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

Short running title

Fish response to hydrology in strongly anthropized marshes

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Abstract

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

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

Keywords

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

Introduction

At the interface between aquatic and terrestrial systems, wetlands are crucial habitats for biodiversity (Williams et al., 2003). They are dynamic ecosystems where aquatic organisms typically experience changes in hydrology following seasonal pulses of rainfall (Williams 2006), or a decreased water supply because of water regulation and evapotranspiration. Intra-annual variability in hydrology results from climatic patterns but also reflects human control of water for a large range of uses (Rideout et al., 2021). In temperate wetlands, and more specifically in marshes, water 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).

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

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

The responses of fish communities to hydrological patterns in marshes are expected to differ from the responses of fish communities in streams. The fish communities of these two habitats are normally different. Marshes are mostly characterized by eurytopic to limnophilic species and to a lesser extent by rheophilic species. Furthermore, particular human uses of marshes – e.g. agricultural 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 (Laffaille et al., 2004; Rehage & Trexler, 2006; Rideout et al., 2021). Such high fluctuations of water depths at a key stage of the fish life cycle (i.e. spawning) should disadvantage equilibrium species and benefit periodic species better adapted to seasonal environmental variations (Winemiller, 2011). By contrast, where the water depth is very low throughout the year, fish communities are expected to support a much lower proportion of large-bodied periodic species, highly sensitive to hypoxia compared to small-bodied species (as showed experimentally by Robb and Abrahams, 2003).

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

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

Lavoy & Allen, 2010; Jopp, Deangelis & Trexler, 2010; Volcan & Guadagnin, 2020). Despite the 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 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.

This study aims to address this research gap by examining the influence of hydrology on the composition of fish communities in canals of a large marshland, according to their LHS. We sampled fish communities in independent hydrological units differing in hydrology management over a six-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 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 conditions, it was not possible to control all environmental factors, so we also studied the possible influence of water physico-chemistry and canal morphology known to be of importance for fish communities (Smiley et al., 2008; DeZiel et al., 2019; Koschorreck et al., 2020).

Materials and methods

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

40%, respectively), and the remaining areas are mostly woodlands (Godet & Thomas, 2013). Important land-use changes have occurred over the last century, notably the conversion of more than 50% of meadows into croplands and the intensification of agricultural practices (Duncan et al., 1999; Godet and Thomas, 2013). The Marais poitevin is also composed of an 8200-km long network of drainage canals that have been progressively established since the Middle Ages (EPMP, 2015). It 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 management committees. This leads to different hydrological patterns across units. We selected eleven hydrological units to represent the diversity of hydrology conditions in the study area (Figure 1; a detailed description of the hydrological units is provided in EPMP, 2015; Mauchamp et al., 2021). One section of a canal was selected in each hydrological unit to monitor the fish community from 2015 to 2020. The sampled canals were wide (8.8 ± 1.2 m) and never dried out.

Fish sampling

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

Environmental variables

The water depth was calculated for different periods (see below), and measured at two different spatial scales: locally, in the canal where fish were sampled (“fish canal” thereafter), and across 10 small nearby canals connected to the fish canal in order to better characterize the hydrological conditions of the hydrological unit (average value). Given that the daily water depth in any canal of a hydrological unit can be calculated using a limnigraph deployed in a permanent (always full of water) canal (taking into account the altitude of its bottom), we calculated the average water depth for two seasons: i) in winter (from November to February, prior to the spawning season and the fish monitoring campaign) because flooding peaked mostly during this period and could influence the spatial distribution of several fish species (Heermann & Borchering, 2006; Scharbert & Borchering, 2013; Morat et al., 2018), and ii) in spring (from March to June, before fish sampling) because it covered the spawning season of most of the studied species (Keith et al., 2020). Two additional hydrological variables were calculated at the hydrological unit scale to describe the rate of water depth changes at the pivotal period in early spring, namely the coefficients of variation of water depth in March and in April. We also assessed the amount of temporary fish-accessible aquatic habitats as expressed by the flooding duration (days) of at least 5% (a maximum water depth ranging from 6 to 21 centimeters depending on the hydrological unit) and at least 20% (a maximum water 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 metrics at the hydrological unit scale because they better reflected the conditions experienced by fish before refuging in the largest canals in late spring. Preliminary tests were carried out using other 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 \times two seasons) were used for subsequent analyses.

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

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).

A body of literature supports the idea that juvenile fish respond differently to environmental conditions, and more specifically to hydrology, than older ones (Grenouillet et al., 2001; Gouraud et al., 2008; Bergerot & Cattaneo, 2017). Since the relationship between fish communities and environmental variables yielded similar results when using all fish data or when removing the young-of-the-year from the dataset (they represented 38% of all fish caught, Appendices B and C), we only presented the results from the complete dataset. In practice, we computed a co-inertia analysis between a scaled principal component analysis (PCA) on environmental variables and a non-scaled PCA on fish abundances (11 sites \times 6 years, Hellinger transformed). By optimizing the covariance of the multivariate axes of the two tables, the co-inertia analysis summarizes variations of fish 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 (Jude et al., 2021). The significance of the RV coefficient, which describes the strength of the correlation between the two tables, was tested with a Monte-Carlo test (999 permutations) on the sum of eigenvalues of the co-inertia (Heo & Gabriel, 1998). All these analyses were computed using the ‘dudi.pca’, ‘coinertia’ and ‘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 *ecspa* package; Rot & Blanco-Moreno, 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.

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

Results

Description of the environmental conditions of the hydrological units

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

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

Description of fish communities

We caught 8070 individuals belonging to 25 species over the six years of the experiment (Table 2). The species pool was composed of three equilibrium species, 10 periodic species and 12 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%), *Anguilla anguilla* (7%) and bream (6%). These species were also the most frequently recorded (occurrence $\geq 77\%$, Table 2). Periodic, opportunistic and equilibrium species represented 57%, 24% and 19% of all individuals, respectively.

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 annual species richness was relatively stable over the study period in most of the canals. However, species turnover occurred (Fig. 3a). Between-years similarity calculations of species composition 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).

Associations between environmental variables and fish communities

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

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

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).

