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Multi-year movements of potamodromous cyprinid species within a highly anthropized river assessed using RFID-equipped fishways

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ABSTRACT

Movements of potamodromous fish are poorly understood, especially in large rivers, because studies often focus on fishway evaluation and diadromous species. Here, we assessed the movements of 808 fish of five potamodromous species (Barbel, *Barbus barbus*; Common bream, *Abramis brama*; Nase, *Chondrostoma nasus;* Asp, *Leuciscus aspius* and chub *Squalius cephalus*) over 14 years in a highly anthropized river system, the Rhine River, where hydropower plants were progressively equipped with fishways including RFID antennas. The objectives of the study were 1) to characterize long-term and large-scale individual movement patterns of five potamodromous fish species 2) to assess inter- and intra-specific variations based on quantitative movement metrics and 3) to create a typology of individuals based on their movements. Results showed that, despite high intra-specific variability, the inter-specific differences were strong enough to highlight long-term and large-scale species-specific behaviors. Breams exhibited movements that occurred essentially during spawning migration period and at the reach scale. In contrast, barbels were more active, with more movements outside their spawning migration period, showed more large-scale and downstream movements, and used navigation locks more often than other species. For this species, the maximum distance between the two furthest recorded positions at the basin scale was exceptionally high (max = 155 km). We conclude that potamodromous species undoubtedly perform large-scale movements, which are characterized by both species-specific and common features. Therefore, efforts need to be made to better consider their ecological needs and swimming capabilities when planning and designing effective fishways for the diverse range of species that move within river systems.

1. Introduction

Potamodromous fish species exhibit upstream and downstream movements between reproduction, feeding and refuge habitats within freshwater environments to complete their life cycle or perform their biological functions (Benitez et al., 2018; Lucas and Baras, 2001). The temporal and spatial extents of these movements vary greatly between species, ecological groups and life stages, and also depends on environmental conditions, habitat diversity and fragmentation (Baras, 1992; Benitez et al., 2015, 2022; Lucas and Baras, 2001). Specifically, when these movements are predictable at certain life stages, involve a large proportion of the population and are directed upstream or downstream, they are considered as migrations (Northcote, 1984, 1978).

While the most studied and emblematic migratory species are diadromous ones (i.e. species that migrate between freshwaters and the sea), migration features of potamodromous species, are much less well understood, especially in large rivers (Panchan et al., 2022) even if studies increased in the last 10 years. Among the wide range of purposes for which potamodromous fish move, spawning activity is the best documented. Spawning migrations are performed by adult individuals, are seasonal and usually directed upstream. These movements can display homing to a previously occupied spawning site (i.e., reproductive

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homing, Lucas and Baras, 2001) and post-reproductive homing to original location (Fredrich, 1996; Ovidio et al., 2007; Panchan et al., 2022; Whelan, 1983). They can also involve a large number of individuals, e.g. several thousands of individuals in some large lowland rivers (Zbinden and Maier, 1996), and sometimes occur over long distances (Baras, 1992; Fredrich, 2003; Povž, 1988; Whelan, 1983). Many rheophilic cyprinids (e.g.*, Barbus sp., Chondrostoma sp., Squalius sp. and Leuciscus sp.*) can accomplish long spring migration to find gravel or stony habitats for spawning, either in the main river channel or in tributaries (Baras, 1992; Lucas and Baras, 2001). The spatial extent of the migration can vary from several hundred meters to more than 100 km depending on habitat heterogeneity, river size and longitudinal fragmentation (Benitez et al., 2018; Lucas and Baras, 2001; Panchan et al., 2022): an asp was for example observed over a 166 km distance (Fredrich, 2003). Eurytopic cyprinids like common bream (*Abramis brama*) also show regular shoal movements during spring migration. These movements usually cover relatively short distances (several kilometers up to 25 km; (Lucas and Baras, 2001; Winter et al., 2021)), but some authors reported exceptionally long bream movements of up to 59 km (Whelan, 1983). Movements can also occur in the summer between feeding habitats (e.g., shoal of nase *Chondrostoma nasus* which shows high mobility; (Huber and Kirchhofer, 1998)), which are generally over shorter distances (Philippart and Baras, 1996). Young of the Year (YOY) fish also show diel migrations from off-shore to in-shore areas of lake and rivers to feed at night or from backwaters to main channel at night when dissolved oxygen declines (Lucas and Baras, 2001). Synchronized migrations of juveniles and subadults to lentic habitat to find refuge during periods of high flow, usually in fall or winter, are also observed (Baras and Nindaba, 1999), with a possible homing to a previously occupied area afterwards (Lucas and Baras, 2001). Similar behaviors are observed in summer during periods of low-flow or intense heat to find deeper or cooler habitats (Lennox et al., 2019).

Whether regarding spawning or non-spawning movements, numerous questions remain about their aim, extent, intensity and frequency (Benitez et al., 2015), partly because studies often focus on fishway evaluation and diadromous species (Benitez et al., 2018; Noonan et al., 2012; Roscoe and Hinch, 2010). Long-term and large-scale monitoring of potamodromous species are necessary to obtain such knowledge, as a great majority of studies have been conducted over a short duration and within small rivers (Radinger and Wolter, 2014), with some exceptions that have been conducted over more than one year and in large rivers (e.g. Benitez et al., 2018; De Leeuw and Winter, 2008; Kärgenberg et al., 2022) Such monitoring also requires to include a sufficient number of individuals as a high inter-individual variability in habitat selection and fish movement in potamodromous species has often been observed (Capra et al., 2017; Winter et al., 2021).

In river systems, obstacles, such as dams and weirs, can lead to local extirpation of diadromous species (Limburg and Waldman, 2009) but can also have a strong impact on potamodromous (Penáz and Stouracova, 1991; Waidbacher and Haidvogl, 1998) acting both through the blockage of migration routes and habitat modifications (Lucas and Baras, 2001). To re-establish longitudinal continuity at anthropogenic obstacles, fishways of different nature were developed in the 19th century (Clay, 2017; Silva et al., 2018). At first, they were mostly designed for species with high swimming capacities, which were also generally of cultural and economic importance (e.g., anadromous salmonids) (Noonan et al., 2012; Silva et al., 2018). Since the 1980s, efforts have been made to make fishways more suitable to a wider range of species and life stages (Silva et al., 2018), although selectivity problems may remain (Foulds and Lucas, 2013; Knaepkens et al., 2006; Noonan et al., 2012; Ovidio et al., 2017). As a secondary service, fishways can be used to monitor fish flux, phenology and global characteristics of movements using capture traps or video-counting stations (Benitez and Ovidio, 2018; Benitez et al., 2022, 2015; Legrand et al., 2021). Overall, individual behavior of fish can be assessed with surgically implanted transmitters detected using acoustic hydrophones (Capra et al., 2017; Tétard et al., 2019, 2016), Radio Frequency Identification (RFID) antennas (Benitez et al., 2018; Celestino et al., 2019; De Leeuw and Winter, 2008; Thiem et al., 2013) or radiotracking (Larinier et al., 2005; Ovidio et al., 2007, 2002), within fishways or along river reaches.

RFID and telemetry studies of fish behavior have often focused on fishway overall or passage efficiency and related standardized behavioral metrics (Ovidio et al., 2017). These studies are often conducted on a single site (but see Benitez et al., 2018 for a multi-site case study) and over a short period, usually one or two years. Very few river systems have RFID arrays installed in several successive fishways that have been kept continuously active and functional for a long time, with a large number of tagged fish able to move and be passively detected throughout the river system and during their whole life (but see Benitez et al., 2018)

In this study, we assessed the multi-year movements of five common potamodromous species in a highly anthropized river system, Rhine, where Hydropower Plants (HPPs) were progressively equipped with fishways including RFID antennas. The monitoring of individual movements covers the period 2010–2023. The objectives of the study were 1) to characterize long-term and large-scale individual movement patterns of five potamodromous fish species, 2) to assess inter- and intra-specific variations based on quantitative movement metrics and 3) to create a typology of individuals based on their movements.

