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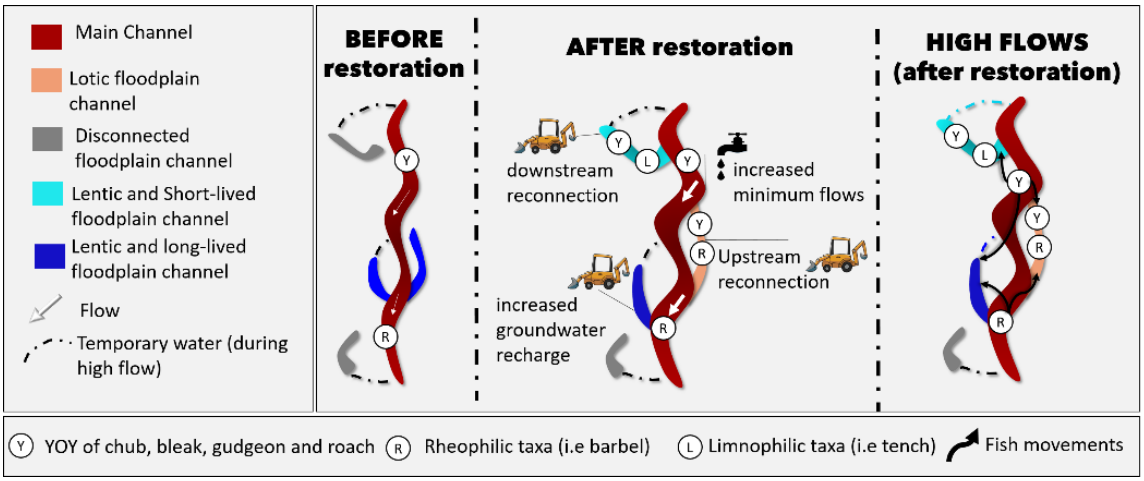


Key word: Habitat Complementarity, River restoration, Flow, Water temperature, Connectivity

Abstract:

River floodplain channels can serve as reproduction, nursery or refuge areas for fish. Although the complementary use of floodplain and main channels is known, few studies attempted to quantify this use and even fewer analysed its controlling factors. The objectives of this study are (1) to describe the spatio-temporal use of floodplain habitats and to identify their roles as complementary habitats for fish and (2) to analyse how abiotic variations and their modifications under restoration impact habitat use by fish. To meet these objectives, we analysed (Principal Components Analysis and Coinertia Analysis) multi-site data collected over 20 years in eight main channels and 23 floodplain channels of eight restored sectors of the French Rhône River. Results show that habitat use by fish is mainly related to spatial effects, with 37% of within-sector variance in taxonomic assemblages explained by the stations. As expected, rheophilic species were more abundant in lotic stations and limnophilic species in lentic ones. In addition, we identified an euryecious guild, grouping young of the year taxa (roach,

gudgeon, chub, bleak) that used all types of habitats and particularly lentic floodplain channels with short life-span. Temporal effects (with ~10% of the variance explained by years) combine (1) the effect of restoration, that increased the diversity of fish assemblages across the floodplain, with stronger changes in floodplain channels whose connectivity regime was modified, (2) the effect of high flows on fish habitat use, that reinforces the nursery and refuge functions of floodplain channels. Our results demonstrate the importance of restoring the diversity of habitats and connectivity because floodplain habitats have complementary functions for fish. Furthermore, our results also suggest to account for temporal variations in order to better estimate the potential effects of restoration on river and their floodplains.

1. Introduction

A tenet of the patch dynamics concept (Townsend, 1989) is the fundamental link between aquatic biodiversity and the spatio-temporal heterogeneity of the environment. This concept builds on major ecological theories and states that biodiversity increases with spatial heterogeneity and intermediate levels of temporal variability of the environment. River floodplains are suited for testing such relationships. In their aquatic components, they include the main river channel and a diversity of floodplain channels more or less connected to the former. These habitats and their connections are frequently modified by temporally variable water and sediment fluxes (Petts & Amoros, 1996).

In large river floodplains, aquatic habitat heterogeneity is known to favour fish diversity (Amoros & Bornette, 2002; Pander et al., 2018; Manfrin et al., 2020; Stoffers et al., 2022). Indeed, fish may use different habitat types during their life cycle (Werner, 2002; Stoffels et al., 2022), based on a trade-off between their habitat requirements (feeding, shelter and reproduction; Lévêque, 1995; King, 2004; Brönmark et al., 2014) at different stages (larvae, juvenile and adult) and the accessibility of suitable habitats (Plichard et al., 2020; Stoffels et al., 2022). According to Junk et al. (1989), fish mainly use floodplain channels to accomplish their life cycle and use the main channels as migratory routes. But Galat & Zweimüller (2001) also demonstrated the importance of main channels in the life cycle of rheophilic species. For example, in the Danube River many larval rheophilic species use the banks as nursery areas (Schiemer & Spindler, 1989; Keckeis et al., 1997). Most studies on fish communities in riverine floodplains identified a spawning or nursery function in floodplain channels (Copp & Peňáz, 1988). These functions depend on channel accessibility (via passive drift for some Youngs Of the Year (YOY) or active movement for all fish), characteristics of flood events and connectivity to the main channel (Burgess et al., 2013). In floodplain channels the abundance of YOY is favoured by reduced hydraulic constraints that limit energy expenses (Keckeis et al., 1997; Fustec & Lefeuvre, 2000; Silva et al., 2012) and an abundance of food (e.g. plankton) (Fustec & Lefeuvre, 2000; Marle et al., 2023). Other studies reported a refuge function promoted by habitat diversity that attenuates the impact of disturbances like floods (Townsend, 1989; Townsend & Hildrew, 1994). Indeed, during floods, organisms can access slow-flowing habitats in the floodplain (Holcik, 1988; Roux & Copp, 1993).

Human activities worldwide have affected the diversity and connectivity of habitats in most alluvial rivers (Klingeman, 1998; Nilsson et al., 2005; Paillex et al., 2015), reinforcing the need to better quantify the role of habitat complementarity for aquatic communities (Stoffels et al., 2022). Historically, regulation for navigation, hydropower production, irrigation and/or flood protection often reduced flows (Poff & Zimmerman, 2010; Lehner et al., 2011; Lamouroux et al., 2015) and decreased the lateral and longitudinal connectivity (Schiemer et al., 2004; Tockner et al., 2010; Lamouroux et al., 2015; Hein

et al., 2016; Higgisson et al., 2020). During the last decades, many river restoration programs were undertaken to improve the ecological conditions of degraded rivers (e.g. Statzner et al., 1997; Schiemer et al., 2004; Palmer et al., 2005; Funk et al., 2019; Stoffers et al., 2021). Yet, the ecological effects of restoration remain rarely evaluated (Palmer et al., 2005; Funk et al., 2009; Olden et al., 2014; Lamouroux et al., 2015) due to a lack of funding or sufficient and representative before-after monitoring (Morandi et al., 2014). Long-term studies on the effects of floodplain restoration on fish communities are needed to better quantify the ecological benefits of habitat diversity improvements. However, such studies are expensive and remain uncommon (Lamouroux et al., 2015). Among exceptions, a 30 years-long study in the Rhine (Stoffers et al., 2021) highlighted the importance of the age of restored floodplain channels in their role as nurseries for rheophilic fish, with an optimum reached 13 to 14 years after restoration. Conversely, a 25 years-long study (1993 to 2018) in a tributary of the Colorado River (Pennock et al., 2022) showed that both native and non-native fish declined in recent years despite flow management mimicking natural flows.

The Rhône river restoration programme that started in 1998 is a long-term and multi-site programme particularly suited for testing the ecological effects of floodplain restoration and identifying their key habitat drivers (Lamouroux et al., 2015). The French part of the Rhône River is highly regulated with 16 hydroelectric plants situated on artificial channels bypassing 162 km of the river, built between 1952 and 1986 (Fig.1; Olivier et al., 2022). Bypassed sectors of the Rhône received a reduced minimum flow [1-20% of the unregulated mean flow before their restoration] during most of the year, but also large floods when the discharge capacity of the artificial channel is exceeded (Lamouroux et al., 2015; Fig. 1). Restoration operations that occurred between 2000 and 2014 increased minimum flows by a factor up to 10 (Table 1) and reach-averaged current velocities by a factor up to five (Lamouroux & Olivier, 2015). At the same time, about forty floodplain channels were restored, by dredging and/or increasing their connection to the main channels.

The scientific monitoring of the Rhône river restoration programme has involved data collection over more than 20 years, both before and after restoration, in eight restored river sectors, with an objective to develop and test quantitative predictions of the ecological effects of restoration. Syntheses available so far (Lamouroux et al., 2015) showed a significant increase after flow restoration of the proportion of fluvial specialist fish species, up to a factor of 2.4 in the main channels in some restored sectors (Lamouroux & Olivier, 2015). Studies on the Rhône restoration have not yet considered the combined influence of main and floodplain channels on fish assemblage dynamics. The purpose of the present study was to fill this gap.

