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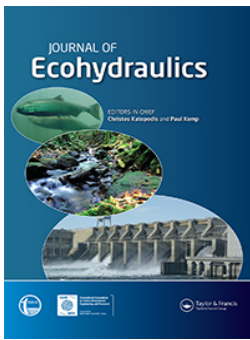
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Consistent but secondary influence of hydropeaking on stream fish assemblages in space and time

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ABSTRACT

Hydropeaking corresponds to rapid artificial discharge variations, designed to address sub-daily peaks in electricity demand. It generates rapid changes in physical habitat (e.g., flow velocity and water depth) with potential impacts on stream assemblages. For assessing the generality of hydropeaking effects on fish assemblages, we present an original combination of spatial (among 45 reaches, including six groups of nearby reaches) and temporal (over 3-17 years) analyses of these effects. Our analyses involved descriptions of natural and artificial hydraulic variations in reaches, obtained after translating hourly discharge data into hydraulics. We found that the influence of hydropeaking was secondary compared to well-known spatial variations in fish assemblage structure along longitudinal gradients, and negative influences of floods on annual densities. However, the spatial and temporal analyses consistently suggested that hydropeaking may disfavour fish species typical of medium-sized streams relative to species of headwater streams (*Salmo trutta*, *Phoxinus phoxinus*, *Cottus gobio*). The magnitude of hydropeaking effects observed here, as well as an apparent weaker effect of ramping rates than the frequency of hydropeaks, may be due to lower ramping rates in our data set than in other studies.

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Hydropower; flow management; hydraulic habitat; fish community structure; high flow variations

Introduction

Hydropeaking corresponds to rapid artificial flow fluctuations downstream of hydropower plants, designed to address sub-daily peaks in electricity demand. Hydropeaking management concerns a large number of dams and river reaches (e.g., 144 of about 600 large dams in France and around 800 km of rivers in Austria; Lauters 1995; Metcher et al. 2017), a number expected to increase with the development of renewable energies (IPCC 2011). The flow regime (e.g., flow magnitude, timing and rate of change, frequency and duration of extreme flow events) is strongly modified downstream of hydropeaking power plants, with more rapid and frequent flow variations than occurring naturally. Because many characteristics of the flow regime influence the structure and functioning of river ecosystems (Schlosser 1991; Poff et al. 1997; Humphries et al. 1999; Magoulick and Kobza 2003), an improved understanding of the ecological effects of hydropeaking is needed. This is particularly true for fish assemblages, which can be affected by hydropeaking at several levels: increased drift of

individuals during rapid flow velocity increases (Lechner et al. 2016), stranding due to rapid shoreline dewatering (Leclere et al. 2012; Hauer et al. 2014; Sauterleute et al. 2016), and repeated drying and scouring of spawning grounds (McMichael et al. 2005; Malcolm et al. 2012; Casas-Mulet et al. 2014, 2016).

An attractive method for estimating the ecological impacts of hydropeaking on aquatic communities is to perform “pressure-impact” spatial analyses among numerous river reaches (Gehrke and Harris 2001; Schmutz et al. 2015). Their principle is to build correlative models involving descriptors of hydropeaking intensity (e.g., frequency of events, ramping rates: rate of change in water level) and descriptors of fish responses (e.g., species richness or indices of biotic integrity). The work of Schmutz et al. (2015) is to our knowledge the most comprehensive study of this type, analysing the impacts of hydropeaking descriptors in 74 reaches of 16 rivers in Austria, with estimated down-ramping rates typically ranging between 5 and 40 cm h⁻¹. Using the national Austrian fish index,

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they found that the ecological status of natural-like streams was significantly degraded (the index lost two points on a scale of five) for the largest ramping rates observed. A difficulty with these “pressure-impact” approaches is to appreciate if the variables finally retained in the models, often after removal of several intercorrelated variables, are the actual drivers of observed responses. In other words, intercorrelation between environmental variables along natural and anthropogenic gradients may complicate the interpretation of such spatial analyses. Another difficulty with these large-scale approaches is that they often lack proximate habitat variables, such as wetted-width ramping rates or rate of changes in flow velocity (Moreira et al. 2019), because these are rarely available across many reaches. Nevertheless, these approaches are extremely useful for identifying thresholds beyond which environmental pressures can become problematic (e.g., hydropeaking ramping rate above 15 cm h^{-1} ; Schmutz et al. 2015).

Interpreting spatial analyses of the ecological effects of hydropeaking among reaches can be facilitated when nearby reaches with contrasting hydropeaking pressures are included in the analyses. Such groups of reaches ideally have similar general characteristics (e.g., morphology, temperature, water quality) and differ only by their hydropeaking regime. These approaches have revealed that hydropeaking can reduce fish biomass and diversity (Liebig et al. 1999; Freeman et al. 2001; Smokorowski et al. 2011; Enders et al. 2017), with different responses among species. For example, Bain et al. (1988) compared two nearby rivers and showed that hydropeaking reduced the abundance of small fish species (and small size classes) living in shallow and slow-flowing habitats (see also Travnicek and Maceina 1994). Nevertheless, these comparisons generally involved one or a few reaches only, limiting the transferability of their results.

Temporal studies (either *in situ* or experimental) of the ecological effects of hydropeaking regime may also contribute to better identify thresholds in hydropeaking characteristics triggering a response of aquatic organisms or assemblages, while limiting problems associated with confounding environmental factors. For example, Saltveit et al. (2001) monitored juvenile fish in a river section during rapid down-ramping events (90 cm h^{-1}) and found that 60% became stranded. Consistently, in artificial channels, Bradford et al. (1995) reported that the proportions of stranded juveniles of rainbow-trout increased from 6% to 30% with down-ramping rates increasing from 5 cm h^{-1} to 60 cm h^{-1} . At the population level, reducing the frequency of hydropeaks may favour the reproduction of several salmonid species (Connor and Pflug 2004). Such

experimental studies improve our mechanistic understanding of the ecological effects of the different hydropeak characteristics. However, as for comparisons of nearby reaches, temporal analyses deserve repeated field validations in multiple reaches. Difficulties for gathering hydraulic and fish data in many hydropeaking reaches over several years explain why few or no studies have carried out combined spatial and temporal analyses.

The originality of our study is to combine three approaches: (1) a spatial analysis of the effects of hydropeaking on fish assemblages between stream reaches, (2) a temporal analysis of these effects within reaches, and (3) a comparison involving groups of nearby reaches subjected to different intensities of hydropeaking (Figure 1). Our objective was to test whether these different approaches reveal consistent effects of hydropeaking on fish assemblages. For this purpose, we used a unique dataset from 45 reaches of 26 rivers covering 3-17 years. The dataset included six groups of nearby reaches close to hydropower plants, hourly discharge data, hydraulic descriptions of reaches, and electrofishing surveys. We used fish species abundances as response variables to account for differential responses among species (Bain et al. 1988). We expected the spatial analysis to indicate how hydropeaking influences the classical longitudinal organisation of fish assemblages (Vannote et al. 1980). We expected the temporal analysis to better indicate the relative influence of hydropeaking on fish compared to the well-documented influence of high and low flows on fish recruitment (Bischoff and Wolter 2001; Thieme et al. 2001). We expected the comparison between nearby reaches to help disentangle the effect of hydropeaking on fish assemblages from those of other environmental drivers.