2. Materials and methods

2.1. Study area

The Rhine River flows through six countries and, with its 1320 km length and 185,000 km² drainage area, is one of the largest river systems in Europe (Fig. 1). It has been intensely used for freight transport and hydro-electrical production for a long time (24 hydropower plants have been progressively constructed on its main course since 1898). This resulted in a high degree of hydromorphological alteration: straightening and bank stabilization, loss of connectivity with its floodplain, change of runoff dynamics and impairment of ecological continuity (ICPR, 2021).

The upper Rhine River delimitates the Franco-German border and has a mean annual discharge of 1190 $m^3.s^{-1}$ at the Lauterbourg station (Hydroportail, 48°57’29.2"N 8°11’44.9"E). Over a reach of about 160 km, ten run-of-river HPPs are in operation, with discharge capacities ranging from 1100 to 1500 $m^3.s^{-1}$, each associated with a dam and high-capacity locks (60,000 m³ of water in each of the two lock chambers). The downstream end of the study site (Iffezheim HPP) is located about 680 km from the North Sea.

In the upstream part of the study site, at Kembs, the river is partially diverted into the Grand Canal d’Alsace (GCA), where 4 HPPs are in operation. Consequently, a reach of 50 km of old riverbed called the “Old Rhine” (OR) is bypassed from Kembs to the dam of Brisach, with a minimum flow ranging from 52 $m^3.s^{-1}$ in winter to 115 $m^3.s^{-1}$ in summer. Downstream of the “GCA/OR” confluence, the following six HPPs are either of the diversion type, with a bypass reach of 5–10 km downstream of the dam on one side and HPP-lock on the other (Marckolsheim, Rhinau, Gerstheim, Strasbourg), or of the “run-of-the-river” type (Gambsheim, Iffezheim), i.e, with HPP, lock and dam in the same alignment with short channels. The OR is equipped with two secondary HPPs: the Kembs K HPP close to the dam at its upstream end (maximum discharge of 90 $m^3.s^{-1}$) and the Brisach HPP at its downstream end (maximum discharge of 60 $m^3.s^{-1}$).

Over the 160 km of the study river reach, 6 HPPs have been progressively equipped with large fishways for upstream migration, which are all of the pool type with vertical slots, with two of them including a long natural bypass channel (Appendices A and C): Iffezheim (since 2000), Gambsheim (since 2006), Strasbourg (since 2016) and Gerstheim

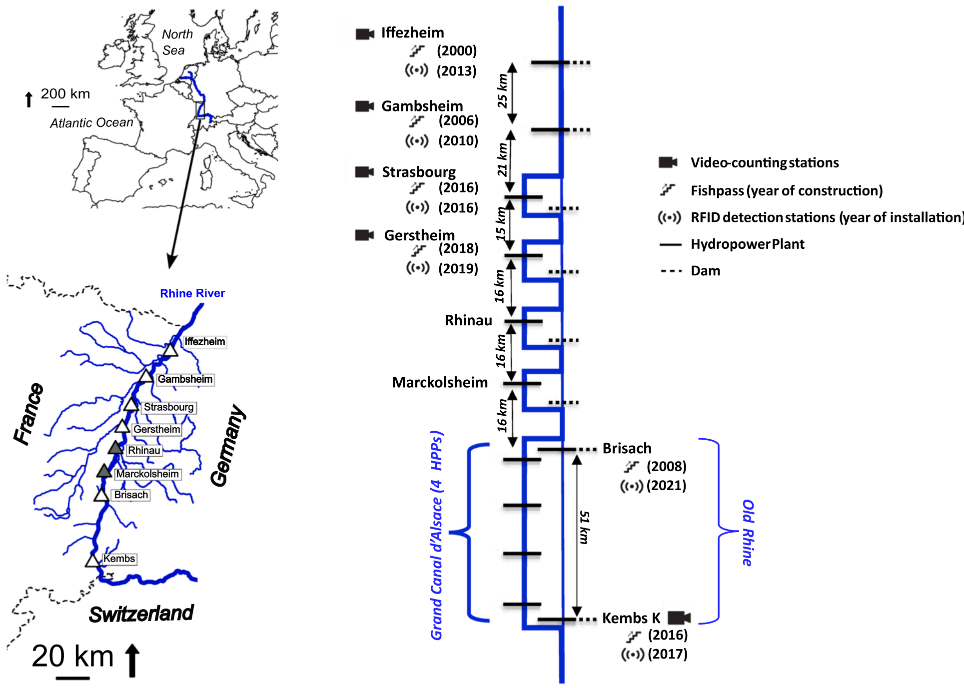

Fig. 1. Top-left map, location of the upper Rhine River in western Europe. Bottom-left map, zoom on the upper study river reach along the French-German border. Triangles indicate hydropowerplant (HPP) along upper and old Rhine River. The color of the triangle indicates if the HPP is equipped with a fishway (white) or not (dark grey) at the time of the study. Right, schematic view of the studied river system.

(since 2018) on the main course of the river; Brisach (since 2008) and Kembs K (since 2016) on the OR. To date, longitudinal continuity was not fully restored over a linear of 48 km between Gerstheim HPP (the distance from Iffezheim in kilometer along the river, hereafter ‘kp’, 61) and Brisach HPP (kp 109). To reach the OR from Gerstheim, fish have to cross Rhinau and Marckolsheim obstructions through navigation locks. Fishways at these two sites are under construction since 2023. For downstream migration protection, only Kembs K and Brisach HPPs are equipped with fine spaced racks (20 mm) associated to bypasses.

2.2. Brief description of the fish community of the upper Rhine River

The fish community of the upper Rhine River can be somehow described as a transition between the “barbel” and the “bream” zone (Huet, 1959). Except for Brisach, all fishways are equipped with a video-counting station. At Gambsheim’s fishway, counts over the 2006–2020 period show a mean number of 16,688 fish individuals passing the fishway each year (42,909 including yellow eels), with a predominance of cyprinids. Aside from the European eel *Anguilla anguilla,* (mean annual number = 26,289 individuals), the most numerous species are: the common bream (*Abramis brama,* mean = 5559), barbel (*Barbus barbus,* mean = 3504), common nase (*Chondrostoma nasus,* mean = 2850), asp (*Leuciscus aspius,* mean = 1734) and common bleak (*Alburnus alburnus,* mean = 1692). Diadromous species such as the Atlantic salmon (*Salmo salar*, mean = 63), seatrout (*Salmo trutta*, mean = 64), allis shad (*Alosa alosa*, mean = 32), sea lamprey (*Petromyzon marinus*, mean = 35) and river lamprey (*Lampetra fluviatilis*, mean = 2) are also observed, but in relatively small numbers.

2.3. Fish detections, captures and behavioral variables

From 2010 to 2021, RFID detection stations (CIPAM®) were progressively installed in the fishways. The detection stations were connected to a variable number of antennae (Appendix A) that were installed along the fishways, with the primary aim of assessing individual behavior and passage efficiency of target species after fishways construction (Tétard et al., 2014). Antennae detection distance and station operating status were regularly checked. Fish passing by the antennae are recorded and each detection is associated with a date and time. In the present study, the detection data of all sites were gathered to examine the pluriannual behavior of individuals of five fish species along the upper Rhine River: barbel, common bream, nase, asp and chub (*Squalius cephalus*). These species were the five most common species caught in the fishway trap (see below “2–4 fish tagging and release campaigns” section for more details). This dataset was complemented by one-time capture data from recreational or professional fishermen, with each capture being associated with a location, date and time.

