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An innovative bivariate approach to detect joint temporal trends in environmental conditions: Application to large French rivers and diadromous fish

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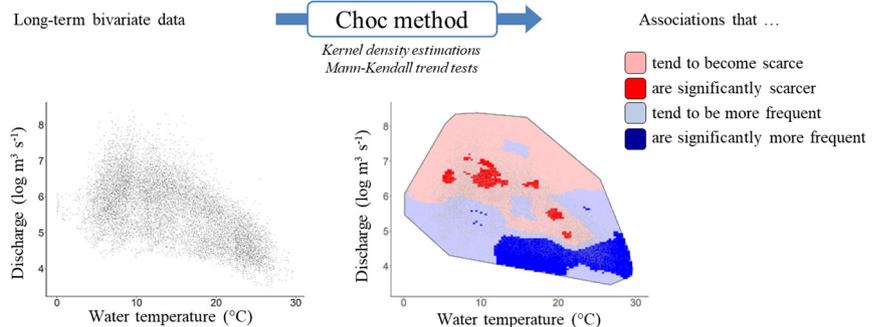
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HIGHLIGHTS

- Organism life-cycle events are synchronized and triggered by abiotic factors.
- Global changes are concurrently modifying many of these environmental factors.
- We developed a method to detect joint temporal trends in abiotic factor time series.
- We related the joint abiotic trends to diadromous fish ecological preferences.
- Changes in thermal and hydrological regimes threatened many migratory processes.

GRAPHICAL ABSTRACT



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ABSTRACT

Most key life-events of organisms are synchronized by complex interactions of several environmental cues to ensure optimal survival and growth of individuals and their offspring. However, global change is known to affect multiple components of ecosystems and cues at the same time. Therefore, detecting joint trends in covariate time series is a crucial challenge in global change ecology that has rarely been addressed so far. In this context, we designed an innovative combination of kernel density estimations and Mann-Kendall trend tests to detect joint temporal trends in a pair of environmental variables. This methodological framework was tested on >30 years (1976–2019) of water temperature and discharge data for 6 large French rivers (the Garonne, Dordogne, Rhône, Rhine, Loire and Vienne rivers). The implications of such trends in both temperature and discharge for diadromous species key life-cycle processes were then explored by checking if significant bivariate environmental changes occurred during seasons of upstream and downstream migration, and reproductive activities. Results were contrasted between rivers and seasons: many rivers displayed an increase in the number of days with high water temperature and low river discharge, but local discharge regulation measures could have mitigated the trend in discharge. Our findings showed that species migrating or spawning in spring were likely to be strongly impacted by the new environmental conditions in the Garonne, Loire and Rhône rivers, given the marked changes in water temperature and discharge associations detected by our new method. Conditions experienced by fall-running and spawning species have been strongly affected in all the rivers studied. This innovative methodology was implemented in a new R package, *ChocR*, for application to other environments and ecosystems.

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1. Introduction

Climate change is expected to have contrasting consequences between seasons and geographical regions. In Europe, precipitation is predicted to increase in winter and decrease in summer and fall (+20%, -20% and -10% respectively by 2100; Dankers and Feyen, 2008). In spring, the situation is expected to be more contrasted, with drier conditions in Mediterranean regions (-5%) and wetter conditions in northern and eastern Europe (+5%). Concurrently, air temperature is expected to increase from 3° to 5 °C by 2100 according to the RCP 8.5 scenario (Brown and Caldeira, 2017; IPCC, 2014). In freshwater environments, climate change has led to a reduction in annual river discharge (e.g., in large French rivers; Maire et al., 2019) and this trend is expected to intensify in the future (Dayon et al., 2018). Extreme events such as floods and droughts are expected to become more frequent, intense and unpredictable (Blöschl et al., 2017, 2019), along with an increase in mean water temperature of up to +1.6 °C (Bal et al., 2014; van Vliet et al., 2013a). Additionally, water withdrawal for human consumption, irrigation and industry, as well as discharge regulation for hydro-power production are also altering natural hydrological regimes in the short and long term (Nohara et al., 2006; Palmer et al., 2008; Postel and Richter, 2003; van Vliet et al., 2013a; Wada et al., 2013).

Water discharge and temperature are key abiotic factors in riverine systems. River dynamics is driven by discharge that controls sediment transport (Malavoi and Bravard, 2010). Discharge shapes the geomorphology of the channel, determines the composition of the substrate (Hart and Finelli, 1999) and defines the quality and quantity of available habitats. It also influences ecosystem processes by delivering nutrients and dissolved gases, and by limiting habitat deterioration by dilution of waste water and toxic contaminants (Rice and Westerhoff, 2017). For aquatic organisms, discharge directly determines movement and the associated energy cost (Giller and Malmqvist, 1998). Water temperature affects processes as diverse as leaf breakdown, nutrient uptake and biological productivity (Brown et al., 2004; Ficke et al., 2007). Since many aquatic organisms are ectotherms, they are restricted to a specific range of water temperatures within which physiological processes can take place (e.g., respiration, digestion, muscle activity, photosynthesis, vulnerability to diseases; Richter and Kolmes, 2005). This thermal range constrains geographical distribution and, indirectly, interactions with other organisms, e.g., predation, competition, parasitism (Allan and Castillo, 2007; Graham and Harrod, 2009). Water temperature and discharge are intricately correlated. There is a relationship between water and air temperatures in rivers (Larnier et al., 2010; Morrill et al., 2005), but hydrology greatly influences thermal regime through discharge variations (Webb et al., 2003), seasonal melt runoff (Mohseni and Stefan, 1999; Mohseni et al., 1998) and discharge barriers (Erickson and Stefan, 2000). Consequently, global change is expected to jointly modify the thermal and hydrological regimes of rivers, leading to major changes in habitat availability and quality for organisms (Lennox et al., 2019): if water temperature is likely to increase with warm conditions arriving earlier during the year, the effects on discharge are more heterogeneous. More specifically, some associations between water temperature and discharge conditions may become rarer or more frequent.

Key events in the life-cycle of organisms are often synchronized with congeners (for reproduction) or with other species (e.g., prey-predator or pollination-plant interactions; Bewick et al., 2016; Cushing, 1969; Durant et al., 2013; Memmott et al., 2007). Key events are also linked with abiotic factors (Pau et al., 2011; Tétard et al., 2019). For example, the rise in air temperature in spring triggers the migration of many birds (Saino et al., 2011) or the flowering of plants (Wheeler et al., 2015). This synchronization allows key events to occur when conditions are optimal, leading to increased growth and survival of individuals and their offspring. For fish, migration and spawning are two critical seasonal processes intrinsically related to environmental factors such as water temperature, discharge and photoperiod (Pankhurst and Porter,

2003; Pankhurst and Munday, 2011). However, expected climatic variations interacting with anthropogenic activities can send “misleading” cues to organisms and stimulate key life events when conditions are unfavorable or suboptimal. The greater the mismatch, the more severe the consequences for individual fitness and thus for population demography (Anderson et al., 2013; Miller-Rushing et al., 2010). In this context, diadromous species characterized by a high seasonality in their life cycle events appear as a relevant biological model for examining the risks associated to joint seasonal changes in environmental cues.

