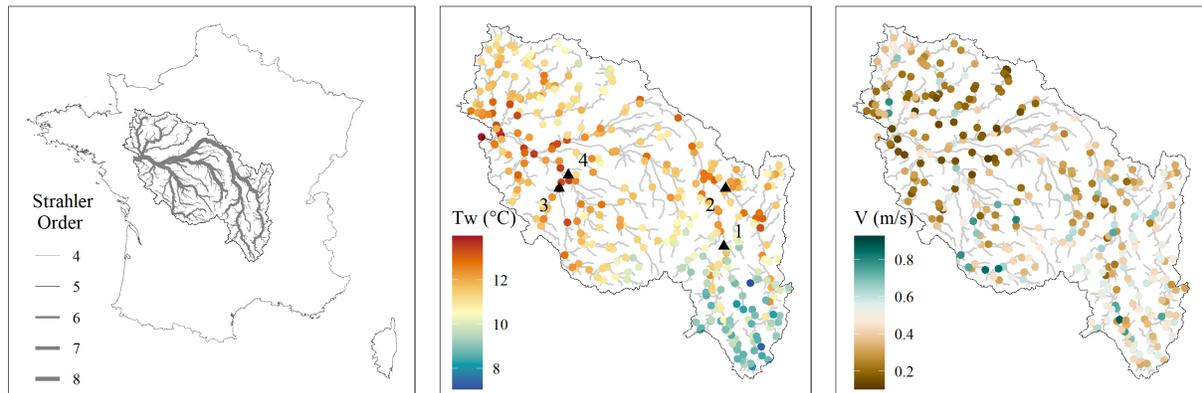


Figure 1: Maps of the Loire River basin showing interannual average of simulated  $T_w$  ( $^{\circ}\text{C}$ ) and  $V$  (m/s) over the 1963-2019 period at the 368 primary sub-basin outlets (in circles), which are representative of the entire basin heterogeneity. The black triangles indicate the locations of the fish monitoring stations, and the numbers correspond to the station ID presented in Table 1. To maintain focus on the study area, the maps exclude the downstream region under tidal influence, up to 110 km upstream of the estuary. Map projection is Lambert-93.

## 2.2 Fish Passage Data

Daily counts of upstream migration at fish monitoring stations located in fishways were provided by LOGRAMI ([www.logrami.fr/actions/stations-comptage](http://www.logrami.fr/actions/stations-comptage)). We focused on three anadromous fish species—Atlantic salmon, allis shad, and sea lamprey—for which recorded passages were sufficiently numerous and frequent (Legrand, Briand, and Besse 2019; Legrand, Briand, Laëtitia Buisson, Artur, et al. 2020; Legrand, Briand, Laëtitia Buisson, Besse, et al. 2021). Anadromous species refer to species that spawn in freshwater, but spend their growth phase at sea before returning to continental waters for reproduction (Brönmark et al. 2014). The video-counting data were collected at four monitoring stations—Vichy on the Allier River, Decize on the Loire River, Châtellerault on the Vienne River, and Descartes on the Creuse River—over a period ranging from 14 to 23 years, depending on the station, between 1997 and 2021 (Table 1). These stations are not in a linear upstream-downstream sequence and no barriers were constructed downstream of these monitoring stations during the study period. While not covering the entire spatial extent, the data collected from these four monitoring stations offer a valuable and extensive long-term record of fish migration. This dataset stands out as the most comprehensive and enduring one within this basin and encompasses key migration routes of the studied species. LOGRAMI also provided a

comprehensive overview of the historically documented presence of the species across the Loire River basin (Figure S1).

Depending on individuals, we considered different migration seasons. Atlantic salmon return to their natal ground after having spent one winter (1WS) or multiple winters (MWS) at sea (Thorstad et al. 2008). While MWS salmon generally migrate in spring (here, referred to as spring salmon), 1WS salmon migrate later in the season, up to late fall (here, referred to as fall salmon). Considering 95% of monthly fish passages at the four fish monitoring stations (Figure S1), fall salmon (1WS) migrated upstream from July to December (Jul-Dec) and spring salmon (MWS) migrated from February to June (Feb-Jun). Therefore, two migration seasons were considered for Atlantic salmon (i.e., Feb-Jun and Jul-Dec) as spring and fall individuals may display distinct behavior, physiology, life history strategies and ecological interactions (Arevalo, Maire, et al. 2021; Thorstad et al. 2008). Using a similar approach, we found that allis shad and sea lamprey migrate from March to June (Figure S2).

Table 1: Mean ( $\pm$  standard deviation) number of adults of Atlantic salmon, allis shad, and sea lamprey caught per year over the data period at each monitoring station.