The following behavioral variables were calculated for each detected fish, based on all detections and captures over the period 2010–2023 (last dataset extraction on 4th July, 2023):

- **Outside_migration**; boolean variable indicating whether or not the fish has ever been detected outside the March-June time period, which delimitates the spawning migration period of the five studied species (Keith et al., 2020);
- **Maximal longitudinal amplitude (Dmax, in river km)**; the distance between the two furthest recorded positions (detections or captures by fishermen);
- **Mean progression time (in days/river km);** as defined in Benitez et al. (2018), metric obtained by calculating the ratio of the time (in days) to the distance (in river km) between the last detection at a fishway and the first detection at the following upstream fishway. For fish that exhibited several inter-sites upstream movements, the mean progression time was calculated;
- **Passage occurence**; variable with 3 modalities: *no_passage/1_passage/2 + _passages*, indicating whether the fish has never/once/several times passed a site by a fishway;
- **Navigation lock use**; boolean variable indicating whether or not the fish has ever used a navigation lock. The use of a navigation lock by a fish was confirmed either by detection or capture upstream of a site not equipped with a fishway (i.e. Rhinau and Marckolsheim HPPs), or by detection of a fish at a given site and no detection, or detection

without passage, at the downstream site. To prevent any misinterpretation (e.g. a missed detection), the assignment of a 'lock passage' in the latter case was only made when the RFID array consisted of at least 5 detection zones along the fishway, i.e., at all sites except Brisach and Kembs (no lock at Kembs, only 3 antennas at Brisach, one at each entrance and one at the exit);

- **Site downstream movement**; boolean variable indicating whether or not individual fish has ever been detected downstream of a fishway after passing it;
- **Reach downstream movement**; boolean variable indicating whether or not the individual was detected at least once at a site located downstream of a site where it was previously detected, thus indicating downstream movement;
- **Movement activity index**; variable with 4 modalities: *VLF_activity/LF_activity/MF_activity/HF_activity* ("very low", "low", "medium" and "high" frequency activity, respectively) was calculated either over the last five years (2019–2023) for the fish that were released before 2017 or over the last three years (2021–2023) for the fish that were released in 2021 (see Table 1 for more details on release campaigns). To compute this variable, we first calculated the percentage of years in which the fish was detected (e.g. a fish detected one year out of five gets a value of 20 %) before transforming it arbitrarily into four classes: *VLF_activity* for 0 %, LF_activity for 0–40 %, MF_activity for 40–80 % and HF_activity for 80–100 %;
- **Mean detection duration during migratory period (in days)**; the mean number of days between the first and last detection during the migratory period (March-June) calculated over all the years in which the fish was detected;
- **Mean detection duration outside migratory period (in days)**; the mean number of days between the first and last detection outside migratory period (July-February) calculated over all the years in which the fish was detected. The two latter variables aimed at characterizing the level of activity of an individual during or outside migratory period in terms of time span.

2.4. Fish tagging and release campaigns

Several fish tagging campaigns were conducted for site-specific behavioral studies (Table 1) between 2011 and 2021. The trap located within the Gambsheim's fishway was used to capture the majority of the fish (92.4 %); the others were caught by electro-fishing (HERON®) in the natural bypass channel of Gerstheim fishway in 2021. The Gambsheim's trap consists of a capture cage (3 ×1.9 ×2.3 m) in which fish are trapped with an inverted funnel. During each tagging campaign, the trap was monitored every morning. Of all the fish individuals captured, a total of 1146 individuals belonging to the five most common fish species (257 barbels, 349 common breams, 338 nases, 156 asps and 46 chubs) were anesthetized in a solution of 10 %-Eugenol at 0.4 $ml.l^{-1}$, identified, measured (± 1 mm, fork length), weighed (± 1 g) and tagged with a PIT-tag (Texas Instruments, HDX, 134.2 KHz, 32 *2 mm and 0.9 g) injected subcutaneously into the dorsal zone. The surgical procedure lasted a few seconds and was carried out by a team of trained and experienced operators from the Rhin-Meuse Migrateurs association (under the A-67–350–3 agreement). After tagging, the fish were kept in a pool with water from the Rhine, where they recovered and swam normally after a few minutes. Fish were mostly released between 60 and 200 m downstream of different fishways, except for two batchs of fish in 2016 and 2017 that were released upstream of Gambsheim fishway. 89 % of fish (1025/1146) were tagged and released between 1st March and 30th June.

2.5. Data analysis

Firstly, the multi-year periodicity of daily fish detections at all sites equipped with RFID arrays was compared with fish counts at the four most downstream video-counting stations (Iffezheim, Gambsheim, Strasbourg and Gerstheim) to check if multi-year movements of detected fish meet the periodicity of fish counting. The counting and detections per species were summed by julian day over the 2006–2022 period.

Secondly, in order to analyse data at multi-species scale, the multi-year movements of individuals assessed by RFID were qualitatively analysed by comparing individual movement patterns and assigning them to a group of movement patterns according to similarity in behavior based on amplitude, direction and recurrence of movements. The assignment of individuals was made independently by three operators, resulting in high congruency between operators (>95 %). The final assignment of the < 5 % of individuals whose assignment differed between operators was decided by the three operators collectively.

Thirdly, we analysed inter-specific variations in multi-year movement variables. The influence of species identity on the quantitative movement metrics (i.e., Dmax, mean progression time, mean detection duration during migratory period and mean detection duration outside migratory period) was tested using the non-parametric Kruskal-Wallis test (because of the non-normality of the data). When the Kruskall-Wallis test was significant, we examined pairwise differences between species using a post-hoc Dunn's test.

Finally, to define a typology of movement behaviors, we used Multiple Correspondence Analysis (MCA), which allows to illustrate the most important relationships among the modalities of categorical response variables (Sourial et al., 2010), followed by a Hierarchical Clustering on Principal Components (HCPC). These two analyses were run using the *FactoMineR* R package (Lê et al., 2008). Before performing

Table 1
Number of fish released by release site and year. The minimum, median and maximum size of all fish of each species are also provided. kp = 'kilometric point', the distance from Iffezheim in kilometer along the river.

Species	Number of tagged fish by release site and year (% of individuals of the species)						TOTAL	Size (mm)		
	Downs. Gamb (kp=24.5)	Downs. Gamb (kp=24.5)	Upstr. Gamb (kp=25)	Upstr. Gamb (kp=25)	Downs. Stras. (kp=46)	Downs. Gerst. (kp=61)				
	2011	2012	2016	2017	2017	2021		Min.	Med.	Max.
Barbel (*Barbus barbus*)	71 (27.7 %)	38 (14.8 %)	/	35 (13.6 %)	51 (19.8 %)	62 (24.1 %)	**257**	248	600	902
Common Bream (*Abramis brama*)	48 (13.8 %)	77 (22 %)	2 (<1 %)	35 (10 %)	86 (24.6 %)	101 (28.9 %)	**349**	400	490	700
Nase (*Chondrostoma nasus*)	/	63 (18.6 %)	30 (8.9 %)	4 (1.2 %)	84 (24.9 %)	157 (46.4 %)	**338**	290	440	590
Asp (*Leuciscus aspius*)	/	9 (5.8 %)	/	28 (17.9 %)	24 (15.4 %)	95 (60.9 %)	**156**	250	559.5	785
Chub (*Squalius cephalus*)	/	12 (26.1 %)	/	13 (28.3 %)	/	21 (45.6 %)	**46**	190	462	530
TOTAL	**119**	**199**	**32**	**115**	**245**	**436**	**1146**			

the MCA, the quantitative variables Dmax and Mean detection duration during migratory period were transformed into classes. Mean progression times and Mean detection duration outside migratory period variables had to be removed from the MCA because of too many missing data. As Dmax is derived from punctual detections between sites with a fixed distance, a new qualitative variable called "Number of river reaches travelled" was created. This variable had three modalities: "0" (detection at a single site), "1reach" (Dmax = 0–26, 25 river km being the maximum distance of a single reach, i.e. between Iffezheim and Gambsheim) and "2reachs+ " (a distance of at least two reaches between the two most distant positions). The variable Mean detection duration during migratory period was transformed into three classes based on quartile distribution (Short duration for values <1st quartile; Medium for values >1st quartile and <3rd. The dataset used for the MCA contained 808 observations of 9 variables:

- "**Species**" (with possible modalities = *Barbel / Bream / Nase / Asp / Chub*);
- "**Outside migration**" (*Detection_outside_migratory_period / No_detection_outside_migratory_period*);
- "**Passage occurrence**" (*no_passage / 1_passage / 2 +_passages)*;
- "Navigation Lock Use" (*Lock_use / No_lock_use*);
- "**Site downstream movement**" (*Site_downstream_movement / No_site_downstream_movement*);
- "**Reach downstream movement**" (*Reach_downstream_movement / No_Reach_downstream_movement*);
- "**Number of river reaches travelled**" (*0_reach / 1_reach / 2 +_reaches_travelled*);
- "**Activity index**" (*VLF / LF / MF / HF_activity)*;
- "**Mean detection duration in migratory period**" (*Short / Medium / Long_migration_activity_duration*);

An imputation of missing value (46 values representing 0.6 % of the dataset) was performed with the missMDA package (Josse and Husson, 2016). The uncertainty associated with the imputation of missing values was checked to ensure that it did not bias the analysis. To avoid biasing the analysis towards interspecific classification, we defined 6 active variables ("Outside migration", "Site downstream movement", "Reach downstream movement", "Number of river reaches travelled", "Activity index" and "Mean detection duration in migratory period") and 3 illustrative ones ("Species", "Passage occurrence" and "Navigation lock use") in the MCA.

Following MCA, the HCPC was performed using Ward's criterion to compute the hierarchical clustering on the selected principal components (n = 5). The number of clusters was obtained using k-means clustering (Lê et al., 2008).

All statistical tests were performed using the *ggplot2*, *ggpubr*, *Addcluster2biplot*, *missMDA*, *FactoMineR* and *factoextra* packages of the R software (R Development Core Team, 2018).

3. Results

3.1. Multi-year periodicity of fish counts and detections

The multi-year daily fish counts recorded at the 4 most downstream video-counting stations showed species-specific patterns of activity over the year. All species displayed an activity peak in spring centered on April-May except for nase for which the peak occurred earlier in March-April (solid black line, Fig. 2). We found different durations for the main activity period (defined as 90 % of fish counts between the 5th and 95th percentiles) depending on the species: 16th April-5th November for barbel (203 days), 10th April-7th September for bream (150 days), 17th March-23rd August for nase (159 days), 7th April-16th September for asp (162 days) and 10th March-5th October for chub (209 days). Nases

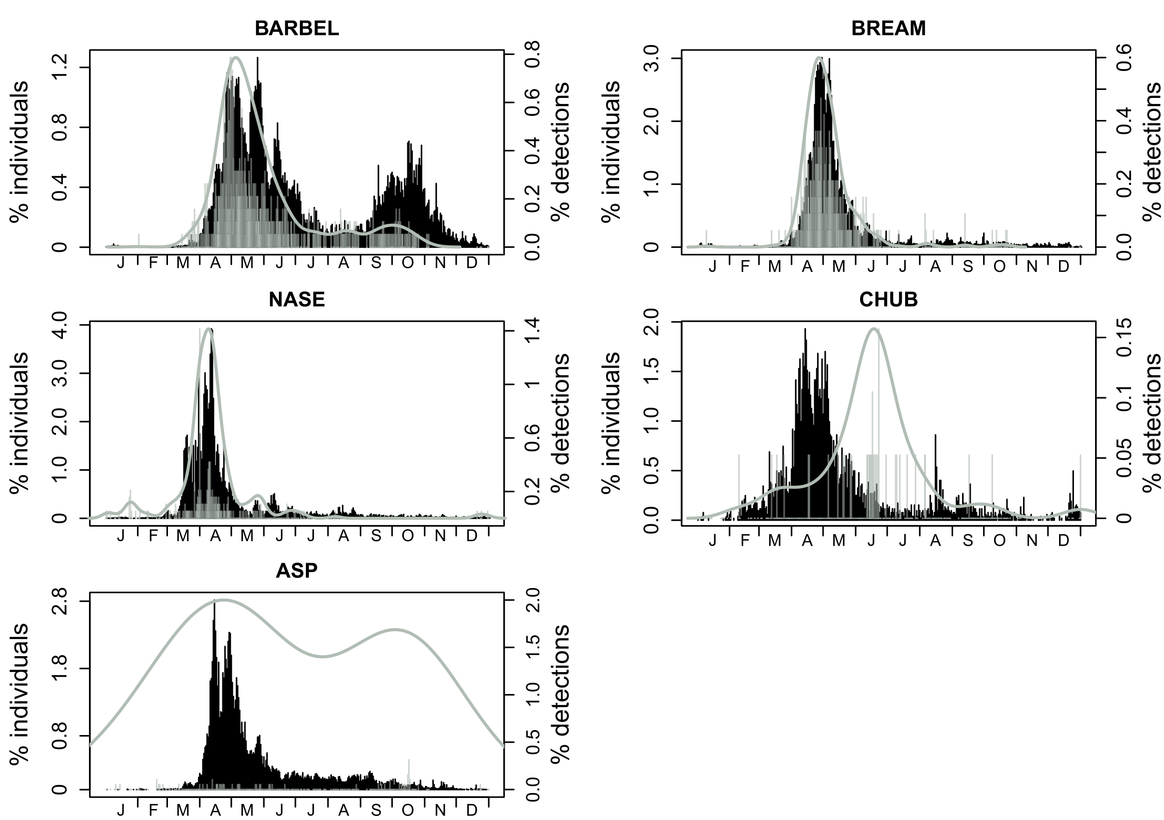

Fig. 2. Multi-year distribution of video-counting and RFID detections from all sites (4 video-counting stations and all RFID stations): daily % of total video counts (black vertical bars), daily % of total RFID detections (grey vertical bars) and density function with adj = 1.5 (solid grey line) of total RFID detections. Daily values were cumulated over all the years available.

and chubs become active earlier than other species. Barbels, which showed a second activity peak in fall between September and November and chubs, which showed an extended activity from late summer to early winter with a small peak in late summer, have the longest period of activity. Breams and nases were less active outside the spring migration peak than other species.

Overall, the main patterns of activity were consistent between video counts and RFID detections (Fig. 2), except for chub and asp. For these two species, the number of RFID detections was not sufficient to obtain representative patterns of activity throughout the year, unlike the video counts.

3.2. Individual movement patterns

We identified 7 groups of individual movement patterns, which were defined based on all detections of 808 fish individuals, possibly over several years (Fig. 3 and Table 2). These groups are described below, sorted by decreasing frequency of occurrence in our dataset. At the time of the study, 338 tagged individuals were still not detected (29.5 % of all tagged individuals).

3.2.1. Pattern A: ascending individuals detected only at one fishway

This pattern is characterized by detections in the fishway of the release site shortly after release (i.e., within the same year for fish released in spring or at the latest, the year after, for fish released in fall), which may or may not have resulted in a successful passage, with no further detections in subsequent years. The individual of common bream shown as an example on Fig. 3 was released downstream of Gambsheim fishway in 2012, passed it the same year, and was never detected afterwards. This pattern concerned 51.9 % of all detected individuals.

3.2.2. Pattern B: ascending individuals with at least one fishway crossed

This pattern is characterized by multi-year detections in the fishway located directly upstream of the release site and with at least one successful passage. The individual of barbel shown on Fig. 3 was released in 2012 and successfully crossed Gambsheim's fishway the same year. The next year, it was again detected downstream of Gambsheim but no successful passage was observed this year. It was again detected downstream of Gambsheim in 2014 and successfully passed Gambsheim's fishway for the second time. This pattern concerned 14.7 % of all detected individuals.

3.2.3. Pattern C: multi-year ascending individuals with no fishway crossed

This pattern is characterized by multi-year detections in the fishway located directly upstream of the release site with no successful passage detected. The individual of chub shown on Fig. 3 was detected several times from 2021 to 2023 at the Gerstheim's fishway without successfully crossing it. This pattern concerned 14.6 % of all detected individuals.