Materials and methods

Reach selection and characteristics

The dataset consisted of fish assemblage surveys ($n = 318$ reach x year combinations) conducted in 45 French stream reaches between 1990 and 2017, and corresponding hourly discharge time-series. Fish reaches were selected from two available databases ($n = 33$ from the national fish survey database www.naiades.eaufrance.fr; $n = 12$ surveyed by the national hydropower company “Electricité de France”, EDF). These reaches had inter-annual median daily discharges between 2.2 and $128 \text{ m}^3 \text{ s}^{-1}$, slopes between 0.1 and 73.8 ‰ and widths at mean discharge between 7 and 89 m (Table 1), according to the national extrapolation of environmental data available in Pella et al. (2012). Most selected reaches were situated downstream of hydropeaking power plants,

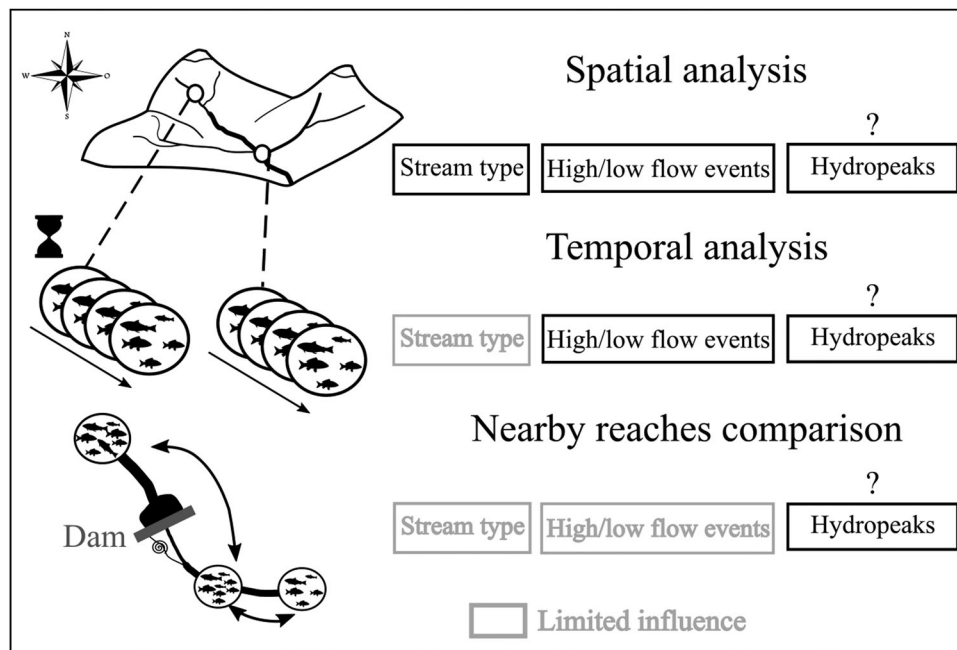


Figure 1. Schematics of the three approaches used to study the relative influence of natural environmental drivers and hydropeaks on fish assemblage structure. For each approach, factors assumed to have a major influence on the structure of fish assemblages are shown in black whereas others are in grey.

except four reaches that were not influenced by hydropeaking. Two of them were situated upstream from hydropower plants, two others in bypassed sections not influenced by hydropeaking. These four reaches belonged to a subset of 15 reaches involved in the analysis of nearby reaches. These 15 reaches were themselves grouped into six groups of two or three nearby reaches, which were used for paired comparisons (Figure 2).

Reach selection was strongly constrained by the availability of hourly discharge data measured close to the fish reaches (we imposed a distance < 25 km and the absence of major obstacles or tributaries between the gauging and fish reach). We used the database of Pella et al. (2012), which includes estimates of reach mean annual flow over the French river network, to check the mean annual discharge of tributaries relative to the fish reach discharge; this relative discharge was on average 2% of mean annual discharge, with only 3/45 cases above 10% (kept in the analyses to avoid removing long fish time-series).

Fish data

Fish were sampled by electrofishing between 1990 and 2017 between July 1 and October 30 (average sampling date September 5; SD = 25 days), when young-of-the-year individuals are catchable and easily identifiable. Three sampling methods were used among surveys. For 10 reaches, generally small ones, the whole reach was most frequently prospected by wading (De Lury 2014). This method could involve several passages, but we retained only the first one for consistency among reaches. In 30 larger reaches,

fish were most frequently sampled by wading or by boat using point abundance samples (Nelva et al. 1979), i.e., more than 75 electrofishing points (estimated sampling area of each point: 7 m^2) distributed throughout the reach. For five reaches, fish were most frequently sampled in more than 30 larger habitat units of varying areas, distributed between geomorphic units (e.g., a riffle or a pool) in proportion of their availability within the reach (Vadas and Orth 1993; Lamouroux et al. 1999). The area of these habitat units depended on the size of distinct habitat elements (e.g., a group of boulders in the centre of the channel) and the inherent variability of areas sampled without enclosures (e.g., in the centre channel, the area sampled depended on current velocity).

When the sampling method changed at a reach over years, which occurred in seven reaches, we split the data as sampled in two different reaches to avoid bias in the temporal analysis. Finally, fish individual length was reported for only 40% of the data, strongly reducing the statistical power of analyses of size class density variations. Therefore, analyses of size class variations are not reported here.

The sampled area was reported in all cases, allowing the estimation of fish species densities per survey (number of individuals per 100 m^2). These values were $\log(1+x)$ -transformed to approach normality in our analyses.

Environmental data

Defining seasons

We used two seasons for describing annual reach environmental conditions at the most important

Table 1. Reach characteristics (see Table 2 for variable codes). Reaches considered for the nearby reaches analysis are linked using brackets. Note that the two reaches indicated by a * correspond to a unique reach but with different dates.