ID	Station (River)	Period	Salmon	Allis shad	Sea lamprey
1	Vichy (Allier)	1997-2021	575 ( $\pm$ 270)	411 ( $\pm$ 720)	470 ( $\pm$ 903)
2	Decize (Loire)	1998-2021	17 ( $\pm$ 11)	2917 ( $\pm$ 4522)	1411 ( $\pm$ 1942)
3	Châtellerault (Vienne)	2004-2021	9 ( $\pm$ 6)	1852 ( $\pm$ 2546)	17249 ( $\pm$ 13596)
4	Descartes (Creuse)	2007-2021	80 ( $\pm$ 50)	1276 ( $\pm$ 2151)	14772 ( $\pm$ 12963)

### 2.3 River Temperature and Current Velocity Data

Daily  $T_w$  ( $^{\circ}\text{C}$ ),  $Q$  ( $\text{m}^3/\text{s}$ ) and  $V$  ( $\text{m}/\text{s}$ ) were reconstructed over the 1963-2019 period across the Loire River basin (Figure 1) using the T-NET physical process-based model coupled with the EROS hydrological model (Beaufort et al. 2016; H. Seyedhashemi, F. Moatar, et al. 2023; H. Seyedhashemi, Vidal, et al. 2022; Thiéry 2018). The EROS model simulated natural daily  $Q$ , i.e., without the influence of water abstractions, at the outlet of 368 sub-basins (with a drainage area ranging from 40 to 1600  $\text{km}^2$ ; mean = 300  $\text{km}^2$ ), which were designed to be as homogeneous as possible with respect to land use and geology. These simulated natural  $Q$  were then employed in a hydraulic geometry model based on discharge statistics and basin physical characteristics (Morel et al. 2020) within the T-NET model to estimate daily stream width, water depth, and current velocity at each sub-basin outlet.

To estimate natural daily  $T_w$ , while accounting for thermal propagation and confluence mixing, the heat fluxes at the water-air and water-stream bed interfaces were computed within the T-NET model. This computation employed reconstructed daily  $Q$  data, river hydraulic geometries, meteorological data, and riparian vegetation cover (Beaufort et al. 2016; Loicq et al. 2018; H. Seyedhashemi, Vidal, et al. 2022). Further details on the thermal, hydrological, and hydraulic geometry models employed in this study can be found in (H. Seyedhashemi, Vidal, et al. 2022).

## 2.4 Suitable Temperature-Velocity Associations for Upstream Migration

To identify suitable conditions for upstream migration (referred to as "suitable conditions"), at each monitoring station, we compiled daily fish passage counts and their corresponding reconstructed  $T_w$ -V associations to construct a convex hull encompassing 90% of fish passages, delineating pair points of suitable  $T_w$  and V associations (Figure 2). To determine 90% of the passages, we first sorted the daily fish passages in descending order, prioritizing the days with the highest passage counts. We then performed a cumulative summation of these passages, starting from the day with the highest count, until 90% of the total fish passages were accounted for. This enabled us to select the most active migration days to define the suitable conditions for migration.

After visually verifying the proper alignment of the convex hulls obtained at each of the four monitoring stations (Figure S3) and confirming their consistency with the ecological tolerance thresholds for water temperature and current velocity reported in the literature (Table S1), we constructed an overall convex hull for each species. This was done by aggregating the data from all stations for each species, while distinguishing between the two salmon ecotypes—those migrating in spring and those migrating in fall. The  $T_w$ -V associations within this convex hull were defined as the "suitable" associations for fish to migrate. For each species during migration season and sub-basin outlet, we considered days with  $T_w$ -V associations that fell within the convex hull of suitable associations as suitable days. Then, we calculated the percentage of suitable days during the migration season for each year and each species, which were averaged over the period 2009–2019 to provide an overall assessment of the contemporary level of suitable days. All monitoring stations recorded data during this period, allowing for a clearer understanding of the average number of suitable days within this recent timeframe.

To assess temporal changes in the percentage of suitable days during the migration season, we calculated the percentage of days that fell within the convex hull of suitable associations for each species and sub-basin outlet. We then applied the non-parametric Theil–Sen estimator (Sen 1968) to quantify the trend magnitude in suitable days, and tested for statistical significance at the 95% confidence level using the non-parametric Mann–Kendall test (Mann 1945). Trends were categorized according to the sign of the Theil–Sen estimator (i.e., positive: increasing; negative: decreasing) and their significance ( $p$ -value < 0.05: significant; otherwise non-significant). This resulted in four trend categories: significantly increasing, non-significantly increasing, non-significantly decreasing, and significantly decreasing.

To assess the sensitivity of the definition of the convex hull, we constructed convex hulls encompassing 80% and 50% of fish passages in addition to the 90% used previously. We then replicated the analyses using these alternative convex hulls. The corresponding ranges of  $T_w$ -V associations for the three different convex hulls are presented in Table S2. Trends in the percentage of suitable days were found to be robust to the way the convex hull was constructed (Table S2, Figures S4 and S5) and therefore, only results using the convex hull covering 90% of fish passages were presented hereafter.

### 3 Results

#### 3.1 Comparison of Migration-Selected Suitable Associations With the Literature

Over the migration period, the convex hulls of suitable associations were very similar across the fish monitoring stations (Figure S3). Spring and fall salmon exhibited a wider range of suitable  $T_w$ -V associations than allis shad and sea lamprey (Figure 2; and Table S1). The minimal temperatures suitable for allis shad and sea lamprey were around to be 10°C, while Atlantic salmon could use colder temperatures. Fall salmon (~3-28°C) displayed a wider range of suitable  $T_w$  compared to spring salmon (~4-26°C). The associations of reconstructed  $T_w$  and V used by fish at the fish monitoring stations were within the range of theoretical suitability thresholds of  $T_w$  and V documented for upstream migration of these species (grey dashed lines on Figure 2). In view of this, we used the convex hulls from Figure 2 as the associations for the migration of the different species/ecotypes at the scale of the whole river basin.