Discussion

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

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

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

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

Opportunistic fish – the most species-rich group (12 out of 25 species) – were most abundant in narrow, turbid and vegetated canals. This is consistent with previous observations, notably in floodplain lakes (Miranda & Lucas, 2004; Miyazono et al., 2010); the results of these studies suggest that turbidity may favor small-bodied species by limiting predation by piscivorous fish. Similarly, vegetated areas can provide refuges for small-bodied species, such as mosquitofish, and suitable feeding grounds (Linden & Cech, 1990). Opportunistic fish have also been found to be more abundant where water depth is less variable, contradicting the results of other studies (Mims & Olden, 2012; Hitt, Landsman & Raesly, 2022). However, even if opportunistic fish benefit from 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 seasonal hydrological variability in early spring would not be suitable for opportunistic fish. Furthermore, although small-bodied opportunistic species can benefit from flooded meadows (Poizat & Crivelli, 1997; Hohausová et al., 2010; Volcan & Guadagnin, 2020), we found no evidence of such an association. This may be due to the possible inadequacy of flooded meadows for the reasons 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.

The under-representation of the equilibrium strategy in our study (only three species) is typical of the biogeographic area of western Europe (Pont et al., 1995). This group was almost exclusively composed of *A. melas* (84% of the total of equilibrium fish), so that the relationships we found with the environmental conditions mainly reflected the ecology of *A. melas* and were probably not representative of the ecological niche of all equilibrium species. The abundance of *A. melas* was negatively correlated with variations in the water depth in the canals in April. This finding is in agreement with previous results in lotic habitats (Winemiller, 2011; Mims & Olden, 2012). Furthermore, the abundance of *A. melas* was positively correlated with aquatic vegetation cover and turbidity, congruent with its benthic activity and detritivorous habits (Braig & Johnson, 2003; Cucherousset et al., 2006).

Lastly, the unexplained part of the variation in fish community composition reached 65%. This can be partly attributed to the high mobility of fish, which are often able to leave when faced with unsuitable environmental conditions like progressive drying out (Cucherousset, Paillisson & Roussel, 2013). Interspecific and intraspecific interactions were beyond the scope of the present study, but they likely influence the fish community composition of wetlands (Hanson et al., 2005). For instance, when fish take refuge in permanent canals when other aquatic habitats start to dry out, density dependence could be an important driver of the composition of fish communities (Rehage & Trexler, 2006), and weaken the relationships with environmental drivers. In addition, we observed a turnover of almost half of the species between years in the canals, but this was largely due to 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., 2010).

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

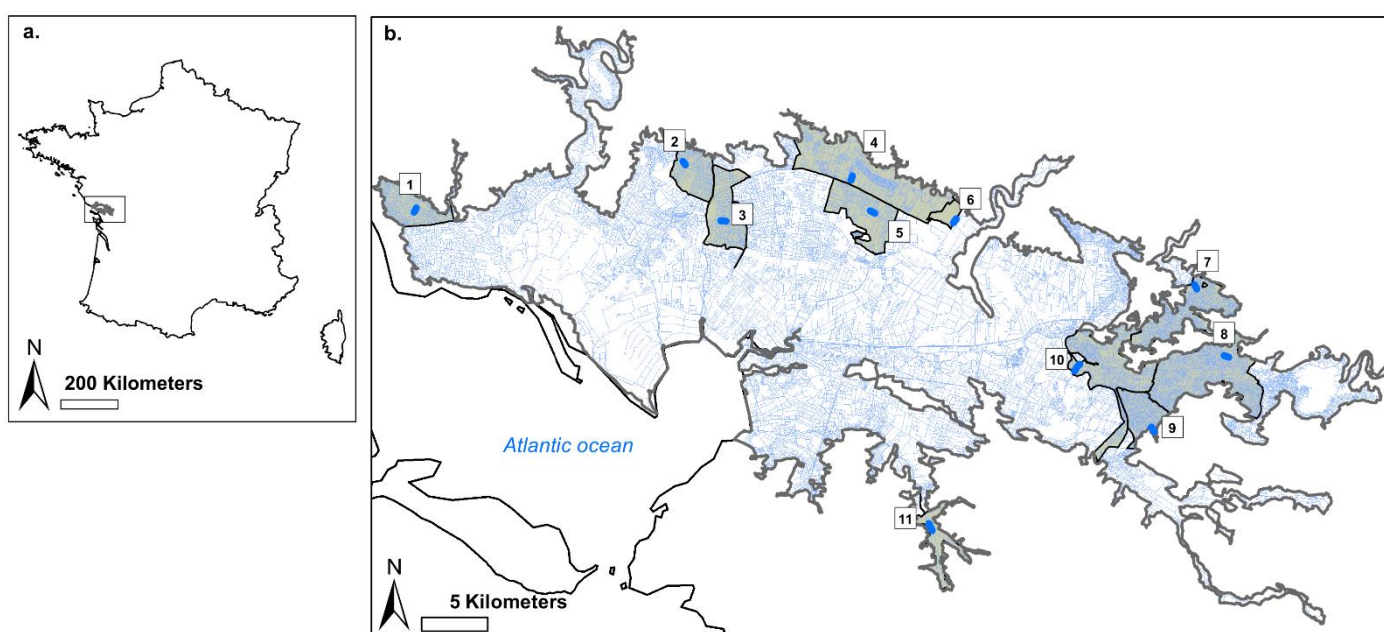


FIGURE 1. Location of (a) the Marais poitevin on a map of France, and (b) the 11 hydrological units (gray areas) and the canals where fish were monitored (blue bold lines). The 11 hydrological units are isolated from the surrounding ones (not showed for clarity reasons) by hydraulic structures, and water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