Reach code	Geographical coordinates (X; Y) in Lambert 93	Median		Width at mean discharge (m)	Mean air temperature		Rr_Vgrad (m s ⁻¹ h ⁻¹) Mean ± sd	Fr_Dec Mean ± sd	Fr_Inc Mean ± sd
		discharge Q50 (m ³ s ⁻¹)	Slope ‰		Spring; Summer (°C)	Spring; Summer (°C)			
Ain	871774.242; 6526504.737	70.5	2.0	76.3	13.2; 21.0	0.05 ± 0.01	0.43 ± 0.12	0.37 ± 0.12	
Allier	738589.163; 6446380.559	15.3	2.1	38.1	10.8; 17.9	0.06 ± 0.02	0.75 ± 0.32	0.70 ± 0.35	
Ardeche	811952.726; 6384583.096	9.8	0.1	32.4	14.1; 22.2	0.09 ± 0.01	0.70 ± 0.25	0.77 ± 0.34	
Besbre	752029.166; 6600455.770	4.1	1.1	20.6	12.6; 17.1	0.03 ± 0.01	0.20 ± 0.08	0.11 ± 0.05	
Cepre	608335.903; 6424801.115	17.7	1.2	36.2	14.1; 18.6	0.08 ± 0.04	0.55 ± 0.40	0.55 ± 0.41	
Cher1	669551.775; 6588271.080	7.0	0.4	30.2	13.1; 19.1	0.08 ± 0.03	0.69 ± 0.26	0.45 ± 0.16	
Correze2	587688.181; 6453638.630	13.8	2.3	31.3	14.1; 19.2	0.06 ± 0.02	0.26 ± 0.11	0.15 ± 0.05	
Creuse_D3	566106.558; 6615406.208	22.0	1.8	42.0	13.3; 19.6	0.04 ± 0.01	0.37 ± 0.08	0.32 ± 0.10	
Creuse_D4	545127.844; 6622154.201	22.5	0.4	44.7	13.0; 19.5	0.03 ± 0.01	0.32 ± 0.09	0.25 ± 0.11	
DordA_D1*	600865.545; 6424853.320	96.1	0.8	87.6	13.8; 19.8	0.04 ± 0.01	0.08 ± 0.10	0.10 ± 0.08	
DordA_D2	570227.164; 6419870.682	115.6	4.1	84.5	13.9; 14.7	0.03 ± 0.01	0.08 ± 0.11	0.11 ± 0.11	
DordB_D1	600865.545; 6424853.320	96.1	0.8	87.6	13.9; 20.5	0.05 ± 0.02	0.38 ± 0.27	0.37 ± 0.25	
DordB_D3	558010.860; 6413463.240	128.0	2.1	89.4	14.2; 20.6	0.04 ± 0.01	0.26 ± 0.18	0.23 ± 0.15	
Dordogne	608936.299; 6436765.767	82.7	0.9	83.6	12.7; 18.3	0.05 ± 0.02	0.24 ± 0.25	0.25 ± 0.24	
Dordogne1	664807.474; 6498563.755	3.2	8.2	13.9	10.8; 16.1	0.17 ± 0.1	0.62 ± 0.89	0.59 ± 0.87	
Dordogne3	675890.967; 6500545.354	2.8	12.3	11.3	8.4; 15.8	0.26 ± 0.1	0.21 ± 0.12	0.24 ± 0.17	
Dore	737411.593; 6531059.903	13.4	0.9	32.6	12.2; 18.5	0.03 ± 0.01	0.33 ± 0.23	0.29 ± 0.21	
Doubs1	1005479.584; 6702034.457	32.5	1.3	41.9	9.9; 15.5	0.04 ± 0.01	0.44 ± 0.08	0.41 ± 0.08	
Doubs2	998685.499; 6692083.909	25.9	2.8	39.6	8.7; 14.5	0.07 ± 0.01	0.63 ± 0.08	0.59 ± 0.10	
Dur_D1	867476.940; 6299688.683	122.6	2.9	85.0	15.5; 24.5	0.12 ± 0.02	0.37 ± 0.12	0.34 ± 0.09	
Dur_UP	889882.098; 6293508.414	122.6	2.3	86.1	14.7; 24.0	0.12 ± 0.13	0.03 ± 0.03	0.03 ± 0.02	
Garonne1	557491.117; 6248020.216	91.8	3.0	68.0	13.6; 21.3	0.11 ± 0.03	0.57 ± 0.22	0.54 ± 0.16	
Garonne2	513155.364; 6224770.194	47.6	3.5	48.1	12.3; 19.6	0.08 ± 0.02	0.51 ± 0.23	0.51 ± 0.22	
Golo	1223972.662; 6177578.191	11.2	57.3	18.0	13.7; 21.4	0.09 ± 0.01	0.75 ± 0.39	0.71 ± 0.40	
Loire1	790882.892; 6471148.745	24.8	3.2	44.5	11.0; 17.8	0.05 ± 0.01	0.57 ± 0.27	0.55 ± 0.29	
Loire3	790895.984; 6524644.455	33.5	0.5	59.1	12.5; 18.3	0.11 ± 0.05	0.74 ± 0.12	0.79 ± 0.14	
Loire4	775925.352; 6584819.553	48.1	2.1	72.1	12.1; 17.7	0.03 ± 0.02	0.38 ± 0.15	0.31 ± 0.11	
Lot	638852.847; 6387661.801	68.0	4.9	66.3	12.8; 19.4	0.13 ± 0.03	0.99 ± 0.22	0.95 ± 0.21	
Maronne	616560.143; 6441947.071	9.3	2.9	32.3	12.9; 18.7	0.09 ± 0.05	0.33 ± 0.37	0.33 ± 0.37	
Roya_BP1	1066121.216; 6335287.829	6.4	36.2	13.5	11.1; 19.1	0.24 ± 0.13	0.28 ± 0.29	0.28 ± 0.28	
Roya_D	1064803.026; 6332576.200	6.6	27.7	14.5	11.5; 20.2	0.14 ± 0.04	1.05 ± 0.32	0.94 ± 0.35	
Roya_UP	1067468.239; 6340374.076	2.2	73.8	6.8	10.4; 19.0	0.08 ± 0.03	0.02 ± 0.02	0.03 ± 0.02	
Salat	534701.500; 6230865.410	30.3	2.4	42.8	12.2; 18.2	0.06 ± 0.02	0.30 ± 0.12	0.32 ± 0.13	
Selune	383599.079; 6841493.378	8.2	3.0	26.8	11.6; 17.1	0.06 ± 0.02	0.18 ± 0.08	0.16 ± 0.08	
Siagne	1018695.535; 6280195.484	2.8	0.4	21.1	16.8; 23.0	0.39 ± 0.07	1.03 ± 0.38	1.14 ± 0.48	
Tarn	579398.131; 6308816.030	83.6	1.3	88.7	14.9; 20.6	0.04 ± 0.01	0.51 ± 0.15	0.44 ± 0.13	
Tet	657601.117; 6171763.877	7.1	10.3	18.0	14.0; 21.9	0.08 ± 0.02	0.22 ± 0.17	0.18 ± 0.09	
VerdonD_BP1	934680.457; 6299317.267	16.9	1.0	36.6	14.0; 23.4	0.1 ± 0.17	0.01 ± 0.01	0.01 ± 0.01	
VerdonD_BP2	929722.209; 6297495.920	17.3	5.7	33.3	14.5; 23.9	0.11 ± 0.19	0.01 ± 0.01	0.01 ± 0.01	
VerdonM_BP1	983527.417; 6311283.309	9.5	8.1	23.0	10.2; 19.8	0.11 ± 0.25	0.01 ± 0.03	0.01 ± 0.03	
VerdonM_D1	981513.856; 6310766.070	9.6	4.7	24.3	10.7; 19.4	0.14 ± 0.02	0.22 ± 0.06	0.24 ± 0.05	
VerdonM_D2	976499.250; 6307373.744	9.9	6.2	24.2	11.2; 19.8	0.15 ± 0.02	0.22 ± 0.06	0.24 ± 0.05	
Vezere	578479.213; 6458829.865	17.1	0.3	36.2	14.2; 18.9	0.07 ± 0.02	0.46 ± 0.16	0.42 ± 0.15	
Vien_D1	570177.247; 6530340.952	35.2	1.9	47.2	12.3; 18.1	0.09 ± 0.03	0.48 ± 0.14	0.45 ± 0.10	
Vien_D2	552401.5587; 6528649.95	46.5	1.6	54.1	12.3; 18.0	0.05 ± 0.01	0.29 ± 0.07	0.26 ± 0.07	
Vienne2	518554.183; 6603719.964	63.3	2.3	71.5	12.8; 19.0	0.04 ± 0.01	0.26 ± 0.09	0.25 ± 0.08	

periods for fish life cycle. The “Spring” season lasted from 1st March to 31st May, encompassing most of the spawning period of the studied fish species (except brown trout). “Summer” was defined as the period from 1st June to 30th September (or to the sampling date if earlier), during which young-of-the-year fish are actively feeding.

Hourly discharge and temperature data

Hourly discharge data came from the national gauging network ($n = 38$ reaches, www.hydro.eaufrance.fr) or from EDF ($n = 7$). For the latter, discharge was generally estimated by adding a theoretical bypassed base flow, the turbinated discharge and eventually an overflow discharge over the dam. These recalculations could create additional uncertainty on hourly discharge estimates. Air temperature data came from daily mean estimations based

on the closest air temperature station (SAFRAN, Durand et al. 1993).

Translations of discharge data into hydraulic characteristics and habitat suitability

We translated hourly discharge data into more proximate habitat variables describing reach hydraulics (wetted width, water depth, flow velocity) and hydraulic habitat suitability (weighted usable areas) for fish guilds (groups of species with comparable habitat use).