3.2.4. Pattern D: ascending individuals with at least one reach crossed

This pattern is characterized by individuals detected at two different sites, whether in the same year or not, moving unidirectionally upstream. These individuals typically cross the reach between two successive HPPs, without necessarily crossing the most upstream site. The individual of barbel shown on Fig. 3 was released downstream of Gambsheim, passed it, crossed the river reach between Gambsheim and Strasbourg and was finally detected in the Strasbourg fishway without successfully passing it, all of which occurred in 2017. This individual was not detected in subsequent years. This pattern concerned 11 % of all detected individuals.

3.2.5. Pattern E: individuals showing both ascending and descending movements

Similar to pattern D, pattern E is characterized by individuals being detected at two or more different sites, but with the difference of exhibiting both upstream and downstream movements. Upstream and downstream movements may occur in the same year or over several years, but detections are generally observed over several years. The individual of common bream shown on Fig. 3 was released downstream of Gambsheim in 2012 and was detected in its fishway in 2012 and 2013, without successfully passing it. It was detected again at Gambsheim in 2015, but this time passed it successfully. It was then detected downstream of Iffezheim (the most downstream of the HPPs studied) in 2016 and successfully passed it that year. In 2017, it was detected again at Gambsheim without passing it successfully. It finally successfully passed Gambsheim and then Strasbourg fishways the following year in 2018. This pattern concerned 3.3 % of all detected individuals.

3.2.6. Pattern F: long-distance ascending individuals

This pattern is characterized by individuals detected at three or more different HPPs, moving unidirectionally upstream. This pattern includes individuals with the greatest longitudinal amplitude that very often used navigation locks to cross sites. The individual of barbel shown on Fig. 3 was released downstream of Strasbourg in 2017 and was first detected downstream of Gerstheim in 2020. As no successful passage of the Strasbourg fishway was detected, it likely used navigation locks to cross it. It finally passed Kembs fishway 99 km upstream one year later in 2021, which indicates that this individual likely crossed at least two additional navigation locks (Rhinau and Marckolsheim HPPs were not equipped with a fishway, Brisach fishway was not yet equipped with RFID station). This pattern concerned 3.2 % of all detected individuals.

3.2.7. Pattern G: descending individuals

This pattern is characterized by detection(s) in a single year in a fishway (with or without successful passage) located downstream of the release site. The individual of nase shown on Fig. 3 was released downstream of Gerstheim in 2021 and only detected once in Strasbourg fishway shortly afterwards. This pattern concerned 1.6 % of all detected individuals.

3.3. Inter-specific variations in multi-year quantitative movement metrics

The distance (km) between the two furthest recorded positions (Dmax) was significantly different between species (Kruskal-Wallis test, $p < 0.001$). Barbels had the longest Dmax with distances significantly greater than all species except for chubs (see pairwise comparisons using Dunn's tests in Table 3 and Fig. 4). Some barbels exhibited very long Dmax: of all the individuals with a Dmax > 46 km (i.e. having crossed more than 2 river reaches), 77 % were barbels (10/13 individuals), and all the individuals whose detections covered more than 100 km of river (up to 155 km) were barbels (6 individuals). Mean progression time between two successive HPPs was significantly different between species (Kruskal-Wallis, $P < 0.05$), although pairwise comparisons showed no significant differences between each pair of species. The mean time span between first and last detections during migratory period was significantly different between species (Kruskal-Wallis, $p < 0.001$). Barbels showed longer periods of activity than breams, asps and nases, while breams and nases showed longer periods of activity than asps (Table 3; Fig. 4). Finally, the mean duration between first and last detections outside the migratory period was significantly different between species (Kruskal-Wallis, $p < 0.001$). Chubs had a longer period of activity than all other species except for barbels and breams had a shorter period of activity than barbels and nases (Table 3; Fig. 4).

3.4. Typology of individuals based on migratory behavior

The best MCA model included 6 active variables (*Activity index, Number of River reaches travelled, Outside migration, Site downstream movement, Reach downstream movement and Mean detection duration during migratory period (qualitative))* and 3 illustrative variables (*Species, Passage occurrence and Navigation lock use)* that are synthetized by

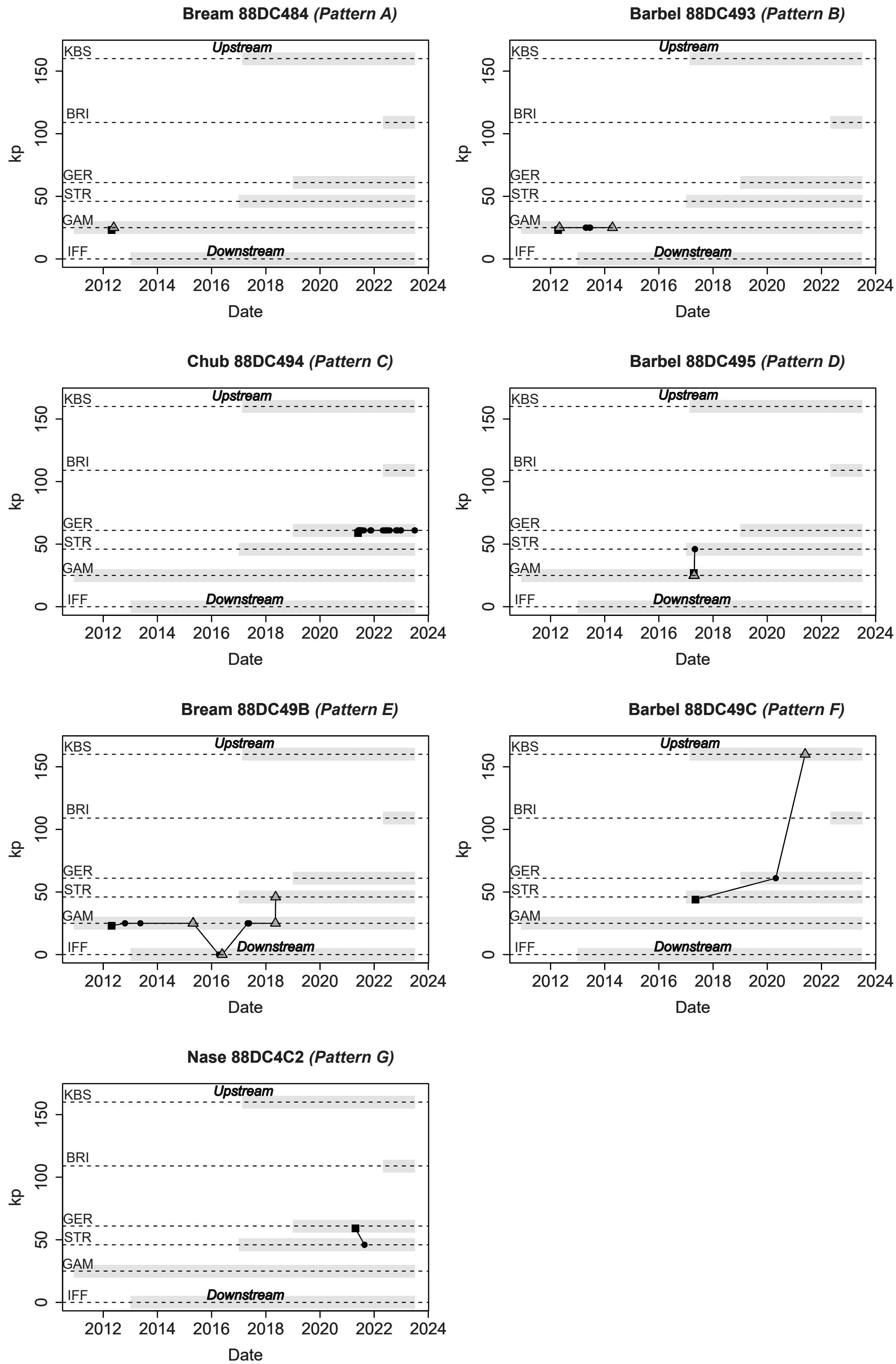

Fig. 3. Movement patterns of seven individuals observed from 2011 to 2023 illustrating the different groups of patterns (A to G) that have been identified. Brief description of the patterns: A = ascending individuals detected only at one fishway, B = ascending individuals with at least one fishway crossed, C = multi-year ascending individuals with no fishway crossed, D = ascending individuals with at least one reach crossed, E = individuals showing both ascending and descending movements, F = long-distance ascending individuals, G = descending individuals. The position of the equipped fishways is represented with horizontal dashed lines, and the period of activity of their respective RFID antennas are indicated with grey shading. Black squares indicate the release site of the individual, black circles indicate detections and grey triangles indicate successful fishway passage. Kp [kilometric point] (Y-axis) = relative distance (in river km) to Iffezheim, the most downstream of the HPPs studied.