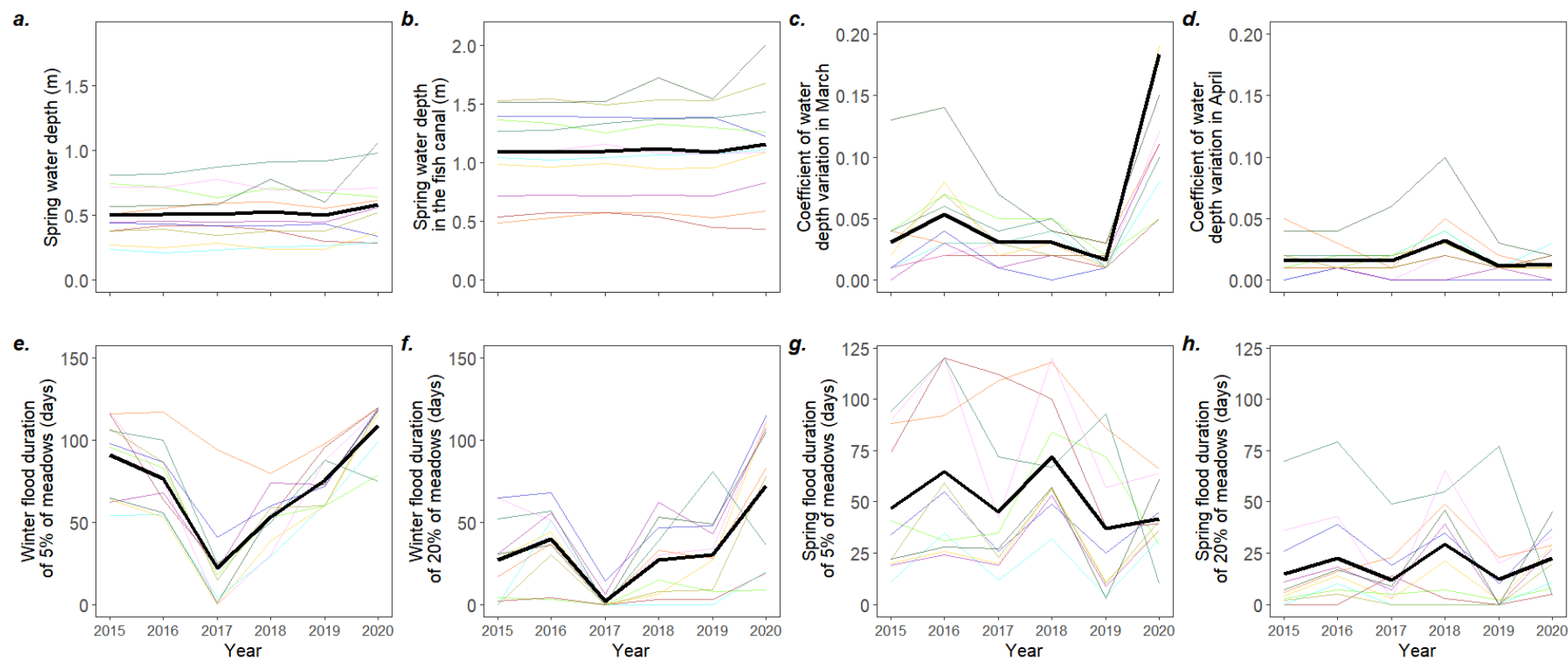


FIGURE 2. Fluctuations of hydrological variables in the 11 hydrological units (unless otherwise indicated) over six years. (a.) Spring average water depth; (b.) spring average water depth in the fish canal; (c.) and (d.) coefficients of water depth variation in March and April; (e.) winter flood duration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

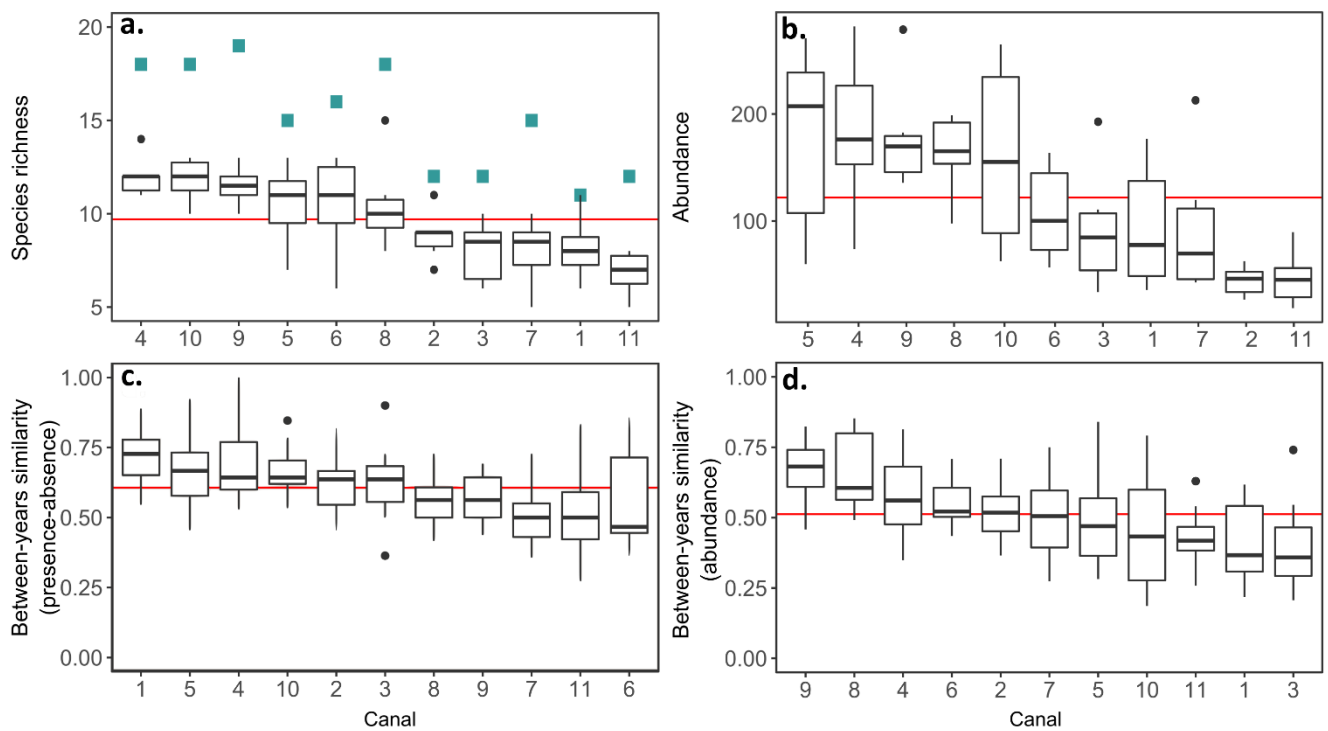


FIGURE 3. Fish species richness (a.), abundance (b.), and between-year similarity in species composition expressed in presence-absence (c.) and abundance (d.) *per* canal (1 to 11) and year. Canals are ranked in a decreasing order for each descriptor. In each panel, the red line represents the mean value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

