

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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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

agricultural purposes. This generally leads to strong changes in the seasonality of water levels, very
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 decreased fish abundance (Bunn & Arthington, 2002), and both elevated and reduced flow 58 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

from opportunism to equilibrium as the dominant strategy within fish communities (Mims & Olden,
2013; McManamay & Frimpong, 2015), or increased connectivity of aquatic patches leads to an
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 early spring water depths is particularly rapid, far from the natural dynamics of rainfall patterns 84 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 & Borcherding, 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:

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

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

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

duration of meadows to be drivers of the fish community composition, with contrasting effects

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

The study was conducted in the Marais poitevin, a ca. 1000-km² French hypertrophic marshland located along the Atlantic coast (46°30′-46°15′N; 1°30′-0°35′W, Figure 1). The region is characterized by a warm Atlantic climate type, with rainfall greater than evapotranspiration in winter balanced by an almost equal deficit of 300 to 350 mm in summer. Flood peaks take place in meadows mostly in winter and the marshland is mostly dry in summer, sometimes until fall depending on the hydrological conditions. It is also characterized by intensive water management practices for 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 controlled independently from the surrounding units because of different water regulations fixed by 132 133 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±1.2m) 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±75V, amperage 7±5A). 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

meters in front of the boat and near the canal bank where fish generally concentrate. All shocked fish
within 1 m² of the impact point of the anode were caught, identified to the species level, measured
(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 & Borcherding, 2006; Scharbert & Borcherding, 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 et al., 2018; Crabot et al., 2022 for a complete description of the calculation). We calculated these 172 173 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

duration values were highly correlated (r=0.9) with those for the 5% and 20% quantiles and with
water depth. Calculations were done for spring and winter, so that four flooding duration variables
(two quantiles × 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 (μ g.L⁻¹), oxygen percentage saturation (%), conductivity (μ 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 (°C), conductivity (μ 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

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

To assess to what extent species composition changed in each hydrological unit over time, we calculated the cumulated species richness over six years and the average between-year similarity (the Jaccard index for presence-absence data and the Bray-Curtis index for abundance data) using 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 & Cattanéo, 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 when the number of variables is high compared to the number of samples (Judes et al., 2021). The 214 215 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).

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

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

recorded(occurrence ≥ 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

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

not vary over the years (0.61±0.08, values for each canal provided in Figure 3c). Roughly comparable

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

distributions of opportunistic (p = 0.010) and equilibrium (p = 0.034) species, which were themselves

comparable (p = 0.577), in line with the species location on the co-inertia plot (Figure 4c).

Lastly, the variation partitioning analysis confirmed that the three groups of environmental variables
(hydrology, physico-chemistry and habitat) significantly explained the composition of the fish

communities (p <0.004), with habitat variables contributing most, followed by physico-chemistry and
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 variable influencing the density of juvenile cyprinids (A. bjoerkna, Scardinius erythrophthalmus and R. 315 316 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 predictable habitats) (Mims and Olden, 2012). By analogy, in our study, the canals with strong 344 345 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

distribution of opportunistic species (notably the most abundant species: *Gasterosteus aculeatus*, *G. holbrooki* and *Lepomis gibbosus*) suggesting that opportunistic fish species were insensitive to the
 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

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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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 .

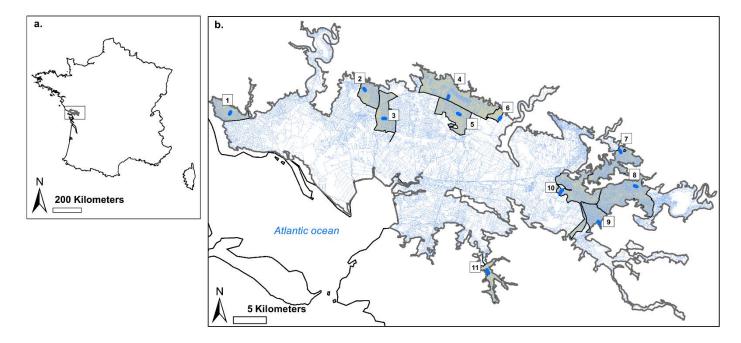


FIGURE 1. Location of (a) the Marais poitevin on a map of France, and (b) the 11 hydrological units (gray areas) and the canals where fish were monitored (blue bold lines). The 11 hydrological units are isolated from the surrounding ones (not showed for clarity reasons) by hydraulic structures, and water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