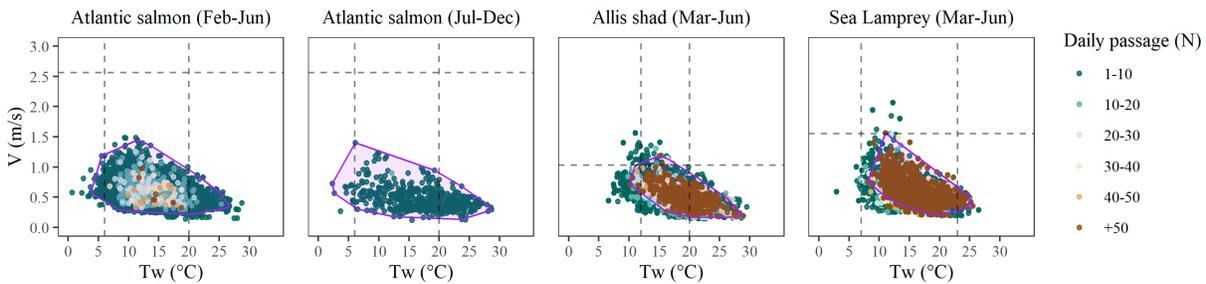


Figure 2: Water temperature ( $T_w$ )-current velocity (V) associations during the migration season of the species of interest over the 1963-2019 period, along with the corresponding number of fish passages. Each point represents a day with a recorded number of passages, with the y-axis showing the daily average of water temperature and the x-axis indicating the daily average of current velocity, both derived from the reconstructed data for that specific day. The combination of associations at four monitoring stations with passage are represented here. The convex hulls (purple lines) are overlaid on the associations during the migration season representing suitable associations/days for the upstream migration of each species (i.e., encompassing 90% of fish passages). The gray dashed lines outline the theoretical upper and lower limits of  $T_w$  and the theoretical upper limits of V for the upstream migration of each species as reported in the literature (see Table S1). Map projection is Lambert-93.

#### 3.2 Temporal Trends in the Number of Suitable Days at the Local Scale of Four Fish Monitoring Stations

For spring salmon, significant positive trends ( $p$ .value < 0.05) in the number of suitable days during the migration season were observed at all fish monitoring stations, except for Decize, where no significant trend ( $p$ .value > 0.05) was found (Figure 3). For fall salmon, no significant trends in the number of suitable days were detected at any of the stations, with the exception of Châtellerault,

where a significantly increasing trend was observed. In the case of allis shad and sea lamprey, significant positive trends were found at all stations, except Decize, where no significant trends were recorded. The absence of significant trends at the Decize station across multiple species suggests that local conditions at this site may differ from the other monitoring stations, potentially influencing migration suitability.