Our objectives were (1) to describe the spatio-temporal habitat use by fish within the whole floodplain, (2) to identify the complementary roles of floodplain and main channels for groups of fish taxa with comparable habitat use (i.e., *a posteriori* guilds), (3) to analyse how annual, quantitative habitat variations (discharge, connection frequencies, water temperature) and restoration measures influenced fish habitat use over time. For this purpose, we used fish and environmental data (daily flows and water temperature) collected before and after restoration in eight sectors of the Rhône River over more than 20 years, including 31 sampling stations (eight main channels and 23 floodplain channels).

We expected (H1) higher spatial variations than temporal variations in fish assemblages, due to the wide range of lateral connectivity levels between stations at the sector scale (Amoros, 2001), (H2) marked changes in fish assemblages where restoration entailed abrupt changes in lateral connectivity

(e.g. full channel reconnections), and (H3) a major influence of hydrological drivers on temporal changes because high waters modify the fish accessibility of floodplain channels (Grift et al., 2003).

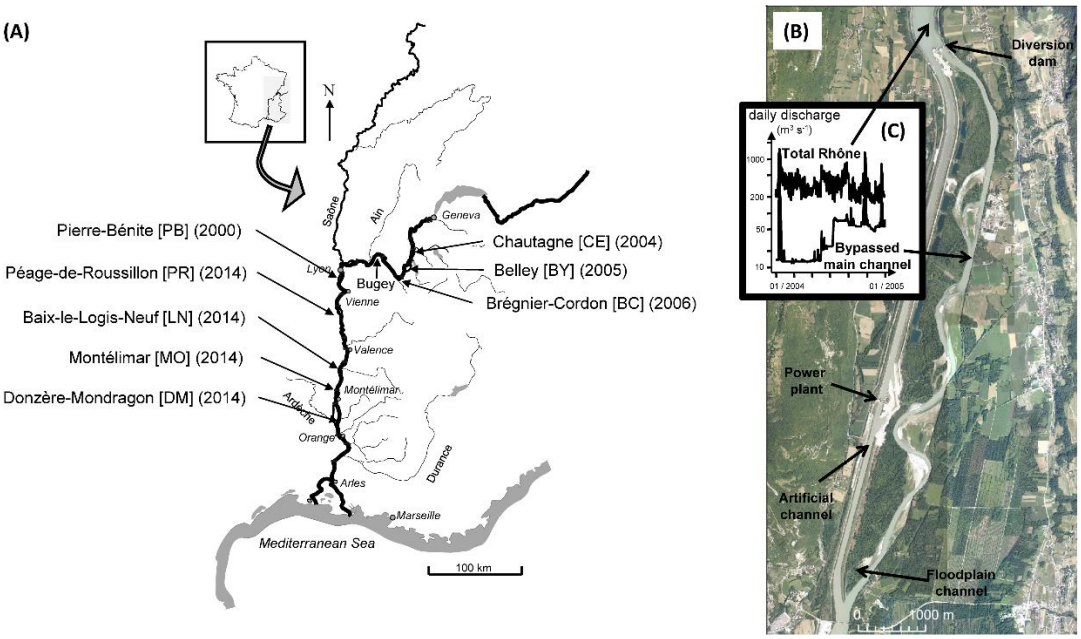


Fig. 1. (A) Map of the Rhône River showing the eight sectors considered in this study. In [] are the code for each sector and in () the year in which restoration occurred. (B) Example of a Rhône sector (CE in Table 1) bypassed by an artificial channel (on the left) for hydropower production © IGN BD Ortho 2013; Lamouroux et al., 2015. (C) Discharge in the bypassed main channel and in the total Rhône for a given year. Bypassed discharge is reduced to a minimum flow except during flood

2. Material and Methods

2.1 Overall study design

Our study design (Fig. 2) included the definition of an *a priori* typology of stations, based on their connectivity with the main channel. Then, we performed a global within-sector principal component analysis (PCA) of the fish data to describe spatio-temporal variations in community structure within sectors. This analysis was used to test our hypotheses H1-H2. Finally, to test our hypothesis H3, we performed within-station co-inertia analyses (CoA), one for each *a priori* group of stations, focusing on the effects of environmental variables (flow and temperature) on annual fish variations.

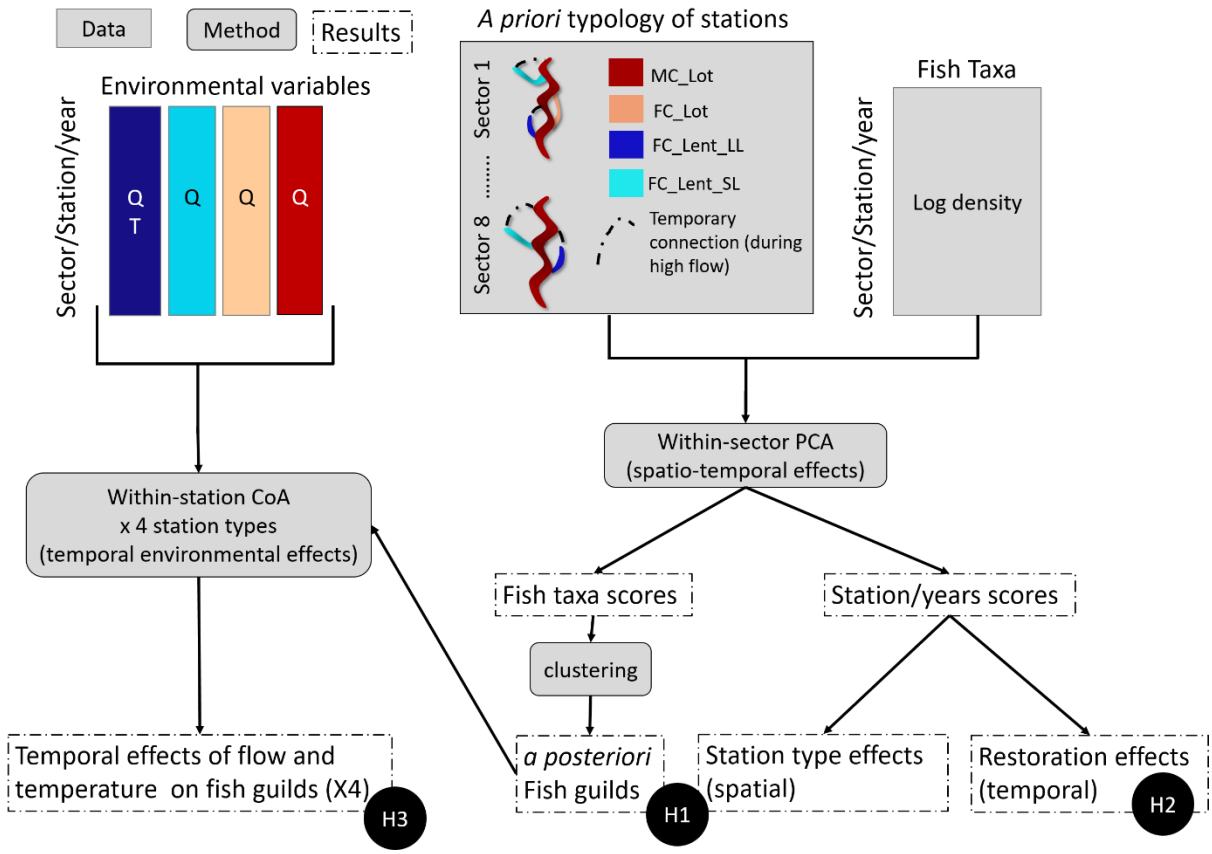


Fig. 2. Conceptual diagram of the study design. Presentation of data, methods and results and their link with our three hypotheses (H1 = Higher spatial than temporal variations in fish assemblages; H2 = Marked changes in fish assemblages where restoration entailed abrupt changes in lateral connectivity; H3 = Major influence of hydrological drivers on temporal changes (Q: discharge, T: temperature). (FC_Lot in orange, FC_Lent_LL in dark blue and FC_Lent_SL in turquoise); see Section 2.2 for station type definitions

2.2 Study sites and a priori *typology*

We considered eight sectors of the Rhône bypassed by artificial channels (Fig. 1, Table 1), corresponding to a total of 31 sampling stations: eight in the main channels and 23 in floodplain channels (up to six by sector). To facilitate graphical interpretations, we used an *a priori* typology of four groups of stations (two lotic and two lentic groups), based on their hydrological characteristics after restoration. For lotic stations, the first group corresponded to main channels (MC_Lot) and the second to floodplain channels permanently connected upstream and downstream to the main channel (FC_Lot); this second group also included floodplain channels connected downstream to the main channel and receiving small tributaries (Bièvre for CERI; Berre for MALA) or water diverted from the head race canal for PLAT (see Table 1 for station codes). Lentic stations were all floodplain channels, permanently connected downstream to the main channel and only temporarily connected upstream. The two groups of lentic stations were differentiated by the channel lifespan, i.e. the duration of the permanent aquatic stage, estimated by Riquier et al. (2017) from observations of fine sediment accumulation rates. The first lentic group (FC_Lent_SL) consisted of floodplain channels with short estimated lifespan (15-30 years) where sedimentation processes were dominant and the rejuvenation

capacity was low (i.e. scouring of fine deposits). The second (FC_Lent_LL) consisted of floodplain channels with longer lifespan (>30 years), due to higher shear stress during flood and lower backflow capacity. Riquier et al. (2017) estimated these lifespans for 10 of the 13 lentic floodplain channels (those of sectors CE, BY, BC and PB in Table 1). We assigned the three remaining stations to the lentic groups based on our expertise and field observations. Lentic stations were often connected to groundwater (Table 1) and could have lower temperatures in summer than lotic stations.

