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Do highly anthropized hydrological conditions in marshes influence fish communities according to their life-history strategies?

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1 **Do highly anthropized hydrological conditions in marshes influence fish communities**
2 **according to their life-history strategies?**

3 **Short running title**

4 Fish response to hydrology in strongly anthropized marshes

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13

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21

22 **Abstract**

23 Alterations of natural hydrology in aquatic ecosystems are known to strongly impact the community
24 composition of different taxa. Surprisingly, literature on the potential influence of hydrology on fish
25 community composition is still very scarce in agricultural marshes, where canals represent one of the

26 few remaining aquatic habitats. This study is aimed to address this research gap by monitoring fish
27 communities in independent hydrological units differing in hydrology management over a six-year
28 period. We predicted variable fish responses to the hydrological context according to different life-
29 history strategies (opportunistic, equilibrium or periodic species). Periodic and opportunistic species
30 were the most frequently observed. Despite differences in hydrology between canals (but little
31 variation among years), we found that hydrology explained only a very low proportion of variation in
32 the composition of fish communities. In particular, flooding duration of meadows in early spring did
33 not influence the composition of fish communities, not even the abundance of periodic species
34 expected to rely on such temporary habitats. Instead, fish communities were more influenced by
35 local habitat variables (aquatic vegetation cover, turbidity, tree roots and refuges under the canal
36 banks). The hydrological management of most hydrological units for agricultural purposes (i.e. severe
37 flood abatement in spring and shallow water depth in canals in summer) was found to be
38 incompatible with conservation goals to promote more diverse fish communities between
39 hydrological units. Therefore, we call for further investigations in similar habitats covering a larger
40 range of hydrological conditions.

41 **Keywords**

42 ditch, seasonal wetland, water level, functional strategies, water regulation

43 **Introduction**

44 At the interface between aquatic and terrestrial systems, wetlands are crucial habitats for
45 biodiversity (Williams et al., 2003). They are dynamic ecosystems where aquatic organisms typically
46 experience changes in hydrology following seasonal pulses of rainfall (Williams 2006), or a decreased
47 water supply because of water regulation and evapotranspiration. Intra-annual variability in
48 hydrology results from climatic patterns but also reflects human control of water for a large range of
49 uses (Rideout et al., 2021). In temperate wetlands, and more specifically in marshes, water
50 management is primarily aimed at draining to lower water levels in late winter and spring for

51 agricultural purposes. This generally leads to strong changes in the seasonality of water levels, very
52 low water levels in summer and low interannual variability (Duncan et al., 1999; Williams, 2006).

53 Alterations of natural hydrology in aquatic ecosystems (e.g. dam construction, river diversion,
54 channelization, pumping or urbanization; see the review by Poff et al. (1997)) significantly affect the
55 community composition of different biological groups; this has been particularly studied for fish and
56 invertebrates, mainly in lotic ecosystems (Poff & Ward, 1989; Poff & Allan, 1995; Bunn & Arthington,
57 2002; Bradley et al., 2017; White et al., 2019). For instance, reduced flow variability leads to
58 decreased fish abundance (Bunn & Arthington, 2002), and both elevated and reduced flow
59 magnitude is associated with declines in fish abundance and diversity (Poff & Zimmerman, 2010). As
60 such, analyzing how hydrological alterations affect fish communities is undoubtedly important. This
61 was first done by focusing on abundance and diversity data (Karr, 1981), however, functional
62 approaches have been increasingly popular over the last decade, especially within the framework of
63 the development of fish-based biomonitoring indices (Karr, 1981; Oberdorff et al., 2001; Pont et al.,
64 2006). Using these approaches, one can compare taxonomically dissimilar communities and identify
65 community assembly rules (Poff & Allan, 1995).

66 To date, life-history strategies (LHS) of fish have been mainly studied in streams. Winemiller and Rose
67 (1992) originally identified three major endpoints of LHS representing different trade-offs among
68 growth, fecundity, life span and parental care. This was later validated using freshwater fish in France
69 (Pont et al., 1995). First, opportunistic strategists are small-bodied, short-lived species with early
70 maturation, and are generally associated with episodically disturbed habitats. Periodic strategists are
71 large-bodied species with late maturation and high fecundity, and are typically favored in seasonally
72 flooded habitats. Finally, equilibrium strategists are species of intermediate body size, displaying high
73 parental care, with few offspring and high juvenile survival; they are usually associated with stable
74 environments. These three species groups behave differently along hydrological gradients; for
75 instance, the conversion of lotic habitats into lentic after the construction of a dam leads to a shift

76 from opportunism to equilibrium as the dominant strategy within fish communities (Mims & Olden,
77 2013; McManamay & Frimpong, 2015), or increased connectivity of aquatic patches leads to an
78 increased proportion of periodic species (Miyazono et al., 2010).

79 The responses of fish communities to hydrological patterns in marshes are expected to differ from
80 the responses of fish communities in streams. The fish communities of these two habitats are
81 normally different. Marshes are mostly characterized by eurytopic to limnophilic species and to a
82 lesser extent by rheophilic species. Furthermore, particular human uses of marshes – e.g. agricultural
83 drainage – drastically control seasonal variations in water depth in such a way that the transition of
84 early spring water depths is particularly rapid, far from the natural dynamics of rainfall patterns
85 (Laffaille et al., 2004; Rehage & Trexler, 2006; Rideout et al., 2021). Such high fluctuations of water
86 depths at a key stage of the fish life cycle (i.e. spawning) should disadvantage equilibrium species and
87 benefit periodic species better adapted to seasonal environmental variations (Winemiller, 2011). By
88 contrast, where the water depth is very low throughout the year, fish communities are expected to
89 support a much lower proportion of large-bodied periodic species, highly sensitive to hypoxia
90 compared to small-bodied species (as showed experimentally by Robb and Abrahams, 2003).

91 Periodic species also need sufficient water depth to move (Poizat & Crivelli, 1997; Meyer & Posey,
92 2009) and to escape predation (as showed in small streams by Harvey and Stewart, 1991).

93 Hydrological management of marshes also modifies the extent of the connectivity between aquatic
94 habitat patches. Above all, it drives the availability of aquatic habitats, e.g. by flooding adjacent
95 habitats within canals and streams. Such temporarily flooded habitats (e.g. wet meadows) provide
96 attractive feeding (Junk, Bayley & Sparks, 1989; Tockner, 2000) and nursing grounds (Cucherousset,
97 Carpentier & Paillisson, 2007, 2008; Miyazono et al., 2010; Scharbert & Borcharding, 2013) that are
98 essential for periodic species. They may also attract opportunistic species displaying early
99 maturation, high habitat tolerance and a short generation time like cyprinid species, and small-
100 bodied species because they offer refuges from large predators (Poizat & Crivelli, 1997; Hohausová,

101 Lavoy & Allen, 2010; Jopp, Deangelis & Trexler, 2010; Volcan & Guadagnin, 2020). Despite the
102 potential influence of hydrology on fish communities in wetlands, this issue is still understudied:
103 about 25 times more articles mentioning hydrology and fish were found on lotic ecosystems
104 compared to wetlands in the Web of Science (6863 *versus* 276). Among those on wetlands, about 20
105 addressed the influence of hydrology on fish in these ecosystems.

106 This study aims to address this research gap by examining the influence of hydrology on the
107 composition of fish communities in canals of a large marshland, according to their LHS. We sampled
108 fish communities in independent hydrological units differing in hydrology management over a six-
109 year period. By conducting a multi-year study, we intended to account for possible annual
110 differences in climate conditions and in turn in hydrology within the hydrological units. We expected
111 hydrology, and more precisely water depth, water depth variation in early spring, and spring flooding
112 duration of meadows to be drivers of the fish community composition, with contrasting effects
113 according to the LHS of the species, as outlined above. As the experiment was carried out in natural
114 conditions, it was not possible to control all environmental factors, so we also studied the possible
115 influence of water physico-chemistry and canal morphology known to be of importance for fish
116 communities (Smiley et al., 2008; DeZiel et al., 2019; Koschorreck et al., 2020).

117 **Materials and methods**

118 *Study area*

119 The study was conducted in the Marais poitevin, a ca. 1000-km² French hypertrophic marshland
120 located along the Atlantic coast (46°30'-46°15'N; 1°30'-0°35'W, Figure 1). The region is characterized
121 by a warm Atlantic climate type, with rainfall greater than evapotranspiration in winter balanced by
122 an almost equal deficit of 300 to 350 mm in summer. Flood peaks take place in meadows mostly in
123 winter and the marshland is mostly dry in summer, sometimes until fall depending on the
124 hydrological conditions. It is also characterized by intensive water management practices for
125 agricultural purposes (EPMP, 2015). Land use is currently dominated by crops and meadows (50 and

126 40%, respectively), and the remaining areas are mostly woodlands (Godet & Thomas, 2013).
127 Important land-use changes have occurred over the last century, notably the conversion of more
128 than 50% of meadows into croplands and the intensification of agricultural practices (Duncan et al.,
129 1999; Godet and Thomas, 2013). The Marais poitevin is also composed of an 8200-km long network
130 of drainage canals that have been progressively established since the Middle Ages (EPMP, 2015). It
131 has been historically divided into different hydrological units in which water management is
132 controlled independently from the surrounding units because of different water regulations fixed by
133 management committees. This leads to different hydrological patterns across units. We selected
134 eleven hydrological units to represent the diversity of hydrology conditions in the study area (Figure
135 1; a detailed description of the hydrological units is provided in EPMP, 2015; Mauchamp et al., 2021).
136 One section of a canal was selected in each hydrological unit to monitor the fish community from
137 2015 to 2020. The sampled canals were wide ($8.8\pm 1.2\text{m}$) and never dried out.

138 *Fish sampling*

139 Each year, fish were sampled between the last week of June and the second week of July. At this
140 time of the year, many aquatic habitats like meadows and narrow canals have dried out, and fish
141 take refuge in larger canals. As a result, monitoring provides a good overview of the fish communities
142 inhabiting the entire hydrological units. Moreover, this time of the season is optimal for sampling fish
143 since the water depth in the canals is sufficient to conduct the fieldwork by boat but not too high to
144 limit the efficiency of electrofishing (0.20 to 1.70m). Lastly, all species had reproduced, so that all
145 young-of-the-year individuals were reliably identifiable in the field, except for some *Blicca bjoerkna*
146 and *Abramis brama* specimens grouped as breams in the analyses. Fish were sampled using the point
147 abundance sampling approach (PAS; Copp and Persat, 1989; Nelva et al., 1979) with an electrofishing
148 apparatus (Heron®, Aigrette®, or EFKO F.E.G. 8000® depending on the year, voltage during fishing
149 operations $255\pm 75\text{V}$, amperage $7\pm 5\text{A}$). A total of 30 PAS were performed *per* canal, spaced out by at
150 least 10 meters to provide independent samples. At each PAS, the anode was immersed about five

151 meters in front of the boat and near the canal bank where fish generally concentrate. All shocked fish
152 within 1 m² of the impact point of the anode were caught, identified to the species level, measured
153 (fork length, mm), and released back into the water.