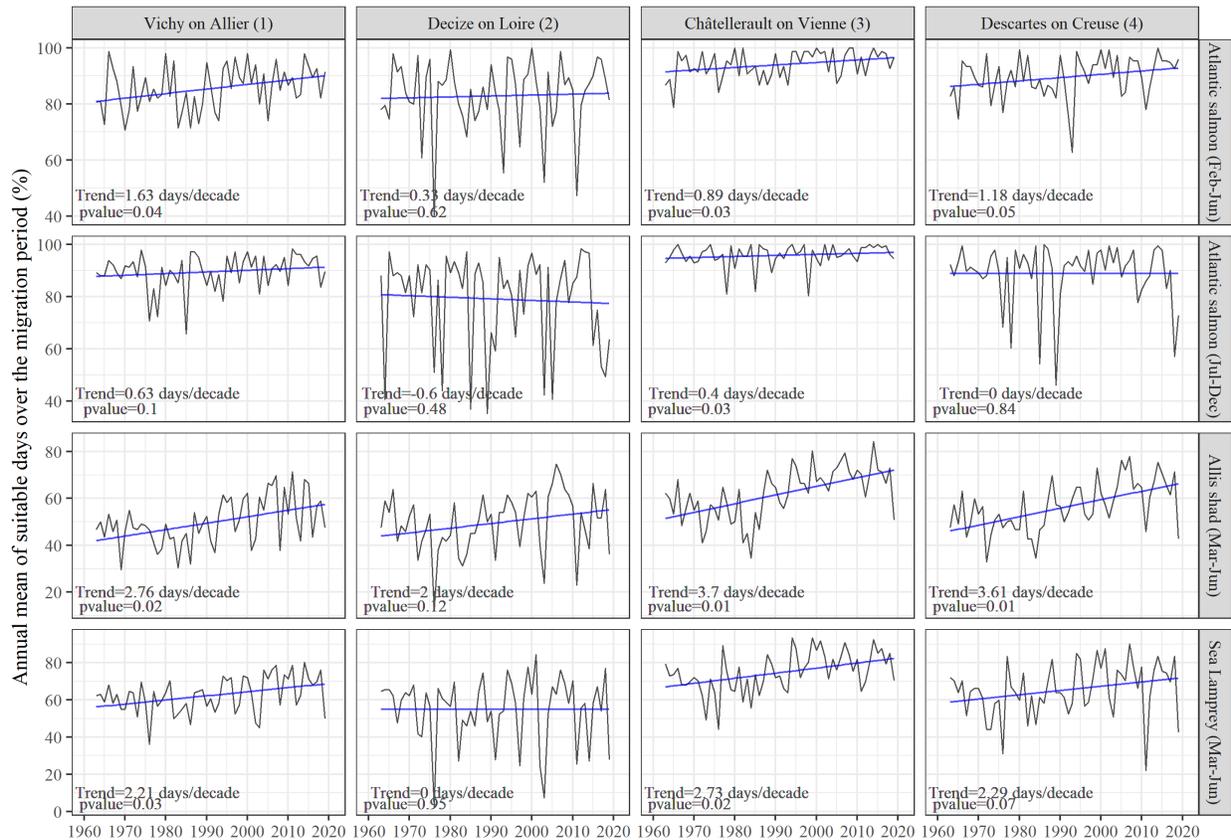


Figure 3: Trends in the percentage of suitable days during the migration season over the 1963-2019 period at the four fish monitoring stations (at the station level) for the species of interest. The blue line shows the Sen's slope of the trend. Direction of the trend in the percentage of suitable days at each each station computed based on a Mann-Kendall test. Map projection is Lambert-93.

### 3.3 Temporal Trends and Spatial Patterns at the Basin Scale

#### 3.3.1 Spatial Patterns

For spring and fall salmon, we found that the mean percentage of suitable days over the 2009–2019 period was generally high across the basin, with 59% of sub-basin outlets showing more than 60% suitable days for spring salmon and 53% for fall salmon (Figure 4). However, there was substantial spatial variability. For spring salmon, 10% of sub-basin outlets had fewer than 23 suitable days, while 10% had more than 89 suitable days. Similarly, for fall salmon, the range was from 20 to 91 suitable days (Figure 4).

However, the mean percentage of suitable days over the 2009-2019 period for allis shad and sea lamprey was lower than that for salmon. Specifically, 77% of sub-basin outlets for allis shad and 66% for sea lamprey had fewer than 40% suitable days. The spatial variability was also lower for these species compared to salmon (variation between the 10th and 90th percentiles: 4-55% for allis shad and 5-66% for sea lamprey).

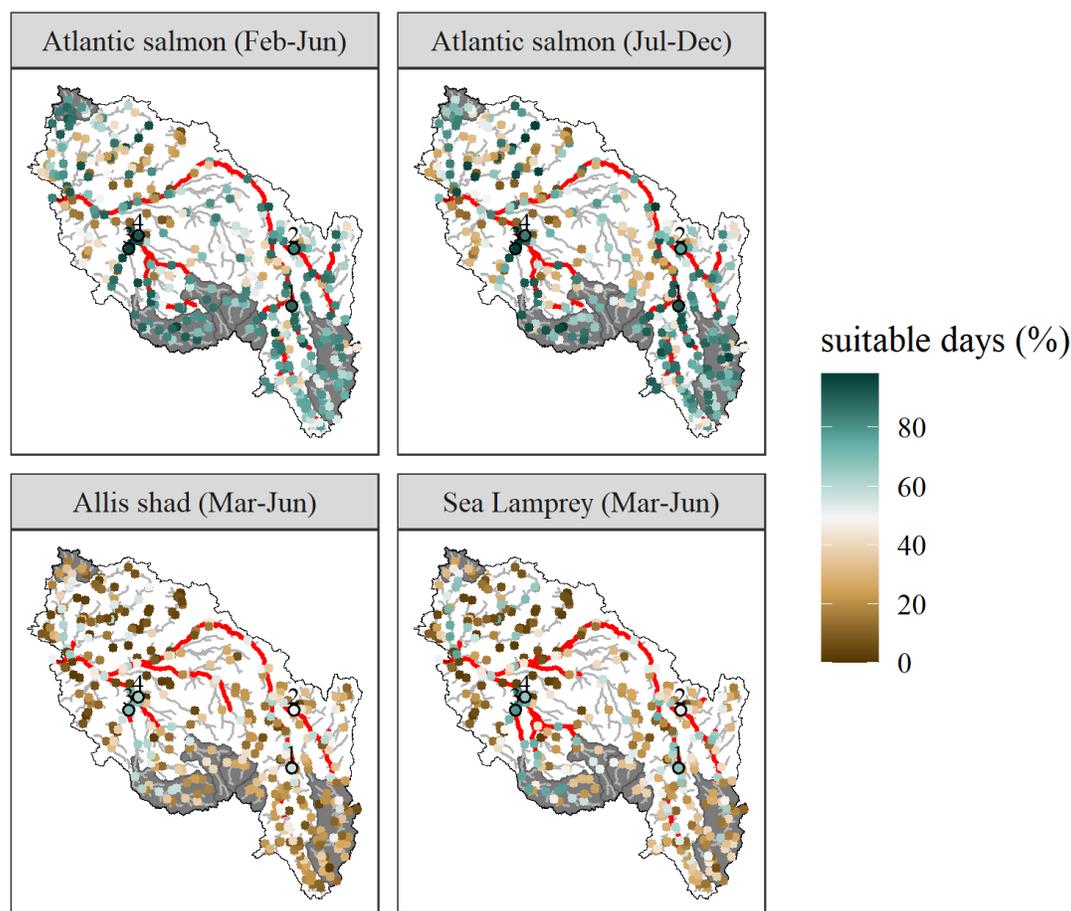


Figure 4: Percentage of days with suitable  $T_w$ - $V$  associations over the migration period for each species: Mean percentage of suitable days for the 368 sub-basin outlets, computed over the 2009-2019 period. The points with black outer edges show the fish monitoring stations. The river network represented in red corresponds to areas where the species of interest has been historically observed (see Figure S2 for more details). Black areas correspond to inaccessible areas, e.g., due to barriers. Map projection is Lambert-93.