Table 1: Sectors/stations considered, their codes, their sampling periods before and after restoration, and their *a priori* group of stations (after restoration). The Restoration field indicates stations whose connection with the main channel was changed by restoration. The *a priori* group names are based on the following rules: MC = Main Channel; FC = Floodplain Channel; Lent = Lentic; Lot = lotic; SL = Short Life span; LL = Long Life span. The upstream connection flows of lentic stations are also indicated (from Riquier et al., 2015); these connection flows are corresponding to discharge rate in the bypassed main channel, except for stations PONT, SAIN and BROT whose connections depend on the total Rhône discharge. The critical discharge (Qcrit, from Lamouroux et al. 2015), indicated for main channels, is a flow threshold that corresponds to the theoretical Shields critical flow rate for moving 20 mm gravel, using a dimensionless Shields criterion of 0.045 (Petit, 1994). The mean temperature (Tmean) during reproduction period (april-june) and growth period (july-august) are calculated from observed and modelled data between 2006 and 2016 in the BY and BC sectors.

Sector/Station	Code	*A priori* group (after restoration) [a]	Fish sampling period [number of surveys]		Restoration [b]		Upstream connection flow (m^3/s)	Qcrit threshold (m^3/s)	Tmean during reproduction period (°C)	Tmean during growth period (°C)
			Before	After	Up	Down				
Chautagne Sector CE										
Main channel	CE_M	MC_Lot	1996-2000 & 2003 [6]	2004-2019 [16]			-	250	-	-
Malourdie	MALO	FC_Lent_LL	2003 [1]	2004-2013 [10]		X	989	250	- [c]	-
Brotalet	BROT	FC_Lent_LL	2003 [1]	2004-2019 [16]			1246	250	- [c]	-
Belley Sector BY										
Main channel	BY_M	MC_Lot	1996-97 & 2003-04 [4]	2005-2019 [15]			-	250	13.4	19.2
Luisettes	LUIS	FC_Lent_LL	2004 [1]	2005-2014 [10]			229	250	12.7 [c]	13.3
Moiroud	MOIR	FC_Lent_LL	2004 [1]	2005-2019 [15]			417	250	12.9 [c]	14.5
Fournier	FOUR	FC_Lent_LL	2004 [1]	2005-2013 [9]			167	250	12.6 [c]	16.4
Béard	BEAR	FC_Lent_LL	[0]	2004-10 & 2012-13 [7]		X	982	250	13.9 [c]	16.9
En-l'île	ENIL	FC_Lot	2004 [1]	2005-2019 [15]	X	X	-	250	13.7	19.3
Brégnier-Cordon Sector BC										
Main channel	BC_M	MC_Lot	1996-97 & 2004-05 [4]	2006-2019[14]			-	200	14.1	20.1
Granges	GRAN	FC_Lent_LL	2004-2005 [2]	2006-2013 [8]			539	200	14.2	15.8

Vachon	VACH	FC_Lot	2004-2005 [2]	2006-2019 [14]	X		-	200	13.7	19.2
Cerisiers	CERI	FC_Lot	2004-2005 [2]	2006-2019 [14]			102	200	-	-
Mathan	MATH	FC_Lot	2005 [1]	2006-2019 [14]	X	X	-	200	-	-
Molottes	MOLO	FC_Lent_SL	2005 [1]	2006-2019 [14]		X	560	200	13.9 [c]	18.1
Ponton	PONT	FC_Lent_SL	2005 [1]	2006-2019 [14]		X	1266	200	14.3 [c]	19.0
Pierre-Bénite Sector	**PB**									
Main channel	PB_M	MC_Lot	1995-96 & 1998-99 [4]	2001-2019 [19]			-	500	-	-
Ciselande	CISE	FC_Lot	[0]	2011 & 2013 [2]	X	X	-	500	-	-
Jaricot	JARI	FC_Lent_LL	[0]	2011 & 2013 [2]		X	1801	500	- [c]	-
Table ronde	TABL	FC_Lent_SL	[0]	2011 & 2013 [2]		X	>3500	500	-	-
Péage-De-Roussillon Sector PR										
Main channel	PR_M	MC_Lot	2007-2013 [7]	2015-2019 [5]			-	900	-	-
Platière	PLAT	FC_Lot	2007-2013[7]	2014-2018 [5]			-	900	-	-
Noyer Nord	NONO	FC_Lot	[0]	2007-2019 [12]	X	X	-	900	-	-
Noyer Sud	NOSU	FC_Lot	[0]	2013-2019 [7]	X	X	-	900	-	-
Ilon	ILON	FC_Lent_SL	2007-08 & 2010-13 [6]	2014-2018 [5]			750	900	-	-
Sainte	SAIN	FC_Lent_SL	[0]	2013-2015 [3]		X	1700	900	-	-
Baix Sector	**LN**									
Main channel	LN_M	MC_Lot	2010-2013 [4]	2014-2019 [6]			-	150	-	-
Montélimar Sector	**MO**									
Main channel	MO_M	MC_Lot	2006-2013 [8]	2014-2019 [6]			-	250	-	-
Roussette	ROUS	FC_Lent_SL	2010-2011 [2]	2013 [1]			1000	250	- [c]	-
Donzère Sector DM										
Main channel	DM_M	MC_Lot	2008-11 & 2013 [5]	2014-2019 [6]			-	550	-	-
Malaubert	MALA	FC_Lot	2010-13 &2015-16 [6]	2017 [1]			-	550	-	-

[a] A priori *group of stations: MC_Lot: Main channel; FC_Lot: Lotic floodplain channel; FC_Lent_LL: Lentic and long-lived floodplain channel; FC_Lent_SL: Lentic and Short-lived floodplain channel*

[b] *Restoration type: Up: upstream reconnection; Down: downstream reconnection*

[c] *stations where restoration increased the connection to groundwater*

2.3 Fish sampling

Fish were sampled at each station on an annual basis, but with gaps and different durations among stations/sectors due to different restoration histories, as well as environmental, logistic and financial constraints (Table 1 and Appendix A). We considered fish samples taken from 1996 to 2019 between late August and mid-November (i.e. between late summer and autumn), when YOY are better identified (Table 1). Sampling effort was higher in the three sectors of the Upper-Rhône (upstream from Lyon, Fig. 1 (A)). The method used was point abundance sampling (Nelva et al., 1979). A fishing point corresponded to an electrode cast, representing a sampling area of about 7 m² (Régis et al., 1981). Points were distributed in the different microhabitats of the station considered (e.g., pools, runs, riffles, along the banks or midstream), in proportion to their availability. However, microhabitats deeper than 2 m were avoided because of the limits of electrofishing in these conditions. Electrofishing was mostly done from boat as detailed in Copp (1987) and Persat and Copp (1990), or by wading in shallower areas using an EFKO FEG 5000 generator delivering a continuous current. The fishing effort (number of fishing points) was relatively constant over years (generally about 25 points in floodplain channels and 100-200 points in main channels). All fish individuals were identified (in the field or at the laboratory for complex species like bream and silver bream), measured and released.

We built a table of abundance of specific size classes, by station × year. Size limits for YOY (noted e.g. "BaBu1" for species code "BaBu"; see Table 2 for species codes) were set for each station × year combination from visual appreciation of size class histograms. Other fish (not identified as YOY) were classified with similar fixed size limits for all species (e.g. BaBu2: < 12 cm, BaBu3: 12-18 cm, BaBu4: >18 cm), because size can be a strong determinant of habitat use (Plichard et al., 2020). The abundance table contained a total of 367 station × year combinations, and 82 specific size-classes of 37 species. Abundance data were transformed to "log-densities": log(1 + abundance per 100 m²) for approaching normal distributions, accounting for variable sampling efforts and reducing the influence of aggregative behaviour, especially observed for YOY.