154 *Environmental variables*

155 The water depth was calculated for different periods (see below), and measured at two different
156 spatial scales: locally, in the canal where fish were sampled (“fish canal” thereafter), and across 10
157 small nearby canals connected to the fish canal in order to better characterize the hydrological
158 conditions of the hydrological unit (average value). Given that the daily water depth in any canal of a
159 hydrological unit can be calculated using a limnigraph deployed in a permanent (always full of water)
160 canal (taking into account the altitude of its bottom), we calculated the average water depth for two
161 seasons: i) in winter (from November to February, prior to the spawning season and the fish
162 monitoring campaign) because flooding peaked mostly during this period and could influence the
163 spatial distribution of several fish species (Heermann & Borcharding, 2006; Scharbert & Borcharding,
164 2013; Morat et al., 2018), and ii) in spring (from March to June, before fish sampling) because it
165 covered the spawning season of most of the studied species (Keith et al., 2020). Two additional
166 hydrological variables were calculated at the hydrological unit scale to describe the rate of water
167 depth changes at the pivotal period in early spring, namely the coefficients of variation of water
168 depth in March and in April. We also assessed the amount of temporary fish-accessible aquatic
169 habitats as expressed by the flooding duration (days) of at least 5% (a maximum water depth ranging
170 from 6 to 21 centimeters depending on the hydrological unit) and at least 20% (a maximum water
171 depth ranging from 14 to 44 centimeters) of the meadows in the whole hydrological unit (see Rapinel
172 et al., 2018; Crabot et al., 2022 for a complete description of the calculation). We calculated these
173 metrics at the hydrological unit scale because they better reflected the conditions experienced by
174 fish before refuging in the largest canals in late spring. Preliminary tests were carried out using other
175 quantiles (notably 10% of flooded meadows), but they were not retained because the flooding

176 duration values were highly correlated ($r=0.9$) with those for the 5% and 20% quantiles and with
177 water depth. Calculations were done for spring and winter, so that four flooding duration variables
178 (two quantiles \times two seasons) were used for subsequent analyses.

179

180 We also considered a series of water physico-chemistry variables, most of them collected as part of a
181 companion monitoring program on the eutrophication of the Marais poitevin (UNIMA, unpublished
182 data). Chlorophyll a content ($\mu\text{g.L}^{-1}$), oxygen percentage saturation (%), conductivity ($\mu\text{S.cm}^{-1}$), and
183 ammonium, nitrite, nitrate and orthophosphate concentrations (mg.L^{-1}) were measured in one large
184 canal representative of each hydrological unit, all year round (more details on the methodology are
185 provided in Appendix A, see also values in Table 1). We also measured basic variables – water
186 temperature ($^{\circ}\text{C}$), conductivity ($\mu\text{S.cm}^{-1}$) and turbidity (m) – in the fish canal once a year, when
187 sampling the fish. Lastly, we measured five habitat features: aquatic vegetation cover (%), tree roots
188 and refuges under the banks (i.e. crucial habitats for certain species to nurse and spawn; Kottelat &
189 Freyhof, 2007), width (m) of the canal section where fish were sampled, and the total network length
190 (km/ha) of large permanent canals and that of narrower temporarily dried canals in the hydrological
191 unit (Appendix A). These latter two variables were used as a proxy of the habitat heterogeneity for
192 fish at the hydrological unit scale (Cucherousset et al., 2006).

193

194 *Data analysis*

195 All statistical analyses were conducted with R software version R-4.1.1 (R Core Team, 2021). We
196 assessed the collinearity between the set of 25 environmental variables with the 'vifcor' function in
197 the *usdm* package (Naimi, 2017), using an excessive correlation threshold of 0.7 as recommended in
198 Dormann *et al.* (2013). The water depth in the fish canals and more broadly at the hydrological unit
199 scale and measured in winter were removed from subsequent analyses.

200 To assess to what extent species composition changed in each hydrological unit over time, we
201 calculated the cumulated species richness over six years and the average between-year similarity
202 (the Jaccard index for presence-absence data and the Bray-Curtis index for abundance data) using
203 the ‘vegdist’ function in the *vegan* package (Oksanen et al., 2020).

204 A body of literature supports the idea that juvenile fish respond differently to environmental
205 conditions, and more specifically to hydrology, than older ones (Grenouillet et al., 2001; Gouraud et
206 al., 2008; Bergerot & Cattaneo, 2017). Since the relationship between fish communities and
207 environmental variables yielded similar results when using all fish data or when removing the young-
208 of-the-year from the dataset (they represented 38% of all fish caught, Appendices B and C), we only
209 presented the results from the complete dataset. In practice, we computed a co-inertia analysis
210 between a scaled principal component analysis (PCA) on environmental variables and a non-scaled
211 PCA on fish abundances (11 sites × 6 years, Hellinger transformed). By optimizing the covariance of
212 the multivariate axes of the two tables, the co-inertia analysis summarizes variations of fish
213 composition and environmental variables among samples simultaneously, and is a suitable analysis
214 when the number of variables is high compared to the number of samples (Judes et al., 2021). The
215 significance of the RV coefficient, which describes the strength of the correlation between the two
216 tables, was tested with a Monte-Carlo test (999 permutations) on the sum of eigenvalues of the co-
217 inertia (Heo & Gabriel, 1998). All these analyses were computed using the ‘dudi.pca’, ‘coinertia’ and
218 ‘RV.test’ functions in the *ade4* package (Dray & Dufour, 2007).

219 We tested whether the species belonging to each of the three LHS (Table 2) were distributed
220 differently using Syrjala’s test (Syrjala, 1996; ‘syrjala’ function in the *ecespa* package; Rot & Blanco-
221 Moreno, 2022). This test is designed to be sensitive to the difference in the spatial distributions of
222 two groups but not to the difference in their abundance (Rot & Blanco-Moreno, 2022). We computed
223 three separate pairwise tests: opportunistic vs. equilibrium, opportunistic vs. periodic and
224 equilibrium vs. periodic.

225 Finally, to evaluate the weight of the hydrological variables as drivers of the composition of fish
226 communities compared to the other environmental variables, we conducted a variation partitioning
227 analysis using fish communities (abundance data) as the response table, and three explanatory tables
228 (a hydrology table, a water physico-chemistry table, and a habitat table). The partitioning was based
229 on a redundancy analysis. The results were plotted on a Venn diagram, using the 'varpart' function in
230 the *vegan* package (Oksanen et al., 2020). The significance of the variation in the fish communities
231 explained by each group of environmental variables was assessed using the 'rda' function in the
232 *vegan* package (Oksanen et al., 2020).

233 **Results**

234 *Description of the environmental conditions of the hydrological units*

235 The hydrology of the canals fluctuated very little in spring between years whatever the hydrological
236 unit (Figure 2a, b, d), but more so in winter (infrequent significant rainfalls in the winter of 2020
237 exceeded the flood mitigation capacities of the hydraulic structures in all hydrological units, while a
238 rainfall deficit was noted in 2017; Figures 2c, e, f). Spring flood duration in meadows fluctuated
239 between years, especially for 5% of the meadows (Figure 2g, h). Overall, hydrological conditions
240 varied between canals (range of values in Table 1). The canals also varied for the other
241 environmental variables (description not given, but ranges of values provided in Table 1).

242 Spring water depth and spring flood duration of 5% and 20% of the meadows in the hydrological
243 units contributed significantly to the first two principal components of the PCA of all the
244 environmental variables (Appendix D). Three other variables also significantly contributed to the PCA:
245 the total network length of the large permanent canals in the hydrological units, the amount of tree
246 root refuges, and the aquatic vegetation cover in the fish canals.

247 *Description of fish communities*

248 We caught 8070 individuals belonging to 25 species over the six years of the experiment (Table 2).
249 The species pool was composed of three equilibrium species, 10 periodic species and 12
250 opportunistic species (Table 2). Overall, the five most abundant species represented more than 70%
251 of all individuals (Table 2): *Rutilus rutilus* (34%), *Ameiurus melas* (16%), *Gambusia holbrooki* (8%),
252 *Anguilla anguilla* (7%) and bream (6%). These species were also the most frequently
253 recorded (occurrence $\geq 77\%$, Table 2). Periodic, opportunistic and equilibrium species represented
254 57%, 24% and 19% of all individuals, respectively.

255 Species richness and abundance differed between canals. Some supported both high richness and
256 high abundance of fish (e.g. canal 4), and some supported few fish (e.g. canal 11, Figures 3a, b). The
257 annual species richness was relatively stable over the study period in most of the canals. However,
258 species turnover occurred (Fig. 3a). Between-years similarity calculations of species composition
259 indicated that on average just over half of the species composition in terms of presence-absence did
260 not vary over the years (0.61 ± 0.08 , values for each canal provided in Figure 3c). Roughly comparable
261 values were found for abundance data (0.51 ± 0.10 , Figure 3d).

262 *Associations between environmental variables and fish communities*

263 There was a significant correlation between the composition of fish communities and the
264 environmental variables ($RV=0.54$, $p < 0.001$). The cumulative projected inertia on the first two axes
265 reached 87% (81% on the first axis and 6% on the second axis, Figure 4). Most canals were very
266 similarly distributed by both the environmental variables and species composition datasets (Figure
267 4a). Only canal 4 had a substantially different relative position between the two datasets. It was close
268 to canal 6 in terms of fish composition, but close to canal 7 in terms of environmental conditions.
269 Overall, the first axis of the co-inertia analysis was primarily structured along a gradient of tree root
270 refuge availability (higher values on the right of the ordination), and large canal length and nitrate
271 concentration to a lesser extent (higher values on the right of the ordination in Figure 4b, see
272 canonical weights of environmental variables in Appendix E). The left part of the ordination was

273 characterized by higher values of conductivity in the hydrological units and turbidity in the fish
274 canals. As for species, the first axis was mostly positively correlated with the abundance of *R. rutilus*
275 and to a lesser extent negatively correlated with the abundances of *Carassius gibelio* and *G.*
276 *holbrooki* (Figure 4c, and canonical weights of species in Appendix E). The second axis of the co-
277 inertia analysis was negatively correlated with two environmental gradients: the coefficient of
278 variation in water depth in April and the width of the fish canals. The lowest scores on this axis
279 corresponded to higher abundances of *A. anguilla*, *Esox lucius* and *Sander lucioperca*, and the highest
280 scores to a higher abundance of *A. melas*.

281 The spatial distribution of periodic species (Figure 4c) significantly differed from the spatial
282 distributions of opportunistic ($p = 0.010$) and equilibrium ($p = 0.034$) species, which were themselves
283 comparable ($p = 0.577$), in line with the species location on the co-inertia plot (Figure 4c).

284 Lastly, the variation partitioning analysis confirmed that the three groups of environmental variables
285 (hydrology, physico-chemistry and habitat) significantly explained the composition of the fish
286 communities ($p < 0.004$), with habitat variables contributing most, followed by physico-chemistry and
287 hydrology variables (Figure 5).

288 **Discussion**

289 Studying the influence of different aspects of hydrology on biodiversity in highly regulated aquatic
290 systems is a critical issue because, whether it is proved to have a key role, water regulations can be
291 adjusted to meet conservation objectives. We showed that hydrology significantly differed between
292 hydrological units, but explained only a small proportion of the variation of fish community
293 composition (18% co-explained with other environmental variables). Contrary to our expectations,
294 the surface area of flooded meadows as well as the water depth in the canals of the hydrological
295 units did not influence the composition of fish communities, especially in early spring, regardless of
296 their LHS group.

297

298 Nevertheless, the distribution of periodic species, recorded most abundantly in the canals (57% of
299 the fish, 10 out of 25 species), differed from the distributions of opportunistic and equilibrium
300 species. This pattern was mainly driven by *R. rutilus* on the first co-inertia axis and by *A. anguilla* and
301 *E. lucius* on the second axis, and this arrangement of periodic species depended on specific
302 environmental conditions. *Rutilus rutilus* was more abundant in canals with many tree roots and
303 refuges under the banks, in line with Brosse & Lek (2000) and Kottelat & Freyhof (2007). The
304 abundance of *R. rutilus* was to a lesser extent positively correlated with spring water depth in the
305 canals, in line with Poizat & Crivelli (1997) and Cucherousset et al. (2008). The other periodic species,
306 notably *A. anguilla* and *E. Lucius*, were associated with large canals with marked variations in water
307 depth in April (reaching up to -0.74 meters over three weeks). This is consistent with the expectation
308 that periodic species are better adapted to seasonally fluctuating environments, as observed in some
309 lotic habitats (Winemiller, 2011; Mims & Olden, 2012).