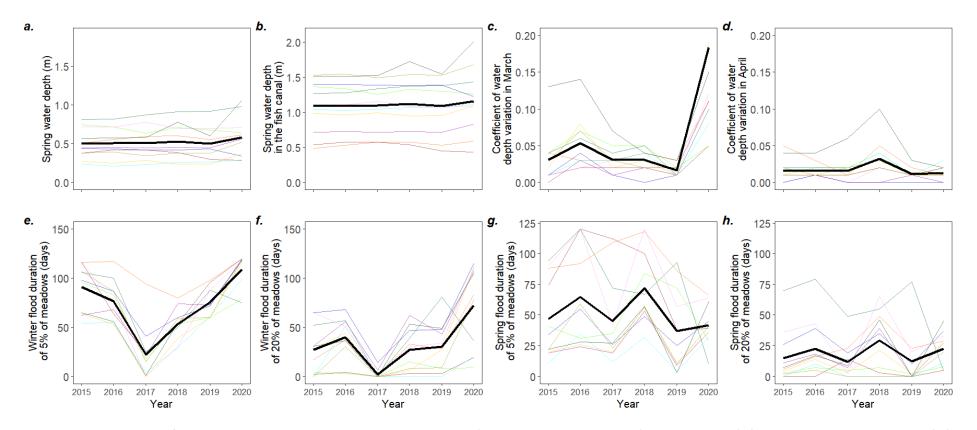


FIGURE 2. Fluctuations of hydrological variables in the 11 hydrological units (unless otherwise indicated) over six years. (a.) Spring average water depth; (b.) spring average water depth in the fish canal; (c.) and (d.) coefficients of water depth variation in March and April; (e.) winter flood duration 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.

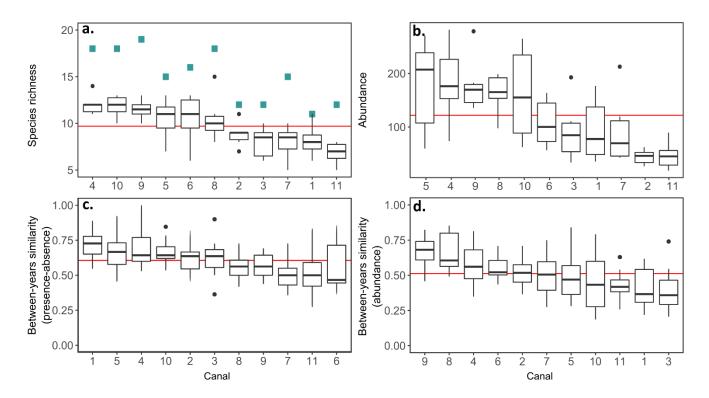


FIGURE 3. Fish species richness (a.), abundance (b.), and between-year similarity in species composition expressed in presence-absence (c.) and abundance (d.) *per* canal (1 to 11) and year. Canals are ranked in a decreasing order for each descriptor. In each panel, the red line represents the mean value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

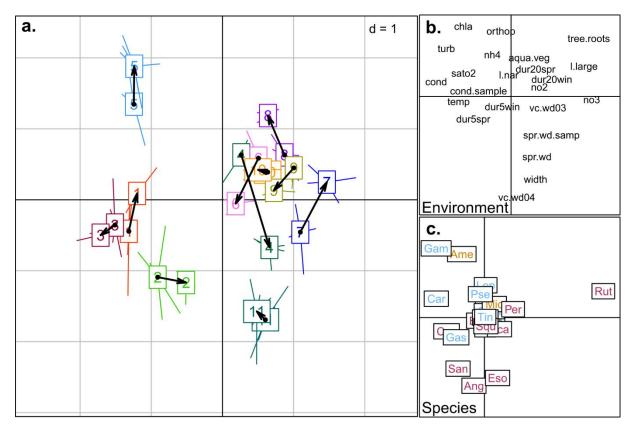


FIGURE 4. Results of the co-inertia analysis. Scores of the canals (six years pooled) (a.). The nock and the head of the arrows indicate the positioning of the canals as described by fish communities and environmental variables, respectively, and their length reflects the divergence between the two datasets. 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.