Diadromous fish share their life cycle between marine and freshwater environments, undertaking regular seasonal migrations between marine and continental waters (McDowall, 2008). These species generally have high cultural and socio-economical values (Aas et al., 2002) and support many ecosystem services such as provision of proteins or energy flow from marine to freshwater environments (Limburg and Waldman, 2009). They present a wide variety of life histories, with species spawning in freshwater (“anadromous”) or at sea (“catadromous”). Therefore, if environmental conditions no longer match the ecological requirements of spawners to complete their migration as a result of a combination of climatic trends and changes in water resource management practices (e.g., favorable temperature but unfavorable discharge), diadromous fish may advance, suspend or delay their migration (Fig. 1; Jonsson and Jonsson, 2009; Bruijs and Durif, 2009; Bell et al., 2017). Such shifts can directly reduce recruitment, by lowering the number of spawners and reproductive acts. Furthermore, recruitment may also be reduced indirectly: higher energy costs associated with migration would reduce the energy allocated to reproduction, resulting in production of lower-quality and less abundant gametes (Farmer et al., 2015). Additionally, if migration is delayed, spawners may have less time to reach the upstream watershed areas that are generally more suitable

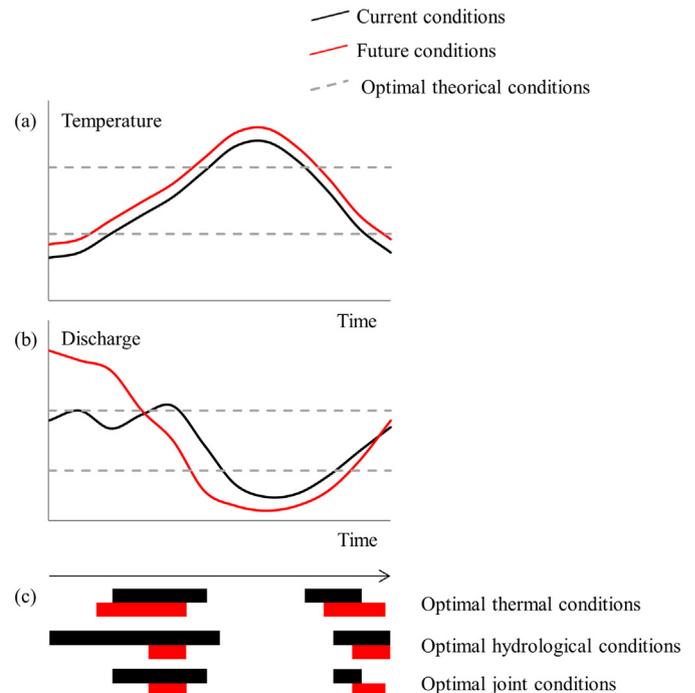


Fig. 1. Schematic representation of potential shifts in thermal and hydrological conditions under climate change. (a) River water temperatures are expected to be warmer in the future. (b) Seasonal hydrological regime of rivers are expected to change in response to climate change, with possibly higher discharge in winter and spring, and lower discharge in summer and fall. (c) Resulting shifts in optimal thermal, hydrological and joint conditions (i.e. combining temperature and discharge) for a given key life-event under climate change. In this hypothetical example, the ecological process that occurs in winter/spring is expected to shrink in the future whereas that occurring in summer/fall is expected to shift later in the season.

for spawning and offspring development. This would in turn restrict reproduction to suboptimal areas (Thorstad et al., 2008).

Studies that simultaneously integrate water temperature and discharge to explain variability in migratory fish stocks are becoming more common (e.g., Battin et al., 2007; van Vliet et al., 2013b; DeBano et al., 2016; Ayllón et al., 2019; Munsch et al., 2019; Paumier et al., 2019), but none have examined joint trends in bivariate time-series. Mann-Kendall trend test is commonly used to test temporal trends in univariate time-series, e.g., hydrological cycles (Yue and Wang, 2004), precipitation anomalies (Xu et al., 2017), water quality (Kisi and Ay, 2014) or fish density and community structure (Maire et al., 2019). However, many environmental factors, such as water temperature and discharge, are expected to be impacted differently by global changes. Since key life-events of diadromous species are triggered by these two environmental factors, it is crucial to go beyond univariate analysis and assess the joint evolution of two cues simultaneously. Recently, Flitcroft et al. (2016, 2019) proposed the "ichthyograph approach" to visually examine the suitability of water temperature and discharge associations for diadromous species. Although highly relevant, this approach did not provide any statistical tools to objectively quantify joint temporal trends in the pair of environmental variables of interest. The lack of such quantitative methods strongly limits our ability to examine the past and future effects of global changes on key life-cycle processes. To address this major methodological gap, we proposed an innovative approach involving the combination of kernel density estimations, which are commonly used to calculate densities of probability in a multi-dimensional space with continuous variables (hypervolume concept; Blonder, 2016, 2018; Blonder et al., 2014; Denoël and Ficetola, 2015), and Mann-Kendall trend tests to characterize joint temporal trends in two variables, here considered as important cues for biological processes. Then, whether the significant changes detected with this new method were taking place during key life-cycle events of emblematic diadromous species was analyzed and discussed.

In the present study, long-term time-series of water discharge and temperature recorded for 6 large French rivers (Dordogne, Garonne, Rhône, Rhine, Loire and Vienne) with contrasting hydrological and anthropogenic characteristics were used to assess and quantify temporal trends in hydrological and thermal conditions at annual and seasonal scales. The aim was to (i) develop a methodology capable of detecting changes in the occurrence of joint water temperature and discharge conditions, (ii) examine the similarities and differences between rivers, and (iii) highlight the seasons that have been most impacted by global change. The implications for diadromous species key biological processes were assessed by analysing if the significant changes were taking place during the upstream and downstream migration and reproductive seasons.

2. Material and methods

2.1. Overview of study sites

We selected 6 large French rivers (Fig. 2) for which time-series of daily water discharge and temperature were available. The hydrological regime of each river was defined according to Sauquet et al. (2008; see the mean monthly discharge per river in Supplementary, Fig. S1). To provide an overview of the anthropogenic pressures that might influence the hydrological regime in each watershed (Table S1), percentage land-cover urbanized or occupied by intensive agriculture (both requiring water extraction) was extracted from CORINE Land Cover 2018 (Büttner and Kosztra, 2007) and storage capacity for hydropower and other uses was extracted from SYRAH-CE (Chandesris et al., 2009; Chandesris et al., 2008). The Dordogne is a pluvial river (i.e., a hydrological regime characterized by a gradual decrease in discharge from January to June, followed by a period of low discharge in summer and an increase in fall). Intensive agriculture in the watershed is moderate and the storage capacity for hydropower is significant on this river.

The Garonne is a pluvio-nival river (i.e., a hydrological regime similar to a pluvial regime but with a significant contribution of snowmelt to spring discharge) with major spring floods. Intensive agriculture is highly developed in this watershed and use of water for hydropower is moderate. The Loire is a pluvio-nival river the hydrological regime of which is still quite natural, with moderate development of intensive agriculture and hydropower. The Vienne River is a tributary of the Loire River but its regime is less influenced by snowmelt than that of the Loire, while water uses (intensive agriculture and hydropower) are similar. The Rhône is a highly anthropized river the pluvio-nival hydrological regime of which is intensively regulated. Intensive agriculture is low to moderate, but the watershed is densely populated and has a large number of hydropower plants. The Rhine is a highly anthropized pluvio-nival river subject to large natural floods. Intensive agriculture and hydropower are highly developed.