Hydraulic translations were made using the hydraulic geometry of Morel et al. (2020). In brief, these models improve the classical hydraulic geometry relationships of Leopold and Maddock (1953). They are based on the analysis of hydraulic data collected at the scale of stream reaches in 1327 stream reaches of France and New Zealand. Their input

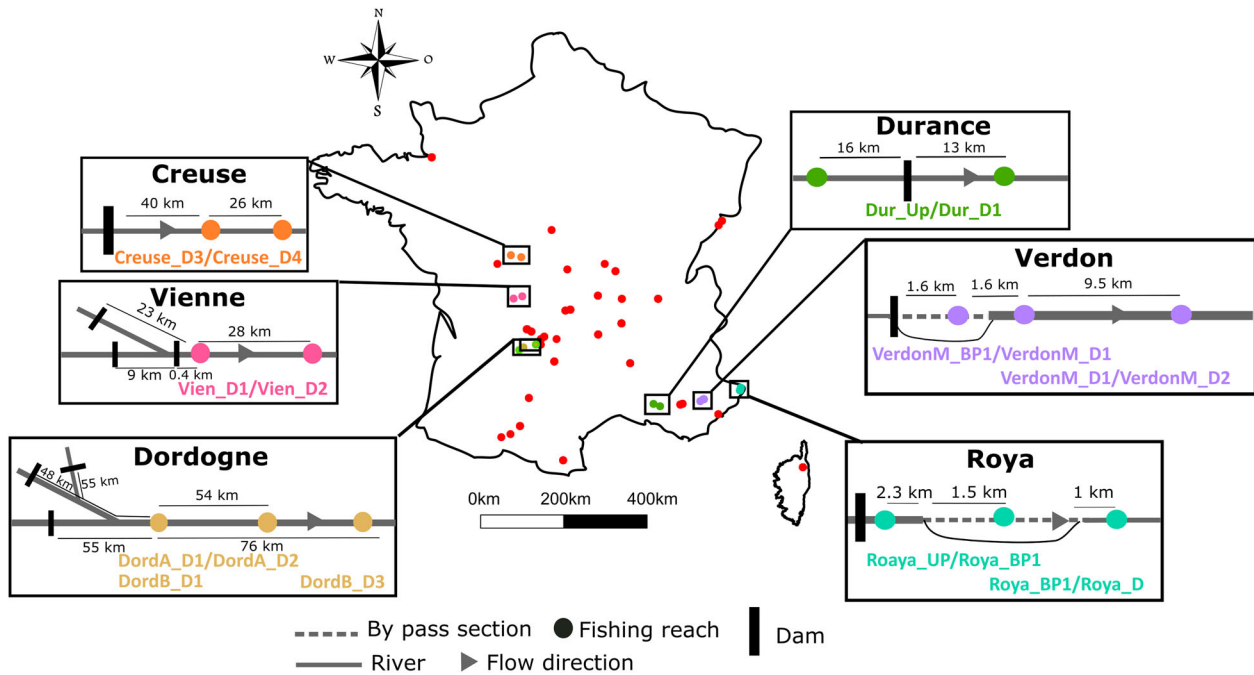


Figure 2. Reach locations in continental France and schematics of nearby reaches (from six rivers) with different hydropeaking pressure. Reach codes are from Table 1.

variables include climatic, hydrologic, topographic and land use descriptors, all available over the French hydrographic network (Pella et al. 2012). These models provide the best estimates of reach hydraulics at a given discharge rate in the absence of detailed field hydraulic measurements. Morel et al. (2020) used cross-validations to quantify how their models predicted hydraulic variations between reaches. For example, they showed that the models predicted 86% and 65% of the variance in observed width and depth among French reaches. However, these models were less accurate when predicting how the rate of change in width and depth with discharge varied among reaches. In detail, the models explained only 35% (width) and 13% (depth) of the exponent of hydraulic geometry for width and depth (Figure 3 in Morel et al. 2020).

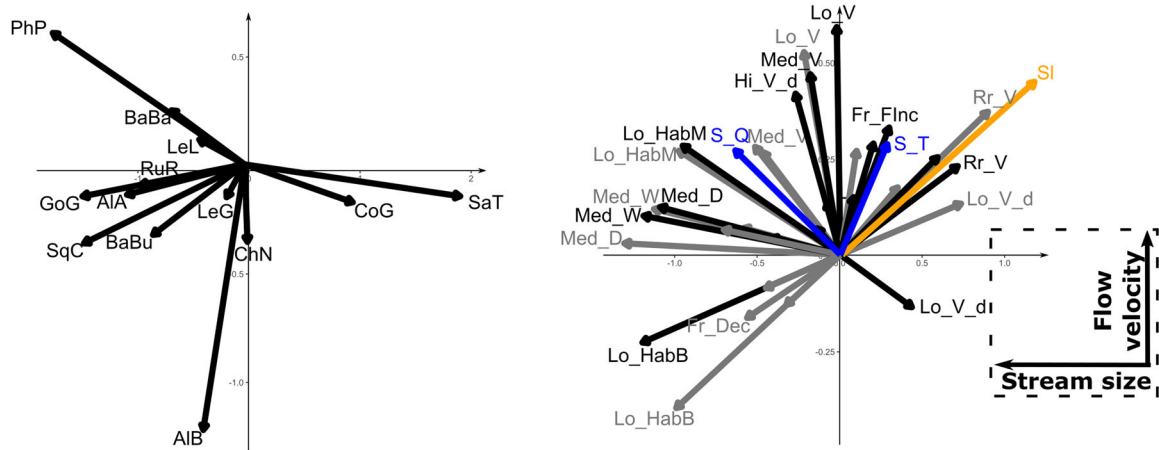
Hydraulic habitat translations were made for two fish guilds using the statistical hydraulic habitat models of Lamouroux and Souchon (2002). These statistical habitat models predict a “weighted usable area” in the reach, at a given discharge rate, as a function of the hydraulic geometry of the reach (described above) and an estimate of average particle size (from Snelder et al. 2011). The weighted usable area is the product of the reach wetted area and a habitat value for the guild that varies between 0 and 1, depending on the suitability of velocities and water depth in the reach for the fish guild. In other words, the weighted usable area increases with both habitat quantity (wetted area) and quality (habitat value). Here, we used weighted usable area for two fish guilds (Lamouroux and Souchon 2002), the “midstream” fish guild grouping species

selecting deep and fast-flowing microhabitats, and the “bank” guild grouping species selecting shallow and slow-flowing microhabitats. The “bank” guild is expected to be more affected by hydropeaking than the “midstream” guild, because hydropeaking generates frequent dewatering and rapid flow velocity variations in shallow habitats.

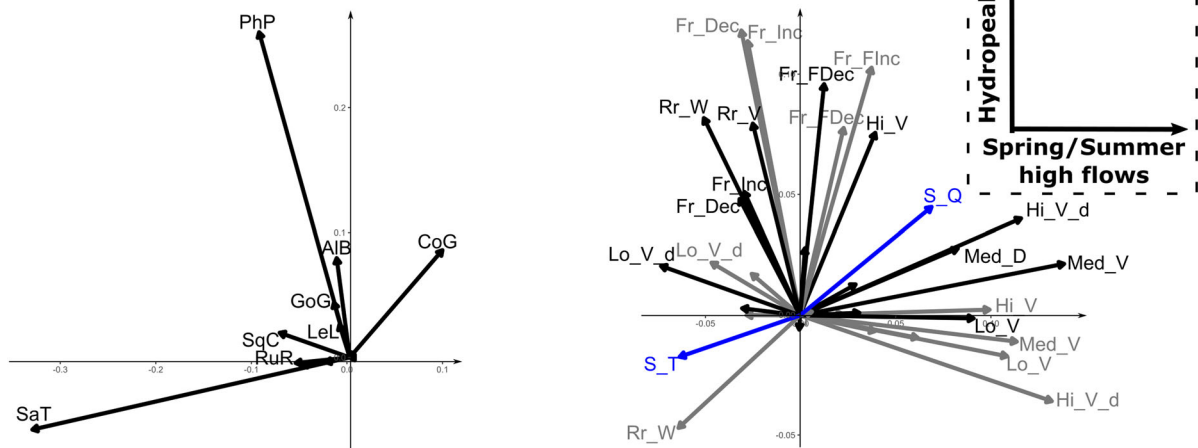
Identifying significant flow events (increases and decreases)

To describe hourly changes in discharge, including both natural and artificial events, we classified each hourly flow variation as “increasing”, “decreasing”, or “stable”. Hours with variations below $0.1 \text{ m}^3 \text{ s}^{-1} \text{ h}^{-1}$ were classified as “stable”. We defined an increasing event (respectively decreasing event) as a concatenation of successive increases (decreases), potentially including periods of “stable” hours if shorter than two hours in total. We defined the peak flow as the highest discharge of the event, at the beginning of the event for decreases and at the end for increases. In the same way, base flow is the lowest discharge of the event. In all subsequent analyses, we considered only significant events having a discharge ratio (i.e., peak to base flow ratio) higher than 30%. We found this empirical threshold appropriate (visually) for selecting major natural changes in flow (typically floods) as well as most hydropeaking events in all study reaches (Appendix S1: Figure S1). With this threshold, the number of events also strongly differed reaches, whether they were subject to hydropeaking or not.