### 3.3.2 Temporal Trends

We found spatially heterogeneous trends in suitable days across the basin for salmon, especially for fall salmon (Figure 5). Decreasing trends in the number of suitable days were observed at 14% of sub-basin outlets for spring salmon (1% significant) and at 43% for fall salmon (6% significant). Particularly, strong decreasing trends (i.e.,  $< -1.5$  suitable days/decade) were found at 10% and

35% of sub-basin outlets for spring and fall salmon, respectively, mostly in the southern part of the basin and in areas where salmon migration has not been observed historically (Figure S6).

For allis shad and sea lamprey, we observed an increase in the percentage of suitable days at nearly all sub-basin outlets (Figure 4), with 100% of sub-basin outlets showing increases for allis shad and 99% for sea lamprey. The percentage of suitable days has increased across the entire basin for both allis shad and sea lamprey. Significant positive trends were found at 59% of sub-basin outlets for allis shad and at 29% for sea lamprey (Figure 5). The median trend in the number of suitable days was +2.27 days/decade for allis shad and +1.40 days/decade for sea lamprey. Strong increasing trends ( $> +1.5$  suitable days/decade) were observed at 68% of sub-basin outlets for allis shad and 48% for sea lamprey, particularly in the southern part of the basin and in areas where these species have not been observed historically (Figure S6).

## 4 Discussion

### 4.1 Consistency of Selected Suitable Conditions for Upstream Migration Across Space and With the Literature

The key strengths of our study lie in its high spatial and long temporal resolution, as well as the incorporation of current velocity ( $V$ ) instead of river discharge to reflect the influence of river hydraulics on fish swimming abilities (Malcolm et al. 2012; Milner, Solomon, and Smith 2012) and the energetic costs associated with migration (Enders, Boisclair, and Roy 2005). Furthermore, the use of  $V$  allowed for comparisons across rivers of different sizes within the basin. However, we considered current velocity as an average across the river section and were unable to account for localized lateral or vertical variations, which fish may exploit during migration (Novak et al. 2023).

The associations between  $T_w$  and  $V$  used by fish were consistent across the fish monitoring stations (Figure S3), suggesting that those two factors are critical cues of diadromous species migration, with species-specific thresholds related to species abilities. Moreover, the  $T_w$ - $V$  associations selected as suitable for fish upstream migration in the Loire basin were in line with documented theoretical suitability ranges of these conditions (see Table S1 and gray dashed lines on Figure 2). These suitable associations were also found to be robust to the way the convex hulls (i.e., encompassing 50%, 80% or 90% of fish passages) were defined.

### 4.2 Species-Specific Trends in Environmental Associations Suitable for Upstream Migration

The frequency of suitable associations for allis shad and sea lamprey has increased over the 1963-2019 period across the Loire River basin. These trends align well with the ecological preferences of these species. Allis shad exhibits a preference for warmer waters (Béguet, Beaulaton, and Eric Rochard 2007; G. Lassalle and E. Rochard 2009; Paumier et al. 2019) compared to salmon, suggesting its potential benefit from water warming. Moreover, the reduction in current velocity during the migration period likely had a positive effect on both allis shad and sea lamprey, as they have relatively lower swimming capacities compared to salmon and require lower current velocities to migrate (see Table S1 and Figure 2), but only when accompanied by sufficient flow to overcome obstructions.