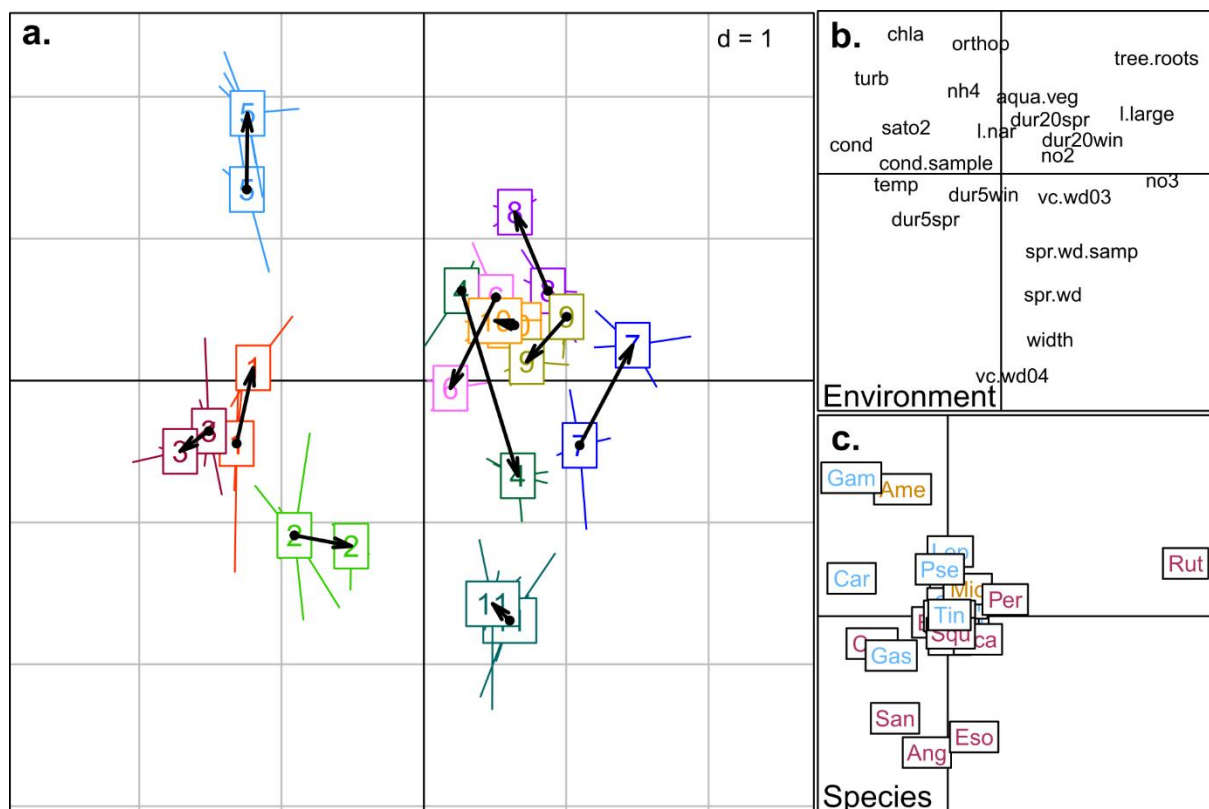


FIGURE 4. Results of the co-inertia analysis. Scores of the canals (six years pooled) (a.). The nock and the head of the arrows indicate the positioning of the canals as described by fish communities and environmental variables, respectively, and their length reflects the divergence between the two datasets.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

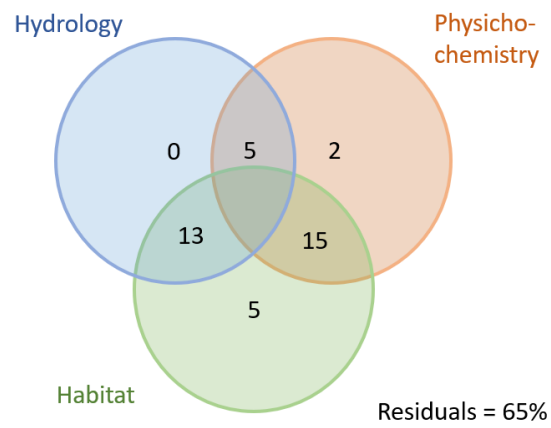


FIGURE 5. Relative contribution (%) of hydrology (8 variables), physico-chemistry (10) and other habitat (5) variables in explaining the variance in the structure of fish communities in the 11 canals over six years.

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.

| 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 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-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 |
| Habitat features | 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 |
| | 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: Czeplédi 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</i> & <i>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 |
| Equilibrium | <i>Squalius cephalus</i> | Squ | | | | | | | | 1 | 1 | | 3 | 5 | 3 | 3 |
| | <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 |
| Opportunistic | <i>Rhodeus amarus</i> | Rho | | | | | | | | | 2 | | | 2 | 1 | 3,5 |
| | <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 | | | |

Figure legends

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.

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).