(A) Spatial analysis



(B) Temporal analysis on "trout" reaches



(C) Temporal analysis on "cyprinid" reaches

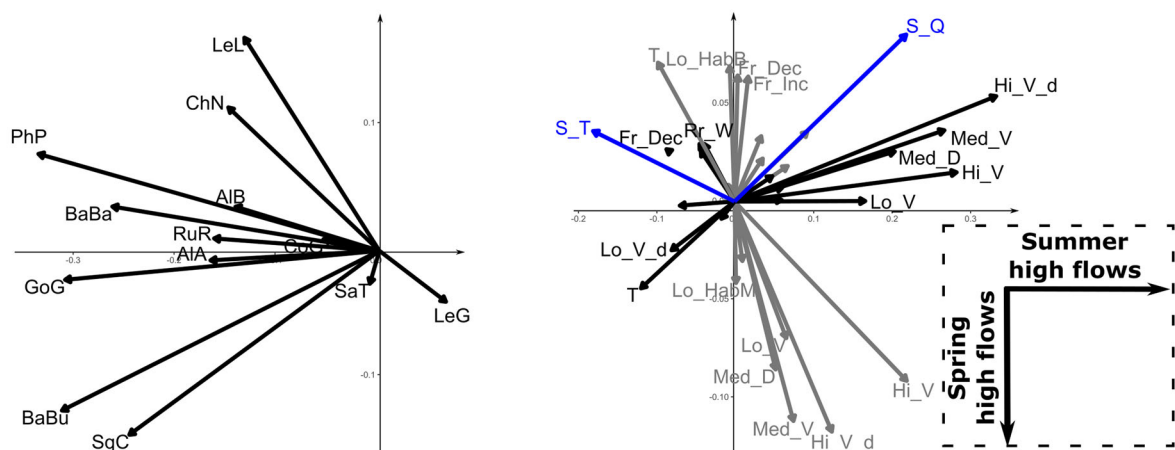


Figure 3. Results of the CoA analyses on the fish and environmental datasets. (A): Between-reach spatial analysis (B): Within-reach temporal analysis on "trout reaches". (C) Within-reach temporal analysis on "cyprinid reaches". Left panels show the fish species scores on the first and second fish axes; right panels show the environmental variable scores on the first and second environmental axes. Environmental variables describing spring conditions are in grey; summer in black; sampling conditions in blue. Slope (in orange) is projected as supplementary variable. The dotted boxes on the right illustrate the interpretation of environmental axes. See Tables 2 and 3 for variable codes and species.

Seasonal environmental descriptions

For each sampling reach \times year combination, we considered a set of environmental variables (Table 2)

potentially affecting annual fish densities and calculated for the spring and summer seasons preceding sampling. These variables describe air temperature

Table 2. Description of the environmental variables considered.

Variable group	Abbreviation	Description	Unit
Topography	SI	Mean reach slope	%
Temperature	T	Air temperature	°C
Median hydraulic conditions	Med_D	Median water depth	m
	Med_V	Median hourly flow velocity	m s ⁻¹
	Med_W	Median hourly wetted surface	m
High flow velocity	Hi_V	Maximum hourly flow velocity	m s ⁻¹
	Hi_V_d	Average daily duration of hourly flow velocity >0.7 m s ⁻¹	hours day ⁻¹
Low flow velocity	Lo_V	Minimum flow velocity	m s ⁻¹
	Lo_V_d	Average daily duration of hourly flow-velocity <0.2 m s ⁻¹	hours day ⁻¹
Low flow weighted usable area	Lo_HabM	Weighted usable area for 100 m of river, for the 'midstream' guild, at low flow 5% quantile (discharge below which hourly discharge is for 5% of the time)	m ²
	Lo_HabB	Weighted usable area for 100 m of river, for the 'bank' guild, at low flow 5% quantile (discharge below which hourly discharge is for 5% of the time)	m ²
Occurrence of flow events	Fr_Dec	Average daily occurrence of decrease events	nb day ⁻¹
	Fr_FDec	Average daily occurrence of rapid decrease events with wetted-width down-ramping-rate >0.6 m h ⁻¹	nb day ⁻¹
	Fr_Inc	Average daily occurrence of increase events	nb day ⁻¹
	Fr_FInc	Average daily occurrence of rapid increase events with flow velocity up-ramping-rate >0.07 m s ⁻¹ h ⁻¹	nb day ⁻¹
Ramping rate	Rr_V	Quantile 90% of flow velocity up-ramping-rate	m s ⁻¹ h ⁻¹
	Rr_W	Quantile 90% of wetted width down-ramping-rate	m h ⁻¹
Fish sampling conditions	S_Q	Flow during fish sampling	m ³ s ⁻¹
	S_T	Air temperature during fish sampling	°C

Table 3. List of the thirteen species studied.

Abbreviation	Scientific name	Common name
SaT	<i>Salmo trutta</i>	Brown trout
PhP	<i>Phoxinus phoxinus</i>	Minnnow
CoG	<i>Cottus gobio</i>	Sculpin
AlA	<i>Alburnoides bipunctatus</i>	Bleak
LeL	<i>Leuciscus leuciscus</i>	Dace
BaBu	<i>Barbus barbus</i>	Barbel
ChN	<i>Chondrostoma nasus</i>	Nase
LeG	<i>Lepomis gibbosus</i>	Pumpkinseed
RuR	<i>Rutilus rutilus</i>	Roach
SqC	<i>Squalius cephalus</i>	Chub
GoG	<i>Gobio gobio</i>	Gudgeon
AlB	<i>Alburnoides bipunctatus</i>	Stream bleak
BaBa	<i>Barbatula barbatula</i>	Stone loach

(T), median hydraulic conditions (variable abbreviations starting by “Med” in Table 2), high flow hydraulics (starting by “Hi”), low flow hydraulics and habitats (“Lo”), frequencies of flow events (“Fr”) and ramping rates (“Rr”). We also described temperature and discharge conditions during fish sampling (“S”). All environmental variables were normalized prior to analyses to give them equal weights.

Correcting ramping rates (attenuation between the discharge station and the fish reach)

The hydraulic ramping-rates attenuate with distance from the water release (Nestler et al. 1989; Hauer et al. 2013; Sauterleute and Charmasson 2014). The attenuation is site-specific and complicated to characterize, depending for example on flow velocity, bed morphology and roughness. Here, we decided to correct ramping rates empirically (for 80% of the studied reaches), as a function of distance between the gauging station and the fish sampling reach (mean = 3.5 km, SD = 6.0 km, max = 24.8 km). For this purpose, we used seven pairs of gauging stations located in the same hydropeaking rivers, with

no flow obstacles or tributaries between them (distance between 1 and 30 km, 1/7 pair being located in a river independent from our dataset). For each pair of stations, we identified the time lag (hours) on the discharge time-series between both stations by numerical optimization, and identified paired significant events. We calculated an average attenuation coefficient for each pair of stations, then regressed attenuation coefficients against distance among pairs (forcing the attenuation to be null at distance zero). An attenuation of 0.4% per km was found for up-ramping rates of flow velocity ($R^2=0.63$) and 0.5% per km for down-ramping rates of wetted width ($R^2=0.45$).