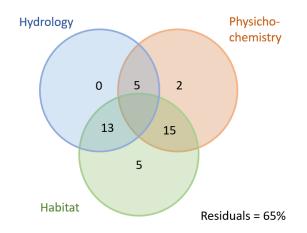


FIGURE 5. Relative contribution (%) of hydrology (8 variables), physico-chemistry (10) and other habitat (5) variables in explaining the variance in the structure of fish communities in the 11 canals over six years.

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.

Hydrological units																									
Metric	Variable	Abbrevia- tion	Unit	:	1	2	2	3	3	4	1	!	5	(6	7	7	8	3	9	9	1	0	1	1
		tion		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 mead- ows)	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-	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
chemistry	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	chla	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 ⁻	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	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	
features	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	

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

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	Life-history Species			Abundance <i>per</i> canal										Total	0	Literature	
strategy	Scientific name	Code	1	2	3	4	5	6	7	8	9	10	11	abundance	Occurrence	source	
Periodic	Abramis brama & Blicca bjoerkna	Bre	87	41	19	84	23	54	27	55	66	59	2	517	11	1,2	
	Anguilla anguilla	Ang	49	45	76	40	60	52	41	40	27	45	72	547	11	1,2	
	Cyprinus carpio	Сур	11	10	97	3	18	3				1		143	7	3	
	Esox lucius	Eso		4		6		1	8	1	7	3	20	50	8	1,2	
	Perca fluviatilis	Per			4	33	4	29	36	15	124	35	9	289	9	1,2	
	Platichthys flesus	Pla											3	3	1	6	
	Rutilus rutilus	Rut	3	11		319	7	235	400	614	633	395	105	2722	10	1,2	
	Sander lucioperca	San	15	53	20	1	5	2		1	8			105	8	1,2,3	
	Scardinius erythrophthalmus	Sca		2	1	80	11	43	5	15	15	16	13	201	10	1,2,3,4	
	Squalius cephalus	Squ								1	1		3	5	3	3	
Equilibrium	Ameiurus melas	Ame	158	25	38	378	371	80	6	28	123	90	2	1299	11	1,3	
	Micropterus salmoides	Mic				11	2	15	3	6	6	211		254	7	1,3	
	Rhodeus amarus	Rho									2			2	1	3,5	
Opportunistic	Alburnus alburnus	Alb							8	13	3	3	18	45	5	1,4,5	
	Barbatula barbatula	Bar							7					7	1	3,4	
	Carassius gibelio	Car	54	4	172	12	64	23	1	2	2	8		342	10	3	
	Gambusia holbrooki	Gam	49	43	70	18	351	21	4	50	5	6		617	10	3	
	Gasterosteus aculeatus	Gas	130	20	52	51	75		10	10	6	43	28	425	10	3	
	Gobio gobio	Gob							3	10	3	1		17	4	3,4,5	
	Gymnocephalus cernua	Gym				1		8		5	23	1		38	5	3,4,5	
	Lepomis gibbosus	Lep	4	10	5	52	60	65		112	15	29	9	361	10	3,4	
	Leucaspius delineatus	Leu				1				1				2	2	3	
	Pseudorasbora parva	Pse	6		2	5	18	14			7	19		71	7	3	
	Pungitius laevis	Pun							1					1	1	1,3,6	
	Tinca tinca	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
- 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.
- 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
- 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
- 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.
- 653 **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 canalsover 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 eutrophisation of the Marais poitevin (UNIMA, unpublished data). These variables were oxygen saturation (%), conductivity (μ S.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 (mg.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 (°C), conductivity (μ S.cm⁻¹), and turbidity (m; using a Secchi disk; Wetzel & Likens).

