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Hervé Capra, H. Pella, M. Ovidio

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1 Individual movements, home-ranges and habitat use by native rheophilic
2 cyprinids and non-native catfish in a large regulated river

3

4 *short title*: Movement behaviour of fish in a large river

5

6 Hervé Capra^{1*}; Hervé Pella¹, Michaël Ovidio²

7

8 ¹Irstea, UR RiverLy, 5 rue de la Doua, CS 20244, 69625 Villeurbanne Cedex (France).

9

10 ²University of Liège, UR-FOCUS. Biology of behaviour Unit, Laboratory of Fish Demography
11 and Hydroecology, 22 Quai Van Beneden, 4020 Liège (Belgium).

12

13 * corresponding author: herve.capra@irstea.fr; Tel +334 7220 8732; Fax +334 7847 7875

14

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16

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26 Individual movements, home-ranges and habitat use by native rheophilic
27 cyprinids and non-native catfish in a large regulated river

28

29 **Abstract**

30 The mobility patterns of two native species, the barbel, *Barbus barbus* (L.) and the chub
31 *Squalius cephalus* (L.) and of one non-native fish species, the catfish *Silurus glanis* (L.) were
32 assessed on a 35.5-km reach of the Upper Rhône River, a strong flowing river with notable
33 thermal regime alterations. An active acoustic tracking technique adapted to large rivers allowed
34 (1) the identification of longitudinal home ranges, movements and preferred habitat at large
35 scale; and (2) the analysis of the influence of discharge and water temperature on the movement
36 patterns of the fish. The active fish-tracking system recorded 1572 fish localisations over seven
37 months on a weekly basis for 80% of the tagged fish (37 barbel, 23 chub and 13 catfish).
38 Compared with the catfish, barbel and chub showed wider longitudinal home ranges, more
39 movements > 1 km and higher inter-individual variability. The catfish preferred artificially
40 heated habitats with less morphological diversity. The three species were more often localised in
41 river sections with high density of woody debris. The results suggest that habitat degradation is
42 more damaging for cyprinids, while the catfish seemed less, if not unimpacted, in large modified
43 rivers.

44

45 **Keywords:** barbel; chub; catfish; Rhône River; seasonal mobility; habitat use.

46

47 **Introduction**

48
49 Many rivers of the northern hemisphere are heavily affected by human activity causing major
50 changes to the rivers' continuity, morphology, flow and thermal regimes. Habitat fragmentation
51 and artificial flow variability are known to modify availability and access to functional habitats
52 for fish (Capra et al., 2017; Fullerton et al., 2010; Nilsson, Reidy, Dynesius & Revenga, 2005).
53 Impassable obstacles limit the possible movements in both upstream and downstream directions
54 (Crook et al., 2015; Jansson, Nilsson & Renöfält, 2000) and artificial high flow variability (e.g.
55 hydropeaking) forces fish to select not the most suitable but the "least-constraining" habitats
56 (Capra et al., 2017). The mobility, spatial distribution and temporal variations of fish are major
57 elements of fish biology that influence their population dynamics and productivity (Benitez,
58 Nzau Matondo, Dierckx & Ovidio, 2015; Fredrich, Ohmann, Curio & Kirschbaum, 2003;
59 Gardner, Deeming & Eady, 2015; Lucas & Baras, 2001; Ovidio, 1999; Radinger & Wolter,
60 2014). The range, frequency and intensity of movements of most holobiotic species remain
61 poorly known or unidentified in large rivers (Booth, Hairston & Flecker, 2013), even though a
62 wide variety of movement behaviours exist in fish at different life stages (adults and juveniles) in
63 different seasons (Benitez et al., 2015; Lucas & Baras, 2001). These studies have shown that
64 flow and temperature variability are significant factors of fish movement behaviour, but this has
65 never been studied in a large hydropeaking river. Although carrying out such behavioural studies
66 in large rivers remains a technical challenge, they are fundamental to understanding the
67 responses of holobiotic fish species to anthropogenic pressures (Benitez et al., 2015; Gardner et
68 al., 2015). In highly regulated and channelized large European rivers, the endemic (i.e. native)
69 rheophilic cyprinid species (e.g. barbel, *Barbus barbus* (L.) and chub, *Squalius cephalus* (L.)) are
70 relevant indicators of the ecological status of the rivers (e.g. Maire, Buisson, Biau, Canal &
71 Laffaille, 2013 (for conservation regulation); Morina et al., 2016 (for sediment contamination);
72 Oberdorff, Pont, Hugueny & Chessel, 2001 (for fish-based index)). Indeed, their high sensitivity

73 to fragmentation, flow change and thermal regime variations is due to specific ecological
74 requirements for the reproduction substrate in certain spawning sites or water quality and leads to
75 dramatic declines of their populations (De Leeuw & Winter, 2008; Ovidio & Philippart, 2008;
76 Poulet, Beaulaton & Dembski, 2011). Barbel and chub could also be considered as relevant
77 indicators to study the impact of river fragmentation (Benitez & Ovidio, 2018). It appears on the
78 other hand, that the non-native species, catfish (*Silurus glanis* (L.)), successfully adapts and
79 seems to take advantage of the general deterioration of river ecosystems (Britton, Cucherousset,
80 Davies, Godard & Copp, 2010; Castaldelli et al., 2013; Guillerault et al., 2015; Poulet et al.,
81 2011). Despite these observations, knowledge on native rheophilic species and non-native catfish
82 movement behaviour in large rivers is lacking. The behavioural ecology and particularly
83 seasonal movement patterns of barbel are well documented but exclusively in fourth order rivers
84 or lower (Baras, 1992; Baras, 1995; Le Pichon, Tales, Gorges, Baudry & Boët, 2016; Ovidio &
85 Philippart, 2008). Benitez and Ovidio (2018) showed that within the same river basin, barbel
86 demonstrate flexibility in movement periodicity and optimise the start date of migration towards
87 spawning grounds in accordance with their local environment and individual experiences. This
88 suggests that movement behaviour of a single species may differ depending on the size of the
89 river. These studies have widely demonstrated frequent seasonal movements between functional
90 habitats and high habitat stringency (substrate, water quality). The documentation of chub
91 mobility in large rivers (i.e. order ≥ 5) is limited to one study with a short tracking duration (5
92 to 17 days) within a 4-km long study site that showed significant occupation of backwaters and
93 cover such as woody debris and boulder clusters (Allouche, Thévenet & Gaudin, 1999).
94 Cucherousset et al. (2017) highlighted a knowledge gap on catfish adaptation to river
95 modification and on their mobility and dispersal patterns and Brevé et al. (2014) showed explicit
96 site fidelity and limited movements for adults in a large river (Meuse River, Netherlands). Capra
97 et al. (2017) showed contrasted habitat selection behaviours among barbel, chub and catfish, on a
98 local scale (i.e. microhabitat) and in a hydropeaking flow regime. However, Capra et al. (2017)

99 assumed that it is more likely that changes in fish habitat selection, considering the available
100 knowledge on specie habitat traits (Lamouroux, Capra, Pouilly & Souchon, 1999; Slavík, Horký,
101 Bartoš, Kolářová & Randák, 2007; Copp et al., 2009; Riffart, Carrel, Le Coarer & Fontez,
102 2009), is related to quick reactions and adapted movements supported by the capacity of fish to
103 remember the spatial structure of the reach and its variations (Reebs, 1996). But, to date,
104 seasonal movement behaviour of native rheophilic species and non-native catfish on a broad
105 scale (a dozen kilometres) has not been studied simultaneously in a large river, which is the
106 typical ecosystem in which their home ranges overlap.

107 Telemetry studies in a broad variety of aquatic environments can now be performed
108 thanks to the technological progress achieved over the last two decades, including the use of
109 radio and acoustic bio-telemetry with manual or automated localisation. Large river ecosystems
110 are somewhat restrictive in terms of the logistical deployment of bio-telemetry techniques mainly
111 because of their size and harsh hydraulic conditions, preventing, for example, the possibility of
112 tracking a large number of individuals in a limited period of time. Therefore, telemetry research
113 in large rivers has been essentially based on passive listening methods to analyse fish trajectories
114 and movement speeds between passive listening stations located several kilometres away from
115 each other (Béguier-Pon et al., 2015; Burke & Jepson, 2006; De Leeuw & Winter, 2008; Gardner,
116 Deeming & Eady, 2013; Verbiest, Breukelaar, Ovidio, Philippart & Belpaire, 2012; Brevé et al.,
117 2014; Wang, Wei, Kynard & Zhang, 2012). Notable exceptions are Daugherty and Sutton
118 (2005), Wang et al. (2012) and Alexandre et al. (2016), who tracked fish over long distances (20
119 to 38 km) during 9 to 14 months on a weekly basis using boats.