310

311 Surprisingly, we did not find any association between the abundance of periodic species and the
312 extent of temporarily flooded meadows in spring, although these habitats are generally used as
313 nursing and feeding areas by periodic species (Cucherousset et al., 2007; Janáč et al., 2010; Miyazono
314 et al., 2010). For example, Janáč et al. (2010) found that flood duration was the only environmental
315 variable influencing the density of juvenile cyprinids (*A. bjoerkna*, *Scardinius erythrophthalmus* and *R.*
316 *rutilus*) inhabiting the floodplain artificial waterbodies. This apparent variable outcome cannot be
317 explained by differences in the range of flood duration experienced by fish because it was
318 comparable and fairly large in both studies (for instance 3-120 and 0-82 days depending on the
319 hydrological unit for the 5% and 20% thresholds we used, respectively). The role played by flood
320 duration in river floodplains varies across studies. King et al. (2003) suggested that flooding for
321 several weeks to months may be required for a floodplain to be successfully colonized by fish
322 because a shorter flooding duration is apparently not enough (Beesley et al. 2012). Janáč et al. (2010)
323 found that a 90-day flood (considering days with water temperature above 16°C) was long enough

324 for an extensive use of floodplain habitats by phytophilous cyprinids. Therefore, the lack of a
325 significant relationship between periodic fish and spring flooding duration of meadows in our study
326 may indicate that: i) although flooding lasted long enough (sometimes up to 120 days), the pattern
327 was too patchy to be suitable for fish (Appendix F), and/or ii) independently of flooding duration,
328 water temperature, water depth and more widely environmental conditions (substrate, vegetation,
329 food resources, see Cucherousset et al., 2007) are also decisive for the colonization of flooded
330 meadows by fish and may have been limiting in the study area. Furthermore, the rapid decrease in
331 water depth sometimes observed in the Marais poitevin in spring can be detrimental for the fish
332 present in flooded areas (Foubert et al., 2019). Further investigations would be needed to explore
333 these hypotheses.

334

335 Opportunistic fish – the most species-rich group (12 out of 25 species) – were most abundant in
336 narrow, turbid and vegetated canals. This is consistent with previous observations, notably in
337 floodplain lakes (Miranda & Lucas, 2004; Miyazono et al., 2010); the results of these studies suggest
338 that turbidity may favor small-bodied species by limiting predation by piscivorous fish. Similarly,
339 vegetated areas can provide refuges for small-bodied species, such as mosquitofish, and suitable
340 feeding grounds (Linden & Cech, 1990). Opportunistic fish have also been found to be more
341 abundant where water depth is less variable, contradicting the results of other studies (Mims &
342 Olden, 2012; Hitt, Landsman & Raesly, 2022). However, even if opportunistic fish benefit from
343 habitats with high hydrological variability, they avoid habitats with strong seasonality (i.e. very
344 predictable habitats) (Mims and Olden, 2012). By analogy, in our study, the canals with strong
345 seasonal hydrological variability in early spring would not be suitable for opportunistic fish.

346 Furthermore, although small-bodied opportunistic species can benefit from flooded meadows (Poizat
347 & Crivelli, 1997; Hohausová et al., 2010; Volcan & Guadagnin, 2020), we found no evidence of such
348 an association. This may be due to the possible inadequacy of flooded meadows for the reasons
349 suggested above. Furthermore, none of the other hydrological variables that we used influenced the

350 distribution of opportunistic species (notably the most abundant species: *Gasterosteus aculeatus*, *G.*
351 *holbrooki* and *Lepomis gibbosus*) suggesting that opportunistic fish species were insensitive to the
352 range of hydrological conditions we studied.

353

354 The under-representation of the equilibrium strategy in our study (only three species) is typical of the
355 biogeographic area of western Europe (Pont et al., 1995). This group was almost exclusively
356 composed of *A. melas* (84% of the total of equilibrium fish), so that the relationships we found with
357 the environmental conditions mainly reflected the ecology of *A. melas* and were probably not
358 representative of the ecological niche of all equilibrium species. The abundance of *A. melas* was
359 negatively correlated with variations in the water depth in the canals in April. This finding is in
360 agreement with previous results in lotic habitats (Winemiller, 2011; Mims & Olden, 2012).

361 Furthermore, the abundance of *A. melas* was positively correlated with aquatic vegetation cover and
362 turbidity, congruent with its benthic activity and detritivorous habits (Braig & Johnson, 2003;
363 Cucherousset et al., 2006).

364

365 Lastly, the unexplained part of the variation in fish community composition reached 65%. This can be
366 partly attributed to the high mobility of fish, which are often able to leave when faced with
367 unsuitable environmental conditions like progressive drying out (Cucherousset, Paillisson & Roussel,
368 2013). Interspecific and intraspecific interactions were beyond the scope of the present study, but
369 they likely influence the fish community composition of wetlands (Hanson et al., 2005). For instance,
370 when fish take refuge in permanent canals when other aquatic habitats start to dry out, density
371 dependence could be an important driver of the composition of fish communities (Rehage & Trexler,
372 2006), and weaken the relationships with environmental drivers. In addition, we observed a
373 turnover of almost half of the species between years in the canals, but this was largely due to
374 occasional or rare species. High between-year variations of fish abundance are also common, related

375 for instance to variations in interannual variations of temperature or flow regime (Piffady et al.,
376 2010).

377 To conclude, our study shows that hydrological fluctuations in the canals of the agricultural marsh of
378 the Marais poitevin are not strongly related to the composition of fish communities, or to the three
379 LHS of fish communities (only a few links were found on a case-by-case basis). The hydrology of the
380 marsh is so regulated (strong flood abatement in early spring and low water depth in summer) that it
381 does not play a pivotal role for fish. Further experimentations is required to cover a wider range of
382 hydrological conditions, and notably more natural hydrological fluctuations (i.e. larger variations over
383 the years). For example, limiting flood abatement in the Marais poitevin in early spring could result in
384 an increase in water depth of about 6 cm in permanent canals, and less patchy flooded meadows
385 (Appendix F). It is assumed that, in such conditions, flooded meadows would be more suitable in
386 particular for periodic species. Lastly, we call for further investigations in other agricultural marshes
387 since the question of the influence of hydrology on fish communities is largely understudied in these
388 systems. Valuable guidelines could follow to conserve fish and the integrity of the remaining aquatic
389 habitats represented by canals in agricultural marshes.

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613

614 **Data availability statement**

615 The data that support the findings of this study are openly available in Dryad at

616 <https://doi.org/10.5061/dryad.mcvdnck5c> .

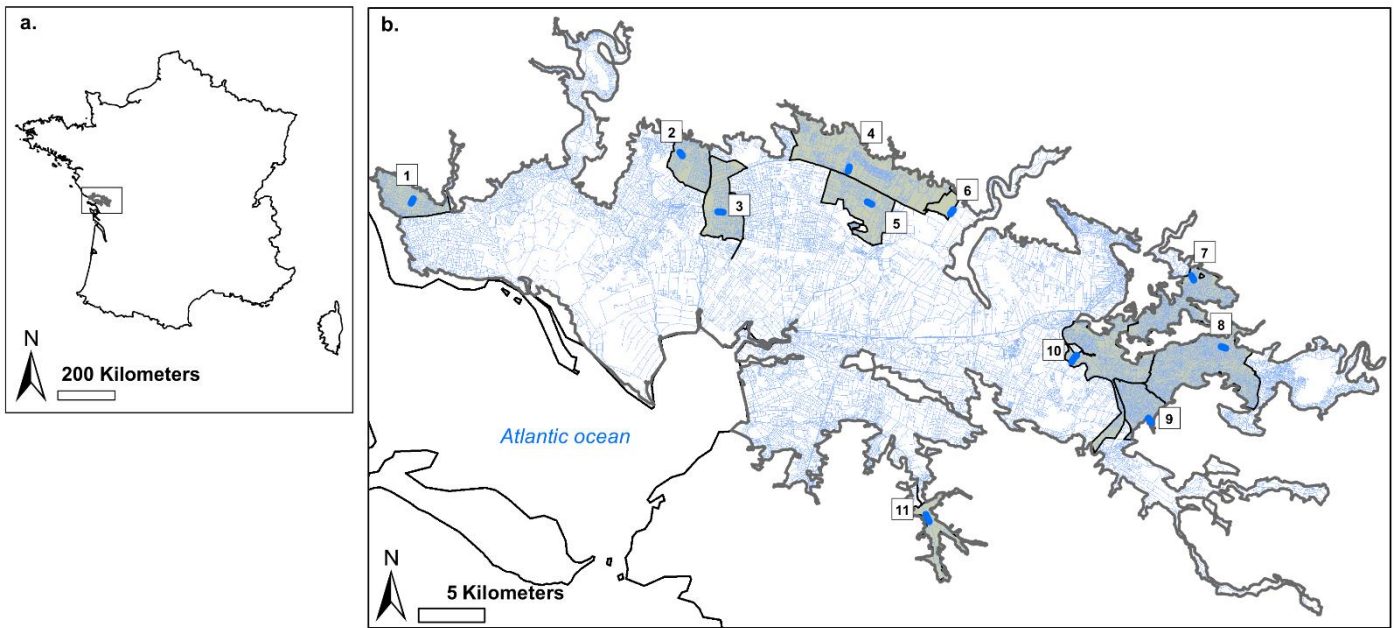


FIGURE 1. Location of (a) the Marais poitevin on a map of France, and (b) the 11 hydrological units (gray areas) and the canals where fish were monitored (blue bold lines). The 11 hydrological units are isolated from the surrounding ones (not showed for clarity reasons) by hydraulic structures, and water management in each unit is based on a special water regulation. Blue thin lines represent the canal networks all over the study area.