Data analyses

Spatial and temporal analyses

To study the link between annual fish densities and seasonal environmental variables, we used Coinertia Analyses (CoA; Dolédec and Chessel 1994; Mérigoux and Ponton 1999), which compute successive pairs of environmental and fish multivariate axes being as covariant as possible. A CoA is a simultaneous analysis of the fish and environmental datasets that is appropriate when the number of variables (biological and environmental) is relatively high compared to the number of surveys. Optimizing the covariance implies that the fish and environmental axes are correlated and simultaneously explain a high variance (i.e., they summarize variations in fish assemblages and environmental variables among reaches). Here, the environmental and fish datasets were analysed following a “principal component analysis” logic. The environmental variables were standardized, but not the

biological variables that had similar units and were only log-transformed.

We performed two different CoAs of the environmental and fish datasets, a “between-reach” CoA and a “within-reach” CoA, to analyse separately spatial effects (between reaches) and temporal effects (within reaches). The between-reach CoA is our spatial analysis among reaches. It is computed on interannual averages of fish and environmental variables. The within-reach CoA is our temporal analysis of the annual variations within reaches. It is computed on differences between annual variables and their interannual average (by reach). In other words, it removes differences between reaches to analyse relative annual changes.

We paid particular attention to the position of nearby reaches on the between-reach fish factorial map (spatial analysis) to appreciate how changes in hydropeaking pressure have influenced the spatial ordination of fish assemblages.

Relations between environmental variables and fish densities

We reported the correlation between reach coordinates on the two CoA axes (environmental and fish axes) to appreciate how environmental variables and fish densities were related. We also used another measure of the overall similarity using a multivariate extension of the Pearson correlation coefficient called the RV-coefficient (Robert and Escoufier 1976). The RV-coefficient ($RV(X, Y) = \frac{COVV(X, Y)}{\sqrt{VAV(X)VAV(Y)}}$) is calculated as the total co-inertia (i.e., sum of eigenvalues of a CoA) divided by the square root of the product of the squared total inertias (sum of the eigenvalues) from the separate analyses of each dataset. RV-coefficient ranges from 0 to 1, with a high RV-coefficient indicating a high degree of co-structure. Finally, a permutation test was conducted on the datasets to check the significance of the co-structure (RV test). All analyses were performed using the R software (R Development Core Team 2020) “ade4” package (Dray et al. 2007).

Results

The dataset concerned 207,386 fish individuals, and we considered the densities of 13 species (Table 3, Appendix S2: Figure S2) with relative survey-averaged density above 1% of the total survey-averaged density. Fish assemblages were typical of those found along longitudinal gradients in Europe (Figure 3A), with 17/45 reaches with relatively high densities of *Salmo trutta* (>10%; hereafter, “trout” reaches) and the other, larger streams dominated by cyprinids (hereafter, “cyprinid” reaches).

Significant flow events were mostly hydropeaking events. For example, flow decreases per day in spring averaged 0.4 (min = 0.01, max = 1.95) in hydropeaking reaches vs. 0.02 (min = 0.01, max = 0.03) in others. The average wetted-width down-ramping rate across all reaches was $0.68 \pm 0.42 \text{ m h}^{-1}$ (mean \pm sd), the average water depth down-ramping-rate was $0.03 \pm 0.01 \text{ m h}^{-1}$ and the flow velocity up-ramping-rate was $0.09 \pm 0.04 \text{ m s}^{-1} \text{ h}^{-1}$ (see details in Table 1). Therefore, environmental variables describing the occurrence of flow events and ramping rates (abbreviations starting by “Fr” and “Rr” in Table 2) mostly described hydropeaking intensity. By contrast, variables describing high flows, low flows and median conditions (“Hi”, “Lo” and “Med”) were strongly influenced by floods and droughts.

Spatial analysis and positions of nearby reaches

The first and second axes of the between-reach CoA (Figure 3A) explained 81% and 11% of the total inertia, respectively (see Table 4 for the proportion of variance of the initial datasets taken into account by each CoA axes). Pearson correlation between the two datasets was 0.64 for the first axis and 0.49 for the second axis, and the two datasets were significantly related ($RV = 0.26, P = 0.005$). The first axis of the fish and environmental factorial maps suggested that larger streams (i.e., high median depth and width, high weighted usable area, low slope) had lower densities of *Salmo trutta* and *Cottus gobio* and higher densities of other species such as *Squalius cephalus*, *Rutilus rutilus*, *Gobio gobio* and *Barbus barbus*. The second axis indicated that faster-flowing reaches had higher densities of *Phoxinus phoxinus* and *Barbatula barbatula* and lower densities of *Alburnoides bipunctatus*.

Accordingly, positions of reaches on the fish factorial map (Figure 4A) indicated a traditional longitudinal gradient, with smaller “trout” reaches on the right and larger “cyprinid” reaches on the left. Positions of pairs of nearby reaches on the map (black arrows on Figure 4A) suggested effects of hydropeaking intensity for cyprinid reaches more than for trout reaches. In particular, for four pairs of reaches on the left of the map, the reach with higher hydropeaking pressure was consistently situated towards the top or top-right of the map relative to its less impacted corresponding reach. This globally indicated, for paired reaches, higher relative abundance of *Phoxinus phoxinus* and/or *Salmo trutta* in the reaches with highest hydropeaking intensity. Figure 4B highlights these differences for two species: higher densities of *Phoxinus phoxinus* were observed in reaches with higher hydropeaking

Table 4. Summary statistics of the CoAs: RV coefficients; P-values of permutation tests; proportion of variance of each initial datasets taken into account by the two first axes; and Pearson correlation coefficients between the fish and environmental axes.

Analysis	Reaches involved	RV coeff.	P-value	Environment:	Fish density:	Pearson correlation
				variance explained	variance explained	$F1_{env} \times F1_{fish}$; $F2_{env} \times F2_{fish}$
Between-reach CoA (Spatial)	All	0.26	0.005	F1: 30%	F1: 47%	F1: 0.64
				F2: 15%	F2: 16%	F2: 0.49
Within-reach CoA (Temporal)	"Trout" reaches	0.05	0.01	F1: 27%	F1: 42%	F1: 0.54
				F2: 22%	F2: 20%	F2: 0.33
	"Cyprinid" reaches	0.14	0.002	F1: 29%	F1: 34%	F1: 0.48
				F2: 18%	F2: 22%	F2: 0.44

intensity whereas higher densities of *Squalius cephalus* were found in reaches with lower hydropeaking intensity.

Temporal analysis

We decided to apply the within-reach CoA separately on "trout" reaches (Figure 3B) and on "cyprinid" reaches (Figure 3C), because pooling these reaches made the axes hardly interpretable due to the different species involved.

The first and second CoA axes for "trout" reaches explained 44% and 27% of the total inertia, respectively (Table 4). Pearson correlation between the two datasets was 0.54 for the first axis and 0.33 for the second axis and the two datasets were significantly related ($RV = 0.05$, $P = 0.04$). The first axis of the fish and environmental factorial maps suggested that the major temporal effect was a decrease in density of *Salmo trutta* with high-flow events during spring and/or summer. The second axis, for which the correlation was low, suggested that the densities of *Phoxinus phoxinus* and secondarily *Cottus Gobio* were positively related to hydropeaking occurrence.