Table 2: The 37 fish species sampled. The species code is based on the Latin name and is accompanied by size classes which are present in the sample (1 = YOY; 2 = fish <12 cm; 3 = 12 cm> fish <18 cm and 4 = fish > 18 cm; - = no size class). The table indicates species average post-restoration densities in the four *a priori* group of stations (see Table 1 for codes). Species are ranked by decreasing density

			Mean density (fish/100m²)			
Species code [size class]	Species name	Common name	MC_Lot	FC_Lot	FC_Lent_SL	FC_Lent_LL
SqC [1,2,3,4]	*Squalius cephalus*	Chub	25.7	28.9	37.4	17.6
AlA [1,2,3]	*Alburnus alburnus*	Bleak	29.0	41.7	33.0	0.3
GoG [1,2,3]	*Gobio gobio*	Gudgeon	13.0	28.7	17.7	5.3
RuR [1,2,3,4]	*Rutilus rutilus*	Roach	17.8	13.4	9.3	11.3
RhS [1,2]	*Rhodeus sericeus*	Amur bitterling	6.3	2.4	80.3	5.7
PhP [1,2]	*Phoxinus phoxinus*	Minnow	14.3	3.9	1.1	7.9
PsP [1,2]	*Pseudorasbora parva*	Stone moroko	4.9	1.5	57.0	1.2
BaBu [1,2,3,4]	*Barbus barbus*	Barbel	15.1	11.1	0.5	0.7
BaBa [1,2]	*Barbatula barbatula*	Stone loach	6.8	10.7	0.5	3.3

BlB [1,2]	*Blicca bjoerkna*	Silver bream	2.7	2.6	21.3	0.2
GaA [1,2]	*Gasterosteus aculeatus*	Threespine Stickleback	0.6	2.7	1.0	12.6
ChN [1,2,3,4]	*Chondrostoma nasus*	Nase	3.3	7.3	0.1	0.1
LeG [1,2]	*Lepomis gibbosus*	Pumpkinseed	1.2	1.0	13.0	1.6
AlB [1,2]	*Alburnoides bipunctatus*	Spirlin	5.7	2.1	0.0	0.0
TiT [1,2]	*Tinca tinca*	Tench	0.3	0.7	7.5	3.2
LeL [1,2]	*Leuciscus leuciscus*	Dace	1.8	4.3	0.3	0.7
AmM [1,2]	*Ameiurus melas*	Black bullhead	0.0	0.0	15.9	0.0
AbB [1,2]	*Abramis brama*	Bream	0.3	0.3	9.6	0.6
PeF [1,2]	*Perca fluviatilis*	European perch	1.2	1.7	1.4	1.0
ScE [1,2]	*Scardinius erythrophthalmus*	Rudd	0.2	0.4	4.8	1.3
CaG [1,2]	*Carassius gibelio*	Prussian carp	0.3	0.1	1.5	0.4
EsL [1,2]	*Esox lucius*	Northern pike	0.2	0.2	1.1	0.6
SiG [1,2]	*Silurus glanis*	Wels catfish	0.6	0.4	0.0	0.0
GyC [1,2]	*Gymnocephalus cernua*	Ruffe	0.5	0.1	0.0	0.1
CoG [1,2]	*Cottus gobio*	European bullhead	0.2	0.7	0.0	0.0
AnA [1,2]	*Anguilla anguilla*	European eel	0.3	0.1	0.0	0.0
LeS [1,2]	*Leuciscus souffia*	Soufie	0.3	0.3	0.0	0.0
CyC [1,2]	*Cyprinus carpio*	Common carp	0.1	0.1	0.5	0.0
SaT [1,2,3]	*Salmo trutta fario*	Brown trout	0.2	0.2	0.0	0.0
IcF [1,2]	*Ichthyocoris fluviatilis*	Freshwater blenny	0.2	0.3	0.0	0.0
ThT [1,2]	*Thymallus thymallus*	Grayling	0.3	0.0	0.0	0.0
SaL [1,2]	*Sander lucioperca*	Pike-perch	0.0	0.1	0.0	0.0
LaP [1,2]	*Lampetra planeri*	European brook lamprey	0.0	0.1	0.0	0.0
LoL [2]	*Lota lota*	Burbot	0.0	0.0	0.0	0.0
LeI [1,2]	*Leuciscus idus*	Orfe	0.0	0.0	0.0	0.0
MiS [1,2]	*Micropterus salmoides*	Largemouth black bass	0.0	0.0	0.0	0.0
PaT[-]	*Parachondrostoma toxostoma*	South-west European nase	0.0	0.0	0.0	0.0

2.4 Environmental data (flow and temperature)

Environmental variables were described for post-restoration years only and pre-restoration dates were not included, to avoid confounding annual environmental effects and those of restoration. Flow variables were derived from daily discharge records at eight gauging stations located in the main channels of each sector (Fig. 1A). We also used daily flows at three gauging stations in the "total Rhône" (downstream of the junction between the tail race and the bypassed channel, see Fig. 1B) for estimating the connection frequency of stations connected to this part of the river (BROT, PONT and SAIN, Table 1). For each station × year, we described mean flows (Qmean) and high flows (the 90% high flow percentile: Q90, and the duration exceeding the critical flow threshold moving fine gravel: Dcrit) in the relevant main channel, and connection durations (Dconn) of floodplain channels at three

periods of importance for fish dynamics (see Table 3 for variable definitions). These three periods were reproduction (April-June), growth (July-August) and pre-sampling (the month preceding sampling; Daufresne et al., 2003). These fixed period definitions did not account for complex variations in life cycle dynamics between species and years, but we considered them suitable for a community-wide analysis.

Table 3: Definitions of the four flow variables and three water temperature variables used. The three periods used to calculate these variables (from Daufresne et al., 2003) are reproduction (R: April-June), growth (G: July-August) and the month preceding sampling (S).

Environmental variables	Definition	Period
Qmean (m^3/s)	Average of daily discharge (log-transformed)	R,G,S
Q90 (m^3/s)	High flows quantile 90% (log-transformed)	R,G,S
Dcrit (day)	Number of days when flows exceeded the critical discharge Qcrit for sediment in the main channel (Table 1)	R,G[a]
Dconn (day)	Number of days when flows exceeded the upstream connection flow threshold (Table 1) calculated only for FC_Lent_LL and FC_Lent_SL	R,G[a]
Tmean (°C)	Water temperature average	R,G,S
T90 (°C)	High water temperature quantile 90%	R,G,S
T10 (°C)	Low water temperature quantile 10%	R,G,S

[a] *Calculations of these flow variables was not relevant for the sampling period, due to many zero values.*

Water temperature variables for post-restoration years were derived from Marle et al. (2022), for the BY and BC sectors only. These authors used hourly temperature records at main and floodplain channels stations between 2006 and 2016 and modelled missing values (~31% of data) with random forest algorithms (R package missForest; Stekhoven & Buehlmann, 2012). At each station × year, we calculated mean temperature (Tmean) and temperature extremes (T10 and T90 quantiles) for the three periods used for discharge (Table 3). The mean temperature (Tmean) during reproduction and growth periods are given in Table 1 to assess variations of temperature conditions among stations.

2.5 Spatio-temporal use of a priori *groups of stations and effect of restoration (within-sector PCA)*

We first performed a within-sector PCA of the fish table including all eight sectors in a single analysis (Dolédec & Chessel, 1989; R package ade4; Chessel et al., 2004; R Core Team, 2020). We chose a within-sector PCA to remove average differences in densities between sectors, which can be due to regional difference and the general organization of fish communities along longitudinal gradients (Huet, 1959). Therefore, the analysis focused primarily on the spatio-temporal variations in community structure within sectors. We also calculated the part of variance of the within-sector community variation explained by space (stations) and time (years).

On the factorial map of the within-sector PCA, we identified stations according to the four *a priori* groups presented above, in order to assess spatial differences in community structure. Based on the results of the within-sector PCA, we created *a posteriori* guilds (groups of specific size-classes) with comparable habitat use, in order to simplify the interpretation. For this purpose, we used a hierarchical

clustering analysis (Müllner, 2013) with the Ward method (Murtagh & Legendre, 2014), based on the Euclidean distances between the scores of the taxa along the within-sector PCA axes.

In order to assess the effects of restoration on fish community composition, despite the limited number of pre-restoration samples, we compared the fish compositions on the within-sector PCA factorial maps before and after restoration. We particularly focused on floodplain channels that underwent changes in connectivity after restoration and for which pre-restoration data were available (Table 1). No statistical test was made to analyse these changes, as most floodplain channels were sampled only once before restoration. Indeed, observed changes may be due to restoration, but also to particular conditions during the pre-restoration year.

2.6 Inter-annual variations in fish habitat use after restoration and influence of flow and temperature (within-station coinertia analyses)

We analysed the influence of flow and temperature variables on fish density variations, for each of the four *a priori* groups of stations, with dedicated within-station coinertia analyses (CoA; Dolédec & Chessel 1994). Although this choice generates several multivariate analyses, we preferred CoA over other methods, such as mixed-effects regressions, due to the fact that our analyses involved a fairly high number of environmental variables compared to the number of statistical individuals (station x years). Regressions have low statistical power and are difficult to interpret in such conditions. Conversely, CoA calculates pairs of multivariate environmental and fish axes that are the most covariant. Therefore, CoA results express a compromise between the fish variance, the environmental variance, and the correlation between them. CoA is adapted to our situation with a high number of explanatory variables and enables multivariate interpretations (Dray et al., 2003). Using within-station CoA enables to remove average differences between stations, and thus to focus on temporal changes within all stations of the group considered.

To simplify the interpretation of CoAs, we performed the analyses on fish log-densities within *a posteriori* guilds (sum of log-densities of individual life stages). For each CoA, flow variables that were not relevant for the station type were not involved: in detail, Dconn was not considered for lotic stations and Dcrit for lentic ones. Temperature variables were available in a sufficient number of stations for FC_Lent_LL stations only and were not involved in the analyses of other station types. This implied that the CoA for FC_Lent_LL was performed only on data between 2006 and 2016, and only on the FC_Lent_LL stations of the BY and BC sectors (period and sector with available temperature). We tested the significance of each CoA with a Monte-Carlo test on the sum of eigenvalues, with 10 000 iterations (RV.rtest function in the ade4 R package; Chessel et al., 2004).