120 This study assessed the movement patterns of two native rheophilic cyprinid species
121 (barbel and chub) and the non-native catfish in the Rhône River (France) over a seven-month
122 period from spring to autumn. The Rhône River in the Bugey area is characterised by huge flow
123 disruptions due to peak flow management measures and water temperature locally warmed by
124 the cooling system of a nuclear power plant. To overcome the limitations of the active tracking

125 of fish in large rivers (Herrala, Kroboth, Kuntz, & Schramm, 2014), an acoustic tracking
126 protocol adapted from the homing protocol presented in Eiler (2012) using scanning acoustic
127 equipment from a boat was used, allowing easier and a more efficient localisation of many
128 individuals. The purpose of this study was to test (1) if the non-native catfish develop, as
129 expected, different movement behaviours, home range exploitations and habitat uses than the
130 native rheophilic cyprinids, barbel and the chub, (2) if their movements are influenced differently
131 by discharge and water temperature and (3) if the catfish take advantage of the river degradation
132 unlike the native rheophilic cyprinids.

133

134 **Methods**

135 *Study site*

136 The study reach is a 35.5-km undiverted section of the French Upper Rhône River located north-
137 east of Lyon (Figure 1) between the Sault-Brénaz hydroelectric facility (located upstream;
138 Compagnie Nationale du Rhône - CNR) and the Jons-Cusset hydroelectric facility (located
139 downstream; Électricité De France - EDF). The upstream limit (river kilometer Km 0;
140 45°51'19.74"N; 5°24'23.40"E) of the study reach is distinguished by an artificial riprap weir
141 (which cannot be crossed by boat). The downstream limit (Km 35.5; 45°46'4.23"N;
142 4°54'49.90"E) is identified by the dam of Jons. Sault-Brénaz's and Jons-Cusset's hydroelectric
143 facilities cannot be crossed by fish in an upstream direction but downstream passages remains
144 possible through the turbines or spillways. A nuclear power plant located on the right bank of the
145 study reach at Km 17.5 pumps ≈ 100 m³/s to cool its four reactors and discharges warmed-up
146 water (between 7 and 10 °C warmer than the upstream water). The warm water discharge creates
147 a strong transversal temperature difference between the left bank and the right bank (Ginot,
148 Souchon & Roger, 1996; Capra et al., 2011).

149 Daily mean discharge at the study site varied between 160 and 742 m³/s 90% of the time,
150 for a mean annual flow of 473 m³/s (<http://www.rdbrmc.com>; stream gauging station of the CNR
151 at Lagnieu, Km 6). The low-flow period stretched mainly from the end of summer to autumn (5-
152 year mean monthly low flow = 200 m³/s). The high-water periods were linked either to the end
153 of spring snowmelts or autumn rains (2-year flood = 1300 m³/s). The peak production of
154 hydroelectricity (hydropeaking), operated by upstream dams, created daily flow variations of 150
155 to 500 m³/s over the study reach (real-time information on <http://www.inforhone.fr>). The daily
156 mean water temperature (data recorded from 1980 to 2010 by EDF at Km17) varied between 1°C
157 and 26°C, and annual mean water temperature was 12.1°C.

158

159 *Capture and tagging*

160 The fish capturing and tagging took place between 15 and 19 March 2010. Close to 20% of the
161 study reach was sampled per day during the capture and tagging period in the upstream direction.
162 The fish were captured by boat using electrofishing or net fishing techniques (gillnets were left
163 for a maximum of two hours) and the capture location of each individual was recorded. The fish
164 were placed in containers, which were set-up on the riverside and supplied with water using
165 pumps immersed in the Rhône River, for a minimum duration of one hour before and after being
166 tagged. The fish were then selected for tagging according to their weight (minimum = 600 g).
167 Acoustic transmitters were implanted in the fish's intraperitoneal cavity, in accordance with the
168 technique described by Ovidio and Philippart (2008). The fish were anaesthetised with a 0.08
169 mL/L AQUIS-S[®] (Aquis-S, NZ Ltd.) solution before the tagging and an antibacterial medication
170 (Marbocyl 2%) was injected in the dorsal muscles to prevent post-operative infections. One hour
171 after the surgery, the fish's recovery was verified (correct resting position and respiration, no
172 bleeding) before release at their capture site to avoid post-tagging artificial movements (Gardner,
173 Deeming, Wellby, Soulsbury & Eady, 2015).

174 The fish tags (Model 795 Acoustic Tags: frequency of 307kHz; transmit power level of
175 155dB relative to 1 μ Pa at a distance of 1m, Hydroacoustic Technology Inc. (HTI), Seattle,
176 Washington) lasted between 180 days and three years (manufacturer data) and their weight in air
177 was 13g or 24g (respectively 795LX and 795Z models). The tags weighed less than 2% of the
178 fish's body weight (Brown, Cooke, Anderson & McKinley, 1999; Winter, 1983).

179 A total of 83 fish belonging to the three most abundant species during the sampling were
180 tagged: barbel (n=37), chub (n=31) and catfish (n=15). A few other individuals (n=1 to 6) of
181 seven other species were also tagged but not considered herein. Some fish tagged for a previous
182 study, in 2009 (Capra et al., 2017; barbel, n=3; catfish, n=5), with a potentially still active tag in
183 2010, were tracked as well as the newly tagged fish in this study. The behaviour, in terms of
184 distances travelled and linear range of newly tagged fish and previously tagged fish, were
185 deemed comparable (Gardner, Deeming, Wellby, et al., 2015).

186

187 ***Fish tracking***

188 Each tagged individual was identified by its tag's HTI configured sound emission period (field
189 programmable; http://www.htisonar.com/acoustic_tags.htm). The emitting period of the tags
190 ranged between 2995 and 3884 ms. A second signal (subcode), replicating the first, was used to
191 improve the detection probability, thus enabling the simultaneous localisation of several hundred
192 fish without risking the collision of tag signals and suppressing any noise interference that could
193 have been on the same frequency.

194 During tracking campaigns, fish detection was performed from a motorboat equipped
195 with four hydrophones (two hydrophones on either side) attached to a metal crossbar set up on
196 the bow of the boat, perpendicular to the navigation axis (Figure 2). On both sides of the
197 crossbar, a directional hydrophone (Model 592 directional Hydrophone 30°, HTI) and a 180°-
198 angle limited omnidirectional hydrophone (Model 590-series Hydrophone 330°, HTI) were set
199 up. This provided large monitoring areas on either side of the boat towards the riverbank and the

200 riverbed (Figure 2). A 291 HTI Portable Acoustic Receiver was linked to the four hydrophones
201 with 690-100 HTI Hydrophone cables. The portable receiver was connected and synchronised to
202 a laptop computer that recorded, via the Acoustic Tag© software, hourly files including all
203 surrounding noises detected by the four hydrophones. The laptop recorded the GPS localisation
204 (compass Crescent V100 Series - Hemisphere GPS with an accuracy inferior to 60 cm) of the
205 crossbar, and therefore that of the hydrophones, every second. The laptop time drew a link
206 between the recording of the tags' sound emissions and the GPS coordinates of the hydrophones.

207 Between 1 April 2010 (two weeks after the fish tagging) and 19 October 2010, the
208 tracking campaigns were carried out on a weekly basis over the entire study reach. Each tracking
209 campaign (around 7 hr each) was boat-monitored in the downstream direction by drifting in the
210 middle of the channel (i.e. along the curvilinear axis from Km 0 to Km 35.5) with the water
211 current to minimise the use of the motor; this was also done in the backwaters and secondary
212 channels when enough water flow was available.

213 Hourly files were recorded using the MarkTags© software, which automatically detected
214 the exact time (to the second) at which the fish tag emission was the nearest to the hydrophones
215 (see NP time on Figure 2), thus allowing precise localization of fish within the study reach after
216 each tracking campaign. Each fish localisation was pinned by the curvilinear coordinates (i.e.
217 ranging from Km 0 to Km 35.5 km; Figure 1) of the hydrophone at the NP time. Only fish
218 localised at least ten times (the third of the tracking campaign number) were retained for
219 analysis.