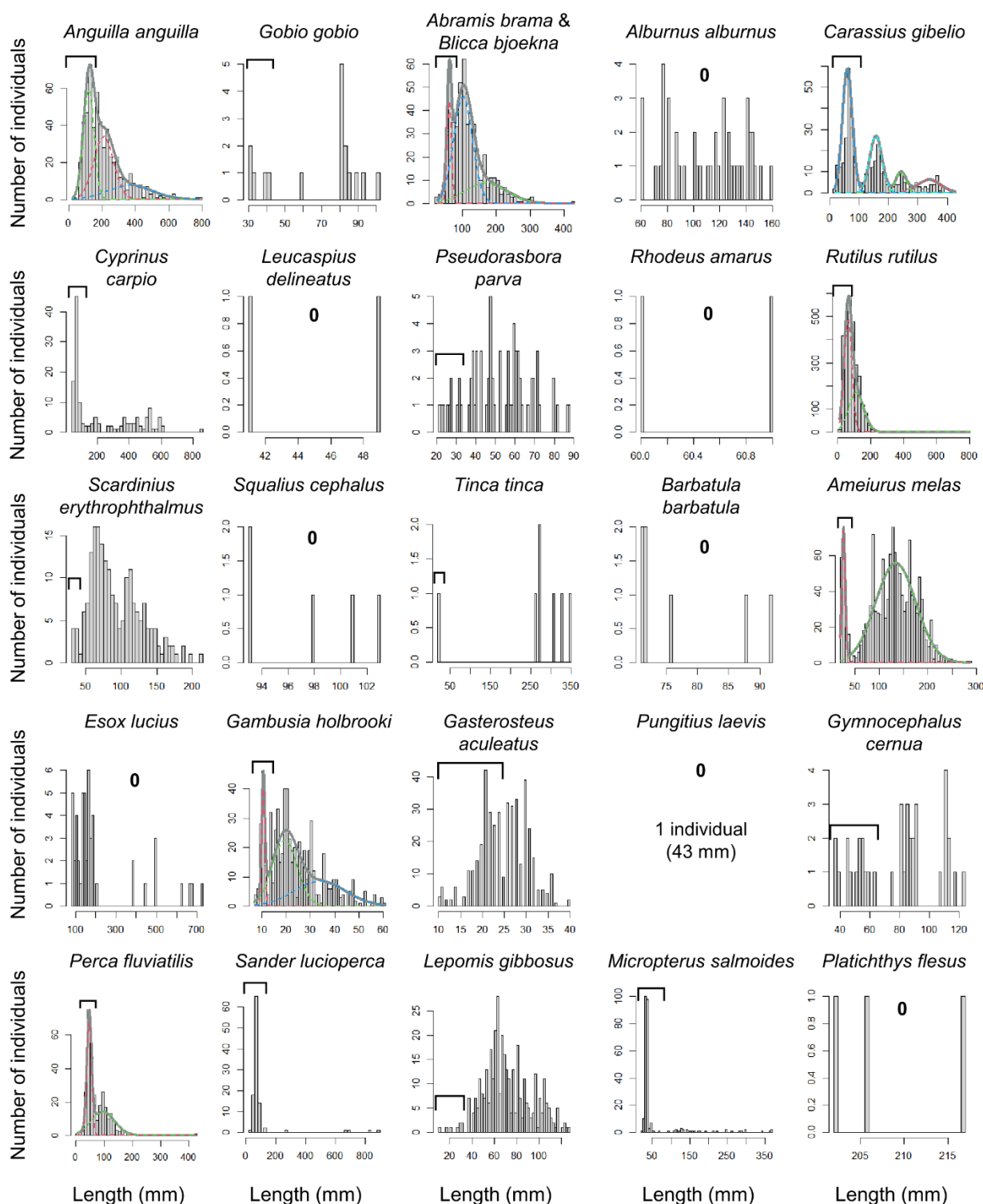
Five other variables described the habitats for fish in the sampled canals and the hydrological units. The number of refuges for fish along the two banks of each sampled canal stretch was visually measured once at the time of the first electrofishing, and converted into five classes: 1/ scarce roots, 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 (Lebre 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) | |
| <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) | | |
| <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 |

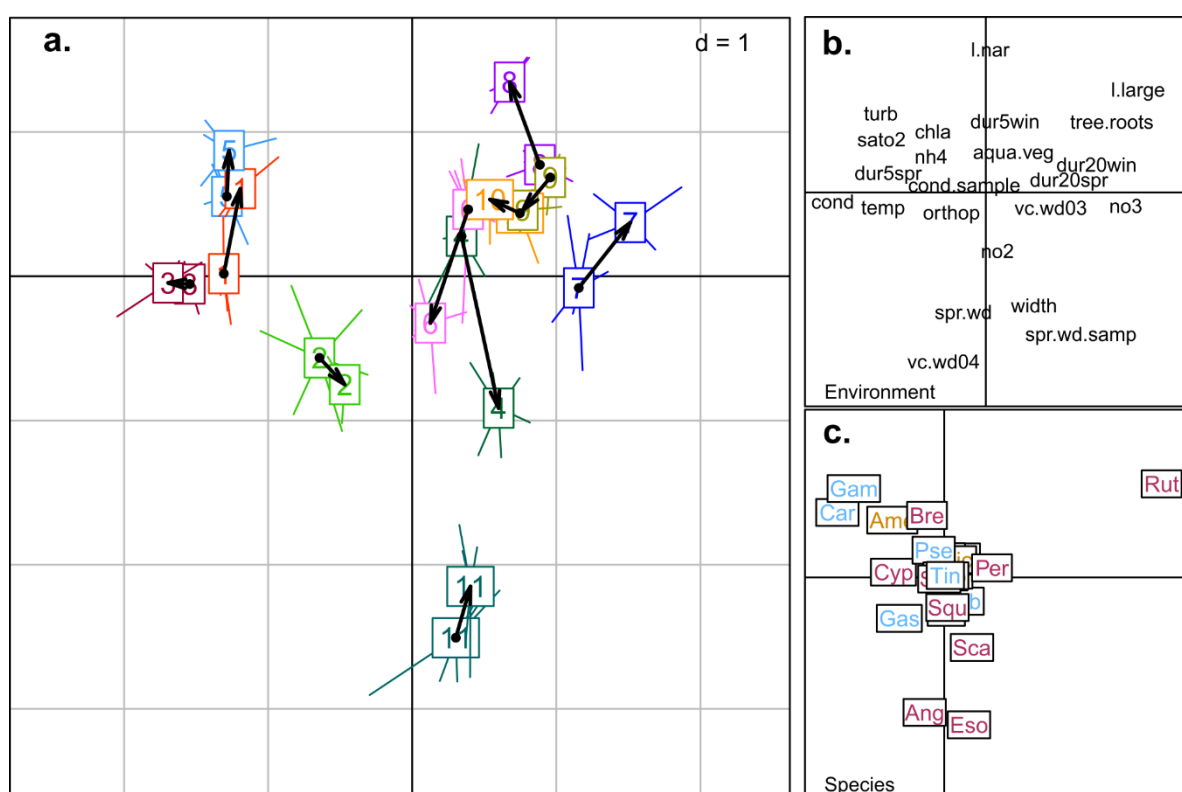
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Appendix C – Co-inertia analysis of the fish communities from the 11 hydrological units (1 to 11) without the Young-of-the-year from the complete dataset.