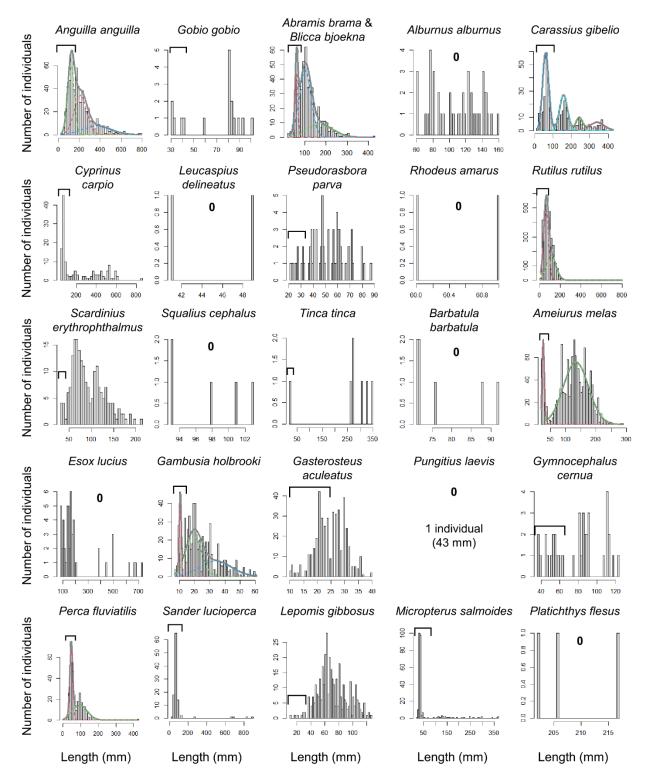
Five other variables described the habitats for fish in the sampled canals and the hydrological units. The number of refuges for fish along the two banks of each sampled canal stretch was visually measured once at the time of the first electrofishing, and converted into five classes: 1/ scarce roots, 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 described habitat heterogeneity: the total length of the network of large permanent canals, and the total length of narrower, temporarily dried canals (both in km.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.

			indiv	gth of iduals nm)	Number of cohorts	Retained BIC model	log- likelihood		0+			1+			2+			3+	
Species		Nb	Min	Max				Nb	Le	ngth	Nb	Len	igth	Nb	Le	ngth	Nb	Lei	ngth
Scientific name	Code		IVIIII	IVIAX					Mean (sd)		Mean (sd)		n (sd)		Mean (sd)		ND	Mean	
Abramis brama& Blicca bjoerkna	Bre	517	28	428	3	5436	-2693	67	63	(6)	315	103	(28)	135	170	(62)			
Ameiurus melas	Ame	1299	20	286	2	13557	-6761	130	27	(4)	1169	134	(42)						
Anguilla anguilla*	Ang	547	22	782	3	6572	-3261	225	123	(32)	210	211	(59)	112	367	(134)			
Carassius gibelio	Car	342	16	428	4	3854	-1895	171	60	(17)	31	2442	(18)	99	157	(21)	41	338	(39)
Gambusia holbrooki	Gam	617	7	61	3	4576	-2262	68	12	(1)	308	20	(5)	241	34	(11)			
Perca fluviatilis	Per	289	6	426	2	2797	-1384	139	48	(8)	150	95	(42)						
Rutilus rutilus	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.

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

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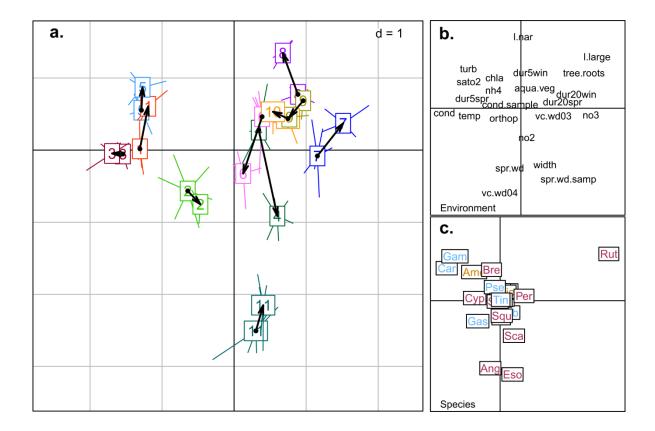
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Appendix C – Co-inertia analysis of the fish communities from the 11 hydrological units (1 to 11) without the Young-of-the-year from the complete dataset.

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.