220

221 ***Data analysis***

222 The spatio-temporal patterns of fish movements were first determined by the longitudinal home
223 range (HR, m) which is defined as the distance between the most downstream NP curvilinear
224 coordinate minus the most upstream NP curvilinear coordinate (Ovidio, Seredynski, Philippart &
225 Nzau Matondo, 2013). For each species the link between HR and the fish size and weight (all

226 variables transformed into $\log(x+1)$ to approximate normal distribution) allowed detection of all
227 possible individual effects (Aarestrup, Jepsen, Koed & Pedersen, 2005). Lastly, several basic
228 indicators related to the complexity and variability of individual fish longitudinal movements in
229 the rivers were calculated (Ovidio, Baras, Goffaux, Giroux & Philippart, 2002; Ovidio et al.,
230 2013). These were:

231 - total net travelled distance (D_{nt} , m), from the sum of the net travelled distances between
232 two subsequent localisations within seven days (D_n , m/7d). D_n was the absolute value of the raw
233 travelled distances, which was negative when fish travelled in an upstream direction;

234 - mean net travelled distance within seven days ($\overline{D_n}$, m/7d), from D_{nt} divided by the
235 number of intervals between two subsequent localisations;

236 - maximum of D_n (D_{nx} , m/7d);

237 - number of $D_n > 1$ km (D_{n1k}). Note that the 1-km threshold has been considered as a
238 significant location change (see Figure 1 in Radinger & Wolter (2014); see also Peñáz, Barus,
239 Prokes & Homolka (2002) who defined resident barbel as all marked individuals that did not
240 move more than 780 m). This indicator was used to infer the variability of the large-scale habitat
241 changes of the fish, in contrast with local scale habitat (microhabitat) selection studied in 2009
242 by Capra et al. (2017) over the same study reach in the Rhône River. Fish that moved, at least
243 once, further than 1 km in seven days (i.e. $D_{n1k} \geq 1$) were called roaming individuals. The
244 proportion of roaming fish, the proportion of D_{n1k} for each species and the proportion of
245 roaming fish that travelled upstream first were calculated and compared to a random distribution
246 with a Pearson's χ^2 -test for count data. Finally, the roaming fish showing $D_n > 5000$ m were
247 detected to outline long-distance movements.

248 - intensity of exploitation (IE) of the HR as the ratio of D_{nt} divided by HR (see Ovidio et
249 al., 2002 and 2013).

250 The distributions of HR, $\overline{D_n}$, D_{nt} , D_{nx} , D_{n1k} and IE are shown as box-plots, using one
251 box-plot per species. The distributions of the three species were compared using Kruskal-Wallis

252 rank sum tests (Kruskal & Wallis, 1952). If these tests showed a difference among species, their
253 distributions were then compared between pairs of species with a Wilcoxon signed-rank test
254 (Wilcoxon, 1945) using a Bonferroni adjustment of the α value (here $\alpha /3$).

255 The influence of mean daily temperature and discharge between two successive locations
256 on Dn was tested fitting a GLM-Poisson model for each species, grouping all data from the same
257 species (i.e. data of all individuals). To illustrate the interaction between temperature and
258 discharge, for each species, a bubble chart was plotted as x = mean temperature values, y = mean
259 discharge values and z (size) = Dn values.

260 To complete the analysis of the effect of the water temperature on the spatial distribution
261 of fish over the study reach, a contingency table was created of the recorded locations between
262 the nuclear power plant of Bugey (Km 18) and Loyettes (Km 24; Figure 1). The right riverbank
263 locations (heated areas downstream of the heated effluents from the nuclear power plants) were
264 distinguished from those located on the left riverbank (non-heated zone) on the entire 6-km-long
265 section. The physical habitat availability on the right and left riverbanks of this section are
266 comparable. The contingency table was tested using a Pearson's χ^2 -test for count data.

267 Finally, to identify possible habitat determinism over fish spatial distribution, the study
268 reach was divided into adjacent 500-m long sections (Figure 1) and then the preferences of the
269 fish for general habitat characteristics were tested. The general habitat of each 500-m long
270 section was differentiated using categorical variables: channel type (single or multi-channel),
271 river morphological unit (rapid or homogeneous lotic channel) and the density of woody debris
272 spots inventoried (three classes with comparable density in a 500-m long section). During the
273 tracking campaigns on 9 August 2010 and 27 September 2010 woody debris spots were
274 inventoried and GPS-localised along both riverbanks. The density of woody debris spots was
275 calculated for both riverbanks of each 500-m long sections as the mean number of spots
276 inventoried from both tracking campaigns. Woody debris density per 500-m long sections in
277 different classes of channel types and morphological units were compared to a random

278 distribution with a Pearson's χ^2 -test for count data. Calculations for each tracking campaign
279 (shown as a date) and for each class of each variable, were necessary, this included: the total
280 number of fish located in each 500-m long section belonging to this particular class divided by
281 the number of 500-m long sections belonging to this particular class (equivalent to the population
282 density in this class). Then, a Wilcoxon signed-rank test (Wilcoxon, 1945) was used on the
283 variables with two classes and a Friedman rank sum test (Friedman, 1940) for the variables with
284 three classes to determine whether a class (i.e. the type of a section) was more densely populated
285 (preferences for these classes) than another one throughout the tracking period, or whether the
286 location distribution among the various types of sections varied over time (no preference). A post
287 hoc test among the different classes was performed when the Friedman rank sum test was
288 significant. The α value for the post hoc tests was divided by the number of classes (Bonferonni
289 adjustment).

290 All statistical tests were conducted using the R software (R Core Team, 2014) with a
291 significant threshold set to $\alpha = 5\%$.

292

293 **Results**

294

295 Daily mean flow during the tracking campaigns varied from 150 to 900 m³/s (mean = 385 m³/s;
296 SD = 165 m³/s; Figure 3 for weekly mean flows). The daily mean temperatures varied from 7.9
297 to 24.4 °C (mean = 16.6 °C; SD = 4.0 °C) the highest values being noted in July and August
298 2010 (Figure 3 for weekly mean temperatures).

299 Between 1 April and 19 October 2010, 29 tracking campaigns were carried out with an
300 average duration of 7.2 days (quartiles = 6.8, 7.0 and 7.3 days) between each campaign. Among
301 the 91 fish of the three species tagged, 73 individuals (80 % of the tagged fish; barbel, n = 37;
302 chub, n= 23; catfish = 13; Table 1) were located at least ten times during the study and
303 considered for analysis. The time between two successive localisations ranged from 5 and 70

304 days (quartiles = 7.0, 7.0 and 9.0 days) for the 1572 recorded fish localisations (all using the 30°-
305 directional hydrophones). The number of individuals located during each campaign varied from
306 43 (59% of the 73 studied fish) to 63 (86%) and on average, 54 fish (74%) were located,
307 although fewer positions were recorded after 27 September. The total number of localisations for
308 barbel was 828, 457 for chub and 287 for catfish (Figure 3). Note that seven localisations for
309 four individuals (barbel, n=1; chub, n=3) were recorded upstream of the weir of Km 0, due to
310 manual studies carried out between 20 May and 28 June 2010 (reproduction period). These four
311 fish returned downstream of the weir one to two weeks after their localisation (Figure 3). Among
312 the 18 individuals with less than ten localisations (20% of the tagged fish; barbel, n=3; chub,
313 n=8; catfish, n=7) and removed from the analysis, nine fish (10%) were poorly detected (1 to 9
314 localisations), six fish (7%) disappeared from the study site early on (before the seventh tracking
315 campaign) and three fish (3%) were never detected.