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.

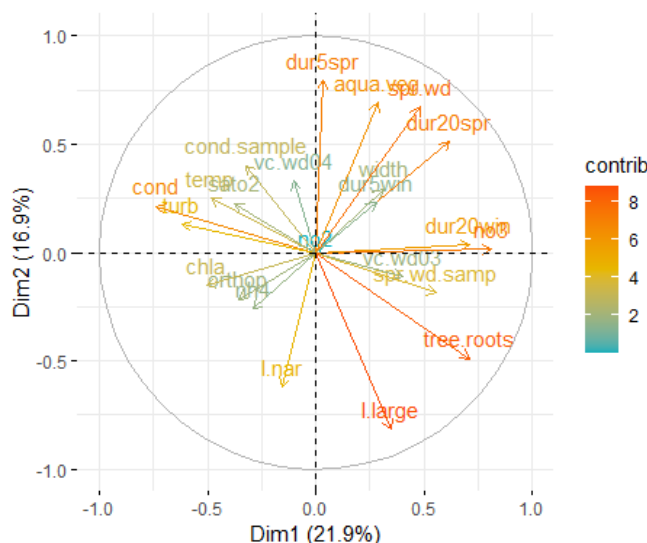


C2 – Canonical weights of the species (left) and the environmental variables (right) in the co-inertia analysis. Colors indicate the lowest (blue) and highest (red) values for each of the first two axes. The full species names and the environmental variables are available in Appendices B2 and D2, respectively.

| 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 | | | |

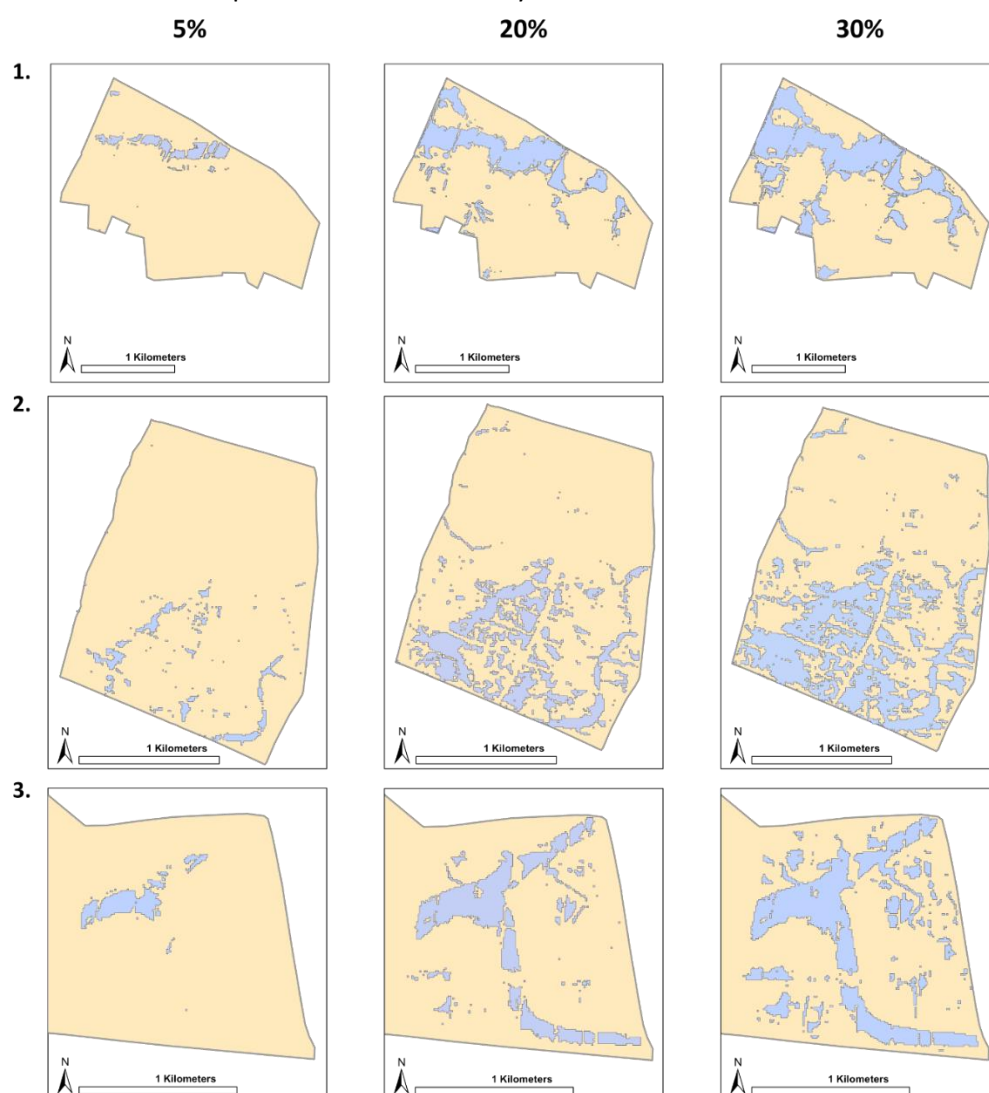
Appendix F – Spatial pattern of flooded meadows in the 11 hydrological units

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.