Table 2
Number of individuals and species showing each movement pattern and associated frequency of occurrence in the RFID dataset. Brief description of the patterns: A = ascending individuals detected only at one fishway, B = ascending individuals with at least one fishway crossed, C = multi-year ascending individuals with no fishway crossed, D = ascending individuals with at least one reach crossed, E = individuals showing both ascending and descending movements, F = long-distance ascending individuals, G = descending individuals.

Pattern	Number of individuals	Number by species					Overall Frequency	Frequency among all detected individuals
		Barbel	Bream	Nase	Asp	Chub		
Never detected	338	24	85	143	74	12	29.5 %	/
A	419	109	136	96	64	14	36.6 %	51.9 %
B	119	38	39	33	/	9	10.4 %	14.7 %
C	118	26	43	37	10	2	10.3 %	14.6 %
D	89	34	32	14	3	6	7.8 %	11 %
E	27	9	9	7	2	/	2.3 %	3.3 %
F	23	15	2	3	/	3	2 %	2.9 %
G	13	2	3	5	3	/	1.1 %	1.6 %
TOTAL	1146	257	349	338	156	46	100 %	100 %

Table 3
Median [minimum – maximum] values of the 4 quantitative movement metrics calculated on all individuals of each species detected at least once. Only the individuals presenting suitable detections were considered in the calculation of each metric (e.g., mean detection duration outside migratory period was calculated only on individuals detected at least once outside the migratory period). The two last columns show results of the Kruskal-Wallis and pairwise comparisons tests. BAR = barbel; BRE = bream; NASE = nase; ASP = asp; CHUB = chub.

Metric	**Median value [min – max]**					**Kruskal-Wallis test**	**Pairwise comparisons (Dunn's test)**
	Barbel	**Bream**	**Nase**	**Asp**	**Chub**		
Dmax (km)	0 [0–155]	0 [0–46]	0 [0–48]	0 [0–36]	0 [0–48]	$p < 0.001$	BAR-BRE ($p < 0.05$)
Number of individuals	*233*	*264*	*195*	*82*	*34*		BAR-ASP ($p < 0.01$) BAR-NASE ($p < 0.01$)
Mean progression time (d/km)	0.4 [0.1–23.3]	0.7 [0.1–18]	0.8 [0.1–38.3]	0.1 [0.1–0.3]	0.4 [0.1–7.8]	$p < 0.05$	All pairwise comparisons were non-significant ($p > 0.05$)
Number of individuals	*36*	*31*	*20*	*3*	*7*		
Mean detection duration during migratory period (d)	7 [0–58.4]	1.5 [0–76]	1.4 [0–106.5]	0.38 [0–49]	3.6 [0–41.8]	$p < 0.001$	BAR-BRE ($p < 0.001$) BAR-ASP ($p < 0.001$) BAR-NASE ($p < 0.001$) BRE-ASP ($p < 0.001$) ASP-NASE ($p < 0.05$)
Number of individuals	*224*	*259*	*175*	*73*	*34*		
Mean detection duration outside migratory period (d)	14 [0–96.4]	0.1 [0–26.3]	1.1 [0–157]	0.8 [0–23.7]	36.6 [0.1–144.2]	$p < 0.001$	BAR-BRE ($p < 0.001$) BRE-CHUB ($p < 0.001$) BRE-NASE ($p < 0.05$) ASP-CHUB ($p < 0.01$) CHUB-NASE ($p < 0.05$)
Number of individuals	*74*	*21*	*52*	*16*	*13*		

species in Appendix B.

The HCPC analysis, performed on the outputs of the MCA yielded 5 clusters (Appendix D, Table 4). Most individuals belonged to cluster 1 (47.4 %), 20.2 % to cluster 2, 11.4 % to cluster 3, 14.2 % to cluster 4 and 6.8 % to cluster 5. The first cluster is mainly characterized by individuals that have a very low activity in frequency and usually for a short time. These individuals were detected almost exclusively at one site (99.2 % of them) that they passed in majority through the fishway (62.7 % of them passed one site, no lock passage was observed in this group). The individuals in the first cluster showed very few downstream movements and almost all their detections occurred during the migratory period (only 15.7 % of them were also detected outside the migratory period). The common bream is the indicator species of this cluster (54.5 % of the bream individuals of the dataset, 37.6 % of all individuals in this cluster were bream). Cluster 2 is mainly characterized by individuals that have a low activity in frequency (98.8 % of them and 69.1 % of the individuals that have this modality are in this cluster). They were active for a medium duration and were detected almost exclusively at one site (96.9 % of them) with an over-expression of the "no_passage" modality (50.3 % of individuals in this cluster vs. 39.2 % for the whole dataset). Nase and asps are the two indicator species of this cluster (33.7 % and 14.7 % of nases and asps, respectively; and almost one third of the individuals of each of these species are in this cluster). Cluster 3 is characterized by more active individuals in frequency (72.8 % of them have a medium frequency activity), usually at one site (92.4 % of them) with an important proportion of downstream movements (38 % of them, 55.6 % of all individuals in the dataset exhibiting downstream movements) and with detections outside the migratory period (47.8 % of them). Cluster 4 is mainly made up of individuals that have crossed one reach (86.1 % of the "1-reach" individuals in the dataset are in this cluster, 91.3 % of the individuals in this cluster crossed one reach) and that have shown reach downstream movements (i.e. detected at a site after having been detected at an upstream site; 79.4 % of the "Reach downstream movements" individuals of the dataset are in this cluster) and site downstream movements (i.e. detected downstream of a fishway after having passed it; 31.7 % of site downstream movements of the dataset). These individuals were often active for a long time (47 % of them) and during the migratory period (87.8 % of them showed no movement outside migratory period). The modality « 2 + _passages » was also over-expressed in this cluster (40.9 % of individuals of the dataset). Finally, cluster 5 regroups the most active and explorer individuals ("2reachs+", "HF activity" and "lock" are over-expressed modalities in this cluster). These individuals were usually active for a long time (63.6 % of them) and were detected outside the migratory period (41.8 % of them). Barbel is the indicator species of this cluster (61.8 % of individuals in this cluster are barbels).

The classifications of movement patterns made either visually (patterns A-G) or using HCPC (clusters 1–5) was partially congruent but not redundant, as shown by the contingency table (Appendix E).