316 Barbel and chub showed a high inter-individual variability in movement patterns, from
317 highly resident to very mobile subjects who roamed the upstream and downstream limits of the
318 study area (Figure 3). Catfish showed lower individual-specific movement variability with the
319 majority of individuals showing only very short movements (Figure 3). The proportion of
320 roaming individuals was higher for barbel (73%; n = 27) and chub (70%; n = 16) than catfish
321 (46%; n = 6; Pearson's $\chi^2 = 5.93$; $p = 0.05$). The proportion of Dn1k, overall, was low but higher
322 for barbel and chub (10% for both species) than catfish (7%), with no significant difference from
323 random distribution (Pearson's $\chi^2 = 2.91$; $p > 0.05$). The first Dn > 1 km was travelled in the
324 upstream direction for most barbel (63%; n = 17) and chub (87%; n = 14), compared with only
325 half of the catfish (50%; n = 3), but without significant difference with a random distribution
326 (Pearson's $\chi^2 = 4.06$; $p > 0.05$). Finally, among roaming fish, 17 individuals (barbel, n = 8; chub,
327 n= 7; catfish = 2) showed a Dn > 5000 m (Figure 3). Most of these individuals remained for
328 some weeks in the newly occupied habitat before coming back near to the place they left a few

329 weeks before (Figure 3). Very few fish stayed in their new habitat, without returning during the
330 studied period.

331 Comparison of the movement indicators showed no significant differences among the
332 three species (Figure 4, Table 2) and there was no correlation (correlation coefficients ranging
333 from -0.17 to 0.14 with all p values > 0.05) between HR and fish size or fish weight. The median
334 HR of barbel and chub were close (respectively 3045 m and 2355 m) and two to three times
335 higher than the median HR of catfish (1295 m; Figure 4 and Table 2). D_{nt} , $\overline{D_n}$, D_{nx} and D_{n1k}
336 were not different among species even though the medians for barbel and chub were close and
337 higher than the medians for catfish (Figure 4 and Table 2). Finally, catfish were the species that
338 most intensively exploited their longitudinal home range (Figure 4 and Table 2).

339 GLM-Poisson models found no effect of temperature, discharge or their interaction on D_n
340 (Figure 5). The coefficients for all variables and their interaction were all significantly ($p < 0.05$)
341 close to 0.0 ($-3.4e-01$ to $5.4e-04$). Mean temperature and mean discharge showed no correlation
342 between fish localisations (Figure 5). D_n was higher for higher mean flows for all three species
343 when the temperature was between 14°C and 18°C. A visible gradient was observed among the
344 three species in relation to the temperature associated with D_n . Longer D_n data were observed
345 for temperatures ranging between 13 °C and 19 °C for barbel, from 13 °C to 22 °C for chub and
346 from 15 °C to 24 °C for catfish.

347 Fish localisations between the nuclear power plant and Loyettes, divided between the
348 non-heated left riverbank and the right riverbank, were not significantly different from a random
349 distribution (Pearson's $\chi^2 = 2.85$; $p > 0.05$). However, barbel and chub mainly occupied the left
350 riverbank (34/49 and 45/51 localisations respectively) whereas the catfish were predominantly
351 on the right riverbank (60/53 localisations).

352 Over the 71 defined 500-m long sections, 20 were multi-channel types and 51 single-
353 channel types, predominantly lotic channel types (46 areas) as opposed to rapid types (25 areas).
354 The number of woody debris spots per 500-m long section varied from 1 to 31 with a median of

355 8 and their density per section was no different from random (Pearson's $\chi^2 = 0.42$; $p > 0.05$).
356 During the tracking period, fish were detected in 65, 500-m long sections. The remaining six
357 sections were located in the downstream half of the study reach. The total number of fish
358 localised per 500-m long section varied from 0 to 28 (quartiles were 2.0, 3.0 and 4.5). The total
359 number of fish localisations per 500-m long section varied from 0 to 298 (quartiles were 4.0,
360 11.5 and 23.7). Barbel preferred multi-channel type sections, with rapids and a high number of
361 woody debris (Table 3). Chub preferred main channels without rapids but with a high number of
362 woody debris (Table 3). Catfish showed no particular channel type preferences but appear to
363 prefer sections with a high number of woody debris (Table 3).

364

365 **Discussion**

366

367 By tracking 91 adult fish over seven months, the movement metrics and habitat use of two native
368 rheophilic species (barbel and chub) and a non-native species (catfish) were quantified in the
369 Upper Rhône River. The results showed the movements of cyprinids and catfish recorded
370 simultaneously in a large fast-flowing river (the Rhône River). Unlike the catfish, barbel and
371 chub demonstrated (1) wider home ranges (HR), (2) a higher number of net distances travelled $>$
372 1 km (Dn1k), (3) a higher inter-individual variability and (4) a higher rate of roaming
373 individuals. Catfish were more often localised in artificially heated habitats (downstream from
374 the nuclear power plant), intensively exploited their habitat and have no preference for available
375 morphological habitat types.

376 The portable active-scanning acoustic system proved a relevant technique to locate fish in a
377 large-size and fast flowing river. It could be used to investigate the complexity and the variability
378 of fish individual movements more accurately, as well as habitat and home range exploitation at
379 high temporal resolution. Furthermore, it allowed high detection rates of the tagged individuals
380 (on average 74% per tracking campaign) without data collisions of dozens of tagged fish

381 simultaneously and without increasing the search duration. Such a high-performance of a
382 telemetry system has not been achieved with more traditional active telemetry or fixed detection
383 stations at the scale of a large river and thus could contribute to filling gaps in knowledge on the
384 behavioural ecology of fish in such environments. However, determining why 20 % (n=18) of
385 the 91 examined tagged fish were never or poorly detected or disappeared early from the study
386 reach remained problematic. Authors often suggested reasons such as mortality, predation or
387 movements outside of the study area, but their results generally showed higher rates (29-43 %)
388 lost or poorly detected individuals (Béguet-Pon et al., 2015; De Leeuw & Winter, 2008; Verbiest
389 et al., 2012). The mobile active scanning used in this study allowed a high number of contacts
390 with fish in comparison to fixed listening stations and consequently increased the precision of the
391 movement metrics quantified (i.e. HR, \overline{Dn} , Dn1k, IE; Figure 4).

392 The evaluation of HR depended mainly on the number of individual localisations recorded,
393 the duration of the study and the telemetry equipment (Alexandre et al., 2016). As in most
394 telemetry studies, seasonal HR and the estimated Dn only partially reflected reality, as fish
395 inevitably travelled outside the tracking periods during other moments of the daily cycle
396 (evening and night-time for example; Horký, Slavík, Bartoš, Kolářová, & Randák, 2007).
397 However, it seemed reasonable to consider in this study that the use of a weekly positioning
398 interval for the three species over seven months was an appropriate way to compare relative
399 mobility patterns among species on a seasonal scale, with acceptable losses of accuracy
400 (Alexandre et al., 2016 [monthly basis; in a stream]; Baras, 1998 [test for successive locations
401 from 1 to 28 days; best cost-effectiveness for barbel = once a week; in a stream]; Hann &
402 Schramm, 2018 [once a week for five months; in a river]; Herrala et al., 2014 [once a month for
403 more than three years; in a river]; Ovidio et al., 2002 [every day to three times a week; in a
404 stream]). HR for barbel and chub (median > 2300 m; Table 1 and Figure 4) were larger than
405 catfish (median < 1300 m; Table 1 and Figure 4), with considerable individual differences. In
406 smaller rivers (median flow < 30 m³/s), the HR of barbel exceeded 10 km on a regular basis and

407 could reach 40 km (tracked using manual mobile radio-telemetry; Baras, 1992; Ovidio,
408 Parkinson, Philippart, & Baras, 2007). Allouche et al. (1999), also using manual mobile radio-
409 telemetry, observed lower HR values for chub, < 600 m in an upstream part of the Upper Rhône
410 River (bypass section of Chautagne; minimum flow 30-60 m³ s⁻¹) over a much shorter tracking
411 period (n = 10 individuals; 3.6 km per reach, max 17 days), which led to an underestimation of
412 the movements compared to the results presented in this study. By contrast, De Leeuw and
413 Winter (2008) found that most rheophilic cyprinids in the Meuse River, Belgium (mean annual
414 flow = 230 m³/s; including barbel and chub) moved over rather short longitudinal distances (< 10
415 km) during the year using the fixed station NEDAP telemetry and De Vocht and Baras (2005),
416 using classic manual mobile radio-telemetry, found HR from 1.05 km to 27.3 km in the Meuse
417 (in between dams; hydropeaking flows; n = 14 individuals; 40 km-reach; 5 to 17 months of
418 tracking). These examples illustrate that the limit of movement for HR of cyprinids often
419 corresponded to the maximum length of the river stretch (Woolnough, Downing, & Newton,
420 2009), which may reflect space-use strategies constrained by habitat fragmentation (Gardner et
421 al., 2015 -bream; Geeraerts et al., 2007 -roach). The HR for barbel and chub recorded here
422 ranged from 150 m to 35 km (i.e. in between the dams of the study reach; Figure 1), which
423 confirmed a possible limitation due to the size of the river stretch. The role of fragmentation on
424 the limitation of the HR size for rheophilic cyprinids was strengthened by their very limited
425 ability to pass over obstacles (Lucas & Frear, 1997; Ovidio & Philippart, 2002; Weibel & Peter,
426 2013). Further, in fragmented rivers the majority of reproduction movements occurred in the
427 upstream direction (Baras, 1992; Ovidio & Philippart., 2002; Reichard, Jurajda, & Ondračková,
428 2002). This is in line with the roaming cyprinids (more than 70%), that also first moved upstream
429 during the circum-reproduction period. But the few tagged barbel (n=1) and chub (n=3) located
430 upstream of the riprap weir at Km 0, after a long upstream migration (from 1.4 to 12 km), were
431 likely blocked by the dam at Sault-Brenaz. De Vocht and Baras (2005) observed that the HR of
432 barbel in the Meuse River was significantly broader in the highly structured part of the river with