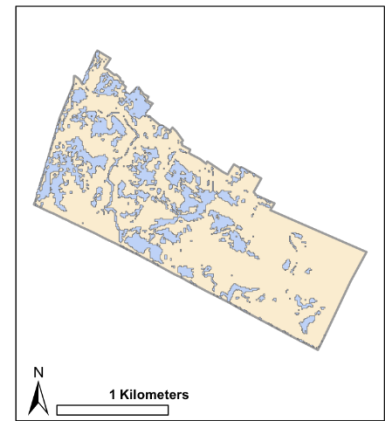
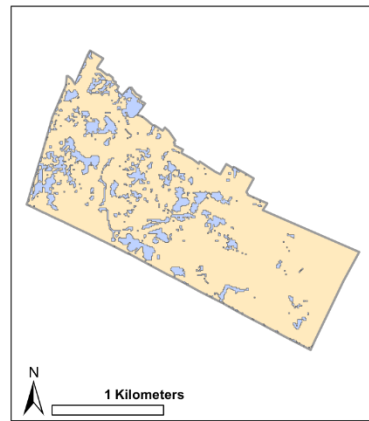
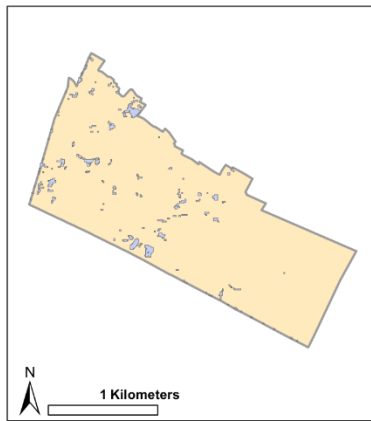


5%

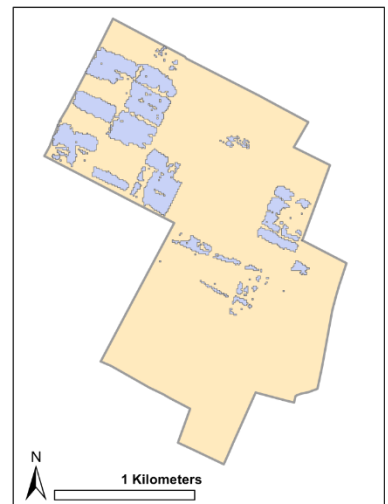
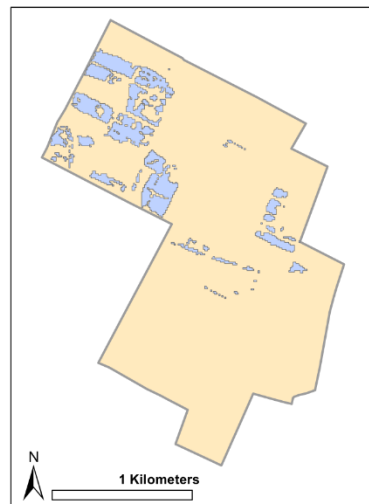
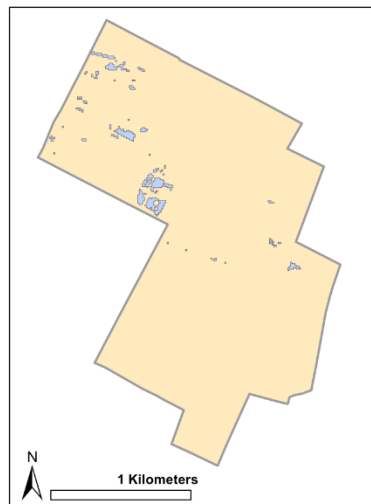
20%

30%

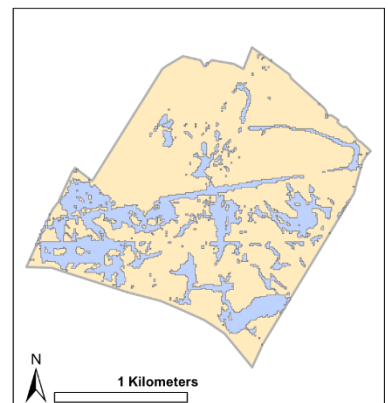
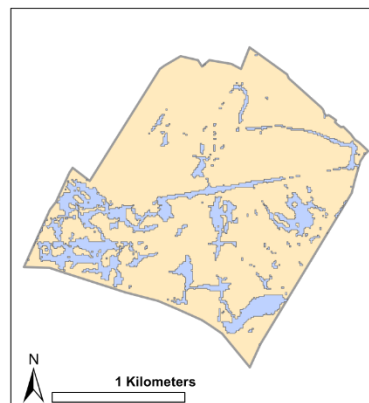
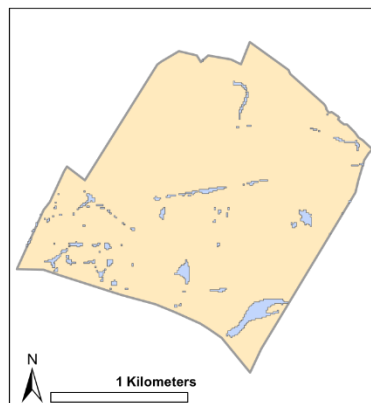
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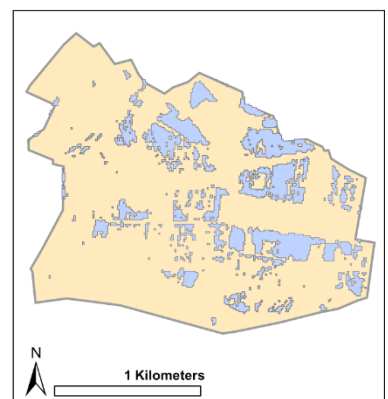
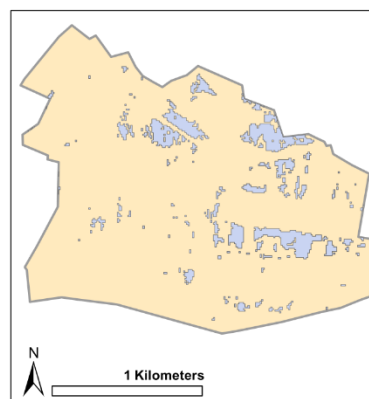
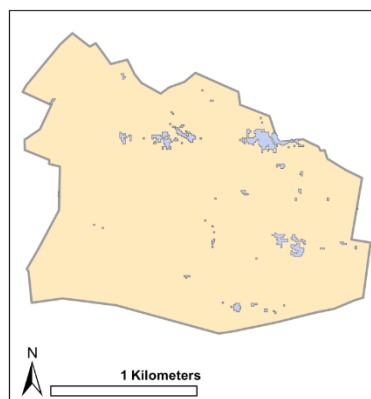
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6.