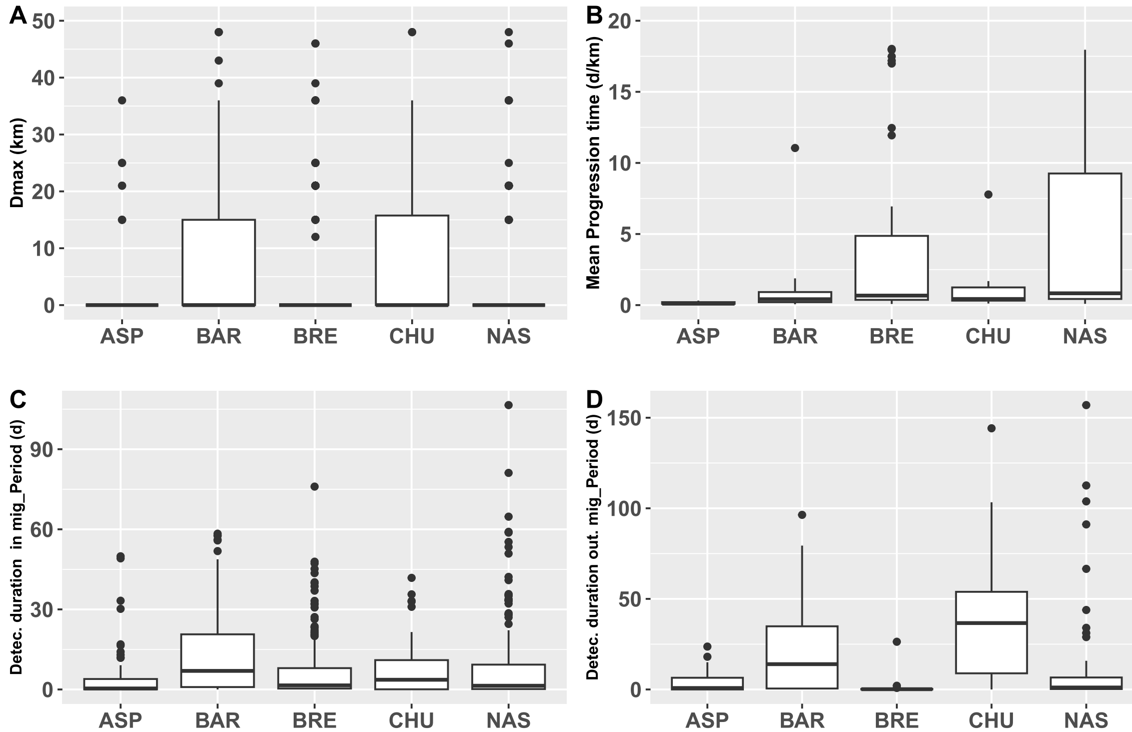

Fig. 4. Boxplots of (A) maximal longitudinal amplitude (D max, in km), (B) Mean progression time (in days/km), (C) Mean duration of the period of activity during the migratory period (in days) and (D) outside the migratory period (in days), according to the species. ASP = asp; BAR = barbel; BRE = bream; CHU = chub; NAS = nase. For visualization purpose, some outliers were removed: 7 values of Dmax > 50 km (all barbels) and 2 values of mean progression time > 20 days/km (1 nase and 1 barbel).

4. Discussion

The multi-year movements of 808 adult fish of 5 species over a maximum 160 km distance and a 12-years period have been studied. This experimental design is rare as most studies usually involve less tracked individuals, and/or focus on smaller river reaches for a limited period of time, usually on one or a few years (Capra et al., 2017; Fredrich, 2003; Horký and Slavík, 2017; Kärgenberg et al., 2022; Ovidio and Philippart, 2008; Pfauserová et al., 2019; Winter et al., 2021) but see Benitez et al. (2018) or De Leeuw and Winter (2008) for multi-sites monitorings involving large numbers of fish and over a long distance for the latter. Such original set-up allowed to (1) characterize long-term and large-scale individual movement patterns of several species, (2) assess inter- and intra-specific variations based on quantitative and qualitative movement metrics and (3) create a typology of individual behaviors based on the type of movements. Regarding the impact of the tagging protocol on fish behavior, it is supposed to be negligible as transponder weight ratio was very low (< 0.5 %) regarding the 2 % rule (Winter, 1996) and as our tagging procedure was already conducted in other studies (Benitez et al., 2018; Ovidio et al., 2023).

Nevertheless, our experimental design is also subject to different biases that must be carefully considered and put into perspective with our results. Firstly, our antenna array did not cover the navigation locks' route. Through deduction, we identified and confirmed 19 navigation lock passages with high confidence. However, estimating the frequency of lock use was not possible without RFID-equipped navigation locks, which is technically challenging for large navigation locks such as those on the Rhine River. Fish could move in and out of the reaches without being detected in the fishways, although the attractivity of the lock's route is certainly low due to the low ratio of lock discharge to total discharge. It could be argued that our deduction approach, based on no detection or no passage in the bypassed fishway, has limitations for the eight individuals subject to deduction (of the 19 navigation lock passages identified, 11 individuals passed sites that could only be passed using navigation locks due to the absence of fishways). However, given the number of consecutive detection zones in each fishway (between 5 and 6), the good detection performance of RFID antennas in vertical slot fishways, the backup systems (backup batteries and diagnostic supervision systems) and the regular monitoring of antenna status and detection performance by operators, the risk of completely missing the passage of a tagged fish in the fishways concerned is very low. Nevertheless, we acknowledge that while the probability of a tagged fish passing through an entire fishway undetected is extremely low, the possibility of a misassignment of a 'navigation lock passage' still exists. Such an assignment error, however, would have a negligible effect on the results and conclusions of this study as it involves a marginal number of fish (19 out of a total of 808 fish). Additionally, although extensive, the spatial coverage is made up of distant detection stations (between 15 and 51 km apart) that did not allow us to study short-range movements, and which have not been built sequentially in an upstream direction (e.g. between 2017 and 2019, fish may have passed and been detected at Strasbourg, then not detected again until Kembs, 114 km upstream).

Finally, fish release campaigns and fishway RFID installations were sequential. This resulted in a dataset mixing fish that passed a fishway

Table 4
Main modalities characterizing each cluster obtained from the HCPC analysis (illustrative variables' modalities in italic). Cla/Mod is the % of individuals with the modality that belong to the cluster. Mod/Cla is the % of individuals in the cluster that have this modality. Global is the % of individuals having the modality in the whole dataset.

Cluster	Nb. Ind.	Modality	Cla/mod	Mod/Cla	Global
1	383	VLF_activity	74.5	90.9	57.8
		River reaches travelled_0	58.7	99.2	80.1
		Short_mig_activity duration	88.2	46.7	25.1
		No_site_downstream movements	51.0	99.2	92.2
		No_reach_downstream movements	51.0	99.2	92.2
		No_lock_use	48.5	100.0	97.6
		No_detection outside migratory period	51.1	84.3	78.2
		1_passage	53.7	62.7	55.3
		Bream	54.5	37.6	32.7
2	163	LF_activity	69.1	98.8	28.8
		Medium_mig_activity duration	30.5	76.1	50.2
		0_reach travelled	24.4	96.9	80.1
		No_site_downstream movements	21.9	100	92.2
		No_downstream movements	21.9	100	92.2
		No_passage	25.9	50.3	39.2
		Nase	28.2	33.7	24.1
		No_lock_use	20.7	100	97.6
		Asp	29.3	14.7	10.1
3	92	MF_activity	81.7	72.8	10.1
		Site_downstream movements	55.6	38	7.8
		Out_mig_period_detection_yes	25	47.8	21.8
		No_reach_downstream movements	12.3	100	92.2
		0_reach_travelled	13.1	92.4	80.1
4	115	1_reach_travelled	86.1	91.3	15.1
		Reach_downstream movements	79.4	43.5	7.8
		Long_mig_activity duration	27.1	47	24.6
		VLF_activity	19.7	80	57.8
		2 + _passages	40.9	15.7	5.4
		Site_downstream movements	31.7	17.4	7.8
		Out_mig_period_detection_No	16	87.8	78.2
5	55	2 +reaches_travelled	100	70.9	4.8
		Lock_use	100	34.5	2.4
		HF_activity	84.6	40	3.2
		2 + passages	59.1	47.3	5.4
		Long_mig_activity duration	17.6	63.6	24.6
		Barbel	14.6	61.8	28.8
		Out_mig_period_detection_yes	13.1	41.8	21.8
		Reach_downstream movements	15.9	18.2	7.8
		MF_activity	13.4	20	10.1

and entered a reach where they were undetectable, with other upstream moving fish that could encounter several RFID-equipped fishways. Consequently, the analyses we conducted in this study had to take into account the fact that the data available to us were highly informative but partial and potentially biased by the successive installation of detection arrays and fishways.