433 continuous availability of suitable habitat for spawning, resting and foraging than in areas with
434 less habitat diversity. Peñáz et al. (2002) also suggested that barbel movements may be linked
435 with the quality and diversity of the habitats available between obstacles within streams. In the
436 Rhône River, the variability in availability of functional habitats (under Le Pichon, Gorges,
437 Baudry, Goreaud, & Boët, 2009; e.g. feeding, shelter, spawning) under the hydropeaking flow
438 regime, needs to be quantified to understand better its role on fish localisation and movements,
439 as it was suggested by Alexandre et al. (2016). However, the HR sizes (0.1 to 35 km) observed in
440 the study reach, although characterized by high artificial flow variability (hydropeaking), were
441 not larger than those recorded by Ovidio et al. (2007) in a less disturbed and smaller river
442 (Ourthe, Belgium). This suggests that HR, especially for barbel and chub, are not river size
443 dependent but more certainly river continuity dependent (i.e. the length of the river without
444 obstacles).

445 Given the limited knowledge about catfish behavioural ecology (Cucherousset et al., 2017),
446 it is difficult to determine if the low median HR with low inter-individual variability (Figures 3
447 and 4) observed reflects an adaptation to a fragmented (in between dams) environment (Crook et
448 al., 2015), such as in the Upper Rhône River, or if this is the typical behaviour of the species,
449 potentially found in other types of less impacted environments within its natural distribution
450 range. Seasonal mobility remained almost unknown (including in their native areas) despite, the
451 species expansion beyond its natural distribution range in Western Europe and potential
452 competition with other native species (Copp et al., 2009; Guillerault et al., 2015).

453 Barbel, chub and catfish demonstrated high inter-season fidelity to certain preferred habitats
454 within the study area, even after long Dn (Figure 3). Site fidelity was also observed for barbel
455 (Britton & Pegg, 2011; De Vocht & Baras, 2005; Ovidio et al., 2007), chub (Allouche et al.,
456 1999), dace (*Leuciscus leuciscus*; Clough & Ladle, 1997), ide (*Leuciscus idus*; Kuliskova,
457 Horký, Slavik, & Jones, 2009; Winter & Fredrich, 2003) and catfish (Brevé et al., 2014; Carol,
458 Zamora, & García-Berthou, 2007), and may be regarded as a valuable behavioural strategy that

459 minimises energy expenditure (Hart, 1986), or to defend territories in the case of the catfish
460 (Slavik, Horký, Maciak, Wackermannová, 2016). In the present study (a study reach three times
461 longer than the study reach of Brevé et al., 2014), site fidelity mostly appeared with the catfish,
462 that tended to change location less often than the other species and that had lower inter-
463 individual heterogeneity mobility patterns (Figure 3). Unlike barbel and chub, catfish are top
464 predators (Copp et al., 2009) and food availability may influence the mobility patterns of the
465 three species (as suggested by Hansen & Closs (2005) for *Galaxias argenteus*) as other
466 behavioural or genetic features (Woolnough et al., 2009). The superior sedentary behaviour of
467 the catfish, yet with a higher IE, may also reflect a lesser need to move to find food resources
468 within the home range. Even under highly variable habitat availability (hydropeaking), cyprinids
469 and catfish seemed to be able to develop cognitive maps of the surroundings, which can be used
470 to navigate home following a journey (Capra et al, 2017), as suggested by Braithwaite and Burt
471 de Perera (2006) and Odling-Smee and Braithwaite (2003). In the present study, 30% (barbel) to
472 44% (chub) of roaming individuals were located in October near (< 1 km) their first localisation
473 point (in April) after $D_n > 5$ km, suggesting that some individuals of each species moved
474 seasonally to reach specific and well known areas of the Rhône River within the scale of the
475 river reach (tens of kilometres; e.g. Peñáz et al, 2002). It seemed less likely that the fish could
476 memorise habitat structure at a larger scale, but travelling dozens of kilometres downstream in
477 seven days before coming back more or less to the same place a few weeks later (Figure 3)
478 requires spatial knowledge of the environment. Catfish appear to be less inclined to long
479 journeys and could take advantage of this situation to exploit its selected habitat more
480 intensively, even in the warmed water plume of the nuclear power plant.

481 Catfish showed higher mobility when the temperature was 15-24 °C and flows were high,
482 unlike the rheophilic cyprinids which tended to move more within the 13-22 °C range, which
483 corresponds to the circum-reproduction temperatures of the three species (Baras, 1995; Copp et
484 al., 2009; Souchon & Tissot, 2012). Slavik, Horký, Bartoš, Kolářová, and Randák (2007) found

485 that catfish movements in spring, autumn and winter differed strongly from the summer when
486 fish were highly active both during the day and night. They observed a strong positive
487 correlation between movements and flow in catfish during the summer, suggesting an attempt to
488 optimise the use of space and food resources that become restricted during low-flow conditions.
489 In this study, neither species moved much between the end of summer and the beginning of
490 autumn, when water temperature and discharge decreased, as already found for barbel and chub
491 (Allouche et al., 1999; Baras, 1992).

492 In terms of habitat use, while barbel preferred multi-channel rapids and chub preferred single
493 lotic channels, catfish did not show specific preferences for morphological units. All three
494 species preferred habitats with large amounts of woody debris, which provide shelters against
495 flow velocity and predators or can be a source of food. Note here that the localisation accuracy
496 did not determine if a fish was hiding in woody debris. Catfish were more often located in the
497 part of the study area that is heated by the nuclear power plant than chub or barbel, which were
498 mainly located upstream of the nuclear power plant. This result supported a previous experiment
499 with fixed acoustic telemetry performed upstream and downstream of the nuclear power plant
500 effluent, and showed that catfish spent more than 50% of their time in the heated zone, whereas
501 chub and barbel used this zone less than 5% of the time (Capra et al., 2017). These results may
502 explain the increase of the catfish populations in the Rhône River, especially considering the loss
503 of lotic habitats in favour of lentic habitats (Olivier et al., 2009), the water heated by the nuclear
504 power plant's effluents and global warming (Daufresne, Roger, Capra, & Lamouroux, 2004;
505 Daufresne & Boët, 2007). Throughout Europe, similar depletion of habitat quality and diversity
506 could be responsible for the expansion of catfish in other similarly disrupted large rivers (Copp
507 et al., 2009; Poulet et al., 2011). For example, Britton et al. (2010) argued that the predicted
508 temperature increases due to global change would benefit catfish, one of the six non-native fish
509 species currently persistent but not established in England and Wales. Ecological niches in the
510 Upper Rhône River are assumed to be not completely saturated by the 45 potential inhabiting

511 fish species (Olivier et al., 2009) because only 37 species were sampled each year on average
512 between 1979 and 1999 (Daufresne et al., 2004) and that this could allow catfish to establish.