7.

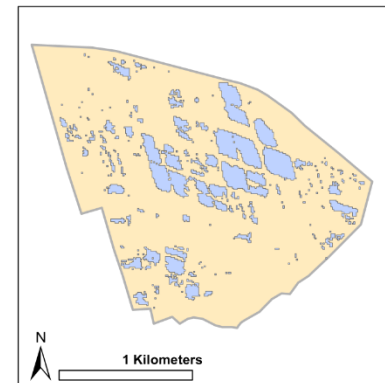
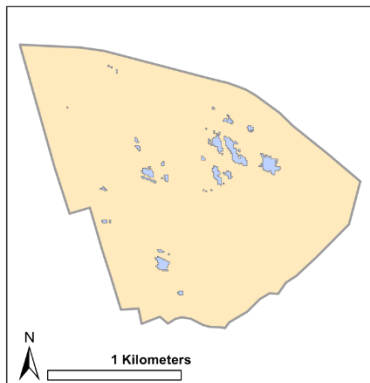


5%

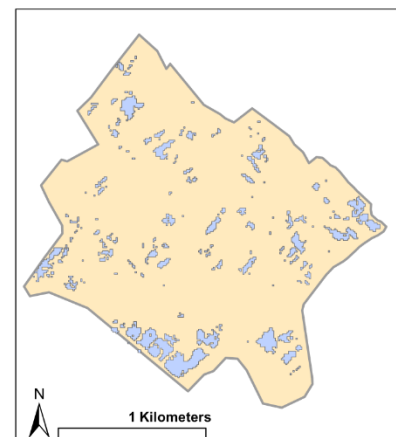
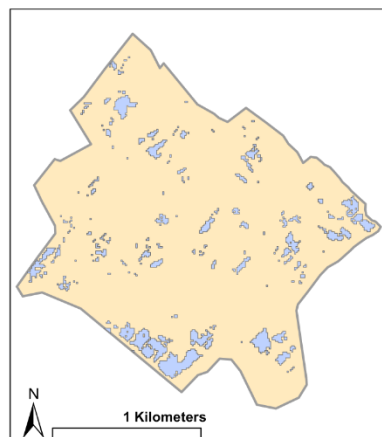
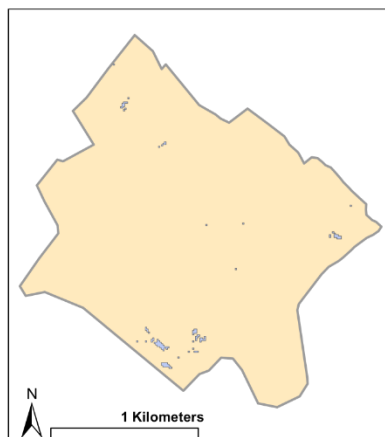
20%

30%

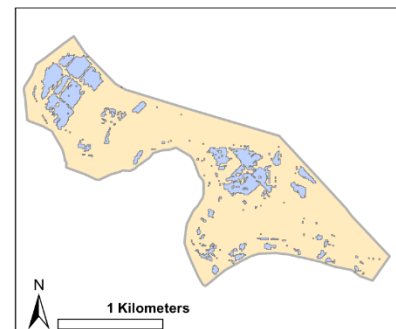
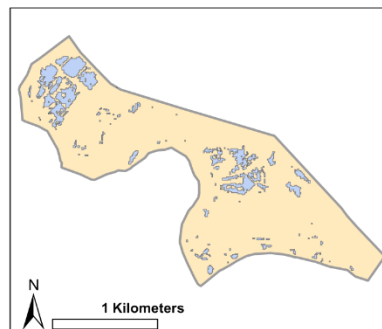
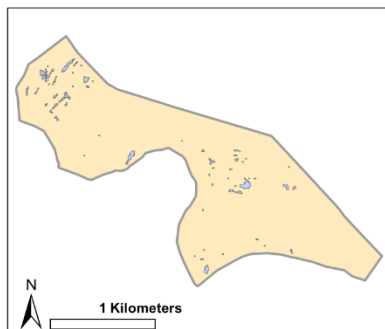
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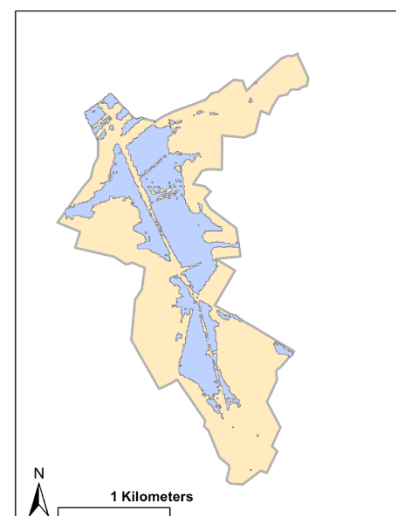
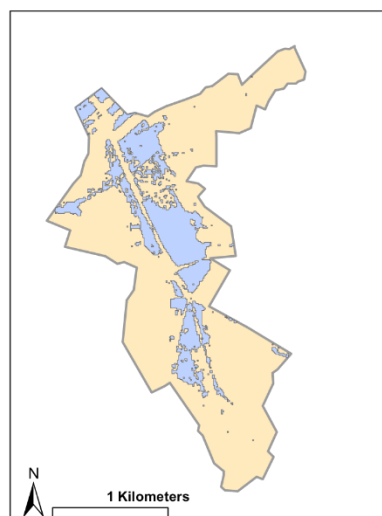
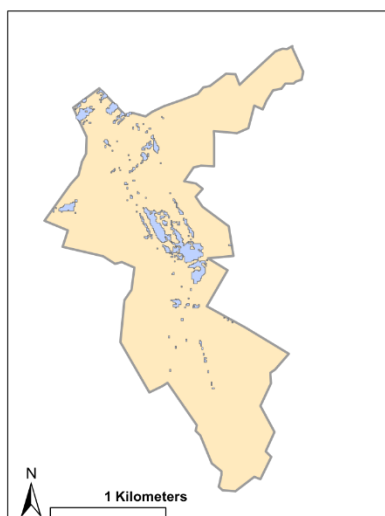
9.



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.