Axis 1

-0.378 -0.229

-0.211

-0.210

-0.206

-0.198

-0.170

-0.168

-0.097

-0.093 -0.046

-0.033

0.025

0.061

0.074 0.079

0.081

0.116

0.187

0.255

0.326

0.330

0.452

Axis 2 0.009

0.212

0.109

-0.006

-0.014

0.130

-0.020

0.086

0.097 -0.487

0.157

0.109

-0.321 -0.336

-0.007

0.384

-0.191

0.068

0.041

-0.346

-0.036

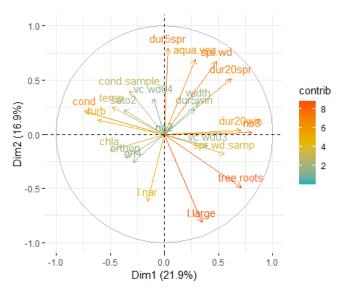
0.242

0.223

Species	Axis 1	Axis 2	Environmental variables
Car	-0.379	0.230	cond
Gam	-0.321	0.315	turb
Ame	-0.184	0.203	sato2
Сур	-0.180	0.019	temp
Gas	-0.159	-0.145	cond.sample
Ang	-0.069	-0.479	chla
Bre	-0.061	0.220	orthop
Pse	-0.037	0.096	dur5spr
San	-0.017	-0.006	nh4
Lep	0.003	0.073	vc.wd04
Tin	0.004	0.007	dur5win
Leu	0.004	0.005	aqua.veg
Rho	0.006	0.006	spr.wd
Pun	0.007	0.002	width
Pla	0.007	-0.124	vc.wd03
Squ	0.011	-0.107	l.nar
Gob	0.025	0.058	no2
Bar	0.029	0.008	dur20spr
Gym	0.033	0.073	dur20win
Mic	0.038	0.063	spr.wd.samp
Alb	0.074	-0.085	no3
Eso	0.088	-0.523	I.large
Sca	0.098	-0.249	tree.roots
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
Сур	-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	I.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).

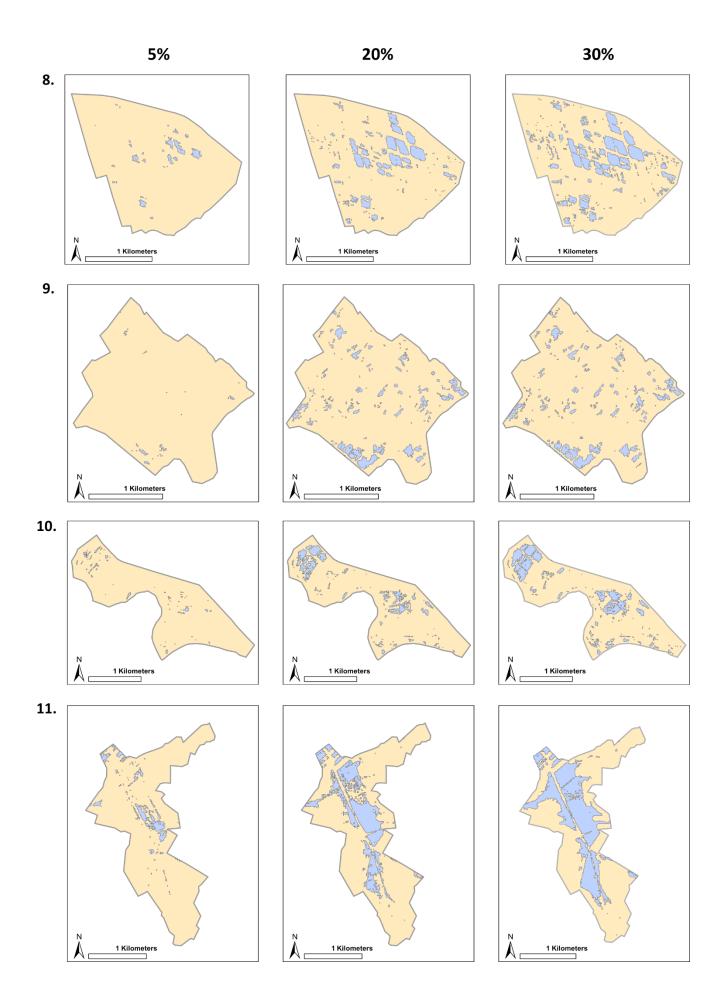
Globally, flooding does not result in one large continuous area in most hydrological units but rather in many small patches. For instance, for the 20% threshold, the surface of the largest flooded patch only reached 1 to 11% of the total meadow cover, depending on the site. The mean patch size increased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





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.