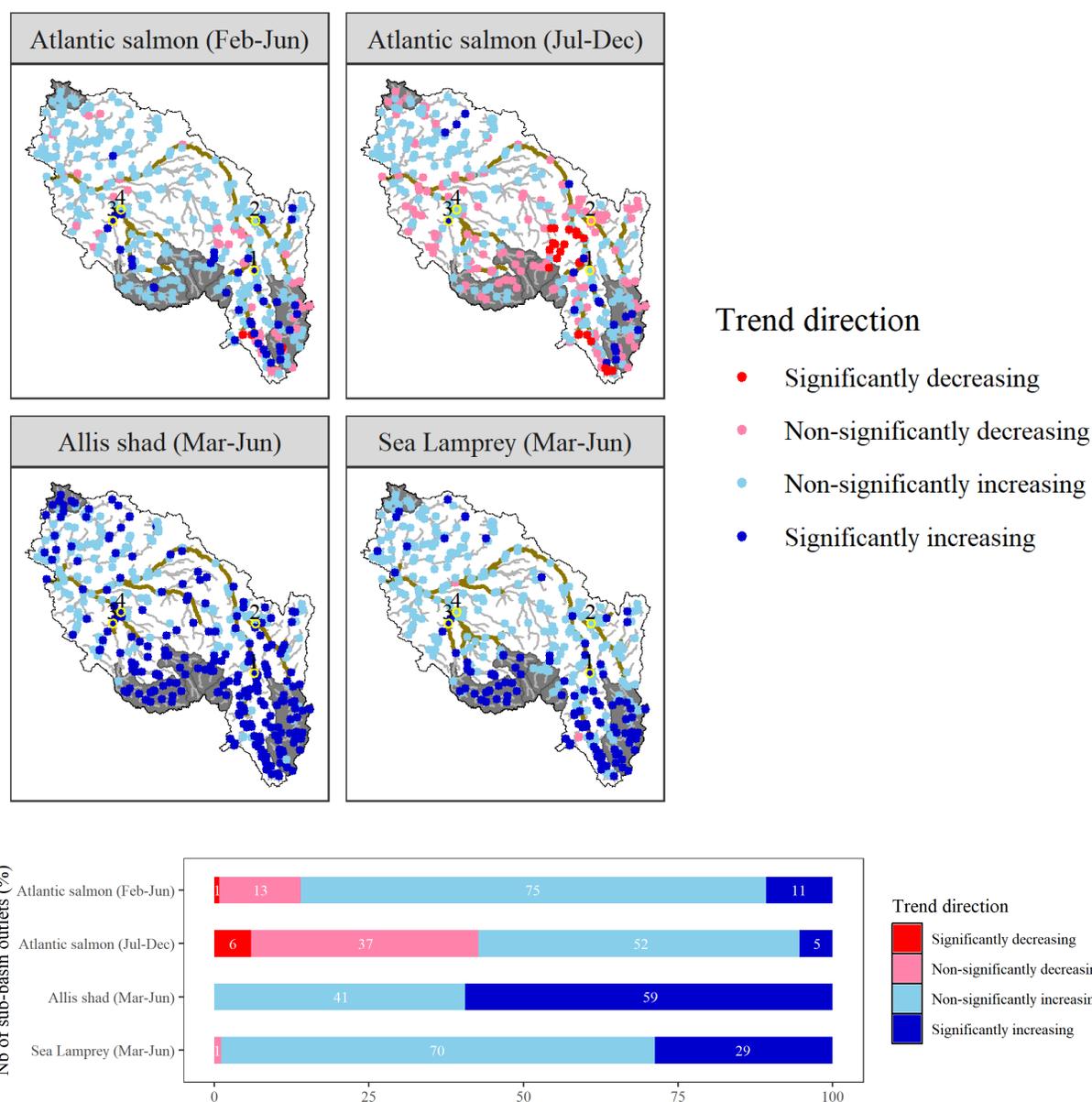


Figure 5: Direction of the trend in the percentage of suitable days at each sub-basin outlet (at the basin level) computed over the 1963-2019 period based on a Mann-Kendall test, with significance assessed at the 95% confidence level ( $p$ -value < 0.05). Map projection is Lambert-93.

In contrast to the relatively consistent trends observed for allis shad and sea lamprey over the entire basin, spatially heterogeneous changes in the frequency of occurrence of suitable associations for Atlantic salmon were observed, in particular for fall salmon. This is in line with prior research that identified a potential mismatch between the ecological preferences of salmon and the local environment due to global climate change in three coastal rivers in France (Arevalo, Maire, et al. 2021). The distinct response of Atlantic salmon to changing river conditions is not unexpected, given that salmonids are cold-water species and the rise in temperature is likely to exert signifi-

cant influences on their population dynamics (B. Jonsson and N. Jonsson 2009). More generally, climate change threatens the persistence of the populations in the southern range of the species distribution area (G. Lassalle and E. Rochard 2009).

### **4.3 Consequences of Temporal Changes in Environmental Associations on Fish Migration at the Basin Scale**

#### **4.3.1 Salmon**

The larger size of the convex hull of salmon compared to that of allis shad and sea lamprey emphasizes the more flexible conditions that salmon can use to migrate upstream and their adaptability. However, the spatial heterogeneity of trends in the number of suitable days for migration suggests that some rivers in the Loire River basin have become less suitable for salmon upstream migration. This may have hindered their migration to the most upstream areas of the basin, which are generally those used for spawning and providing the best survival rate for offspring (Beechie, Moir, and Pess 2008). Nevertheless, our results also highlighted areas that salmon could use as new migration routes due to an increasing number of suitable days, which could spatially offset the negative impacts of climate change observed in other areas of the basin. Salmon are also able to use thermal refuges located in cooler tributaries or river sections whose thermal regime is buffered by groundwater upwelling (Baird and Krueger 2003; Mackenzie-Grieve and Post 2006; Moore et al. 2012; Newell and Quinn 2005).

Another strategy for salmonids to mitigate the impact of climate change on the occurrence of suitable associations involves phenological plasticity and shifts in migration timing (Legrand, Briand, Laëtitia Buisson, Besse, et al. 2021; Otero et al. 2014; Sandlund et al. 2017). However, delaying migration might not be a viable option for fall salmon (1WS), as their suitable associations for upstream migration have been more significantly impacted than those of spring salmon (MWS). Consequently, they might be stopped relatively quickly in their upstream migration, especially in the rivers located in the lower and middle parts of the basin, where river conditions have experienced the most pronounced changes. Indeed, these reaches can serve as temporary physical barriers, impeding further upstream migration, disrupting the connectivity network, and ultimately influencing population dynamics (Alshwairikh et al. 2021). This could also explain why spring salmon seem to be more predominant than fall salmon in the basin (Figure 6). It should be also noted that although no significant decrease in salmon's population was found at the monitoring station but the continue of negative impacts induced by climate change on river conditions may jeopardize the population of these species in the future.

