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

short title: Movement behaviour of fish in a large river

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Abstract

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

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

Introduction

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

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

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

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

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

Methods

Study site

The study reach is a 35.5-km undiverted section of the French Upper Rhône River located north-east of Lyon (Figure 1) between the Sault-Brénaz hydroelectric facility (located upstream; Compagnie Nationale du Rhône - CNR) and the Jons-Cusset hydroelectric facility (located downstream; Électricité De France - EDF). The upstream limit (river kilometer Km 0; 45°51'19.74"N; 5°24'23.40"E) of the study reach is distinguished by an artificial riprap weir (which cannot be crossed by boat). The downstream limit (Km 35.5; 45°46'4.23"N; 4°54'49.90"E) is identified by the dam of Jons. Sault-Brénaz's and Jons-Cusset's hydroelectric facilities cannot be crossed by fish in an upstream direction but downstream passages remains possible through the turbines or spillways. A nuclear power plant located on the right bank of the study reach at Km 17.5 pumps $\approx 100 \text{ m}^3/\text{s}$ to cool its four reactors and discharges warmed-up water (between 7 and 10 °C warmer than the upstream water). The warm water discharge creates a strong transversal temperature difference between the left bank and the right bank (Ginot, Souchon & Roger, 1996; Capra et al., 2011).

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

Capture and tagging

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

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

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

Fish tracking

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

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

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

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

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

Data analysis

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Results

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

Barbel, chub and catfish demonstrated high inter-season fidelity to certain preferred habitats within the study area, even after long Dn (Figure 3). Site fidelity was also observed for barbel (Britton & Pegg, 2011; De Vocht & Baras, 2005; Ovidio et al., 2007), chub (Allouche et al., 1999), dace (*Leuciscus leuciscus*; Clough & Ladle, 1997), ide (*Leuciscus idus*; Kuliskova, Horký, Slavík, & Jones, 2009; Winter & Fredrich, 2003) and catfish (Brevé et al., 2014; Carol, 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

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

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

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

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

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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).

782

	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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784

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	Dnt	$\overline{Dn}$	Dnx	Dn1k	IE
	(m)	(m)	(m/7days)	(m/7days)		
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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Table 3: P values and sum of ranks of Wilcoxon signed-rank test (for two classes) and p value and Friedman χ^2 of Friedman rank sum test (for three classes) of the spatial distribution of the localisations of all the individuals of each species for the 29 tracking campaigns within the 500-m long sections for the three habitat variables (n_{tot} = total number of detection for a species). If $p < 0.05$ ($p < 0.017$ for three classes after Bonferroni adjustment), there was at least one class of the habitat variable that was more or less used than the other ones which was indicated with the $>$ and $<$ symbols. In italics, the localisation numbers for each class of each habitat variable are noted: type of channel (single ($n=20$ 500-m long sections) or multi-channel ($n=51$)), morphological unit (Channel ($n=46$) / Rapid ($n=25$)), and woody debris density (three classes with 6 ($n=25$), 9 ($n=20$), and > 9 ($n=26$) woody debris spots within a 500-m long section).

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>

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.

825

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

(in °C, left outside scale, dash-dotted) and those of the flow (in m³ s⁻¹, right outside scale, solid line) with weekly averages, and the tracking duration (grey rectangle).

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

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

Figure 1

Figure 2

Figure 3

Figure 4

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879 Figure 5