513 In conclusion, while remaining coherent with previous knowledge on the behavioural
514 ecology of the barbel, chub and catfish, the results presented here help to understand better how
515 these three species behave and react to environmental changes and habitat modification when
516 tracked simultaneously in the same river. The new active scanning telemetry system was well
517 suited to track the seasonal movements and habitat use of native rheophilic cyprinids (barbel and
518 chub) and non-native catfish simultaneously in the deep, large and fast flowing Upper Rhône
519 River, with higher detection rates and better ease of fish localisation than with radio telemetry
520 methods. The results presented here indicated that catfish seemed to be less constrained by
521 environmental and habitat changes (high temperature, fragmentation, hydropeaking flow regime)
522 in this modified river, by the adoption of more opportunistic and stable behavioural strategies.
523 This may help explain the expanding range of this non-native species, to the detriment of the
524 more exigent native species, which have to deal with the anthropogenic alterations. Assuming
525 rheophilic cyprinids have some ability to adjust their behavioural strategies to habitat constraints,
526 by limiting their migrations in between dams and by avoiding high temperature areas, it would
527 be interesting to assess what are the reasonable limits of habitat modification to maintain their
528 population size and structure and ensure long term persistence in the 35.5 km of the Rhône River
529 in the Bugey area. A priority would be to reconnect the river stretch and maintain sufficient
530 habitat diversity, adapted to the requirements of the native species.

531
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- 777

778 Table 1: Summary of individual length, weight and number of localisations (minimum, mean and
 779 maximum) for the 73 subjects of the three tracked species (barbel, chub and catfish), with at least
 780 ten localisations between April 1st 2010 and October 19th 2010. (n = number of individuals for
 781 each species).

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	n	Total length (mm)			Weight (g)			Number of localisations			
		min.	mean	max.	min.	mean	max.	min.	mean	max.	total
Barbel	37	462	530	650	700	1312	2000	10	22.4	29	828
Chub	23	382	474	536	600	1360	2000	10	19.9	29	457
Catfish	13	640	829	1265	1600	4280	12501	14	22.1	26	287

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785 Table 2: Medians of the individual movement indicators for each species: longitudinal home
 786 range (HR), total travelled net distance (Dnt), mean travelled net distance (\overline{Dn}), maximum
 787 travelled net distance (Dnt), number of Dn > 1 km (Dn1k) and intensity of exploitation (IE) of
 788 the HR (see Figure 4 for the box-plot type representations) and summary of the rank sum tests
 789 comparing the indicators among the three species (p values and the Kruskal-Wallis χ^2 value)
 790

	HR (m)	Dnt (m)	\overline{Dn} (m/7days)	Dnx (m/7days)	Dn1k	IE
Barbel- <i>Bab</i>	3045	7064	333	2148	2	1.98
Chub- <i>Sqc</i>	2355	4625	274	1814	2	2.02
Catfish- <i>Sig</i>	1295	3291	133	868	1	3.26
	p value (KW χ^2)					
	0.064	0.245	0.142	0.123	0.350	0.074
	(5.5)	(2.8)	(3.9)	(4.2)	(2.1)	(5.2)

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794 Table 3: *P* values and sum of ranks of Wilcoxon signed-rank test (for two classes) and *p* value
 795 and Friedman χ^2 of Friedman rank sum test (for three classes) of the spatial distribution of the
 796 localisations of all the individuals of each species for the 29 tracking campaigns within the 500-
 797 m long sections for the three habitat variables (*n tot* = total number of detection for a species). If
 798 $p < 0.05$ ($p < 0.017$ for three classes after Bonferroni adjustment), there was at least one class of
 799 the habitat variable that was more or less used than the other ones which was indicated with the >
 800 and < symbols. In italics, the localisation numbers for each class of each habitat variable are
 801 noted: type of channel (single (n=20 500-m long sections) or multi-channel (n=51)),
 802 morphological unit (Channel (n=46) / Rapid (n=25)), and woody debris density (three classes
 803 with 6 (n=25), 9 (n=20), and > 9 (n=26) woody debris spots within a 500-m long section).

804

Variable (classes)	Barbel	Chub	Catfish
	<i>n tot = 826</i>	<i>n tot = 452</i>	<i>n tot = 287</i>
Multi (1) / Single (2)	< 0.001 (435) 1>2 <i>559/267</i>	< 0.001 (435) 1<2 <i>206/246</i>	0.133 (251) - - <i>91/196</i>
Channel (1) / Rapid (2)	< 0.001 (0) 1<2 <i>284/542</i>	< 0.001 (424) 1>2 <i>348/104</i>	0.460 (251) - - <i>190/97</i>
Woody debris (1/2/3)	< 0.001 (44) 1-2<3 <i>127/99/600</i>	< 0.001 (35) 1<2-3 <i>67/188/197</i>	< 0.001 (18) 1<2-3 <i>68/101/118</i>

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808 Figure Captions

809

810 Figure 1: The study reach was located in the Rhône River, upstream of Lyon, between the dams
811 of Sault-Brénaz (Km0 along the curvilinear axis) and Jons (Km35.5). The main riverbed is
812 shown within a digital elevation model (elevations in m; grey levels) in order to illustrate the
813 reach's 15 m level difference. The limits of the 500-m long sections used for describing the
814 habitat conditions are marked by lines across the main riverbed.

815

816 Figure 2: The two pictures on the left illustrate the boat's equipment (A) and the position of the
817 two hydrophones on either side of the boat (one example of the 30°-hydrophones on B). On D, a
818 copy of the echogram screen is displayed using MarkTags© (hourly files recorded by the
819 starboard hydrophone during a trip). The two parallel lines (white square) show the recording of
820 a tag's sound emission (top and bottom dash). An explanatory diagram (echogram window in C)
821 illustrates the automated selection process for the nearest tag's sound emission (black pointer,
822 NP) located between the first recording (dark grey pointer) and the last recording (light grey
823 pointer). The time and the GPS coordinates of the boat at NP were used to define the fish
824 localisation.

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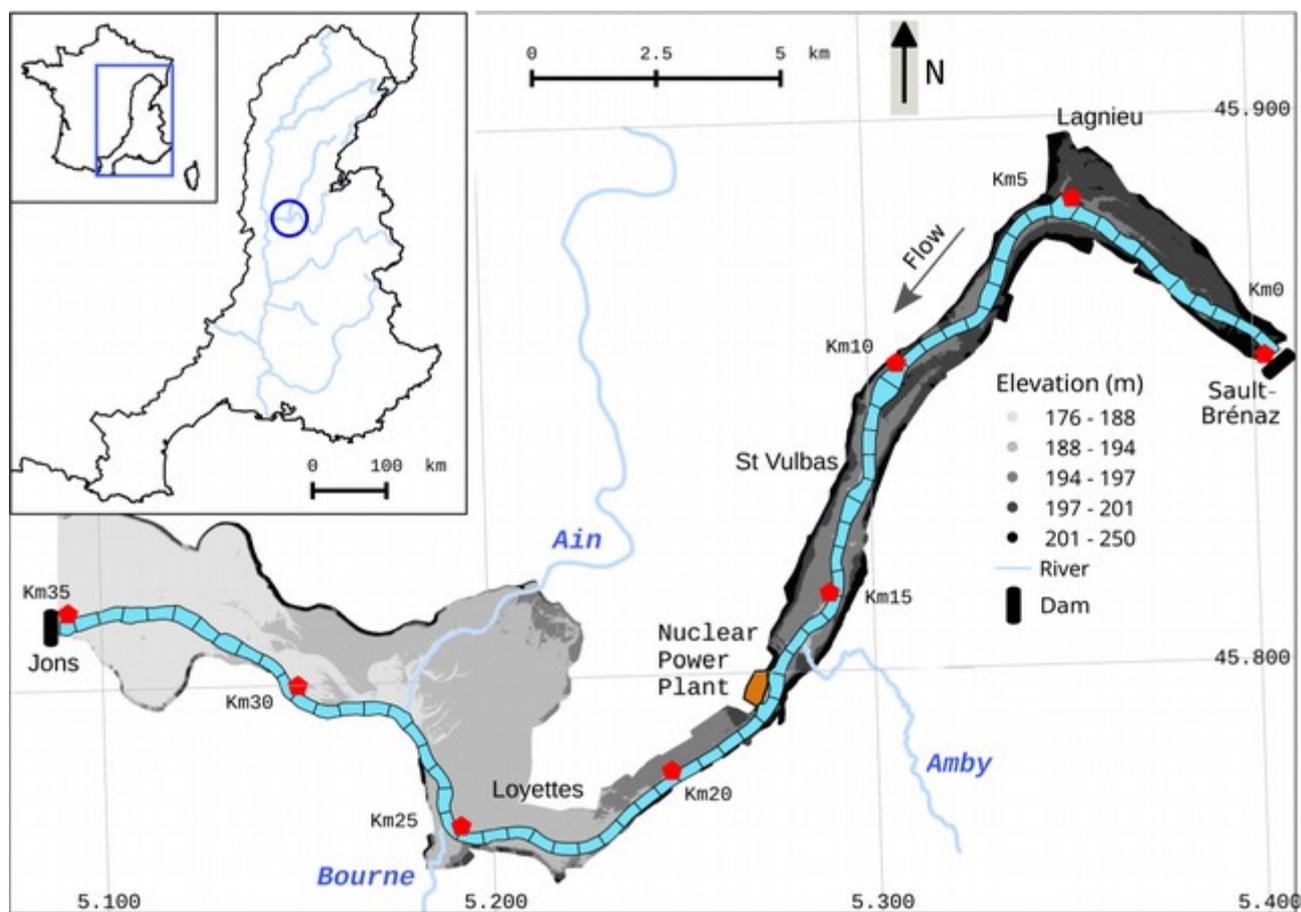
826 Figure 3: Representation of the journeys of the 73 tracked fish selected for analysis between
827 April 1st 2010 and October 19th 2010. Results are presented for each species (barbel, *Bab*, n=37;
828 chub, *Sqc*, n=23; catfish, *Sig*, n=13). The horizontal axis shows the time between March and
829 November 2010. The graphs' vertical axis is the curvilinear coordinate (in km; the origin (Km0)
830 is the upstream part of the study reach; Figure 1) when the fish was located (NP). The first dot
831 corresponds to the fish's capture and tagging location. When there is no capture location noted, it
832 is because the fish had previously been tagged in 2009 (curvilinear coordinate of 2009 tagging
833 location, Km17.5). Below in the fourth graph are shown the timelines of the water temperature