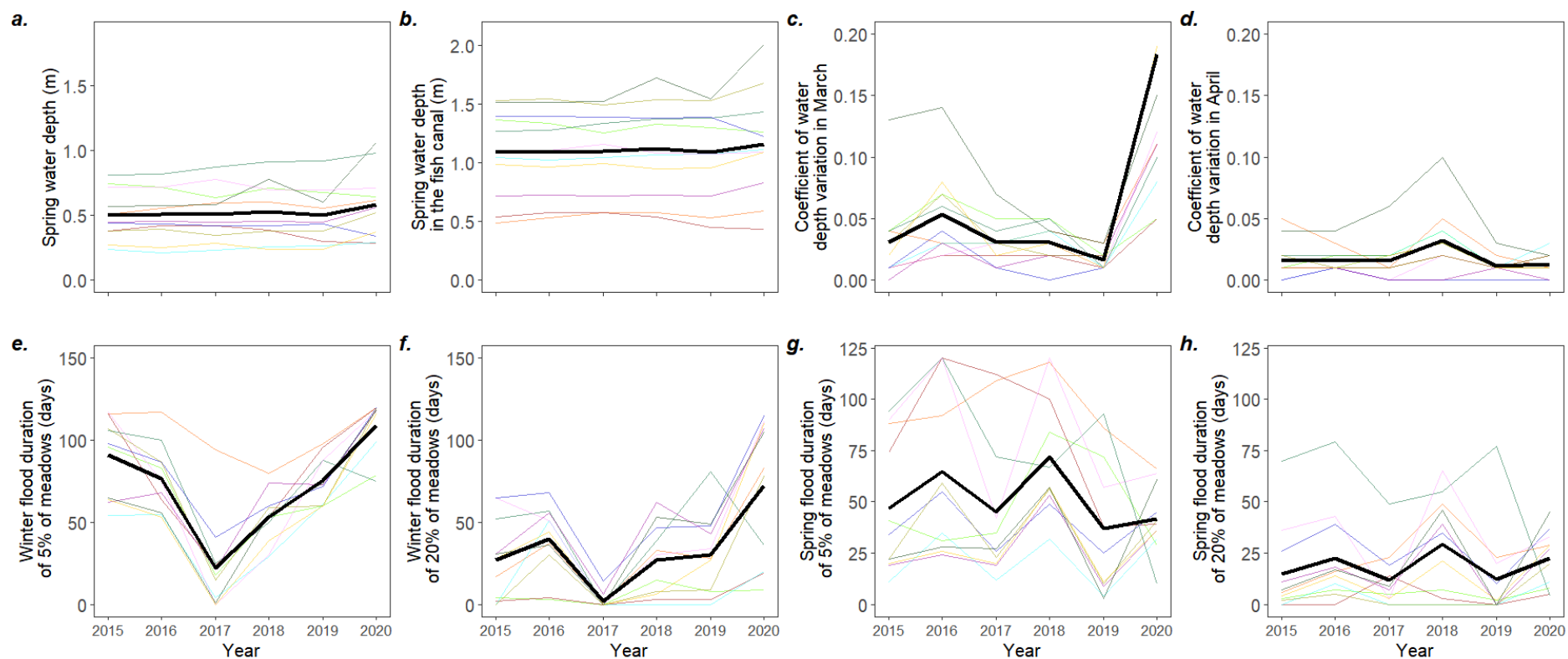


FIGURE 2. Fluctuations of hydrological variables in the 11 hydrological units (unless otherwise indicated) over six years. (a.) Spring average water depth; (b.) spring average water depth in the fish canal; (c.) and (d.) coefficients of water depth variation in March and April; (e.) winter flood duration on 5% of the meadows; (f.) winter flood duration on 20% of the meadows; (g.) spring flood duration on 5% of the meadows; and (h.) spring flood duration on 20% of the meadows. Different colors were used for the 11 hydrological units, and the bold black line represents the average values across all units.

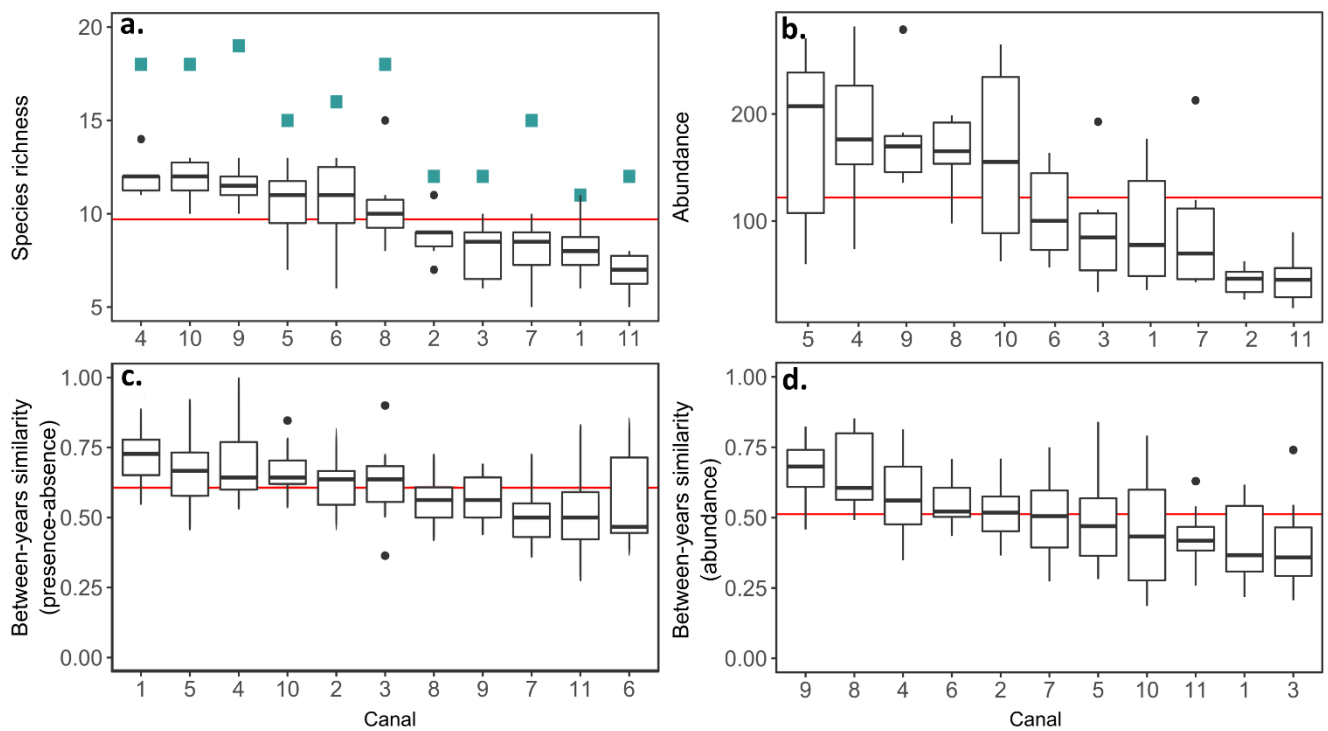


FIGURE 3. Fish species richness (a.), abundance (b.), and between-year similarity in species composition expressed in presence-absence (c.) and abundance (d.) *per* canal (1 to 11) and year. Canals are ranked in a decreasing order for each descriptor. In each panel, the red line represents the mean value calculated for all canals and years. Blue squares indicate the cumulated species richness over six years.

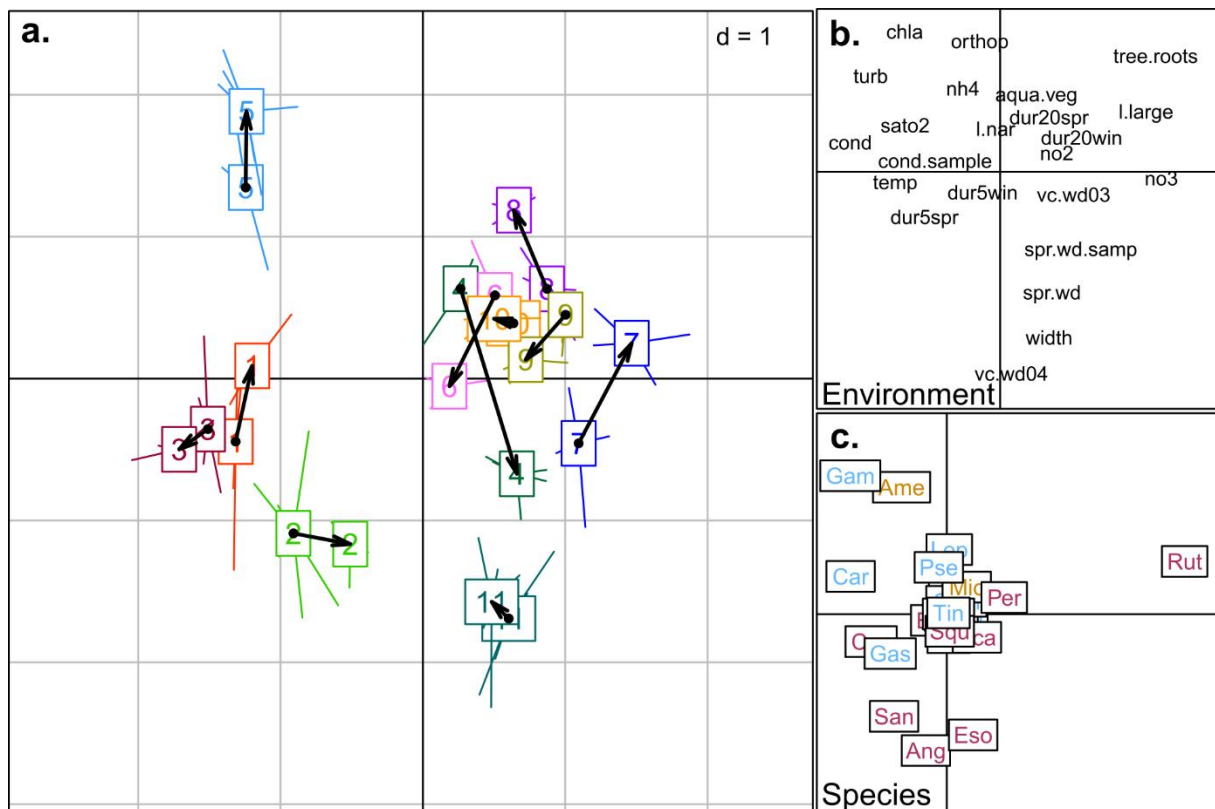


FIGURE 4. Results of the co-inertia analysis. Scores of the canals (six years pooled) (a.). The nock and the head of the arrows indicate the positioning of the canals as described by fish communities and environmental variables, respectively, and their length reflects the divergence between the two datasets. Canonical weights of environmental variables (b.) and species composition (c.). Red, brown and blue labels stand for periodic, equilibrium and opportunistic species, respectively. Environmental variable codes are in Table 1, and fish species codes are in Table 2.

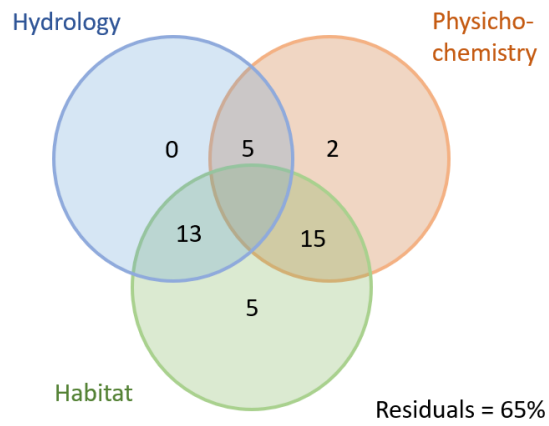


FIGURE 5. Relative contribution (%) of hydrology (8 variables), physico-chemistry (10) and other habitat (5) variables in explaining the variance in the structure of fish communities in the 11 canals over six years.

617 **Tables**

618 **Table 1 –Set of environmental variables (range of values) used to explain variations in fish communities in 11 hydrological units over six years** (only one
 619 value if no change occurred over time). Measurements were done at the hydrological unit scale unless indicated otherwise (* only in the canals where fish
 620 were sampled). See Appendix A for a complete description of the measurement of the variables.