3. Results

3.1 Spatio-temporal use of a priori *groups of stations and effect of restoration*

The sector effect explained 15% of the overall spatio-temporal variation in the abundance of fish taxa. The remaining variation was partly accounted for by differences between stations (37%) and between years (10%).

The cluster analysis of taxa scores along the within-sector PCA axes (Fig. 3, with results of the hierarchical clustering analysis in Appendix B) identified *a posteriori* guilds that we interpreted as

rheophilic (three guilds Rheo_3T, Rheo_16T, and Rheo_4T; with the last two or three digits of each acronym indicating the number of taxa included), limnophilic (two guilds Limno_9T and Limno_4T), euryecious (a single guild Eury_4T), and a last guild grouping the remaining taxa (Other) that contributed little in the analysis. This last guild (Other) includes 42 taxa that did not form an obvious functional group and were grouped because they had low abundance in the samples. We named guilds based on the flow characteristics of the stations where they occur, as revealed by the juxtaposition of Figures 3 and 4.

The three rheophilic guilds were associated with lotic stations (MC_Lot and FC_Lot; Fig. 4). However, taxa of the Rheo_3T guild were more abundant in the MC_Lot stations of the Upper Rhône (BC, BY and CE sectors; Figures 3 and 4, Appendix C). Taxa of the Rheo_16T guild had comparable abundance between most lotic stations. Finally, the Rheo_4T guild was particularly abundant in the MC_Lot of CE and LN sectors, and was also present in significant numbers in two FC_Lent_LL stations (FOUR and MALO stations, see Appendix C).

Taxa of the two limnophilic guilds preferentially used FC_Lent_SL stations (Fig. 4). Limnophilic guilds were also abundant in the MC_Lot station of the PR sector (Fig. 3 and Fig. 4). They used FC_Lent_LL stations to a lesser extent, in particular MOIR and BROT stations (Fig. 3 and Fig. 4; Appendix C). The difference between the two guilds of limnophilic taxa was mainly related to differences in taxon density, with amur bitterling and stone moroko (Limno_4T guild) having larger densities than the taxa of the Limno_9T guild (see Appendix C).

Finally, taxa of the euryecious guild were abundant in three of the four habitat types (MC_Lot, FC_Lot and FC_Lent_SL; Fig. 3 and 4). Taxa of this guild were YOY (chub, bleak, gudgeon, and roach); the other size classes of these species were members of the rheophilic guilds (Fig. 3).

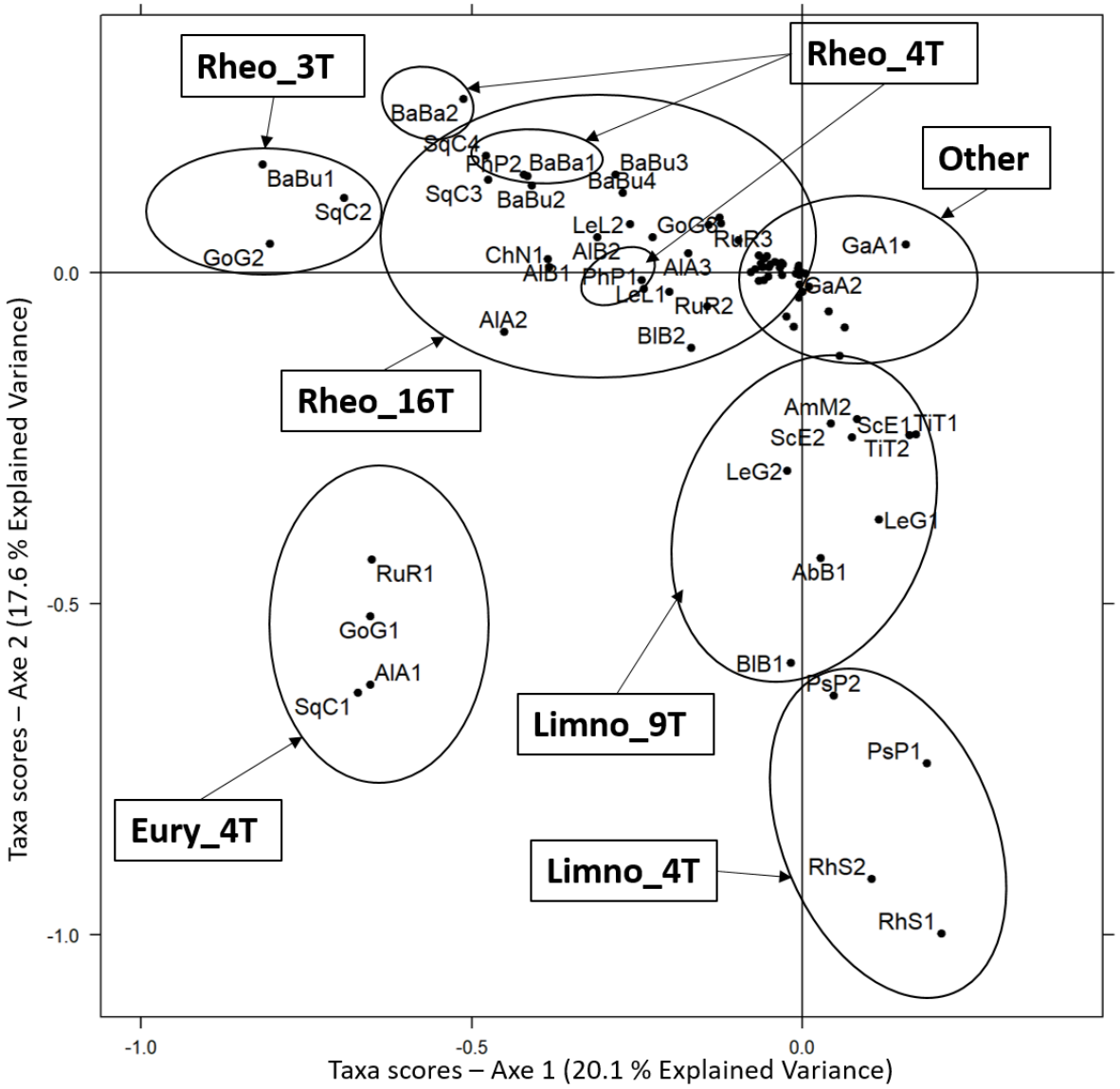


Fig. 3. Scores of taxa on the centred within-sector PCA on fish log-densities (axes 1 and 2). A cluster analysis grouped taxa into seven guilds. Taxa labels are not indicated for the "Other" guild (except sticklebacks, GaG), because they contribute little to the fish structure and would complicate the reading. See Table 2 for taxa codes.

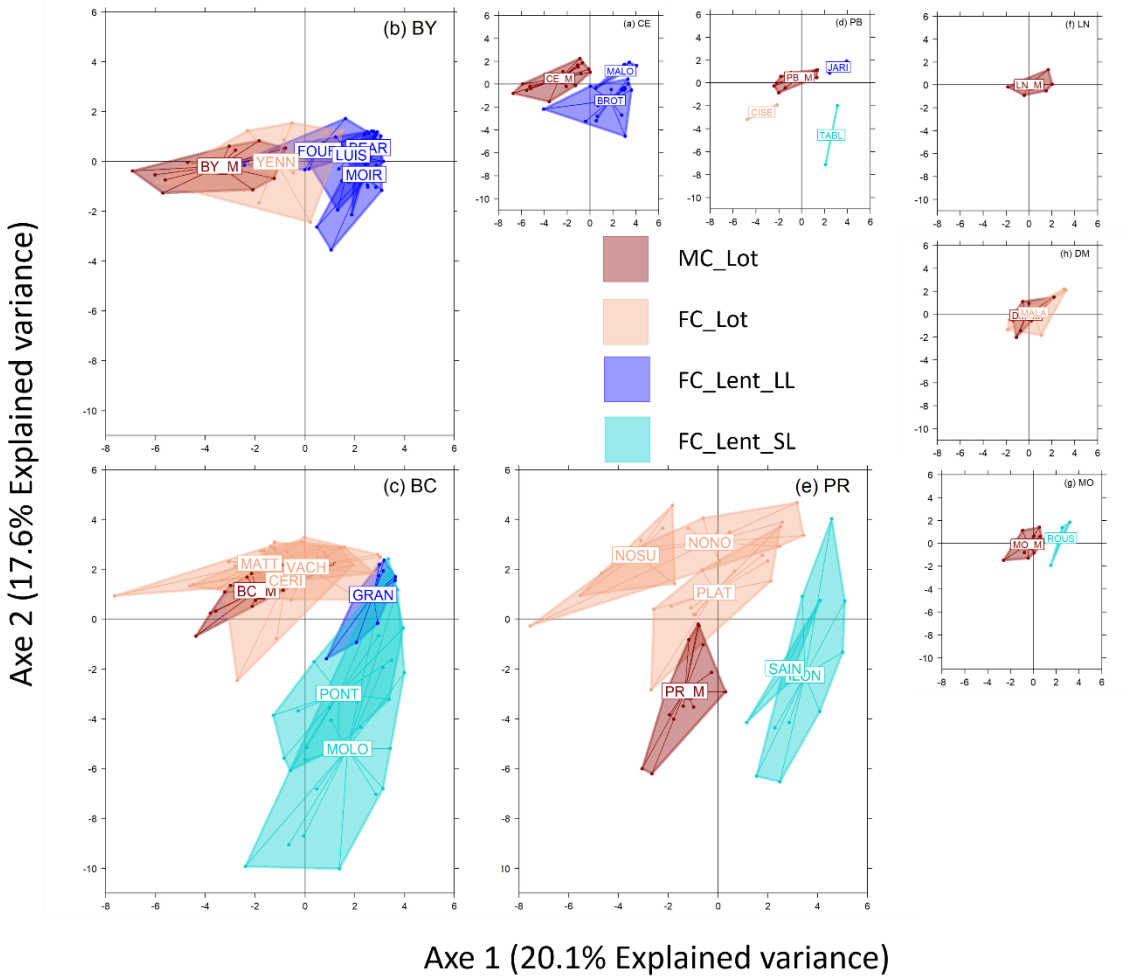


Fig. 4. Scores of stations × years on the centred within-sector PCA on annual log-densities of the 82 taxa sampled in eight sectors. Polygons group scores by station, and their colours indicate their belonging to a priori groups of stations. See Table 1 for stations and sector code.