The first and second CoA axes for "cyprinid" reaches (Figure 3C) explained 71% and 11% of the total inertia, respectively (see Table 4 for details). Pearson correlation between the two datasets was 0.48 for the first axis and 0.44 for the second axis. The relationship between fish densities and the environment was significant ($RV = 0.14$, $P = 0.002$). The first axis of the fish and environmental factorial maps suggested that the major temporal effect was a general decrease in the densities of most fish species with high-flow events during summer. The second axis suggested that spring high flows could increase the densities of *Leuciscus leuciscus* and *Chondrostoma nasus* relative to the density of *Squalius cephalus*. Summer hydropeaks tended to have the opposite effect.

On both within-reach CoA analyses, high discharge and very cold temperature on sampling date tended to reduce observed densities of most species.

Discussion

Secondary influence of hydropeaking compared to stream size and high-flow events

The spatial analysis (between-reach CoA) showed that the influence of hydropeaking on fish assemblage was secondary relative to the influence of stream size. In this analysis, the fish factorial map separated *Salmo trutta* and *Cottus gobio* preferably found in steep headwaters, *Phoxinus phoxinus* and *Barbatula barbatula* in intermediate-sized streams, and all other species in larger streams. Such an organization of fish assemblages along the upstream-downstream gradient has been largely described (e.g., Huet 1949; Vannote et al. 1980). However, we observed two exceptions to this upstream-downstream gradient on the second axis: the position of *Phoxinus phoxinus* and *Barbatula barbatula* (with high densities in faster-flowing reaches) opposed to *Alburnoides bipunctatus*. The computation of the second axis was certainly influenced by the spatial distribution of the studied reaches, some being within and others outside the heterogeneous geographic distribution of *Alburnoides bipunctatus*.

The temporal analysis (within-reach CoA) showed that the influence of hydropeaking on fish densities was secondary relative to the effects of high flows. In line with previous studies, we found that high-flow events in spring or summer reduced the densities of most species (Bischoff and Wolter 2001; Thieme et al. 2001; Cattaneo 2005; Bret et al. 2016). For "cyprinid" reaches, the second axis of the environmental factorial map discriminated the effects of spring and summer high-flow events. Spring high-flows logically affected earlier spawners (i.e., March/April), such as *Leuciscus leuciscus* and *Chondrostoma nasus*, while summer high-flows affected species that spawn later (i.e., May/June), such as *Gobio gobio* and *Phoxinus phoxinus* (Lelek and Penaz 1963; Mills 1981; Lascaux et al. 2013).

Since most studies have shown that hydropeaking was linked to adverse consequences for fish (e.g., stranding, drifting and spawning ground scouring; Halleraker et al. 2003; Connor and Pflug 2004; Auer et al. 2017), frequent hydropeaks and high ramping

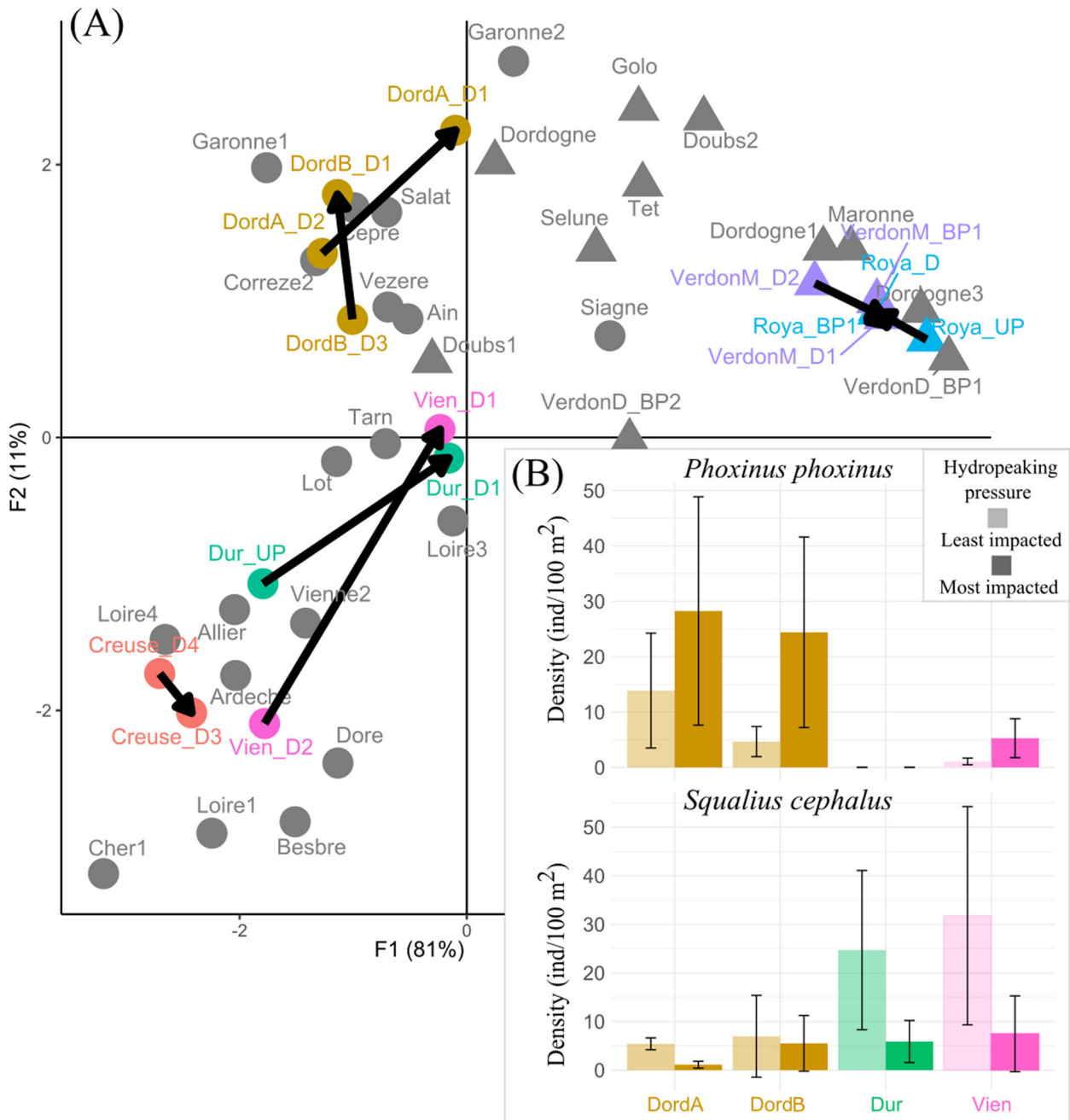


Figure 4. (A): Reach scores on the first and second axes of the fish dataset for the between-reach spatial analysis. Triangles correspond to "trout reaches" and circles to "cyprinid reaches". Black arrows indicate the position of pairs of nearby reaches (same colour), with arrows going from the reach least influenced by hydropeaking to the most influenced. (B): Density of minnow *Phoxinus phoxinus* and chub *Squalius cephalus* in the four pairs of nearby reaches; clear and dark colors are for the reach least and most influenced by hydropeaking, respectively. Reach colour codes are from Figure 2. Reach codes are from Table 1.

rates were expected to be negatively related to the density of most species. However, our temporal and spatial analysis brought different findings. We propose three potential explanations for the secondary influence of hydropeaking observed here. First, within-reach, the variability of hydropeaking intensity between years was low, limiting our ability to show relationships between fish densities and hydropeaking descriptors. For example, the annual within-reach standard deviation for up-ramping rates of flow velocity was 44% of the interannual average. Second, the hydropeaking intensity in the

reaches studied here is relatively low. For example, we found an average water-depth down-ramping-rate of 3.2 cm h⁻¹ for hydropeaking reaches (max = 10.6 cm h⁻¹) whereas Schmutz et al. (2015) showed an adverse effect of hydropeaking on fish assemblages for water level down-ramping rates above 15 cm h⁻¹. Halleraker et al. (2003) observed almost no stranding of juvenile Brown trout for water-depth down-ramping-rates below 18.6 cm h⁻¹. Although we cannot directly compare these values (our ramping rates are based on average depths, others on water levels), the down-ramping rates in

our reaches were clearly lower. Third, since most French hydropower plants were built more than fifty years ago, the fish species that are currently present could have adapted to these highly variable environments. For example, studies have shown that many fish individuals move in response to temporal variations in habitat suitability (Pert and Erman 1994; Shirvell 1994; Bond and Jones 2015) and can adapt their behaviour against hydropeaking risks by using the less constraining habitats (Capra et al. 2017).