Metric	Variable	Abbrevia- tion	Unit	Hydrological units																					
				1		2		3		4		5		6		7		8		9		10		11	
				min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max
Hydrology	Spring average water depth	spr.wd	meter	0.51	0.62	0.64	0.75	0.28	0.42	0.81	0.98	0.21	0.29	0.70	0.78	0.34	0.44	0.45	0.56	0.34	0.52	0.24	0.38	0.57	1.06
	Spring water depth (fish canal)	spr.wd.samp	meter	0.49	0.59	1.26	1.37	0.44	0.58	1.27	1.44	1.03	1.11	1.08	1.16	1.23	1.40	0.72	0.83	1.50	1.68	0.95	1.09	1.52	2.01
	Coefficient of water depth variation (March)	vc.wd03	-	0.03	0.11	0.02	0.07	0.01	0.05	0.01	0.10	0.01	0.08	0.01	0.12	0.00	0.88	0.00	0.11	0.02	0.18	0.01	0.19	0.03	0.15
	Coefficient of water depth variation (April)	vc.wd04	-	0.01	0.05	0.01	0.04	0.01	0.02	0.01	0.03	0.00	0.04	0.00	0.02	0.00	0.01	0.00	0.01	0.01	0.02	0.01	0.03	0.02	0.10
	Winter flood duration (20% of meadows)	dur20win	days	1	83	0	15	0	19	0	81	0	51	0	111	14	115	6	107	0	78	0	110	0	105
	Spring flood duration (20% of meadows)	dur20spr	days	6	49	2	8	0	14	4	79	0	11	3	65	10	39	0	39	0	20	2	29	0	46
	Winter flood duration (5% of meadows)	dur5win	days	80	120	18	96	24	120	25	106	4	99	0	118	41	120	21	118	15	119	0	116	1	118
	Spring flood duration (5% of meadows)	dur5spr	days	66	118	29	84	38	120	10	120	4	35	42	120	25	55	9	53	10	59	11	57	3	61
Physico-chemistry	Oxygen saturation	sato2	%	79.0	128.0	77.8	97.9	58.6	102.4	67.1	112.2	45.2	120.6	51.3	91.8	62.4	74.3	69.9	81.1	67.5	79.2	61.8	98.2	53.2	90.9
	Ammonium	nh4	mg.L ⁻¹	0.02	0.48	0.01	0.05	0.03	0.15	0.04	0.08	0.07	2.03	0.07	0.11	0.05	0.40	0.08	0.15	0.06	0.12	0.04	0.12	0.02	0.12
	Nitrite	no2	mg.L ⁻¹	0.01	0.32	0.08	2.87	0.01	4.07	0.16	17.57	0.01	0.70	0.11	16.57	0.15	5.44	0.08	11.73	0.12	8.41	0.09	4.32	0.10	14.45
	Nitrate	no3	mg.L ⁻¹	0.32	1.07	2.87	12.33	0.67	4.07	17.57	56.35	0.50	1.07	3.65	38.63	5.44	40.80	11.73	30.80	8.41	26.15	4.32	23.10	14.45	42.15
	Orthophosphate	orthop	mg.L ⁻¹	0.02	0.04	0.02	0.06	0.04	0.23	0.02	0.07	0.20	0.94	0.04	0.12	0.02	0.05	0.06	0.12	0.04	0.10	0.04	0.15	0.05	0.55
	Chlorophyll a	chl a	µg.L ⁻¹	37	169	24	57	65	290	4	235	198	1871	8	93	16	58	4	28	7	36	9	78	2	77
	Annual average conductivity	cond	µS.cm ⁻¹	855	1853	671	1031	1851	3985	487	703	1505	2304	468	604	658	803	562	594	577	669	627	702	660	810
	Conductivity at sampling date*	cond.sample	µS.cm ⁻¹	589	2040	600	1531	706	6050	439	3331	531	1589	364	941	486	601	491	584	509	598	507	611	639	774
	Temperature*	temp	°C	20.3	24.6	22.9	27.9	20.1	26.1	19.4	24.2	20.6	26.8	20.2	23.9	15.9	24.1	16.6	24.5	19.9	24.7	19.1	23.7	18.2	23.9
	Turbidity*	turb	m	-5	-1	-15	-2	-8	-3	-35	-10	-3	-1	-15	0	-80	-1	-15	-3	-25	-6	-12	-2	-60	-12
Habitat features	Canal width*	width	m	7.50		10.00		10.00		10.00		7.00		8.50		9.50		7.00		9.00		9.00		9.50	
	Presence of tree root refuges*	tree.roots	-	1		1		1		3.5		2		3.5		5		3.5		4		4		2.5	
	Aquatic vegetation cover*	aqua.veg	%	0.65		0		0.10		0.80		0.15		0.70		0.20		0.05		0.10		0.05		0.15	
	Length of large canal network	l.large	km/ha	18		30		8		32		35		7		57		56		49		54		23	
	Length of narrow canal network	l.nar	km/ha	99		112		78		35		82		32		109		138		166		84		21	

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622

623 **Table 2.** Fish species sampled in the canals (1 to 11, all years pooled) classified according to life-history strategies: abundance, total abundance, and
624 occurrence (number of canals where species were caught). Literature sources used to classify the fish according to a life history strategy: 1: Czeglédi et al.,
625 2021; 2: Winemiller and Rose, 1992; 3: Bergerot et al., 2015; 4: Blanck et al., 2007; 5: Pont et al., 1995; 6: Thorsteinson and Love, 2016). Occasional
626 discrepancies were found in the literature when assigning a species to a life-history strategy group. In that case, we referred to the most comparable papers
627 with ours (i.e. similar biogeographic zone and/or habitat type).

Life-history strategy	Species Scientific name	Code	Abundance per canal											Total abundance	Occurrence	Literature source
			1	2	3	4	5	6	7	8	9	10	11			
Periodic	<i>Abramis brama & Blicca bjoerkna</i>	Bre	87	41	19	84	23	54	27	55	66	59	2	517	11	1,2
	<i>Anguilla anguilla</i>	Ang	49	45	76	40	60	52	41	40	27	45	72	547	11	1,2
	<i>Cyprinus carpio</i>	Cyp	11	10	97	3	18	3				1		143	7	3
	<i>Esox lucius</i>	Eso		4		6		1	8	1	7	3	20	50	8	1,2
	<i>Perca fluviatilis</i>	Per			4	33	4	29	36	15	124	35	9	289	9	1,2
	<i>Platichthys flesus</i>	Pla											3	3	1	6
	<i>Rutilus rutilus</i>	Rut	3	11		319	7	235	400	614	633	395	105	2722	10	1,2
	<i>Sander lucioperca</i>	San	15	53	20	1	5	2		1	8			105	8	1,2,3
	<i>Scardinius erythrophthalmus</i>	Sca		2	1	80	11	43	5	15	15	16	13	201	10	1,2,3,4
	<i>Squalius cephalus</i>	Squ								1	1		3	5	3	3
Equilibrium	<i>Ameiurus melas</i>	Ame	158	25	38	378	371	80	6	28	123	90	2	1299	11	1,3
	<i>Micropterus salmoides</i>	Mic				11	2	15	3	6	6	211		254	7	1,3
	<i>Rhodeus amarus</i>	Rho									2			2	1	3,5
Opportunistic	<i>Alburnus alburnus</i>	Alb							8	13	3	3	18	45	5	1,4,5
	<i>Barbatula barbatula</i>	Bar							7					7	1	3,4
	<i>Carassius gibelio</i>	Car	54	4	172	12	64	23	1	2	2	8		342	10	3
	<i>Gambusia holbrooki</i>	Gam	49	43	70	18	351	21	4	50	5	6		617	10	3
	<i>Gasterosteus aculeatus</i>	Gas	130	20	52	51	75		10	10	6	43	28	425	10	3
	<i>Gobio gobio</i>	Gob							3	10	3	1		17	4	3,4,5
	<i>Gymnocephalus cernua</i>	Gym				1		8		5	23	1		38	5	3,4,5
	<i>Lepomis gibbosus</i>	Lep	4	10	5	52	60	65		112	15	29	9	361	10	3,4
	<i>Leucaspis delineatus</i>	Leu				1				1				2	2	3
	<i>Pseudorasbora parva</i>	Pse	6		2	5	18	14			7	19		71	7	3
	<i>Pungitius laevis</i>	Pun								1				1	1	1,3,6
<i>Tinca tinca</i>	Tin				3	1	1					2	7	4	3	
Cumulated species richness			11	12	12	18	15	16	15	18	19	18	12			

629 **Figure legends**

630 **FIGURE 1.** Location of (a) the Marais poitevin on a map of France, and (b) the 11 hydrological units
631 (gray areas) and the canals where fish were monitored (blue bold lines). The 11 hydrological units are
632 isolated from the surrounding ones (not showed for clarity reasons) by hydraulic structures, and
633 water management in each unit is based on a special water regulation. Blue thin lines represent the
634 canal networks all over the study area.

635 **FIGURE 2.** Fluctuations of hydrological variables in the 11 hydrological units (unless otherwise
636 indicated) over six years. (a.) Spring average water depth; (b.) spring average water depth in the fish
637 canal; (c.) and (d.) coefficients of water depth variation in March and April; (e.) winter flood duration
638 on 5% of the meadows; (f) winter flood duration on 20% of the meadows; (g.) spring flood duration
639 on 5% of the meadows; and (h.) spring flood duration on 20% of the meadows. Different colors were
640 used for the 11 hydrological units, and the bold black line represents the average values across all
641 units.

642 **FIGURE 3.** Fish species richness (a.), abundance (b.), and between-year similarity in species
643 composition expressed in presence-absence (c.) and abundance (d.) *per* canal (1 to 11) and year.
644 Canals are ranked in a decreasing order for each descriptor. In each panel, the red line represents the
645 mean value calculated for all canals and years. Blue squares indicate the cumulated species richness
646 over six years.

647 **FIGURE 4.** Results of the co-inertia analysis. Scores of the canals (six years pooled) (a.). The nock and
648 the head of the arrows indicate the positioning of the canals as described by fish communities and
649 environmental variables, respectively, and their length reflects the divergence between the two
650 datasets. Canonical weights of environmental variables (b.) and species composition (c.). Red, brown
651 and blue labels stand for periodic, equilibrium and opportunistic species, respectively. Environmental
652 variable codes are in Table 1, and fish species codes are in Table 2.

653 **FIGURE 5.** Relative contribution (%) of hydrology (8 variables), physico-chemistry (10) and other
654 habitat (5) variables in explaining the variance in the structure of fish communities in the 11 canals
655 over six years.

Appendices

Appendix A – Protocols for measuring environmental conditions other than hydrology in the hydrological units

We considered ten water physico-chemistry variables. Seven were measured bi-monthly in one large canal in each hydrological unit covered by a companion program on the eutrophication of the Marais poitevin (UNIMA, unpublished data). These variables were oxygen saturation (%), conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$), measured *in situ* in the top 30 centimeters of the water column using a portable electronic multi-parameter probe (WTW 3430, Thermo Fisher Scientific Inc.), chlorophyll a concentration (measured by spectrophotometry after acetone extraction), and ammonium, nitrite, nitrate and orthophosphate concentrations ($\text{mg}\cdot\text{L}^{-1}$), all measured in the laboratory from a water sample also collected from the top 30 centimeters of the water column. Mean annual values were used for subsequent analyses. Three additional variables were measured directly in the canals where fish were caught, at the same sampling date: water temperature ($^{\circ}\text{C}$), conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$), and turbidity (m; using a Secchi disk; Wetzel & Likens).