#### **4.3.2 Allis Shad and Sea Lamprey**

An increase in the frequency of suitable associations for allis shad and sea lamprey due to positive effects of ongoing climate change could potentially open up access to new spawning areas that were previously unsuitable, provided that physical barriers do not hinder access to these newly accessible areas. Despite this rather positive signal, a pronounced decrease in the abundance of migrating allis shad has been observed over the past decades in the Loire basin (Figure 6) and, more globally, in France (Kuczynski et al. 2017; Legrand, Briand, Laëtitia Buisson, Artur, et al.

2020). Population decrease was also observed for sea lamprey but with mainly non-significant trends.

Hence, the decline in the populations of these two species does not seem to be the result of climate-induced changes in the thermal and hydrological conditions encountered during their upstream migration, which appear to have improved with regard to their ecological preferences. Other causes, possibly acting in an additive or synergic ways, have probably contributed significantly to population declines, including pressures in freshwater or at sea, for example, water pollution, overfishing, connectivity loss (Belletti et al. 2020; Bolstad et al. 2021; Tillotson et al. 2021). Nevertheless, the latter is less concerning for our study area since an improvement of longitudinal connectivity has been observed in recent years compared to the beginning of the study period. For example, on the Loire River, the removal of the Blois dam in 2004–2005 has facilitated upstream migrations (Legrand, Briand, Laëtitia Buisson, Artur, et al. 2020). Water quality has also improved these last years but, despite this improvement, populations are not recovering (Diamond et al. 2022; Floury et al. 2012).

Other pressures, such as predation, seem to play a more significant role in the decline of populations. For example, catfish are a major predator of diadromous fish species and intense predation pressure has been reported on sea lamprey on the middle Loire (TRANCART, ROBIN, ACOU, et al. 2023) and in the Garonne-Dordogne basin (Boulêtreau et al. 2020). Furthermore, many increasing pressures, including climate-induced ones, have also affected other key life-cycle stages of the species, including growing phase, estuarine migration, and reproduction (Arevalo, Maire, et al. 2021; Paumier et al. 2019), and may thus have contributed to the decline in sea lamprey and allis shad numbers.

## 4.4 Limitations and Perspectives

### 4.4.1 Extrapolation Across the Basin and Spatial Heterogeneity

In this study, we postulated that the convex hulls obtained from the four monitoring stations could be extrapolated to the rest of the basin. However, the large scale of the basin introduces spatial heterogeneity in thermal and hydrological conditions, local hydro-morphology, and reach sizes (Milner, Solomon, and Smith 2012). This variability may lead to differences in migratory responses, behavior, and life history strategies. Deploying thermographs and limnimeters at unequipped fishways would address the scarcity of long-term joint time series on river temperature, discharge, and fish passages.

### 4.4.2 Anthropogenic Modifications

The reconstructed water temperature and current velocity data used in our study were based solely on natural conditions—climate, local topography, hydro-geometry, and vegetation—and did not account for anthropogenic modifications such as water withdrawals, dams, and reservoirs. These reconstructed time series allowed us to delineate the effects of climate change on the migratory conditions of the three species over the past five decades. However, anthropogenic structures fragment habitats, modify flow regimes, and alter thermal conditions, creating additional pressures on migratory fish populations (Grill et al. 2019). The Loire River basin contains 73 large dams with a total storage capacity of 999  $Mm^3$ , which are used for hydroelectricity, drinking water production,