834 (in °C, left outside scale, dash-dotted) and those of the flow (in $\text{m}^3 \text{s}^{-1}$, right outside scale, solid
835 line) with weekly averages, and the tracking duration (grey rectangle).

836
837 Figure 4: Box-plot of the six mobility indicators (HR, $\overline{\text{Dn}}$, Dnt, Dnx, Dn1t and IE of the 73
838 tracked fish identified between April 1st 2010 and October 19th 2010 (see Table 2 for
839 comparisons among species and Table 3 for the total number of localisation for each species).
840 The whiskers were extended to the data extremes.

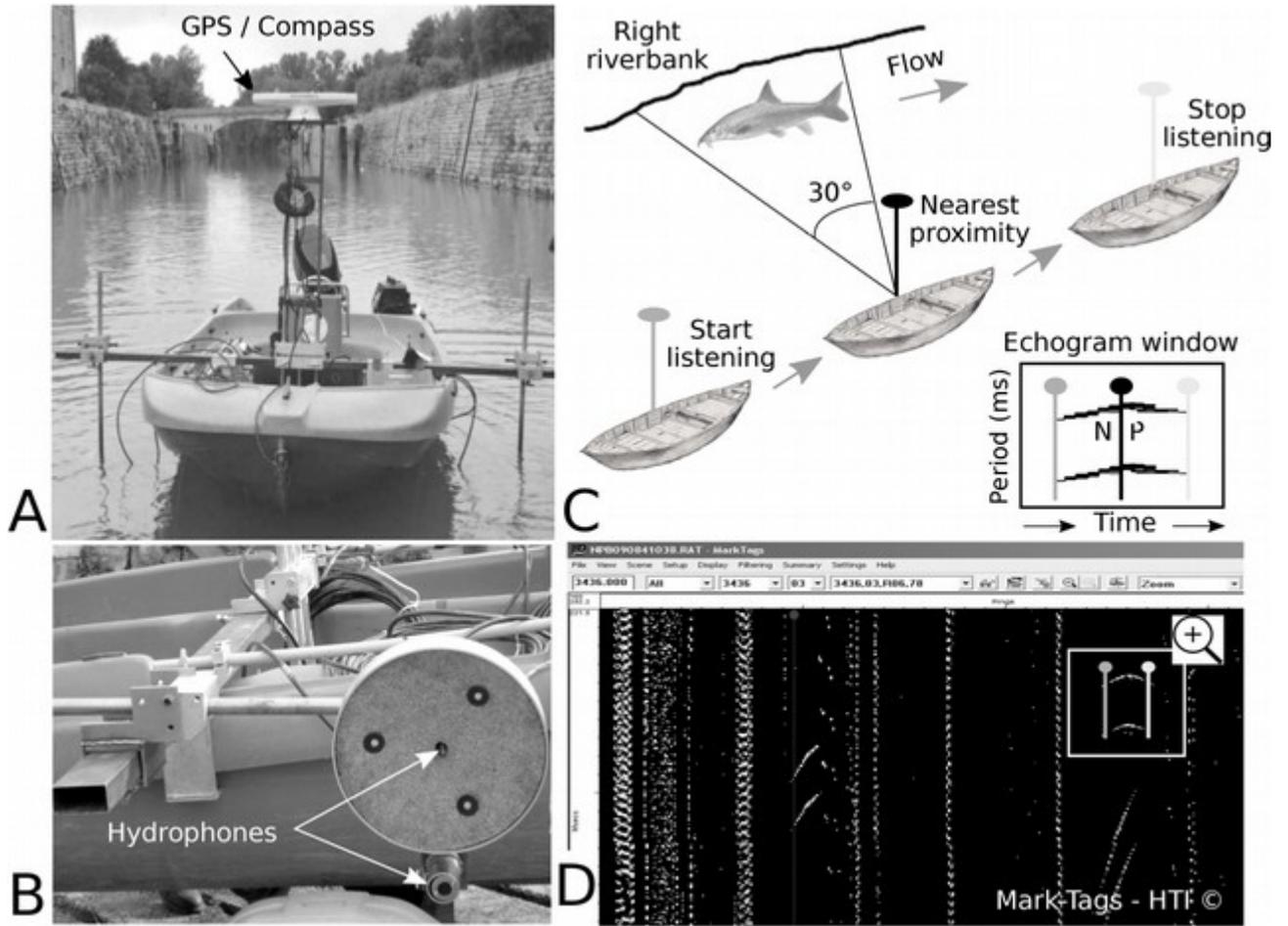
841
842 Figure 5: Bubble charts plotting x = mean temperature values, y = mean discharge values and z
843 values = Dn (size of the circle) between two locations for each species. The shortest Dn, the
844 longest Dn and the number of Dn are given in brackets for each species.