2.2. Water temperature and discharge times-series

For each of these 6 rivers, daily average water temperature (in °C) and discharge (in $\text{m}^3 \text{s}^{-1}$) have been monitored for several decades upstream of nuclear power plants (for the Garonne, Loire, Rhône and Vienne rivers) or large dams (for the Dordogne and Rhine rivers) operated by Electricité de France (Fig. 2). When discharge data were not available at the nuclear power plant or dam, data from BanqueHYDRO (<http://www.hydro.eaufrance.fr/>) at the nearest station (maximum distance between discharge and water temperature monitoring station = 40 km) were used. When data were missing for >3 consecutive weeks for at least one of the two variables, the corresponding year was excluded from analyses. A total of 194 years of combined water discharge and temperature data were included in the analyses (Table 1). This represented an average of 32.3 ± 8.4 (mean \pm standard deviation) years per site. Despite the removal of years (between 1 and 4 years depending on the site; Table 1), the time-series ranged from 21 to 40 years for the Dordogne and Loire rivers, respectively. The main features of the rivers at the study sites (i.e., upstream drainage area, time period covered by the data-set, average annual water temperature and discharge) are presented in Table 1. Summary statistics of seasonal water temperature and discharge are provided in Tables S2 and S3, respectively.

2.3. Statistical analyses to detect joint temporal trends

Analyses were conducted in the same way and independently for each site. Discharge was log-transformed to avoid excess scatter and to normalize the data. To assess univariate monotonic trends in water temperature and discharge series, seasonal Mann-Kendall trend tests were carried out on the monthly averages for each variable (Libiseller and Grimvall, 2002; Zhang et al., 2016). Then, since no method was available to quantify joint trends in the associations between the values of two variables (here, water temperature and discharge), we developed one specifically for that purpose: the Choc method (see Appendix A for its fully detailed description). It consists in two steps. First, to quantify the annual density of probability of any pairs of water temperature and discharge conditions, yearly densities of probability were estimated with kernels at each pair of water temperature and discharge conditions. Second, to detect monotonic temporal trend, Mann-Kendall trend tests were used on the densities of probability over the period for each pair of water temperature and discharge conditions. The smoothness of the kernel density curves depended on the value of the bandwidth parameter (H), which was selected according to the plug-in method (Chacón and Duong, 2010; Duong and Hazelton, 2003; see an in-depth description of the bandwidth's choice in Appendix B). Statistical significance was assessed by comparing results with those from artificial datasets generated under the null hypothesis. The null hypothesis implied that the frequency of a given water temperature and discharge association did not change over time while the alternative hypothesis implied a more or less frequent association over time.

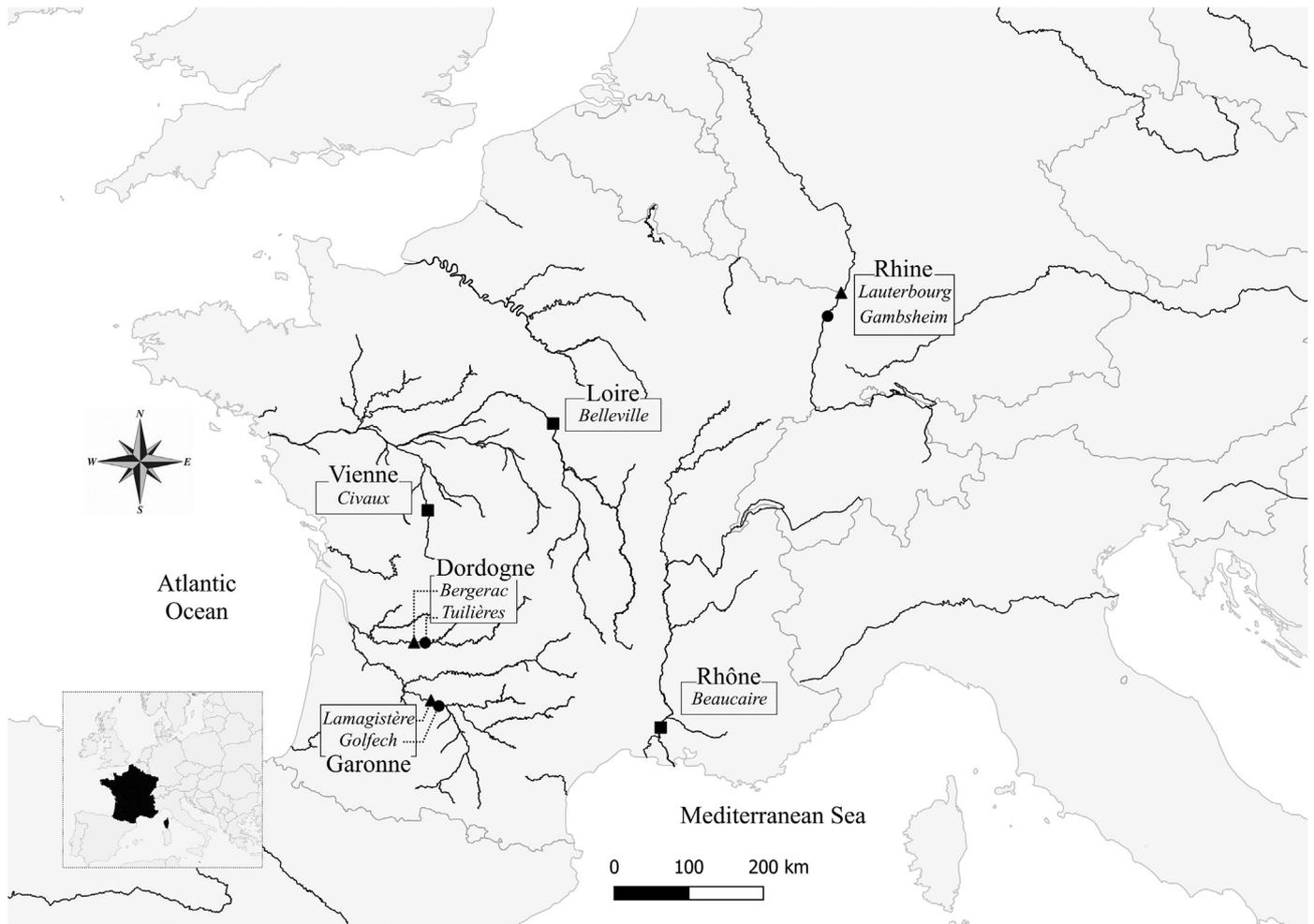


Fig. 2. Location of the monitoring stations for water temperature (●), discharge (▲) or both (■) on the 6 rivers studied.

Two methods were proposed to simulate artificial datasets under null hypothesis, permutations and sampling in kernel, but since both methods provide similar results, we only focused on the second method (see Appendix A, Fig.A1).