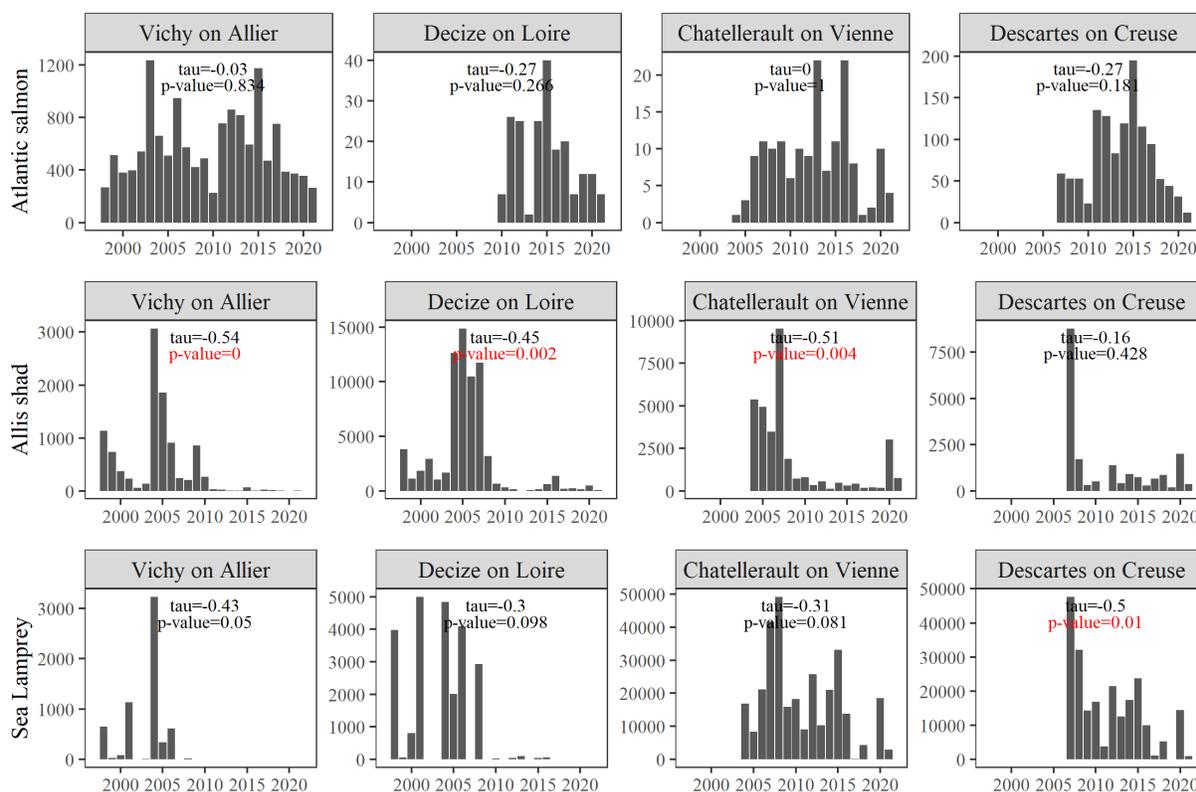


Figure 6: Annual number of fish passages for each species (arranged in rows) at each monitoring station (arranged in columns). The Mann-Kendall tau and p-value of the non-parametric monotonic temporal trend are indicated on each graph. Significant trends ( $p$ -value < 0.05) are highlighted with p-values in red.

recreation, and navigation (see Hanieh Seyedhashemi et al. 2020). Water withdrawals for irrigation and other human uses also divert significant flow volumes from the system. These anthropogenic activities can reduce river discharge during critical migration periods, lowering flow rates and creating thermal barriers that might affect fish upstream migration. Although no major new barriers were constructed downstream of the fish monitoring stations during the study period, upstream barriers can still influence migration, particularly by altering the thermal and hydrological conditions that fish rely on during their journey. This creates a complex interaction between climate-induced changes and anthropogenic pressures, which can exacerbate stress on fish populations (Kovach et al. 2015; Mantyka-pringle, Martin, and Rhodes 2012).

#### 4.4.3 Future Research Directions

Future research should integrate barriers on flow and thermal regimes into the hydrological model to assess the combined effects of climate change and human pressures on fish migration. This integration would provide a more comprehensive understanding of how both natural and human-induced changes interact to shape migration conditions in the basin. Given the long monitoring time series used to define the ‘envelope’ of suitable conditions for migration, and its consistency

with values from the literature, we believe that our characterization reasonably approximates the conditions favorable for migration encountered by migrating fish in the basin over the past decades. In our analysis, we defined suitable associations of water temperature and current velocity based on the days when fish were observed migrating, interpreting any deviations from these conditions as potentially unfavorable. However, it is possible that fish could adapt or even benefit from new river conditions outside the historically observed range (Crozier and Hutchings 2014). Potential adaptive responses in migration timing or behavior are crucial to understanding the resilience and flexibility of migratory fish species under changing conditions (Crozier and Hutchings 2014; Munsch et al. 2019). Exploring physiological limits and behavioral responses to shifting environmental conditions also represents an important avenue for future research, which will help refine our understanding of the capacity of diadromous fish to adapt to ongoing climate change.

## 5 Conclusion

In this study, we analyzed climate-induced changes in river conditions during the upstream migration of three diadromous fish species—Atlantic salmon, allis shad, and sea lamprey—using 57 years (1963–2019) of daily water temperature and current velocity data at the Loire River basin scale, along with 25 years (1997–2021) of fish passage data from four monitoring stations.

Our findings indicated that while river conditions for allis shad and sea lamprey have improved over time, offering more days with suitable conditions for their migration in terms of water temperature and current velocity, these species have experienced population declines over the same period. This suggests that their decline is not driven by climate-induced changes in river conditions, but probably by other pressures such as predation, overfishing, and changes in ocean conditions. For Atlantic salmon, particularly fall salmon, the situation is more concerning, as climate-induced changes have had a negative impact on migration conditions in certain areas.

These findings underscore the need for integrated models that account for both climate- and human-induced changes across all environments encountered by a species during its life cycle, which would allow a more comprehensive understanding of the relative importance of factors affecting the dynamics of diadromous fish populations. Policy-makers would then be able to leverage these insights to develop spatially targeted conservation strategies, identify areas where climate change may provide opportunities for migration, and ensure that access to these areas is not obstructed by barriers.

## Author contributions

Conceptualization and methodology: HS,HD,FM,AM. Software, preparation of figures and tables: HS. Conducting the research and data interpretation: HS,ML,EA. Writing draft: HS. Writing and editing: HS,HD,ML,EA,FM,AM.

## Conflict of interest

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

## Data and Code Availability

The reconstructed daily time series of water temperature and discharge were recently published as a data paper (H. Seyedhashemi, F. Moatar, et al. 2023) and can be downloaded freely in NetCDF format from <https://doi.org/10.57745/LBPGFS>.

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