Floodplain channels whose connection regime changed after restoration (Table 1) showed modifications in the structure of their fish community. Stations that became lotic following upstream and/or downstream reconnection (MATH, ENIL and VACH; Fig. 5A) were rapidly used by rheophilic taxa (Fig. 3). Stations that were reconnected downstream changed in two ways. Stations PONT and MOLO (Fig. 5A) were rapidly used by limnophilic and euryecious taxa. Station MALO (Fig. 5A) remained weakly favourable to fish. The effects of restoration were not obvious in most of the other stations that were only dredged, with no surface reconnection. In particular, FC_Lent_LL stations such as MOIR, LUIS and GRAN, had a low density and diversity of fish both before and after restoration (Fig. 3). Concerning the effects of restoration over time, we did not observe any obvious trend in post-restoration data (Fig. 5). When considering sectors with more than three restored channels with pre- and post-restoration data (BC and BY), the diversity of fish assemblage in each station x date clearly increased in the BC sector (larger ellipses after restoration on Fig. 5B), but not in BY (Fig. 5B).

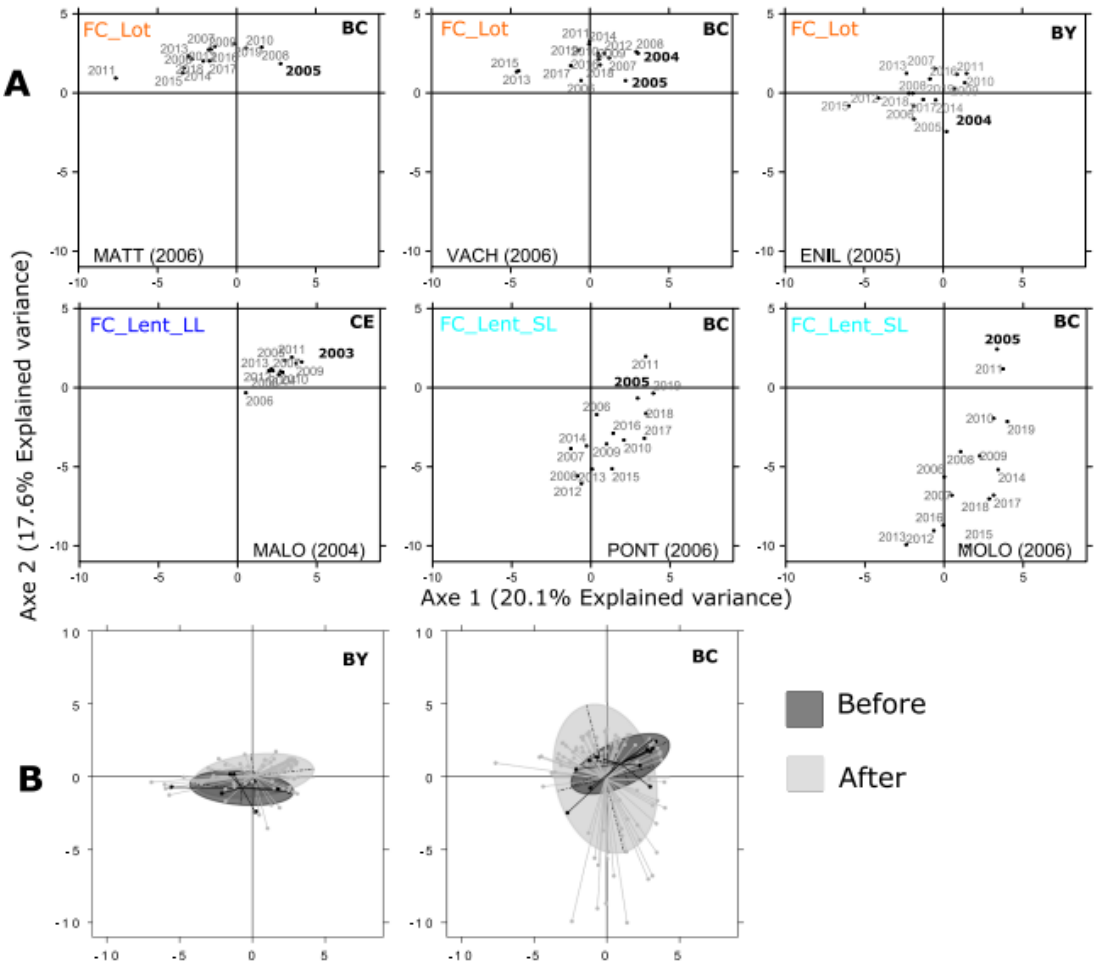


Fig. 5. Scores of stations × years on the centred within-sector PCA, as in Fig. 4. A) At the station scale: detail of the temporal trajectory for the six stations whose connection regime changed after restoration. Labels indicate sampling years, pre-restoration years are bolded. See Table 1 for sector and station codes. The year in brackets corresponds to the restoration year. B) At the sector scale with the Belley sector (BY: in which four stations have been restored and have before and after data, one of which has changed its connection regime see Fig. 6A) and Br´egnier-Cordon sector (BC: in which six stations have been restored and have before and after data, four of which have changed their connection regime, see Fig. 6B). The ellipses show the 67 % normalized distribution of scores, before and after restoration.

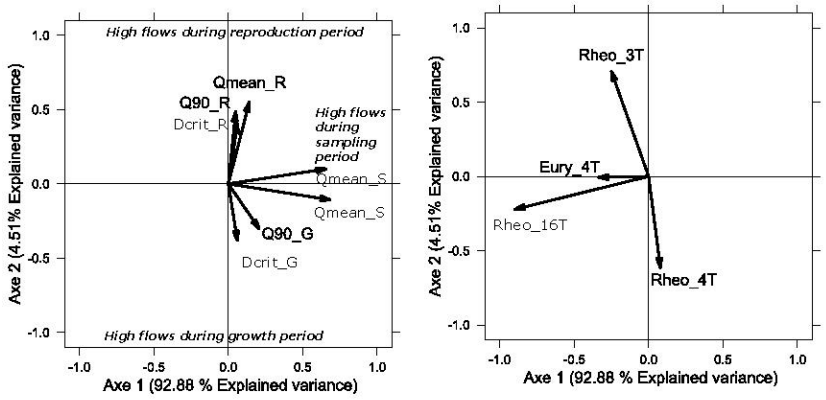
3.2 Inter-annual variations in fish habitat use after restoration and the influence of flow and temperature

The CoA analyses carried out for each *a priori* group of stations indicated which environmental variables were covariant with annual variations in guild densities (Fig. 6). The associated significance were P = 0.002 for FC_Lent_LL, P = 0.055 for MC_Lot and P = 0.09 for FC_Lot. The CoA for FC_Lent_SL, that involved few station x dates, was not significant (P = 0.57). The effects of flow variables are summarized in Table 4. High flows during the reproduction period (April-June) covaried positively with the log-densities of Eury_4T guild observed later in lentic stations (FC_Lent_SL and FC_Lent_LL) and with the log-densities of Rheo_3T and Rheo_16T guilds in lotic stations (MC_Lot and/or FC_Lot). High flows during the growing period (July-August) covaried negatively with the log-density of Rheo_3T

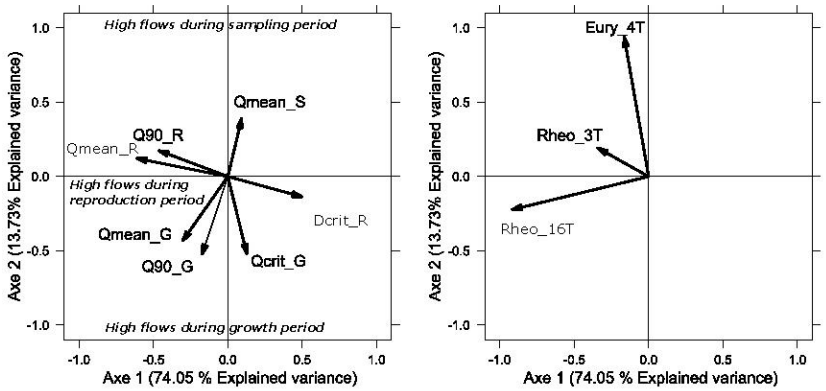
guild in MC_Lot, but positively in FC_Lot. Furthermore, Eury_4T log-densities covaried negatively with long duration of upstream connection (Dconn) in FC_Lent_SL. Finally, during the sampling period, the log densities of guilds covaried negatively with high flows in MC_Lot for 3 out of 6 guilds, and positively in the floodplain channels (Table 4). The log-density of Limno_9T guild covaried negatively with high flows in FC_Lent_SL whatever the period considered.