To visualise how the associations between the two variables have changed over the study period, two-dimensional heatmaps were drawn with water temperature on the x-axis and log-discharge on the y-axis. On these heatmaps, blue areas indicate water temperature and discharge associations that have become more frequent (positive Mann-Kendall's tau coefficient), while red ones indicate water temperature and discharge associations that have become less frequent (negative Mann-Kendall's tau coefficient). Dark colored areas indicate statistically significant trends, while light colored ones indicate non-

significant trends. The plot region was restricted to the convex hull that encompassed all points in the dataset to avoid extrapolation. Then, the area of regions showing a significant negative or positive trend was divided by the total area of the convex hull to obtain an indicator (%) of water temperature and discharge associations that became more or less frequent over the study period.

This approach was applied on the entire dataset (annual scale) and on predefined ecological seasons (seasonal scale). Four seasons were defined according to the life-cycle of most diadromous species: winter from January to March, spring from April to June, summer from July to September and fall from October to December. The entire methodology was implemented in the R software "ChocR" package (R Development Core Team, 2019).

Table 1
Selected sites and corresponding upstream drainage areas, length of the time series, number of years eliminated from and included in the analyses and average (mean \pm standard deviation) annual water temperature and discharge.

River	Stations		Upstream drainage area (km ²)	Time period	Number of years		Water temperature (°C) Mean \pm SD	Discharge (m ³ s ⁻¹) Mean \pm SD
	Water temperature	Discharge			Excluded	Analyzed		
Dordogne	Tuilières	Bergerac	14,000	1993–2018	4	21	14.4 \pm 6.2	252 \pm 235
Garonne	Golfèch	Lamagistère	32,700	1976–2018	4	38	14.5 \pm 6.4	386 \pm 363
Rhône	Beaucaire	Beaucaire	102,200	1977–2018	2	39	14.6 \pm 5.9	1691 \pm 998
Rhine	Gambsheim	Lauterbourg	5000	1994–2019	2	23	13.4 \pm 6.0	1263 \pm 538
Loire	Belleville	Belleville	35,200	1978–2019	1	40	13.1 \pm 6.9	308 \pm 294
Vienne	Civaux	Civaux	5800	1980–2015	2	33	13.9 \pm 6.7	80 \pm 86

2.4. Assessing potential implications for diadromous species

Seven species of diadromous species are frequently found in French rivers and may be impacted by concomitant changes in water temperature and river discharge over the last decades. To detect potential implications in terms of diadromous species life cycle, the first step consisted in identifying their migration and spawning seasons as well as the environmental conditions usually associated with these events at the specific scale. To do so, we reviewed the literature available on this topic for the seven species as presented below:

- Atlantic salmon (*Salmo salar*) begin their upstream migration to reach spawning areas from March to early summer. A second migration period takes place during the fall. Spawners generally migrate when water temperature is between 6° and 20 °C (Alabaster, 1990; Baisez et al., 2011) and when discharge increases (Gowans et al., 1999; Jonsson and Jonsson, 2009; Jonsson, 1991; Thorstad et al., 2008), and reproduce from November to January when water temperature is around 8.5 °C (Armstrong et al., 2003). After 1–2 years' growth in freshwater, juveniles become “smolts” and migrate toward the ocean in spring and early summer (Otero et al., 2014) when the water is cold or cool, with a possible role of increased discharge (Hvidsten et al., 1995).
- Sea lamprey (*Petromyzon marinus*) migrate upstream from February to June and spawn between late May and late June. Adult lamprey seem more active (in both migrating and spawning) when the water temperatures are between 7° and 20 °C, with maximum activity at 15 °C (Binder and McDonald, 2008). In addition, a rapid increase in water temperature seems to stimulate migration and reproduction (Binder et al., 2010). After 2–8 years in freshwater, young lamprey begin their downstream migration from fall to late winter, when river discharge markedly increases. There is no known relationship between water temperature and the downstream migration of lampreys (ICES, 2015).
- European river lamprey (*Lampetra fluviatilis*) migrates upstream from February to April when the water temperature exceeds 8 °C (Keith et al., 2011). Adults spawn in April–May when water temperature is between 10° and 14 °C. Similarly to sea lamprey, juveniles migrate downstream from fall to winter, with no known trigger effect of water temperature (Keith et al., 2011).
- European sturgeon (*Acipenser sturio*) migrate from the ocean to the downstream parts of watersheds in spring, during periods of high discharge and when water temperature is above 12 °C (Rochard et al., 2009). They spawn between May and June when water temperature is generally between 15° and 20 °C (Rochard et al., 2009). After spawning, adults return to the ocean. Juveniles spend a year in freshwater before migrating to the estuary in fall (Rochard et al., 2001).
- Allis shad (*Alosa alosa*) generally migrate to freshwater from late February to June. At water temperature around 10–11 °C, migration has been recorded but is limited (Baglinière et al., 2003). Adults generally migrate when water temperature is between 12° and 20 °C (Baglinière et al., 2003). Adults spawn from May to mid-August when water temperature ranges from 12° to 19 °C, with reproduction peaking at 16–18 °C (Cassou-Leins et al., 2000). After only a few months in freshwater, juveniles migrate to the ocean in late summer and fall (Boisneau et al., 2008).
- For twaite shad (*Alosa fallax*), spawning migration takes place from February to May when water temperature exceeds 10 °C (Aprahamian et al., 2003; Keith et al., 2011). Reproduction is observed between May and June, when water temperature is between 18° and 22 °C (Keith et al., 2011). Then, after 1–3 months' growth in freshwater, juveniles migrate to the estuary in fall. Downstream migration of allis and twaite shad juveniles is closely associated with fall floods (ICES, 2015). Twaite shad in the Mediterranean area (Rhône River in the present dataset) belong to a

specific sub-species, *Alosa fallax rhodanensis*, distinct from the *Alosa fallax fallax* sub-species found elsewhere (Keith et al., 2011).

- The one catadromous species considered here, the European eel (*Anguilla anguilla*), migrates downstream to spawn at sea mainly in fall and early winter, although this period sometimes extends into spring, especially in fragmented rivers (Acou et al., 2008; Bruijs and Durif, 2009; Feunteun et al., 2000), when water temperature is between 4° and 23 °C (optimal range: 6–10 °C) and discharge increases (Acou et al., 2008; Stein et al., 2016). Young stages (glass and yellow eels) begin upstream migration in freshwater from September to April (ICES, 2020), although this period may extend throughout the year, when water temperature is between 12° and 20 °C (August and Hicks, 2008).

Then, potentially impaired seasonal ecological processes (i.e., upstream and downstream migration and spawning) were assessed for each river by comparing the seasons with most changes detected by the “Choc” method in terms of water temperature and discharge with the literature-based timing of these three key life-cycle events (Table 2). Crossing these two types of information will help the detection of processes and species most at risk.

3. Results

According to the seasonal Mann-Kendall trend tests, water temperature increased at all stations over time, mainly due to warmer springs, summers and falls (Table 3). The Rhône River experienced the highest annual and seasonal increases in water temperature, while the Dordogne, Rhine and Vienne rivers showed the lowest. For all rivers apart from the Vienne River, discharge decreased at annual scale over the study period (Table 4). The annual trend in water discharge was mainly driven by decreasing trends in summer and early fall. Discharge in the Vienne River did not exhibit any significant change over the study period.