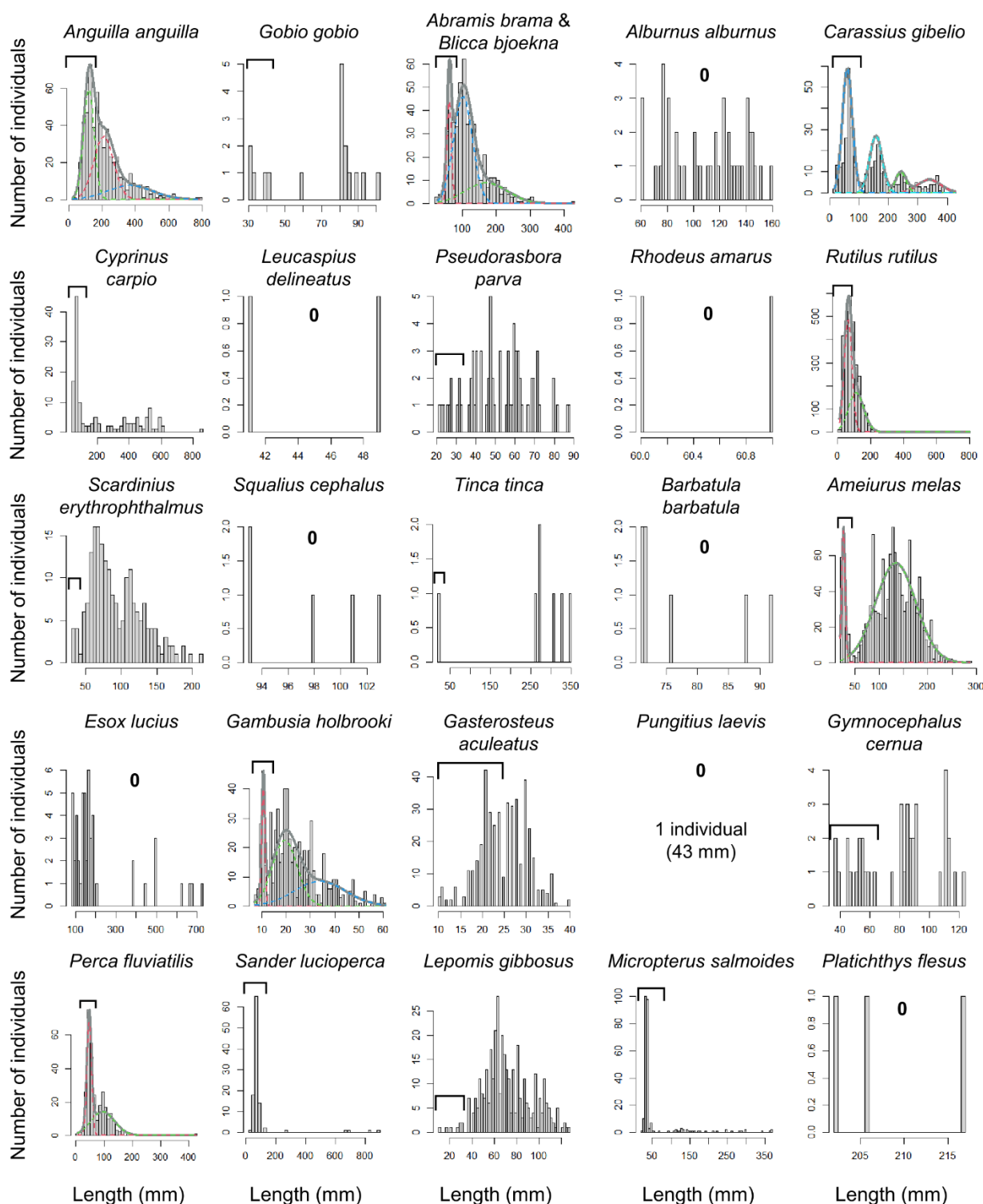
Five other variables described the habitats for fish in the sampled canals and the hydrological units. The number of refuges for fish along the two banks of each sampled canal stretch was visually measured once at the time of the first electrofishing, and converted into five classes: 1/ scarce roots, 2/ frequent roots, 3/ frequent roots and refuges under the banks, 4/ frequent roots, refuges under the banks, and scarce woody debris jams, 5/ frequent roots, refuges under the banks, and woody debris jams. The canal width (m), and the aquatic vegetation cover (%; Mauchamp et al., 2021) were also considered. Measurements were done at the time of electrofishing. Two additional variables were measured at the hydrological unit scale to describe habitat heterogeneity: the total length of the network of large permanent canals, and the total length of narrower, temporarily dried canals (both in $\text{km}\cdot\text{ha}^{-1}$). These variables were measured using QGIS 3.2 (QGIS Development Team, 2021).

Mauchamp, A., Gore, O., Paillisson, J.-M., Bergerot, B., Bonis, A., 2021. Delineating the influence of water conditions and landscape on plant communities in eutrophic ditch networks. *Wetlands Ecol Manage.* <https://doi.org/10.1007/s11273-021-09792-x>

QGIS Development Team (2021). QGIS Geographic Information System. Open Source Geospatial Foundation Project
Wetzel, R.G., Likens, G., 2000. *Limnological Analyses*. Springer Science & Business Media.

Appendix B – Age-specific decomposition analyses based on length-frequency distributions. To explore this issue, we used an age-specific polymodal decomposition method that consists in fitting Gaussian components to the length-frequency histograms for each species (all canals and years pooled) when possible (Benaglia et al., 2010), using the *Rmixmod* package in R software (Lebret et al., 2015). The associated 95% confidence intervals were calculated, and all fish within them were included in the given cohort. The models converged for seven species, and the cohorts were estimated visually for the other species, and then validated based on literature data.

B1 – Length-frequency histograms for all species with age-specific components (different colors) reported for seven species. The bracket indicates the Young-of-the-Year (0+) cohort. “0” indicates that no 0+ was caught. Species are ranked in the same order as in Table 2. Please note that the chart scales may differ across species.



B2 – Size and age-specific cohorts for each species.

Table B2.1. Size and age-specific (0+ to 3+) cohorts for the seven species for which the age-specific polymodal decomposition was successful: number of individuals (Nb), number of cohorts as found in the best model with associated basic statistics (Bayesian Information Criterion (BIC) and log-likelihood), and summary for each cohort.

Species		Nb	Length of individuals (mm)		Number of cohorts	Retained BIC model	log-likelihood	0+			1+			2+			3+		
Scientific name	Code		Min	Max				Nb	Length Mean (sd)	Nb	Length Mean (sd)	Nb	Length Mean (sd)	Nb	Length Mean (sd)	Nb	Length Mean (sd)		
<i>Abramis brama</i> & <i>Blicca bjoerkna</i>	Bre	517	28	428	3	5436	-2693	67	63	(6)	315	103	(28)	135	170	(62)			
<i>Ameiurus melas</i>	Ame	1299	20	286	2	13557	-6761	130	27	(4)	1169	134	(42)						
<i>Anguilla anguilla</i> *	Ang	547	22	782	3	6572	-3261	225	123	(32)	210	211	(59)	112	367	(134)			
<i>Carassius gibelio</i>	Car	342	16	428	4	3854	-1895	171	60	(17)	31	2442	(18)	99	157	(21)	41	338	(39)
<i>Gambusia holbrooki</i>	Gam	617	7	61	3	4576	-2262	68	12	(1)	308	20	(5)	241	34	(11)			
<i>Perca fluviatilis</i>	Per	289	6	426	2	2797	-1384	139	48	(8)	150	95	(42)						
<i>Rutilus rutilus</i>	Rut	2722	11	800	2	27712	-13836	1578	63	(23)	1144	110	(46)						

*Due to the specificity of the ecology of *Anguilla anguilla* (diadromous species), the age-specific cohorts better represent individual residence years in the marsh.

Table B2.2. Cohorts for species (0+ and >0+) for which the age-specific polymodal decomposition was unsuccessful, estimated visually and validated from literature data.

Species	Code	Nb	Length of individuals		0+			>0+			Literature sources
			Min	Max	Nb	Mean length (sd)	Nb	Mean length (sd)	Nb	Mean length (sd)	
<i>Alburnus alburnus</i>	Alb	45	60	159	0			45	111 (28)		Gozlan et al., 2003
<i>Barbatula barbatula</i>	Bar	7	71	92	0			7	77 (9)		Kováč, Copp & Francis, 1998; Vinyoles et al., 2010
<i>Cyprinus carpio</i>	Cyp	143	47	842	90	71 (13)		53	401 (154)		Vilizzi, 1998; Lechelt, Kocian & Bajer, 2017
<i>Esox lucius</i>	Eso	50	81	723	0			50	218 (173)		Cucherousset et al., 2009
<i>Gasterosteus aculeatus</i>	Gas	425	10	40	211	20 (3)		214	30 (3)		Sillett & Foster, 2000; Kume et al., 2006
<i>Gobio gobio</i>	Gob	17	30	102	17	70 (24)		0			Watkins et al., 1997; Pollux et al., 2006
<i>Gymnocephalus cernua</i>	Gym	38	37	123	15	50 (8)		23	96 (14)		Kováč et al., 1998; Lorenzoni et al., 2009
<i>Lepomis gibbosus</i>	Lep	361	11	127	5	25 (8)		356	73 (20)		Copp et al., 2004; Uzunova et al., 2008
<i>Leucaspis delineatus</i>	Leu	2	41	49	0			2	45 (6)		Gozlan et al., 2003
<i>Micropterus salmoides</i>	Mic	254	23	368	221	35 (4)		33	198 (86)		Moyle & Holzhauser, 1978; Hamilton & Powles, 1979
<i>Platichthys flesus</i>	Pla	3	202	217	0			3	208 (8)		Andersen et al., 2005; Mendes, 2019
<i>Pseudorasbora parva</i>	Pse	71	21	88	11	28 (4)		60	57 (13)		Rosecchi, Crivelli & Catsadorakis, 1993
<i>Pungitius laevis</i>	Pun	1			0			1	43 (0)		Keivany & Nelson, 2000
<i>Rhodeus amarus</i>	Rho	2	60	61	0			2	61 (1)		Podobailo, Shukh & Kutsokon, 2021
<i>Sander lucioperca</i>	San	105	37	886	98	68 (13)		7	515 (328)		Persson & Brönmark, 2008; Zingel & Paaver, 2010
<i>Scardinius erythrophthalmus</i>	Sca	201	30	214	9	36 (4)		192	95 (35)		Gozlan et al., 2003
<i>Squalius cephalus</i>	Squ	5	93	103	0			5	98 (5)		Pompei et al., 2011; Nyeste et al., 2019
<i>Tinca tinca</i>	Tin	7	23	349	1	23 (0)		6	299 (35)		Kennedy & Fitzmaurice, 1970; Harka, Sály & Antal, 2007

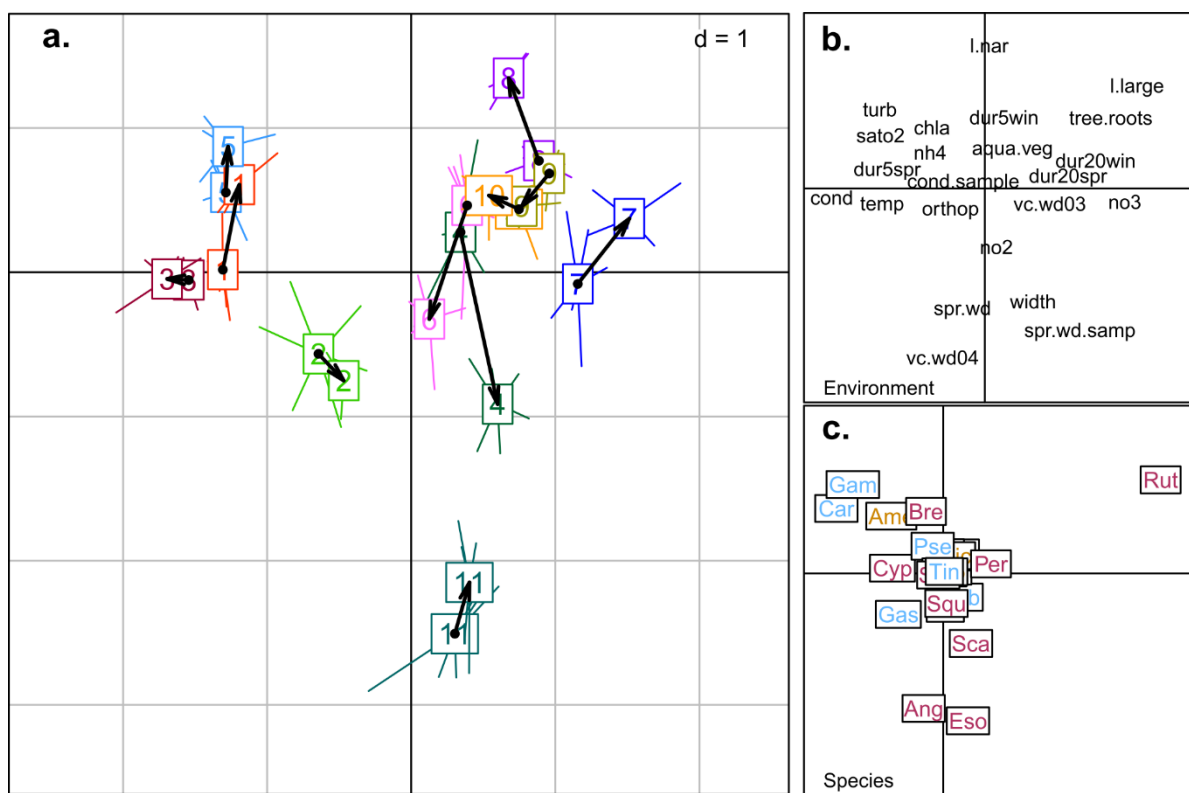
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Appendix C – Co-inertia analysis of the fish communities from the 11 hydrological units (1 to 11) without the Young-of-the-year from the complete dataset.