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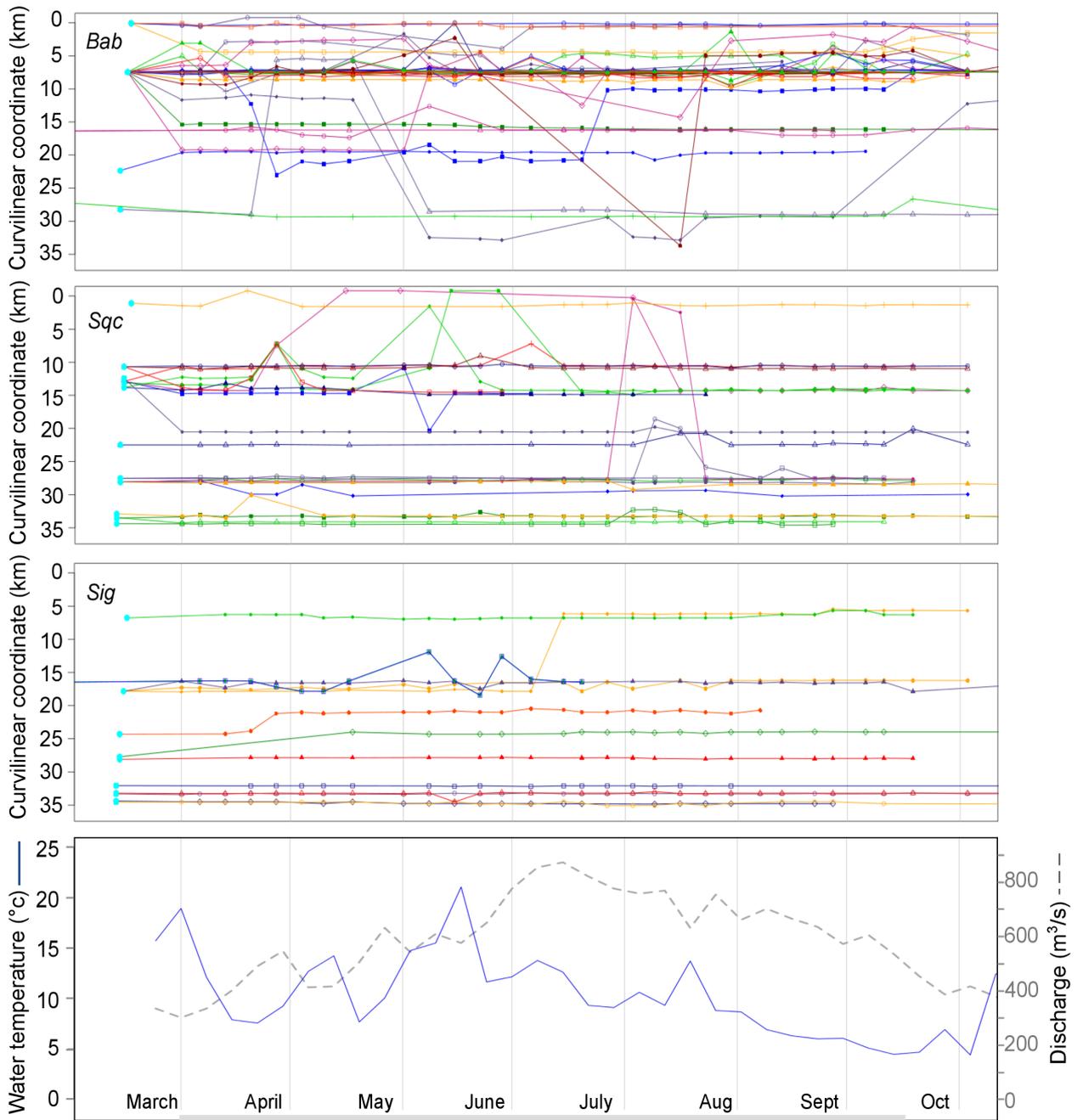


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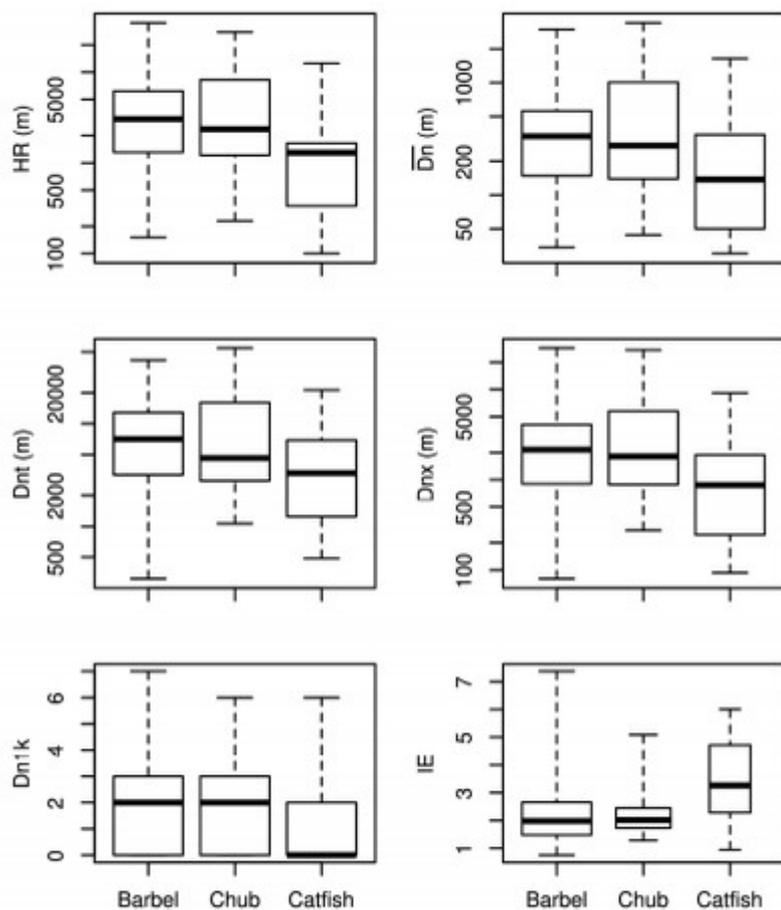
Figure 1



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868 Figure 2

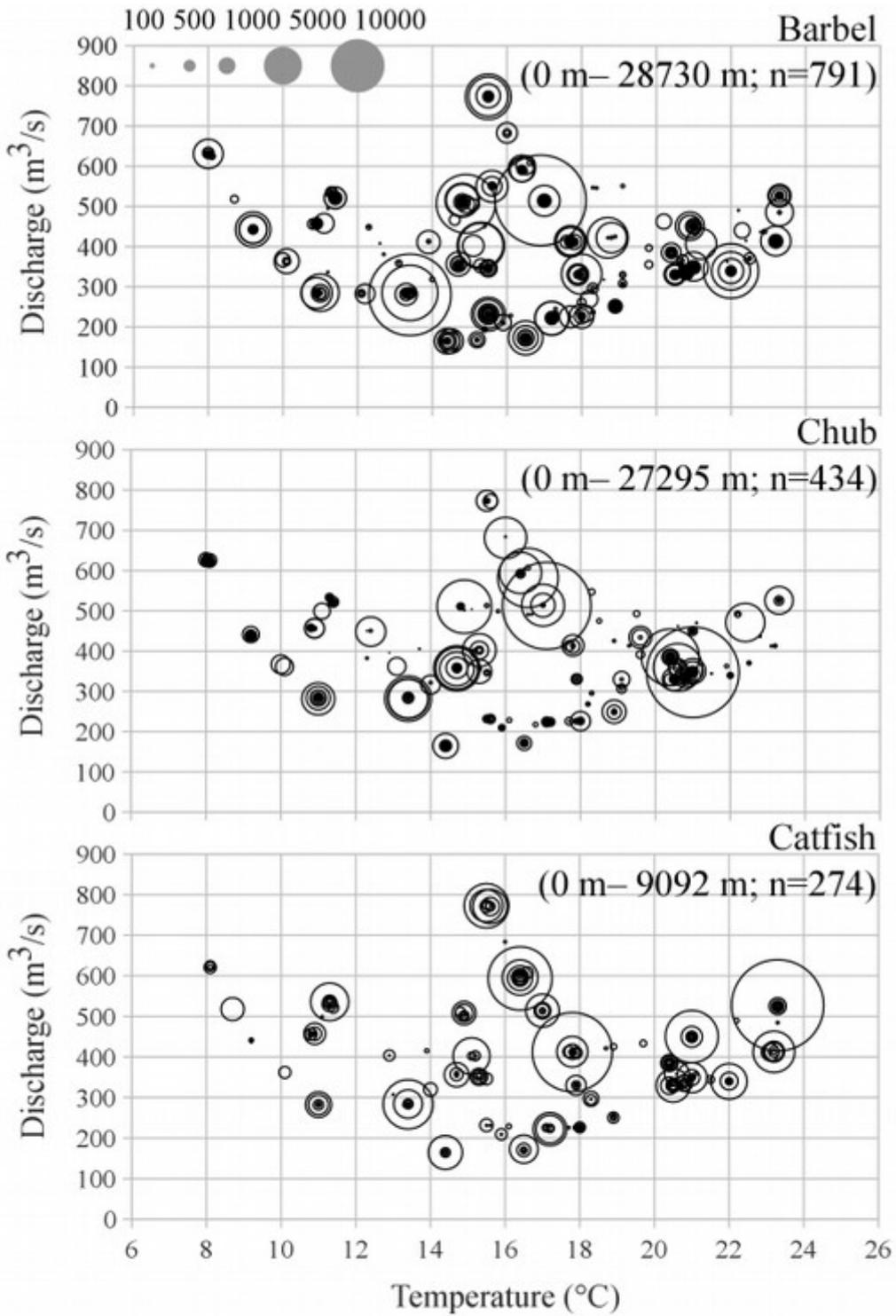


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875 Figure 4

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Figure 5