At annual scale, the Garonne River had the highest percentage of significant trends in associations of water temperature and discharge (19.0%) and the Rhine River had the lowest (0.7%; Table 5). The Rhône River showed substantial changes in all seasons (ranging from 14.7% in fall to 40.5% in summer). The Dordogne River experienced significant changes mainly in fall (43.5%) but also in spring (9.3%) and summer (9.0%) to a lesser extent. For the Loire River, changes were mostly in spring (16.9%), winter (11.7%) and summer (11.1%). For the Garonne, Rhine and Vienne rivers, summer was the season that changed the most (between 14.1% and 45.8%), followed by spring for the Garonne (18.3%) and fall for the Rhine (1.2%) and Vienne (5.2%) rivers.

At annual scale, though rates of days with high discharge and low-to-intermediate temperature tended to decrease for all rivers, different patterns were observed (Fig. 3). For the Loire and Garonne rivers, the number of days with low discharge and high water temperature increased. The pattern for the Rhône River showed an increase in water temperature with a large range of discharge (the blue region being parallel to the y-axis in Fig. 3). The pattern on the Dordogne River was slightly different, with increased occurrence of low discharge associated with moderate temperature. The Vienne and Rhine rivers displayed atypical patterns: almost no significant change in the associations of water temperature and discharge for the Rhine River (consistent with the limited number of significant Mann-Kendall trend tests) and a decrease in occurrence of droughts in the Vienne River (i.e., high temperature and low discharge) compensated for by an increase in the number of days with intermediate discharge and water temperature.

Overall, this classification remains valid at seasonal scale (Fig. 3). Prevalence of warm water and low discharge increased in all seasons in the Garonne and Loire rivers, while days with intermediate discharge and low water temperature became rarer in spring and summer (for the Garonne River especially). For the Rhône River, seasonal patterns were similar to the annual pattern with more frequent warm conditions for

Table 2
Time periods of key life cycle events (upstream migration, spawning and downstream migration) for the 7 European diadromous fish species of interest and the optimal temperature range associated with these events.

Key life-cycle events in freshwater		Winter (JFM)	Spring (AMJ)	Summer (JAS)	Fall (OND)	Temperature range
Atlantic salmon (<i>Salmo salar</i>)						
	Upstream migration					9-20°C ^{1,2}
	Spawning					~ 8.5°C ³
	Downstream migration					Cold-Moderate ⁴
Sea lamprey (<i>Petromyzon marinus</i>)						
	Upstream migration					7-20°C ^{5,6}
	Spawning					7-20°C ^{5,6}
	Downstream migration					No relation with T ⁷
European river lamprey (<i>Lampetra fluviatilis</i>)						
	Upstream migration					> 8°C ⁸
	Spawning					10-14°C ⁸
	Downstream migration					No relation with T ⁸
European sturgeon (<i>Acipenser sturio</i>)						
	Upstream migration					> 12°C ⁹
	Spawning					15-20°C ⁹
	Downstream migration					
Allis shad (<i>Alosa alosa</i>)						
	Upstream migration					12-20°C ¹⁰
	Spawning					12-19°C ¹¹
	Downstream migration					No relation with T ⁷
Twaite shad (<i>Alosa fallax</i>)						
	Upstream migration					> 10°C ^{12,8}
	Spawning					18-22°C ⁸
	Downstream migration					No relation with T ⁷
European eel (<i>Anguilla anguilla</i>)						
	Upstream migration					12-20°C ¹³
	Downstream migration					4-23°C ^{14,15}

Table footnotes: References cited regarding the optimal temperature range of the key life-cycle events for each species. 1: Alabaster (1990); 2: Baisez et al. (2011); 3: Armstrong et al. (2003); 4: Hvidsten et al. (1995); 5: Binder and McDonald (2008); 6: Binder et al. (2010); 7: ICES (2015); 8: Keith et al. (2011); 9: Rochard et al. (2009); 10: Baglinière et al. (2003); 11: Cassou-Leins et al. (2000); 12: Aprahamian et al. (2003); 13: August and Hicks (2008); 14: Acou et al. (2008); 15: Stein et al. (2016).

the whole range of discharge. For the Rhine River, seasonal patterns were consistent with the annual pattern, with few significant changes in occurrence, except in summer with an overall decrease in high discharge associated with low temperature over the study period. For the Dordogne River, patterns differed between seasons, with very few changes in winter and summer, a smaller number of days with low temperature and low discharge in spring, and a decrease in discharge in fall. In addition, discharge seemed more stable in spring and summer, with greater occurrence (significant or not) of intermediate discharge at the expense of high- and low-flow conditions.

The Dordogne and Garonne rivers host the seven diadromous species of interest. In the Dordogne River, intermediate and stable

discharge in spring could be beneficial to spring runners, while reduced discharge in fall could be detrimental to fall runners. On the Garonne River, water temperatures in springs and summers increasingly exceeded 20 °C over the study period, which is the upper threshold for most fish key events in the river. The Rhône River is inhabited by four diadromous species: sea and European river lamprey, European eel and twaite shad. Water temperature in the Rhône River has increased in all seasons and the situation is particularly alarming in spring, summer and fall, when water temperatures increasingly exceeded the optimal thermal range for the key life-events of all these 4 species. The Rhine, Loire and Vienne rivers host five diadromous species: Atlantic salmon, sea lamprey, European eel, and allis and twaite shads. The

Table 3
Seasonal Mann-Kendall trend tests performed on water temperature for each river at annual and monthly scales. Arrows symbolize a significant trend (p-value <0.05) and their direction indicates an upward or downward trend. Empty cells indicate non-significant results.

	Yearly	Winter			Spring			Summer			Fall		
		J	F	M	A	M	J	J	A	S	O	N	D
Dordogne	↗												
Garonne	↗				↗	↗	↗	↗	↗	↗	↗	↗	↗
Rhône	↗	↗		↗	↗	↗	↗	↗	↗	↗	↗	↗	↗
Rhine	↗				↗								
Loire	↗				↗	↗	↗	↗			↗	↗	
Vienne	↗							↗					

Table 4
Seasonal Mann-Kendall trend tests performed on log-transformed discharge for each river at annual and monthly scales. Arrows symbolize a significant trend (p-value <0.05) and their direction indicates an upward or downward trend. Empty cells indicate non-significant results.

	Yearly	Winter			Spring			Summer			Fall		
		J	F	M	A	M	J	J	A	S	O	N	D
Dordogne	↘										↘	↘	↘
Garonne	↘								↘	↘	↘	↘	↘
Rhône	↘							↘	↘				
Rhine	↘												
Loire	↘				↘								
Vienne	↘												

European river lamprey is also found in the Loire River. The few temporal trends in water discharge and temperature observed for the Rhine River raise only minor concerns for the achievement of key life-events of diadromous species. In the Loire River, the increase in water temperature in winter could become problematic for the reproduction of Atlantic salmon, but is not expected to affect other migratory processes. In spring, reduced discharge and higher water temperature (more frequently exceeding 20 °C) probably jeopardize key life-events of all the species of interest. In summer and fall, warm periods increased in frequency, but water temperature mostly remained within the optimal thermal range for the key life-events of interest. In the Vienne River, the situation is almost the same as in the Loire River.