There was a significant correlation between the structure of the fish communities and the environmental variables ($RV=0.53$, $p < 0.001$). The cumulative projected inertia on the two first axes reached 88%, with 81% projected on the first axis and 7% on the second axis.

C1 – Results of the co-inertia analysis. (a.) Scores of the sampled canals (six years pooled). The nock and the head of arrows indicate the positioning of the canals as described by environmental variables and fish communities, respectively, and their length reflects the divergence between the two datasets. Canonical weights of (b.) environmental variables and (c.) species composition. Red, brown and blue labels stand for periodic, equilibrium and opportunistic species, respectively. The full species names and the environmental variables are available in Appendices B2 and D2, respectively.

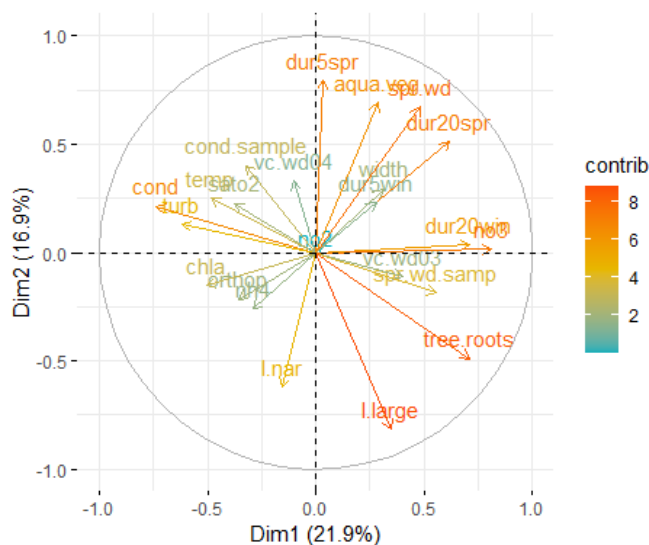


C2 – Canonical weights of the species (left) and the environmental variables (right) in the co-inertia analysis. Colors indicate the lowest (blue) and highest (red) values for each of the first two axes. The full species names and the environmental variables are available in Appendices B2 and D2, respectively.

Species	Axis 1	Axis 2	Environmental variables	Axis 1	Axis 2
Car	-0.379	0.230	cond	-0.378	0.009
Gam	-0.321	0.315	turb	-0.229	0.212
Ame	-0.184	0.203	sato2	-0.211	0.109
Cyp	-0.180	0.019	temp	-0.210	-0.006
Gas	-0.159	-0.145	cond.sample	-0.206	-0.014
Ang	-0.069	-0.479	chla	-0.198	0.130
Bre	-0.061	0.220	orthop	-0.170	-0.020
Pse	-0.037	0.096	dur5spr	-0.168	0.086
San	-0.017	-0.006	nh4	-0.097	0.097
Lep	0.003	0.073	vc.wd04	-0.093	-0.487
Tin	0.004	0.007	dur5win	-0.046	0.157
Leu	0.004	0.005	aqua.veg	-0.033	0.109
Rho	0.006	0.006	spr.wd	0.025	-0.321
Pun	0.007	0.002	width	0.061	-0.336
Pla	0.007	-0.124	vc.wd03	0.074	-0.007
Squ	0.011	-0.107	l.nar	0.079	0.384
Gob	0.025	0.058	no2	0.081	-0.191
Bar	0.029	0.008	dur20spr	0.116	0.068
Gym	0.033	0.073	dur20win	0.187	0.041
Mic	0.038	0.063	spr.wd.samp	0.255	-0.346
Alb	0.074	-0.085	no3	0.326	-0.036
Eso	0.088	-0.523	l.large	0.330	0.242
Sca	0.098	-0.249	tree.roots	0.452	0.223
Per	0.169	0.034			
Rut	0.772	0.332			

Appendix D – Principal component analysis of the 23 environmental variables all six years pooled

D1 – Representation of the PCA variables. The color indicates the relative contribution (contrib.) of a given variable to the principal dimensions.



D2 – Contribution of each variable to the first two axes of the PCA, in decreasing order of importance. Measurements were done at the hydrological unit scale unless indicated otherwise (* only in the canals where fish were sampled).

Variable	Abbreviation	Dim.1	Dim.2	Cumulated contribution
Length of the large canal network	l.large	3	14	18
Spring average water depth	spr.wd	3	13	16
Spring flood duration (5% of meadows)	dur5spr	0	16	16
Number of tree root refuges	tree.roots	12	4	16
Spring flood duration (20% of meadows)	dur20spr	6	9	14
Aquatic vegetation cover*	aqua.veg	1	13	14
Nitrate	no3	13	0	13
Annual average conductivity	cond	12	0	12
Turbidity*	turb	9	2	11
Winter flood duration (20% of meadows)	dur20win	9	0	10
Length of narrow canal network	l.nar	0	9	10
Spring water depth of fish canals	spr.wd.samp	6	0	7
Conductivity at sampling date*	cond.sample	3	3	6
Chlorophyll a	chla	5	1	6
Temperature*	temp	5	1	6
Oxygen saturation	sato2	4	1	5
Orthophosphate	orthop	2	2	4
Canal width*	width	1	3	4
Ammonium	nh4	2	2	4
Coefficient of water depth variation (March)	cv03	3	0	3
Winter flood duration (5% of meadows)	dur5win	1	2	3
Coefficient of water depth variation (April)	cv04	0	2	2
Nitrite	no2	0	0	0

Appendix E – Canonical weights of the species (left) and the environmental variables (right) in the co-inertia analysis performed on all fish data. Colors indicate the lowest (blue) and highest (red) values for each of the first two axes. The full species names and the environmental variables are available in Appendices B2 and D2, respectively.

Species	Axis 1	Axis 2	Environmental variables	Axis 1	Axis 2
Car	-0.312	0.129	cond	-0.369	0.032
Gam	-0.309	0.404	turb	-0.244	0.273
Cyp	-0.244	-0.099	temp	-0.228	-0.022
Gas	-0.185	-0.113	sato2	-0.215	0.071
San	-0.170	-0.349	cond.sample	-0.202	-0.016
Ame	-0.150	0.474	chla	-0.195	0.293
Ang	-0.067	-0.431	dur5spr	-0.164	-0.062
Bre	-0.044	-0.022	orthop	-0.132	0.288
Pse	-0.025	0.153	nh4	-0.092	0.247
Leu	0.004	0.003	vc.wd04	-0.088	-0.465
Tin	0.005	0.009	dur5win	-0.043	-0.038
Rho	0.005	0.000	aqua.veg	-0.024	0.216
Pla	0.006	-0.071	spr.wd	0.038	-0.227
Pun	0.006	-0.002	width	0.048	-0.437
Lep	0.007	0.236	l.nar	0.049	0.100
Squ	0.009	-0.051	vc.wd03	0.075	-0.033
Gob	0.025	0.061	no2	0.087	0.035
Bar	0.027	0.000	dur20spr	0.119	0.123
Gym	0.030	0.041	dur20win	0.208	0.075
Alb	0.065	-0.018	spr.wd.samp	0.272	-0.170
Mic	0.065	0.088	l.large	0.305	0.192
Eso	0.084	-0.369	no3	0.339	0.030
Sca	0.096	-0.025	tree.roots	0.454	0.281
Per	0.187	0.047			
Rut	0.770	0.159			

Appendix F – Spatial pattern of flooded meadows in the 11 hydrological units

In this study, we examined the link between variation in the composition of fish communities and the amount of temporary fish-accessible aquatic habitats as expressed by the flooding duration (days) of at least 5% (corresponding to a maximum water depth ranging from 6 to 21 centimeters depending on the hydrological unit) or 20% (a maximum water depth ranging from 14 to 44 centimeters) of the meadows in the whole hydrological unit, notably in spring. Here, we gather maps of flooded meadows in the 11 hydrological units for the two selected thresholds and three associated landscape metrics. We also provide the results for the threshold of 30% of flooded meadows (i.e. 6 additional centimeters of water on average) as a possible hydrological management scenario (Appendix F1). Then, classical landscape metrics were computed to describe the shape of the flooded surfaces: mean patch size, largest patch index (proportion of the largest patch of flooded surface compared to the total area of meadows on the hydrological unit) and number of isolated patches (Appendix F2).

Globally, flooding does not result in one large continuous area in most hydrological units but rather in many small patches. For instance, for the 20% threshold, the surface of the largest flooded patch only reached 1 to 11% of the total meadow cover, depending on the site. The mean patch size increased on average by 174% and 51% when the flooded surface increased from 5% to 20% and from 20% to 30% of the meadows, respectively. For the same thresholds, the largest patch size increased on average by 516% and 109%. The number of patches increased by 156% when the flooded surfaces increased from 5% to 20%, then reached a plateau.

F1 – Spatial distribution of flooded areas for all sites and quantiles 5%, 20%, 30%

The canal networks were not represented for readability.