The effects of temperature variables, tested for FC_Lent_LL stations only, were secondary compared to the effects of flow. The CoA indicated that the Rheo_16T guild covaried positively with high temperatures during the sampling period, contrarily to the Rheo_4T and Eury_4T guilds (Fig. 6).

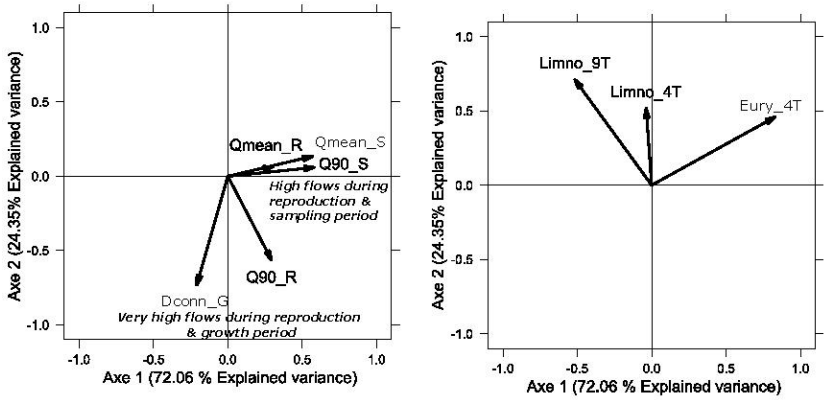
(A) Lotic stations: MC_Lot (N=8)



(B) Lotic stations: FC_Lot (N=7)



(C) Lentic stations with short life span : FC_Lent_SL (N=4)



(D) Lentic stations with long life span : FC_Lent_LL (N=5)

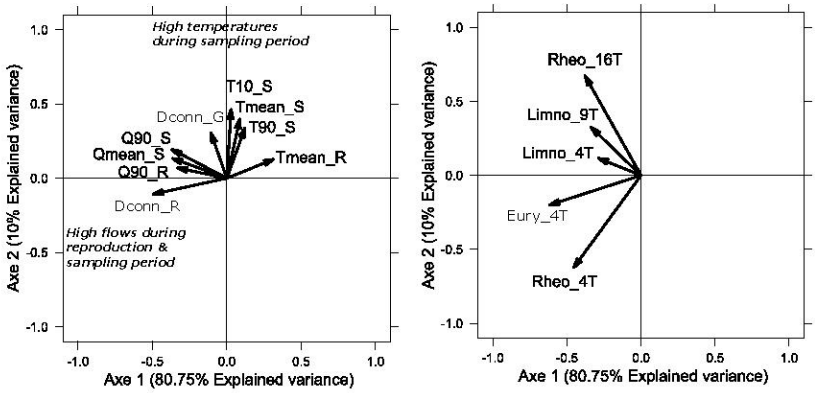


Fig. 6. Results of the four CoA analyses on the six a posteriori guilds of fish defined above and environmental (flow and temperature) datasets. Left panels show the environmental variable scores on axes 1 and 2; right panels show the posteriori guilds scores on axes 1 and 2. The text illustrates the interpretation of environmental axes. See Table 3 and Fig. 3 for variables codes and a posteriori guilds. For reasons of readability, environmental and fauna variables with a score between − 0.3 and 0.3 were removed from the graphs.

Table 4: Summary of the main results of this study. (1) The composition of the six *a posteriori* guilds defined by the hierarchical clustering analysis on the within-sector PCA. (2) The *a priori* groups of stations used preferentially by the *a posteriori* guilds. (3) The effects of high flows during the three selected periods on *a priori* group of stations used by the *a posteriori* guilds thanks to the four within-station co-inertia analyses. ↗ : positive covariance and ↘ : negative covariance between density of taxa and high flow.

Within-sector PCA results (Spatial distribution of *a posteriori* guilds among *a priori* groups)			CoA Results (Temporal change in *a priori* group use with high flows)		
A posteriori Guilds	Taxa (hierarchical clustering)	*A priori* groups used preferentially	Reproduction period (_R)	Growth period (_G)	Sampling period (_S)
Eury_4T	AlA1 GoG1 SqC1 RuR1	MC_Lot; FC_Lot; FC_Lent_SL	↗ FC_Lent_SL ↗ FC_Lent_LL	↘ FC_Lot ↘FC_Lent_SL (Dconn)	↗ FC_Lent_SL ↗ FC_Lent_LL ↗ FC_Lot ↘MC_Lot
Limno_9T	ScE1 ScE2 TiT1 TiT2 AmM2 LeG1 LeG2 AbB1 BlB1	FC_Lent_SL	↘FC_Lent_SL ↗ FC_Lent_LL	↘FC_Lent_SL	↘FC_Lent_SL ↗ FC_Lent_LL
Limno_4T	PsP1 PsP2 RhS1 RhS2	FC_Lot_SL	↘FC_Lent_SL ↗ FC_Lent_LL	↘FC_Lent_SL	↗ FC_Lent_LL
Rheo_16T	AlA2 AlA3 BaBu2 BaBu3 BaB4 BlB2 SqC3 SqC4 RuR2 RuR3 GoG3 ChN1 AlB1 AlB2 LeL1 LeL2	MC_Lot; FC_Lot	↗ FC_Lot (except for Dcrit) ↗ FC_Lent_LL	↗ FC_Lot	↘MC_Lot ↘FC_Lot ↗ FC_Lent_LL
Rheo_3T	BaBu1 GoG2 SqC2	MC_Lot; FC_Lot	↗ MC_Lot ↗ FC_Lot	↘ MC_Lot ↗ FC_Lot (except for Dcrit)	↘ MC_Lot
Rheo_4T	BaBa1 BaBa2 PhP1 PhP2	MC_Lot; FC_Lot; FC_Lent_LL	↗ FC_Lent_LL ↘ MC_Lot	↗ MC_Lot	↗ FC_Lent_LL

4. Discussion

4.1 Habitat complementarity for fish in river floodplain

The spatio-temporal analysis of fish communities essentially reflected spatial effects and indicated a strong influence of habitat types, based upon their hydraulic connection within the floodplain, on observed fish community structure. As expected, rheophilic species were more abundant in lotic stations and limnophilic species in lentic ones. This confirms, with numerous stations and long-term data, the general distribution patterns of floodplain fish communities observed in alluvial rivers around the word (Tales et al., 1996; Galat & Zweimüller, 2001). In addition, we identified an euryecious guild, grouping several YOY taxa (roach, gudgeon, chub, bleak), that used all types of floodplain habitats and particularly floodplain channels with short life duration, even if the corresponding adult stages mostly used lotic habitats. This pattern suggests a nursery function of floodplain channels, confirming previous observations (Grift et al., 2003; Humphries et al., 2006; Bolland et al., 2012).

Our results also indicated that habitat use varied in time as a function of flow. Indeed, covariance between the annual variations of fish after restoration and discharge variables suggested that high flows were major drivers of fish habitat use, with effects depending on the period of high flow occurrence and on the different habitat requirement of fish taxa.

4.2 A functional complementarity between floodplain habitats

The spatio-temporal analysis and our focus on inter-annual variations suggested three main functions of floodplains, each differently influenced by flow variations.

The "**nursery**" function is the main function revealed by our results and was confirmed by elements of the inter-annual analysis, which indicated that high flows during the pre-sampling period increase the use of lentic habitats by YOY of chub, bleak, gudgeon and roach. High flows can facilitate a passive drift of early developmental stages (larvae) present in the main channel towards floodplain habitats (Lechner et al. 2014) because of their poor swimming ability (Reichard et al., 2004). The nursery function was mainly associated with lentic stations where a high sedimentation rate shortened the persistence of aquatic habitats. The other lentic stations of longer duration such as LUIS, FOUR or BEAR had a very limited nursery function, and more generally a low density and diversity of limnophilic species. Several hypotheses can be put forward to explain this functional difference between the two types of lentic habitats. First, water temperature in short-lived floodplain channels such as MOLO and PONT (Table 1) was higher during the juvenile growth period (July-August) than in long-lived floodplain channels, the latter probably receiving a higher groundwater inflow. Higher temperature often has a positive impact on food production that imply a better growth of juveniles (Cowx, 2000; Bruslé & Quignard, 2013). Secondly, in long-lived lentic stations short but intense floods generate high shear stress that can limit sedimentation rates (Riquier et al., 2015; 2017). This may act as hydraulic disturbances for YOY fish, macroinvertebrates and macrophytes (Padial et al., 2009). In particular, macrophytes can provide egg-laying substrate, shelter and feeding areas for fish (Hamilton et al., 1990; Delariva et al., 1994; Casatti et al., 2003). This is consistent with observations of Marle et al. (2021) who reported high abundance of *Elodea nuttallii* (H. St. John, 1920) and *Ceratophyllum demersum* (Linnaeus, 1753) in MOLO station, a short-lived channel associated with shallow depths and silty substrate. Consistently, despite their weak nursery role, the spatio-temporal analysis indicated that long-lived floodplain channels could be used by species living in cooler waters (e.g. minnow, stickleback and stone loach, Huet, 1959). This is particularly the case at the MALO station (in the CE sector).