Focusing on young-of-the-year individuals could have revealed a stronger influence of hydropeaking compared to our analyses made without differentiating life stages. Indeed, young-of-the-year individuals have lower swimming capacity than adults and mostly use near-bank habitats (Moore and Stanley 1988), making them highly susceptible to drifting and stranding (Saltveit et al. 2001; Halleraker et al. 2003; Lechner et al. 2016). However, density-dependence may offset the effects of hydropeaking in some populations (Ratikainen et al. 2008; Puffer et al. 2019). For example, using a population dynamic model for Atlantic salmon (*Salmo salar*) in a hydropeaking river in Norway, Sauterleute et al. (2016) showed that the stranding mortality of young-of-the-year individuals had weak effects on population dynamics.

Hydropeaking favours headwater species at the expense of medium-sized stream species, consistently in space and time

The comparison of nearby reaches showed that, for cyprinid reaches, stronger hydropeaking intensity was associated to higher densities of fish species typical of headwater streams (*Phoxinus phoxinus*, *Salmo trutta* and *Cottus gobio*) and lower densities of species typical of medium-sized streams (*Rutilus rutilus*, *Barbus barbus*, *Squalius cephalus*, *Chondrostoma nasus*). In contrast, for trout reaches, no clear trend was observed, indicating that headwater fish species were less influenced by hydropeaking than others. This result is consistent with the temporal analysis on trout reaches, where years with higher hydropeaking intensity had higher densities of fish species typical of headwater streams. Several previous studies have also shown that fish species typical of headwater streams may better withstand hydropeaking (Garcia De Jalon et al. 1988; Casado et al. 1989; Garcia De Jalon et al. 1994). Garcia De Jalon et al. (1994) found that, after the construction of a hydropeaking power plant on the Tera River (Spain), populations of almost all cyprinid species declined while the trout population persisted. However, on the Rio Duraton (Spain), Camargo and Garcia de Jalon (1990) found the opposite effect: cyprinid

populations persisted or even increased whereas trout disappeared. These differences are difficult to interpret and likely depend on dam management, dam location along the river and/or the particular morphological characteristics of each hydropeaking reach.

Another way to study the influence of hydropeaking is to focus on the individual scale, for example by comparing the growth of individuals under different hydropeaking intensity. Such approaches suggest that Atlantic salmon (Puffer et al. 2017) may thrive in hydropeaking reaches, in contrast to the cyprinid humpback chub (*Gila cypha*) in medium-sized streams (Finch et al. 2015). A possible reason for the greater hydropeaking tolerance of headwater stream species may be their behavioural adaptation to naturally highly variable environments (Horwitz 1978). They may have developed ecological strategies to cope with frequent and rapid flow variations (Schlosser 1982; Oberdorff et al. 2001; Lytle and Poff 2004). For example, rainbow trout (*Oncorhynchus mykiss*) can detect the rising limb of a flood, allowing a rapid search of hydraulic shelter (Gore et al. 1994). The freshwater sculpin (*Cottus gobio*) lives in coarse substrate interstices, limiting the risk of drifting during high flows (Keith et al. 2011). *Phoxinus phoxinus* spawns several times a year (Wootton and Mills 2006), reducing the mortality risk of a whole young-of-the-year cohort after a single intense hydropeaking event. Furthermore, due to the greater availability of rocks, tree roots and woody debris, headwater streams have a greater diversity of habitats and shelter than larger streams (Jackson and Sturm 2002; Benda et al. 2005; Gooderham et al. 2007).

Perspectives

We identified several biases that could have blurred the relationships between hydropeaking descriptors and fish densities. First, variations in electrofishing efficiency between surveys, related to environmental conditions during sampling, probably introduced noise in observed fish densities (Cauvy-Fraunié et al. 2020). Consistently, we found that higher air temperature or lower discharge rates during fish sampling resulted in higher densities. Second, variations in fish sampling methods between reaches could have influenced our spatial analysis. We checked that this influence was limited (results not shown) by repeating our analysis after introducing method-specific correction coefficients (up to a factor 5) on observed densities. This indicated that our spatial analysis was essentially driven by differences in species relative densities and little sensitive to the fish sampling method. Third, environmental

descriptions could be improved. In particular, air temperature alone did not allow to evaluate the potential influence of water temperature variations induced by hydropeaking (known as thermo-peaking, Zolezzi et al. 2011). In addition, although they are relatively accurate for describing hydraulic differences between reaches, the general hydraulic translations of Morel et al. (2020) cannot reflect the presence of shelter or particular substrate configurations. More importantly, hydraulic geometry models are uncertain for describing the rate of change in width and depth with discharge. Field measurements would have been desirable for improving our hydraulic descriptions. However, using more accurate descriptions would unlikely affect our conclusions, because we described many aspects of the frequency and ramping rates of hydropeaks, all of which had a secondary influence on density annual variations. Finally, all environmental characteristics of reaches (hydraulic geometry, substrate composition, shelter availability) could have changed over the study period.

In spite of the large dataset used here, increasing the range of hydropeaking intensity studied would help to identify thresholds over which significant adverse impacts are observed on fish assemblages. In particular, it is possible that higher hydropeaking intensity negatively affects headwater species (*Phoxinus phoxinus* and *Cottus Gobio*). Since each country has its own rules for managing hydropeaking, international comparisons will help to extend the range of hydropeaking intensity considered. The number of reaches considered could also be increased by using environmental DNA techniques that allow rapid, semi-quantitative assessments of fish community structure in a non-invasive way (Lodge et al. 2012; Taberlet et al. 2012; Pont et al. 2018).

In the future, there is a need to improve our understanding of the interactions between hydropeaking and other stresses for aquatic biota (e.g., changes in water temperature or quality; Zolezzi et al. 2011; Bruno et al. 2013; Vanzo et al. 2016) to determine whether their effects are additive, synergistic or antagonistic. This could be achieved with analyses similar to ours, but including complementary environmental descriptors (e.g., turbidity, water temperature) and more reaches with unique or multiple pressures (e.g., Acreman et al. 2014; Bondar-Kunze et al. 2016). Finally, understanding taxa behavioural response to hydropeaking could help identify improved management measures (Metcher et al. 2017). For example, the development of models of habitat selection adapted to highly variable environments, taking into account the history of habitat conditions, could help to predict the amount of suitable habitat for different taxa under different management scenarios.

Conclusion

We found that the influence of hydropeaking was secondary compared to the well-known organization of fish assemblages along the longitudinal gradient of rivers, or the frequently observed negative influence of floods on recruitment. Our temporal analyses suggest that, within the range of hydropeaking intensity considered, small changes in hydropeaking management should have limited effects on fish assemblage structure. However, further analyses covering a wider range of hydropeaking intensity are needed to assess possible threshold effects. Consistently in space and time, we found that hydropeaking affected fish species typical of medium-sized streams more intensively than those of headwater streams. Although this result remains to be confirmed with a larger dataset, it suggests that flow should be managed cautiously in medium-sized streams. Because past studies focused more on salmonid species (Moreira et al. 2019), more attention is deserved on assemblages of larger streams.

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