4. Discussion

4.1. Long-term changes in the hydrological and thermal regimes of large French rivers

In recent decades, hydrology and water temperature were found to have significantly changed for the 6 rivers studied. According to Dayon et al. (2018), projections for 2100 under the RCP 8.5 scenario forecasted an increase in winter and spring river discharge in areas north of the Seine River, while river discharge is expected to decrease in the south. The Rhine River is the only river studied that is located in this northern zone. The Rhine River has the highest water storage capacity (taking all uses together) of the 6 rivers and its hydrology is also highly dependent on the management of the upstream lakes (especially Lake Constance), located in Germany and Switzerland. Its discharge is thus highly regulated and different from what would be normally expected from a pluvio-nival regime. Few significant temporal trends were detected on the present analysis for this river, probably due to the previously described anthropogenic alterations that may have buffered the effects of climate change. Under the RCP 8.5 scenario, Dayon et al. (2018) also projected a slight decrease in precipitation accompanied by a significant increase in evapotranspiration for the Loire and Garonne rivers, which are likely to show reduced discharge from December to June. This expected decrease in discharge is already observed in the Loire River, but not in the Garonne, where the hydrological contribution of snow is greater. Most of the winter precipitation is stored as snow in the Pyrenees mountains and, with the rise in spring temperatures, snowmelt occurs earlier in the season and increases spring discharge (Tisseuil et al., 2010). This early snowmelt could explain the discharge stability in winter observed in the Garonne River, and the decreasing trend in high-flow conditions in spring. The decrease in the discharge of the Garonne River in winter and spring is expected to be exacerbated by 2030 (Hendrickx and Sauquet, 2013) and 2050 (Boé et al., 2009; Caballero et al., 2007). Storage capacity for hydropower is high in the Dordogne River, which likely explains the observed discharge homogenization for this river. Flow barriers reduce discharge variability, convert lotic river sections into more lentic ones and create reservoirs (Assani et al., 2006; Lytle and Poff, 2004; Poff et al., 2007). These hydrological effects

can persist over hundreds of kilometers upstream and downstream of the largest dams and accumulate over consecutive dams, resulting in more intense effects on aquatic ecosystems (Beatty et al., 2009; Grill et al., 2015; McCartney, 2009). The Rhône River has also a pluvio-nival hydrological regime, but no influence of earlier snowmelt has been detected. This lack of trend can be explained by the far downstream location of the monitoring station in the Rhône watershed. The influence of snowmelt has probably been counterbalanced by water withdrawals for agriculture and the large storage capacity for hydropower in upstream tributaries.

In summer, climate change is expected to increase the frequency of droughts (Ledger and Milner, 2015; Reid et al., 2019; Trenberth et al., 2014) in a context of greater water scarcity due to increasing withdrawal (Rodell et al., 2018). The present results showed that such trends can already be observed on the Garonne, Loire and Rhine rivers. Droughts are expected to become more severe in Mediterranean regions (where a significant part of the Rhône watershed is located) than in temperate regions, due to high storage needs and reservoir capacity because of the intrinsic scarcity of water resources (Belmar et al., 2013; Lorenzo-Lacruz et al., 2010). We also found that hydrological and thermal conditions in fall are becoming more and more similar to those usually found in summer (e.g., more frequent ranges of common values between the two seasons), especially on the Rhône River. This finding supports the hypothesis that summer conditions, such as low-flow periods, may increasingly persist in fall (at least until October) in the coming decades (Trenberth et al., 2014). Droughts adversely affect habitat connectivity and water chemistry (Bond et al., 2008; Lake, 2003a, 2003b), and the composition and structure of aquatic communities, in which changes mostly depend on the duration of the low-flow period (Bogan et al., 2015; Lennox et al., 2019; Rolls et al., 2012). Droughts have considerable ecological and economic consequences (Harou et al., 2010; Wilhite et al., 2014) but dams can buffer this hydrological anomaly related to climate change and release water to maintain minimum discharge in rivers during summer (Palmer et al., 2008; Rossi, 2000; Rossi et al., 2005). Such a management strategy is already implemented in the Dordogne and Vienne rivers to support watershed activities, resulting in an artificial increase in summer discharge. However, most of these mitigation measures are still under optimization (Sauquet et al., 2019) and there is as yet no evidence of their long-term effectiveness on aquatic ecosystems.

4.2. Can the desynchronization of water temperature and discharge lead to suboptimal conditions for diadromous species?

The changes in water discharge and temperature highlighted in this study when related to species preferences further raise the question of whether these new conditions are still conducive to the achievement of the key-life events of diadromous species. When environmental conditions change, one of the ways diadromous species can adapt is by shifting the timing of key events to limit adverse consequences. In our literature review, winter and spring were unanimously identified as key seasons for the reproduction of diadromous species (Table 2). The increase in

Table 5

Percentage significant changes in the occurrence of temperature and discharge associations for each river at annual and seasonal scales. Total percentage change and the percentage of associations that became more or less frequent are shown ("Gain" and "Loss", respectively). Bold values indicate the season with the highest percentage change for each river.

River	% change in the occurrence of temperature and discharge associations														
	Yearly			Winter (JFM)			Spring (AMJ)			Summer (JAS)			Fall (OND)		
	Total	Gain	Loss	Total	Gain	Loss	Total	Gain	Loss	Total	Gain	Loss	Total	Gain	Loss
Dordogne	7.0	3.5	3.5	0.1	0.1	0	9.3	0	9.3	9.0	0	9.0	43.5	16.5	27.0
Garonne	19.0	15.2	3.8	2.8	2.8	0	18.3	13.5	4.8	45.8	12.3	33.5	8.9	8.9	0.0
Rhône	16.5	14.1	2.4	19.7	16.5	3.2	28.8	26.7	2.1	40.5	31.0	9.5	14.7	14.7	0.0
Rhine	0.7	0.1	0.6	0.1	0.1	0	0	0	0	14.1	0.3	13.7	1.2	0	1.2
Loire	6.6	5.2	1.4	11.7	11.7	0	16.9	11.8	5.1	11.1	0.9	10.2	2.2	2.2	0
Vienne	11.8	4.1	7.7	2.0	2.0	0	2.4	2.4	0	19.6	4.5	15.1	5.2	4.8	0.4

water temperature observed on the Loire, Garonne and Rhône rivers may have had huge consequences on reproduction timing: warmer temperatures reduce the duration of egg development (Pankhurst and Munday, 2011) and fish generally delay their spawning to maintain the development of juveniles when foraging conditions are optimal (Einum and Fleming, 2000; Letcher et al., 2004; Webb and McLay, 1996). The situation is probably even worse in the Garonne and Loire rivers, where the increase in water temperature has proved to be concomitant with a decrease in discharge, which is a major trigger for migration. Conversely, it seems that warmer water temperatures lead to earlier spawning of allis shad in the Garonne and Dordogne rivers (Boisneau et al., 2008), likely triggering an increase in primary and secondary productivity earlier in spring (Hannesdóttir et al., 2013), so that the favorable period for larvae hatching may be advanced, but it is still difficult to say whether these processes (reproduction, incubation duration, hatching, productivity) shift in time in the same direction and with the same intensity (Crozier et al., 2008). Moreover, Paumier et al. (2019) clearly showed that the spawning was under the combined control of temperature, discharge and photoperiod. Additionally, warmer winters and drier springs may result in advanced fish migrations to avoid high (and possibly lethal) temperatures. In the Loire River, Kuczynski et al. (2017) concluded that all diadromous species migrated upstream earlier in spring, by a few days to several weeks, over the last 20 years. Similarly, an earlier upstream migration in spring was reported for salmonid spawners (Hodgson and Quinn, 2002

and Keefer et al., 2008 in North America), several shad species (Lombardo et al., 2019 in North Carolina), as well as earlier downstream migration of salmonid smolts (Sykes et al., 2009 in North America), with strong selection against late migrants (Sturrock et al., 2020 in Californian river systems).