An "**effective reproduction**" function was suggested by the positive influence of high flows during the reproduction period on the recruitment of the euryecious guild in lentic habitats and the rheophilic guilds (Rheo_3T and Rheo_16T) in lotic habitats. It is likely that YOY of the rheophilic guilds originate from spawning in lotic environments, particularly because barbel, nase and spirlin breed in shallow water with high current velocity and coarse substrate (gravel and pebble) (Keith & Allardi, 2001). Concerning YOY of the euryecious guild, their reproduction could have taken place either directly in lentic environments, or in lotic environments from which they subsequently drifted (Lechner et al., 2014) towards their growth zones; the latter hypothesis is particular likely for chub, which requires gravel substrate for spawning (Keith & Allardi, 2001). A study by Bounket et al. (2021) on chub in the Rhône River showed that 90% of the YOY sampled in a lotic floodplain channel (MALA station in the DM sector) originated from the floodplain channels themselves and that only 6.5% came from the main channel (3.2% of undetermined origin). Conversely, according to our results, high flows during reproduction appear to reduce the recruitment of limnophilic species, especially in short-lived lentic channels. These results must be further investigated because high flows can also be favourable for the reproduction of some limnophilic and phytophylic species such pike by allowing access to spawning areas (Keith & Allardi, 2001). This differential effect of flows on fish reproduction was described in previous research (Cattanéo 2005; Scharbert & Borcherding 2013). For example, a two-year study in the Volga River floodplain (Górski et al., 2010) revealed a synchrony between the spawning of rheophilic fish and flood events that was not observed for limnophilic species.

A "**flow refuge**" function was suggested by the influence of high flows during the growth period on rheophilic species (Rheo_3T), probably moving from fast-flowing main channels (MC_Lot) to lotic floodplain channels (FC_Lot). This refuge function of the floodplain channels was observed in other shorter-term studies with analyses generally based on a single year (Schwartz & Herricks, 2005; Bolland et al., 2012). In addition, high flows preceding sampling reduced the abundance of three guilds (Eury_4T, Rheo_16T and Rheo_3T) in the main channels and increased the abundance in lentic floodplain channels (for Eury_4T, Rheo_16T, Rho_4T), suggesting an escape from fast currents. It should be noted that high flows can also induce movements to the bottom substrate (demonstrated for rainbow trout by Pert & Erman, 1994) that were not detectable given our point sampling method.

4.3 How did restoration favour new habitats, nursery and refuge functions?

In the spatio-temporal analysis, trajectories of stations with pre-restoration data available suggested that the main effects of restoration concerned channels becoming lotic and a limited number of channels becoming short-lived. Restored lotic floodplain channels offered new habitats colonized by rheophilic species, in addition to their role as refuge for these species (see above). In restored short-lived floodplain channels, the increase of limnophilic and euryecious taxa suggested a positive effect of restoration that created habitats for limnophilic taxa and improved the nursery function for euryecious taxa. The weaker changes observed in long-lived floodplain channels were consistent with their weak nursery role, and probably their lower temperature during the growth period. It should be noted that the restoration targeted such increased groundwater inflows in LUIS, FOUR and BEAR stations. However, the low levels of dissolved oxygen in groundwater can limit zooplankton production and therefore impact fish foraging and thus survival (Marle et al., 2023). Concerning the long-term effect of restoration, the absence of trend in fish response after restoration suggests that the temporal variations were mainly due to annual environmental variations.

Overall, restoration increased the diversity of species using floodplain habitats. At Brégnier-Cordon, where four floodplain channels had their connections modified, restoration clearly increased the spatio-temporal diversity of fish assemblages across the floodplain. Such a floodplain-level response was not observed at Belley, where only two channels had their connections restored. It is also possible that the environmental configurations of the sectors (e.g. habitat heterogeneity and connectivity of channels) influenced the success of the restoration. Among restoration measures, the restoration of short-lived floodplain channels enabled them to become habitats of high fish diversity and to play a role in the growth of YOY rheophilic species. These channels became priority habitats for limnophilic species.

4.4 Limits of our interpretation

A full interpretation of the observed temporal variability remains difficult due to the combined influence on fish communities of multiple abiotic and biotic processes (Cauvy-Fraunié et al., 2020). In particular, we mostly related the temporal effect to high flows, in accordance with other studies (Bain et al., 1988; Poff & Allan, 1995; Taylor & Cooke, 2012). However, many other biotic and abiotic variables, not considered here, can impact fish communities. These variables include predation, competition for resources, pollutants, oxygen concentration, nutrients, substrate (considered indirectly in our habitat typology; Riquier et al., 2015, 2017) and light (Bruslé & Quignard, 2013). Finally, as the data were collected over more than 20 years (with only one sampling per year), variability due to sampling efficiency and timing was difficult to avoid (Trenkel et al., 2004).

Another important limitation is the insufficient statistical power of the coinertia analysis of short-lived lentic habitats, which is probably the reason for the lack of significance of this particular analysis. Although the interpretations of this analysis are consistent with our initial hypotheses as well as with the literature, they should be taken with caution. Another important limit concerns the interpretation of the influence of high flows on reproduction success. We defined a fixed reproduction period for all fish species (April - June) in order to perform a general analysis of the fish communities (Daufresne et al., 2003). However, this period does not consider the complexity of each specific life history. The reproduction of early spawners (e.g. pike, nase, dace, roach; Ovidio & Philippart, 2008) and that of species that reproduce later (e.g. bleak, tench, rudd; Tissot & Souchon, 2011) are not influenced by the same flow rates. In addition, due to the limited temperature data, we were unable to look at the interaction between temperature and flow rates, the combination of which influences reproductive mechanisms (Rolls et al., 2013).

4.5 Lessons for efficient restoration measures

Our results demonstrated the importance of restoring habitat diversity and connectivity in riverine floodplains because habitats may have complementary functions for fish (Pander et al., 2018). This complementarity is often discussed in the literature (Lévêque, 1995; Werner, 2002; Schwartz & Herricks, 2005), but has rarely been demonstrated on long-term and multi-site data. Therefore, our conclusions can potentially be transposed to other large alluvial rivers in the temperate zone (see also Ramler & Keckeis, 2019, Manfrin et al., 2020; Stoffers et al., 2021).

Results highlighted the importance of short-lived floodplain channels, which have various functional roles for fish (i.e. nursery and refuge) and are also preferred habitats for limnophilic species. These floodplain channels were often completely disconnected and inaccessible for fish before restoration. They were reconnected at their downstream end to a lotic habitat and share a common trend of rapid

fine sediment infilling after restoration. For the same reason, however, these habitats are not self-sustainable and will likely disappear in less than 30 years (Riquier et al., 2017), with a progressive decrease in their functional roles. This means that the restoration actions carried out in this type of channels might have to be repeated, when the river is no longer able to generate this type of habitat by itself.

We also showed that the presence of lotic floodplain channels permanently connected to the main channel was important, especially for rheophilic species that can use them as refuge areas. Before restoration, these were either completely disconnected from the main channel, or connected downstream. After restoration, most of these floodplain channels are currently shown to be self-sustainable and to preserve a gravel substrate under the prevailing conditions (Riquier et al., 2017).

Finally, we showed that long-lived floodplain channels with higher shear stress during high flows and lower temperature during the growth period are not suitable habitats for YOY and their often oligotrophic nature gives them limited trophic conditions for adults. However, we recommend maintaining some of these channels that seem to be used by a limited number of cold water fish species (i.e. minnow and stone loach). Indeed, they may be used by specific macroinvertebrate assemblages (Brunke et al., 2003) and can be increasingly important in the context of global warming.

4.6 Perspectives

Our study indicates complementary functions of the main and floodplain channels. These functions are influenced by high flows and were improved by restoration in the case of the Rhône River. Further studies could better account for other variables in addition to flows and temperature, such as the magnitude of groundwater inflows, the density and diversity of food resources (i.e. macroinvertebrates), and/or the availability of spawning areas (i.e. combinations of substrate, vegetation and accessibility characteristics). Furthermore, the complementarity of floodplain habitats could be better understood by focusing on population dynamics of selected species, based on a detailed analysis of spatio-temporal variations in size class distributions. This study may contribute to the selection of species for such more detailed analyses of the complementarity between habitats in the floodplain. In particular, it would be important to focus on abundant species that clearly use different habitats, such as bleak. Other candidates are species with periodic reproduction strategy, (e.g. chub, roach, barbel and nase; Blanck et al., 2007) that synchronise their spawning with optimal environmental conditions (Winemiller and Rose, 1992).

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Data availability statement

Restrictions apply to the availability of discharge data, which were used under an agreement for this study. Fish and temperature data are available from the authors upon reasonable request.

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