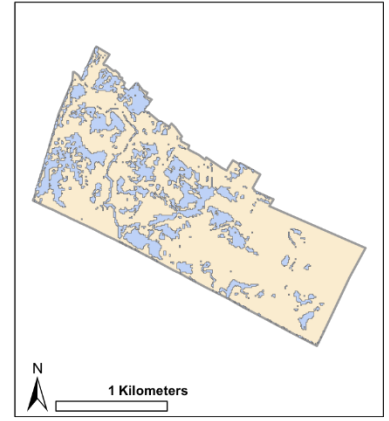
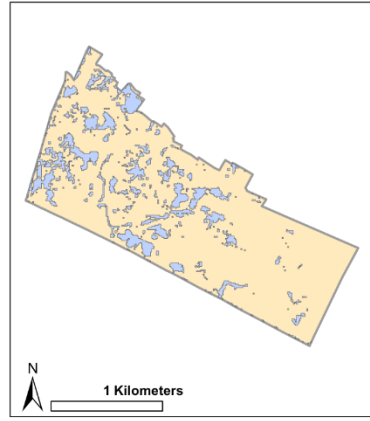
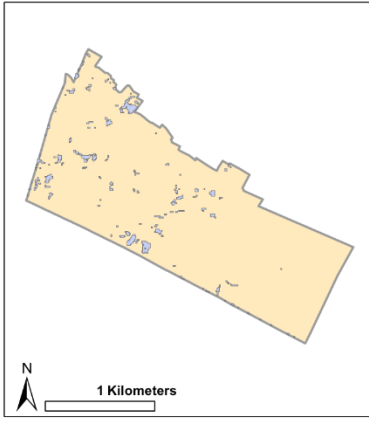


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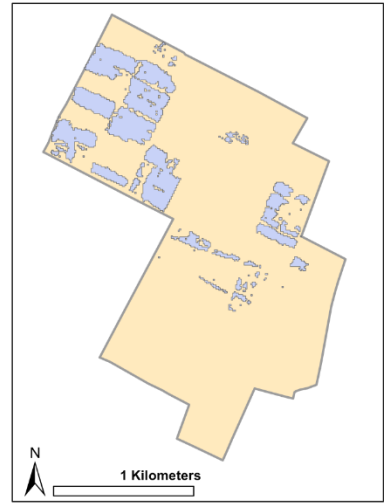
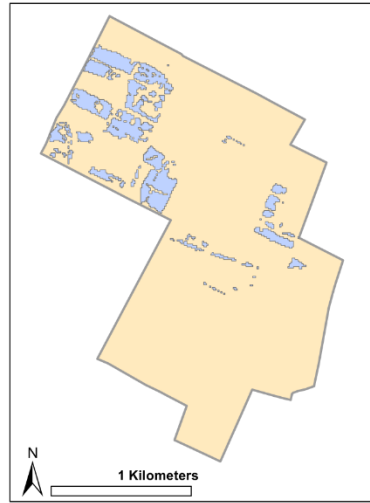
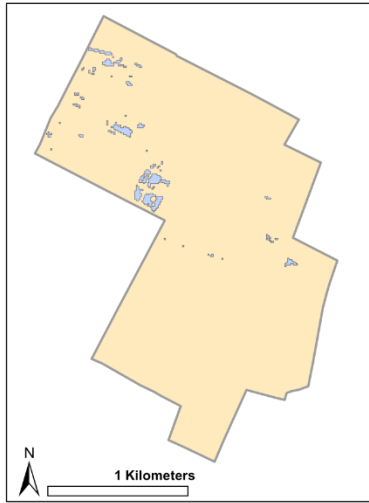
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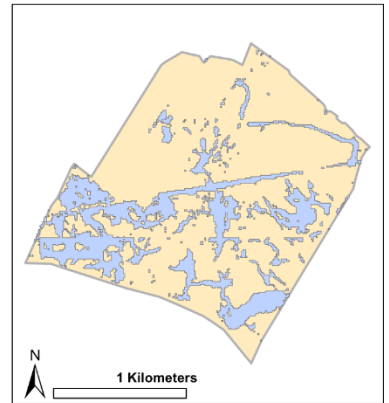
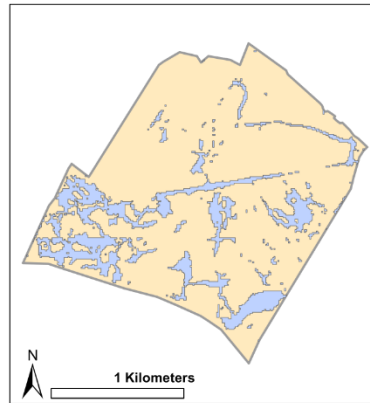
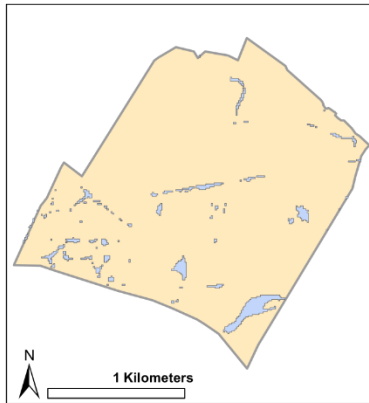
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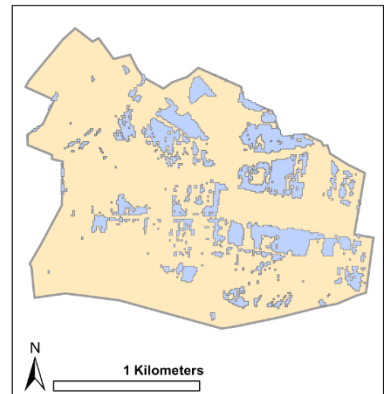
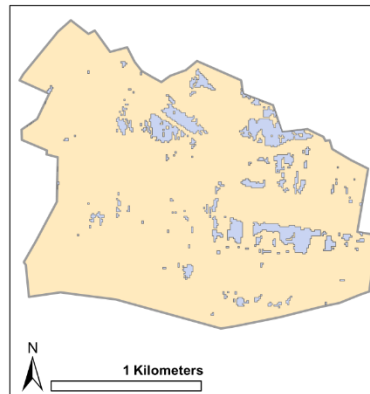
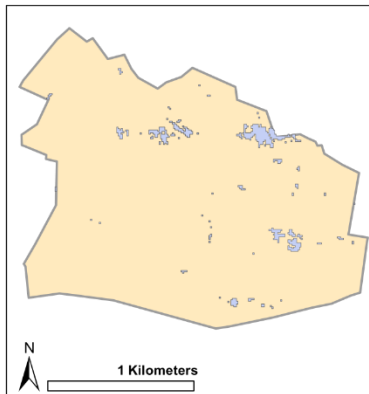
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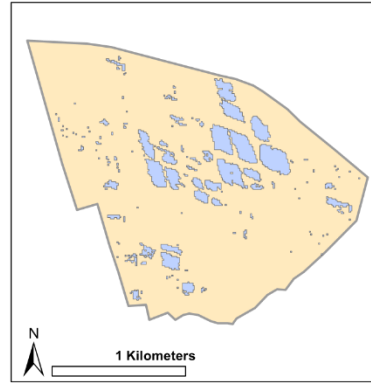
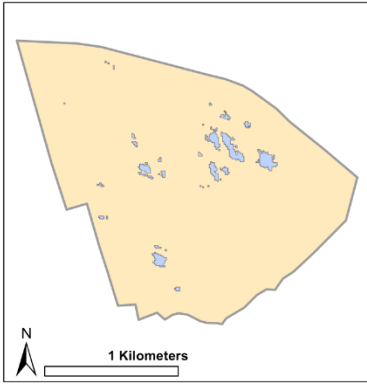


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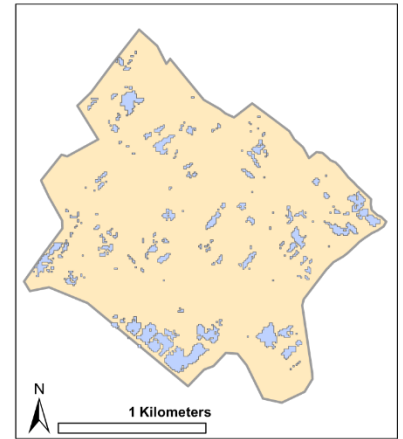
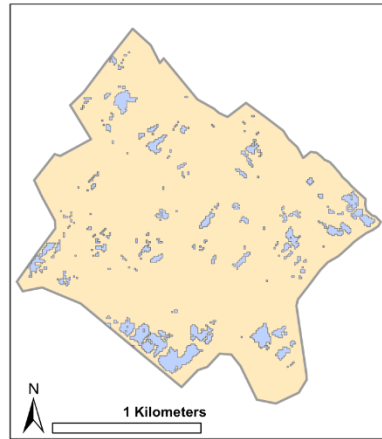
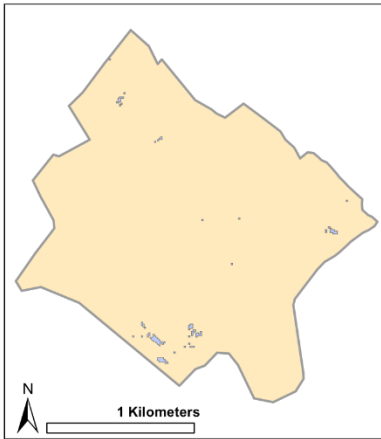
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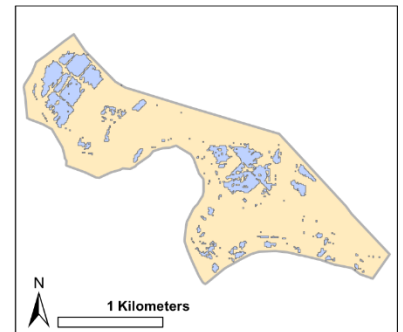
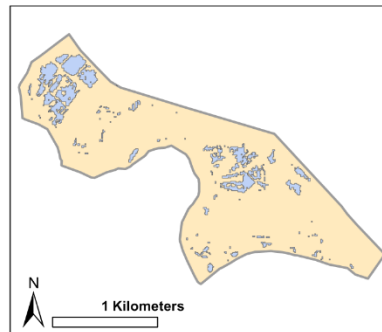
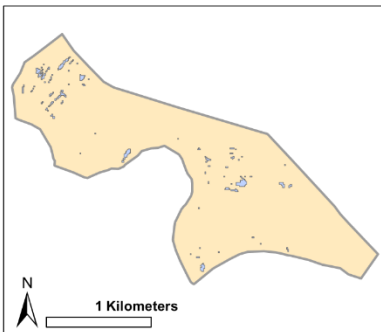
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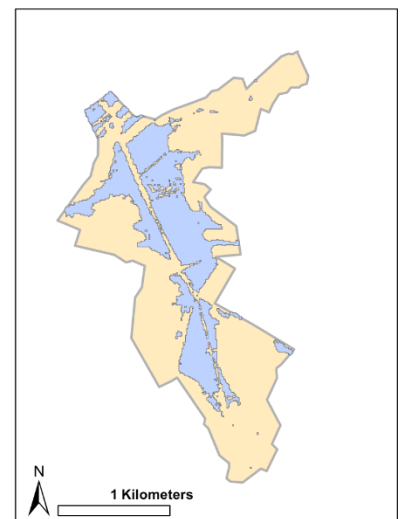
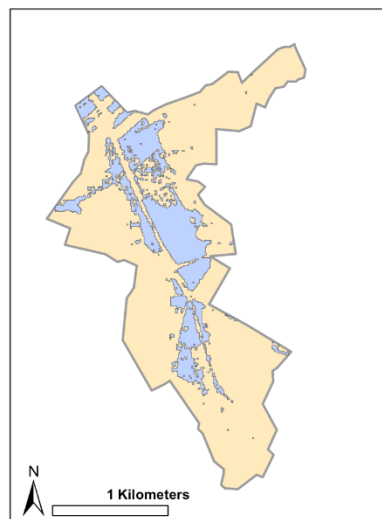
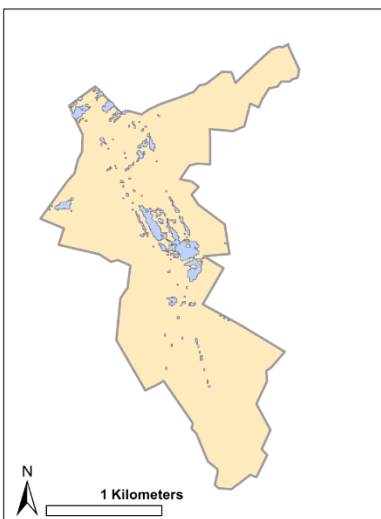
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10.



11.



F2– Landscape metrics characterizing the flooded surfaces for all sites and quantiles 5%, 20%, 30%

Different colors were used for the 11 hydrological units, and the bold black line represents the average values across all units.