In contrast, summer and fall migrations are likely to be postponed until water temperatures drop and discharge rises. Baisez et al. (2011) tracked adult Atlantic salmon in the Loire River and its main tributaries and found that salmon temporarily stopped their upstream migration when the water temperature exceeded 20 °C, resulting in delayed migration, and even in the inability of some spawners to reach the most suitable upstream areas in time to spawn. Drouineau et al. (2017) demonstrated a combined influence of water temperature and discharge on silver eel migration: high discharge associated with warm temperature was crucial for eels to achieve migration to the sea. Diadromous species responded similarly in the Columbia River (Idaho, United States) where Quinn et al. (1997) assessed changes in discharge and temperature caused by water management. These environmental changes were accompanied by marked changes in fish behavior, and by earlier migration of sockeye salmon (*Oncorhynchus nerka*) in spring due to reduced discharge and warmer water temperatures, while the later drop in water temperature in fall delayed the migration of other salmonids. Whatever the season, global changes are also expected to reduce the diversity of traits and life-history portfolios (Sturrock et al., 2020). The

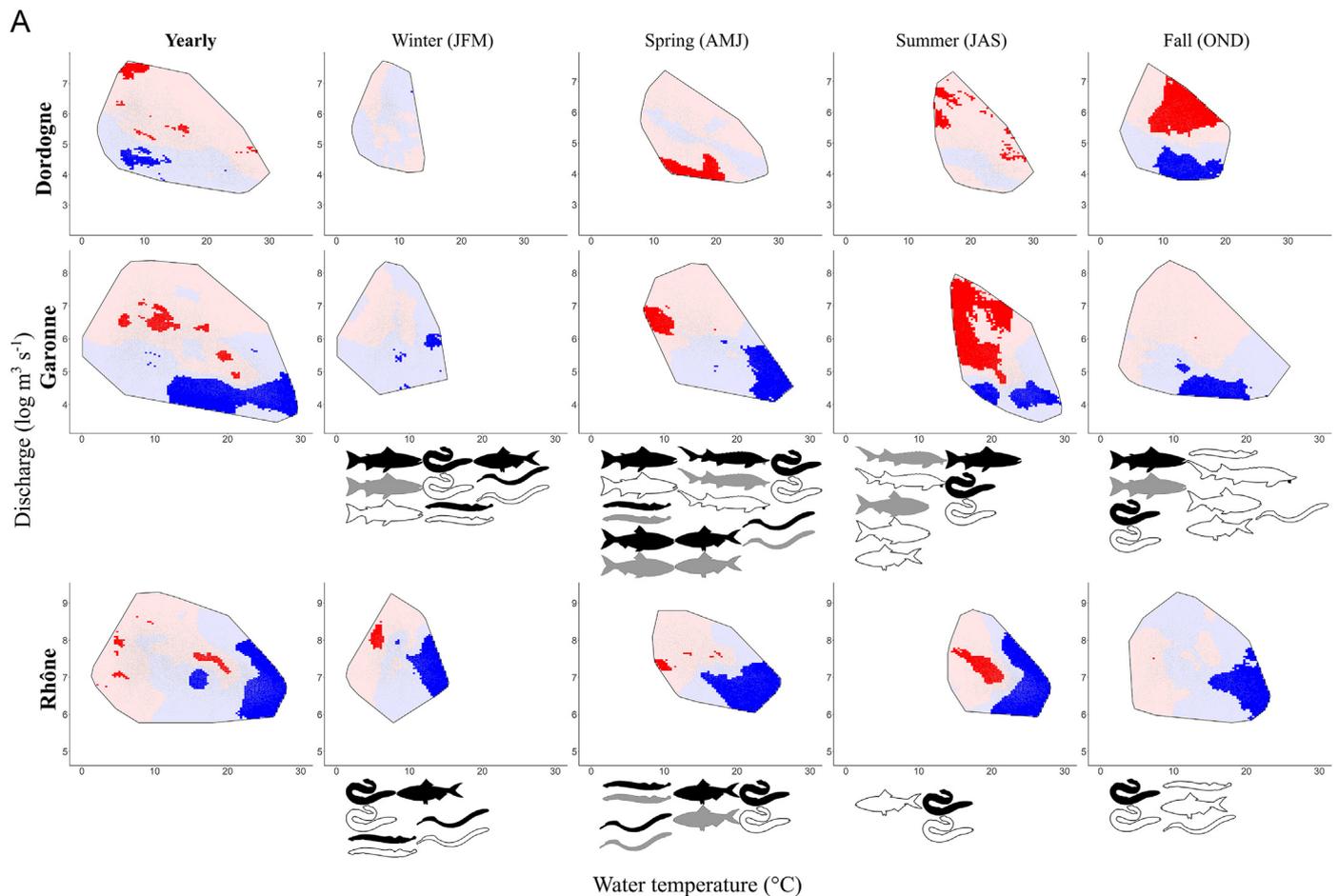


Fig. 3. Two-dimensional space of log-transformed discharge (Y-axis; $\log \text{m}^3 \text{s}^{-1}$) and water temperature (X-axis; °C) for each river at annual and seasonal scales. Water discharge and temperature associations that have become more or less frequent over the study period are shown in blue or red, respectively. Light or dark colors correspond to non-significant and significant trends, respectively (e.g., dark red corresponds to significant decreasing trends, light blue to non-significant increasing trends). The gray line delineates the edge of the convex hull (i.e., the smallest space encompassing all the points of the annual or seasonal datasets). For Atlantic salmon , European eel , sea lamprey , European river lamprey , European sturgeon , allis shad  and twaite shad , the season(s) of upstream migration (in black), spawning (in gray) and downstream migration (in white) are specified for the river(s) in which the species is present.

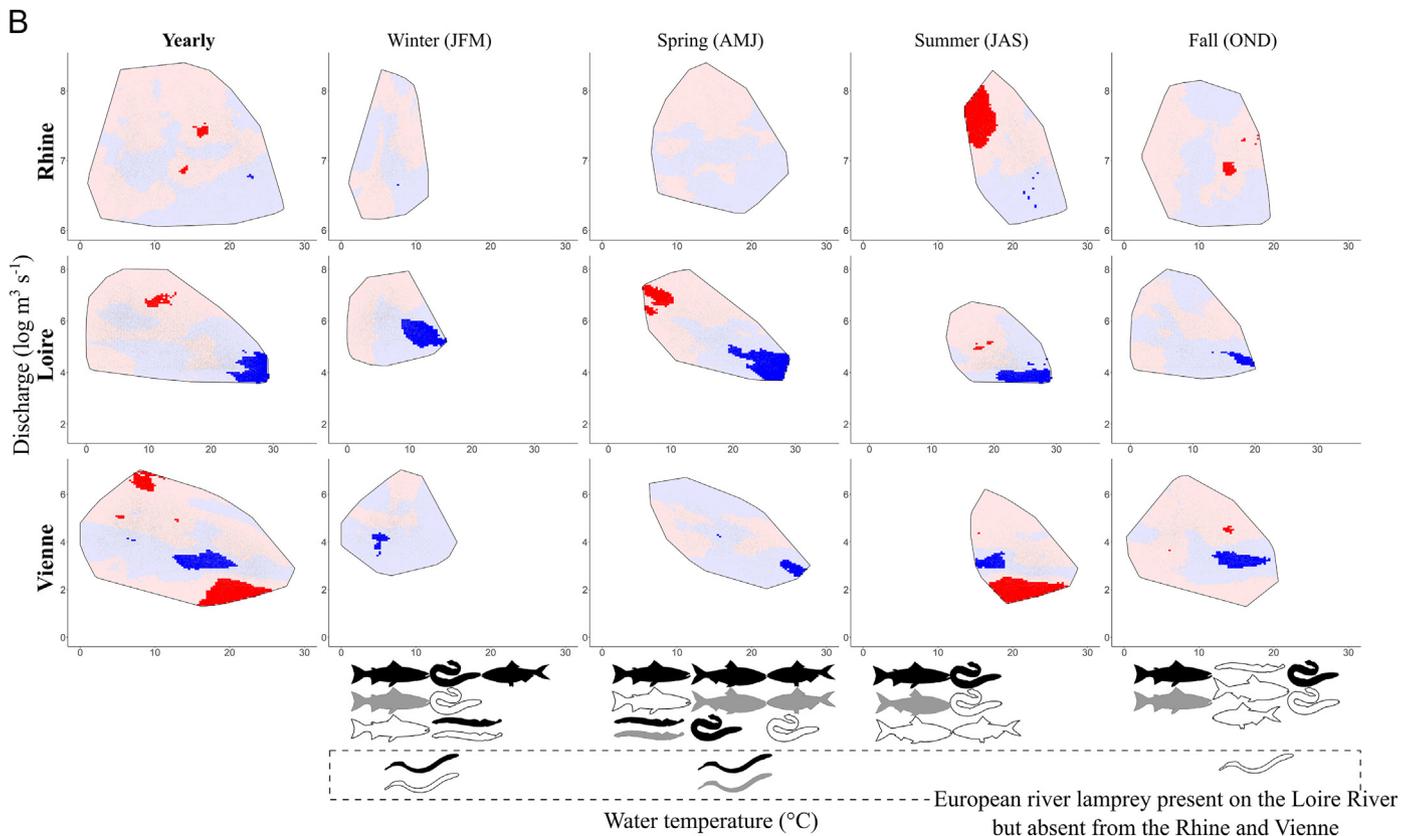


Fig. 3 (continued).

consequences of global changes on the key life-events of most species (e.g., river or sea lamprey) are still largely unknown and urgently need to be further studied. Similarly, key life-events of diadromous species are driven by several factors, including photoperiod and lunar phase, which are not affected by global changes (Lucas and Baras, 2001; Pankhurst and Porter, 2003; Stein et al., 2016). Therefore, experiments on the effect of interactions between these factors on fish events are essential for better understanding and prediction of population dynamics.

4.3. Discussing the methodological approach

This article describes a new methodology for studying temporal changes in the association between two variables, without choosing a reference period. As emphasized by Willis and Birks (2006), it is difficult to determine a relevant and robust baseline that would simultaneously take account of the range of natural variation and reveal impacts related to disturbances. Due to the complexity of hydrological cycles, long time-series are required to overcome the biases due to the inherent variability of hydrological regimes (Burn, 1994) and to detect significant hydroclimatic changes (i.e., the “Invisible Present”; Magnuson, 1990). In the present study, Mann-Kendall trend tests were first applied to monthly means and provided overall monthly trends. In the context of global change, this test is, however, poorly adapted for detecting changes in the variation or occurrence of extreme events. The method here proposed, which combines kernel density estimates with Mann-Kendall trend tests, allows identification of joint water temperature and discharge conditions that have become more or less frequent over the study period. The situation on the Vienne River is a perfect illustration of the relevance of combining the two methods. The management practices to support the Vienne River discharge during low-flow periods probably reduced variation, without changing mean annual or seasonal discharge levels. Therefore, results on the seasonal Mann-Kendall test

were not significant, despite there having been profound changes (Table 4). Nonetheless, it is highly relevant to jointly use these two methods, as the information provided is complementary, the first giving a global overview and the second visualizing changes in conditions over the whole range studied. Kernel density estimates are particularly sensitive to bandwidth H . There are many approaches to select an optimal H value, plug-in and cross-validation techniques being the most commonly used (Duong and Hazelton, 2005). The optimal bandwidth values obtained using a plug-in method (Hpi; Chacón and Duong, 2010; Duong and Hazelton, 2003) or a smoothed cross-validation approach (Hscv; Chacón and Duong, 2011) were similar in the present study (Appendix A). Moreover, sensitivity analysis regarding the value of bandwidth H was performed using different bandwidth values (value of H doubled or halved), and results led to similar conclusions (Appendix A).

5. Conclusion

Through the development and application of an innovative statistical method, we demonstrated that the thermal and hydrological regimes of 6 large French rivers have been significantly affected by climate change and local anthropogenic pressure over the past 30 years. Direct and indirect human-induced disturbances may lead to suboptimal environmental conditions for diadromous species to complete their entire life cycle. It seemed that spring-running and -spawning species are likely to have experienced less suitable thermal and hydrological conditions in the Garonne and Loire rivers over the last decades. Fall-running species have been more threatened in the Dordogne and Vienne rivers. Given the numerous significant environmental changes observed in the Rhône River, all the species of interest have doubtless been impacted, in all seasons. The situation for diadromous species does not seem alarming in the Rhine River, as thermal and hydrological regimes have changed little over the study period. The differences between rivers are likely due to differences in natural hydrological regime, but also to anthropogenic factors

and management practices. The method here proposed can also be extended to other study cases. Air temperature and precipitation drive many processes, such as the reproductive cycle of anurans (Montezol et al., 2018) or the migration of birds (Haest et al., 2019) and this bivariate analysis could help anticipate whether changes in environmental conditions cause a species to persist, disappear or expand according to its ecological requirements.

CRedit authorship contribution statement

Elorri Arevalo: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft. **Géraldine Lassalle:** Conceptualization, Writing - review & editing. **Stéphane Tétard:** Conceptualization, Methodology, Data curation, Writing - original draft. **Anthony Maire:** Conceptualization, Methodology, Data curation, Writing - original draft. **Eric Sauquet:** Validation, Writing - review & editing. **Patrick Lambert:** Writing - review & editing. **Alexis Paumier:** Writing - review & editing. **Bertrand Villeneuve:** Data curation, Writing - review & editing. **Hilaire Drouineau:** Conceptualization, Methodology, Software, Writing - original draft.

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.

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Data availability statement

Data available on request due to privacy/ethical restrictions: The data that support the findings of this study are available on request from the corresponding author, EA. The data are not publicly available due to private restrictions.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.141260>.

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