For the reasons outlined above and the fact that the studied river system was fragmented (mixing site non-equipped with a fishway and site with one, which is, at best, a mitigation measure), the maximal longitudinal amplitude D_{max} cannot be directly transcribed into a 'Home range' (Gerking, 1953) but rather as a conservative estimation of it. The greatest value of Dmax observed for each species was 155 km for barbel, 48 km for nase, 46 km for common bream, 48 km for chub, and 36 km for asp. These values are in the lower range of what has already been observed for asp [31–166 km] (De Leeuw and Winter, 2008; Fredrich, 2003; Horký and Slavík, 2017; Pfauserová et al., 2019); in the medium range for nase [4–100 +km] (De Leeuw and Winter, 2008; Ovidio and Nzau Matondo, 2024; Ovidio and Philippart, 2008; Panchan et al., 2022; Povž, 1988), common bream [5–59 km] (Whelan, 1983; Winter et al., 2021); above the upper range for chub [13–25 km] (De Leeuw and Winter, 2008; Fredrich, 1996); and exceptionally high for barbel, for which, to our knowledge, such a distance has never been reported ([25–40 km] (Baras, 1992; Capra et al., 2017; De Leeuw and Winter, 2008; De Vocht and Baras, 2005; Panchan et al., 2022). The low to average values observed for D_{max} for asps and nases could be linked to the fact that a larger fraction of individuals of these two species were released at Strasbourg and Gerstheim, the two most upstream sites. This implies that the D_{max} values observed for these individuals were possibly constrained by the absence of fishways at the upstream dams, Gerstheim being the most upstream fishway built on the main course of the Rhine River. Such limited values of Dmax could also be explained by the possible low passage efficiencies of the studied fishways for these species (the "asp" and "nase" categories were over-expressed in the 2nd cluster in which 50 % of individuals were never detected successfully passing a fishway). Ovidio et al. (2023) observed high and medium adjusted passage efficiency (i.e. not taking attraction efficiency into account) for asp (94.9 %) and nase (close to 60 %), respectively. Site-specific analyses of fish behavior showed difficulties in attraction flow injection pools (Tétard et al., 2014) and high proportion of barbels, nases and asps stopping their upstream movements in the natural bypass channel section of the Gerstheim fishway (53.5 %, unpublished data), which could reveal their settlement and/or spawning in this stony/-gravel microhabitat. The search for favorable habitats to spawn which are globally lacking in a very anthropized environment like the Rhine River might be a good explanation of the high maximum values of Dmax observed for the other species, like already observed in other studies, especially for rheophilic species (Baras, 1992; De Leeuw and Winter, 2008; De Vocht and Baras, 2005; Ovidio et al., 2023). On the other side, the median values of 0 for Dmax of all species would tend to demonstrate that, unlike some long-range individuals, most individuals rather move over short distances. However, this assumption might only be true for common bream, the only eurytopic species, that can more easily find functional habitats in the main course of the Rhine River. Despite the presence of very high mobile individuals of rheophilic species that explore the main course of the Rhine River, the majority of the others may actively search for functional habitats in bypassed river reaches below dams and in tributaries (Ill, Rench, Kinzig and Elz-Dreisam systems) that have a great potential of living and spawning habitats for these species (Schneider, 2017). These species can therefore travel dozens of kilometers without these distances being recorded by our metrics. The median progression times calculated in our study were consistently lower than those reported in Benitez et al., (2018) (0.4 vs 0.8 d/km, 0.4 vs 1.1 d/km, 0.8 vs 1.3 d/km and 0.1 vs 0.9 d/km, for barbel, chub, nase and asp, respectively), but with similar variability within species. These differences may be explained by the absence of attraction flow, a key element of fishway efficiency (Larinier, 2002; Williams et al., 2012) in one fishway studied by Benitez et al. (2018), and the fact that our fish were larger than theirs (median TL of 600 vs 572 mm, 462 vs 396 mm, 440 vs 397 mm and 560 vs 483; for barbel, chub, nase and asp, respectively). Active telemetry tracking would be a more appropriate tool to study the spatial scale of these inter-sites movements, as well as their intra- and inter-specific variations.

Our study also confirmed that high-capacities navigation locks were used by several individuals of all tagged species, except for asp, although this was only verified for a limited number of individuals (2.3 % of the fish detected at least once). Barbels appear to be comparatively more regular users of navigation locks (‘Lock use’ and ‘barbel” are both over-expressed in cluster 5). As already reported in the literature (Argent and Kimmel, 2011; Lin et al., 2013), navigation locks can be used by an unknow proportion of upstream moving fish. Although they cannot be the only means to restore longitudinal connectivity, in relation to their low attractivity (position and low lock/HPP discharge ratio), this might be an interesting complementary passage route. In some highly fragmented ecosystems with impassable barriers, it can even be the only way for fish to reach some upstream areas of the river system (e.g. the 8 individuals that reached the Old Rhine reach in this study could only have done so thanks to navigation locks). Moreover, their management has the potential to be optimized for fish passage like it was already tested for shads (Baumgartner and Harris, 2007; Finger et al., 2020; Guillard and Colon, 1998; Moser et al., 2000).

Downstream movements at the site scale and at the reach scale were also observed for 7.8 % of the tracked individuals, although our estimation is again imperfect, as the downstream movement is in our case only detected after a reascending movement. Apart from methodological issues, such as arrival in a reach where they are not detectable, fish that do not reascend can be explained by changing upstream migration strategy or by natural (fish tagged and released in this study were overall old fish, predation) or anthropic mortality (fishing or turbine mortality). Most of the HPPs studied here (all except Kembs K and Brisach) are not equipped with Fish Downstream Passage Solution, such as angled or inclined racks with reduced bar spacing associated to bypasses, which are considered best practice to protect downstream migrating fish but not yet applicable for large HPPs (recommended for HPPs receiving up to 100 $m^3.s^{-1}$ water flow) (Courret and Larinier, 2008). The causes of the downstream movements were multifactorial and might imply homing behaviors (Fredrich, 1996; Gelder et al., 2024; Ovidio et al., 2007; Whelan, 1983) but their frequency and spatial extent were very variable, which reflects the high diversity of behaviors and ecological needs at the origin of potamodromous species movements within their home-range. Large scale unidirectional upstream movements were also observed, which could reflect processes such as colonization of new habitats or home-range shifts (Crook, 2004; Gelder et al., 2024; Stott, 1967), especially in the context of the reconnexion of reaches after fishway construction like it was observed specifically with rheophilic cyprinids species (Gelder et al., 2023).

Finally, our results revealed that, although there was a high intra-specific variability, the inter-specific differences were strong enough to highlight species-specific behaviors: breams were over-represented in the group characterized by short range movements mainly during migratory period, asps and nases in the group associated with low activity in frequency and possible passage difficulties, and barbels in the group characterized by the more active individuals both in frequency and spatial extent, with a higher rate of downstream movements and lock uses. Although the biases mentioned before call for a cautious interpretation of these results and the fact that studies must still rely on standardized precise metrics to allow inter-sites and inter-species comparisons (Ovidio et al., 2023, 2017; Silva et al., 2018), our approach was able to capture ‘the global picture’ of a large dataset, which was individually confirmed by several metrics taken separately. Finally, our study emphasizes the fact that some potamodromous fish species undertake large-scale movements, not only during spawning period, and that their ecological needs and swimming capacities should be systematically considered in fishway planning and design. In terms of fishway design itself, efforts are to be made to improve fishway efficiency for these species whose movement capabilities and characteristics have been overlooked in comparison to diadromous species. This calls for further research to better understand their behavior in space and time, in the vicinity of obstacles and beyond in river systems.

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CRediT authorship contribution statement

COLL Marie: Writing – review & editing, Resources, Investigation, Data curation. **SCHAEFFER Frédéric:** Writing – review & editing, Resources, Investigation, Data curation. **ROY Romain:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Tétard Stéphane:** Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **MAIRE Anthony:** Writing – review & editing, Methodology, Data curation, Conceptualization. **BENITEZ Jean-Philippe:** Writing – review & editing. **OVIDIO Michaël:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A
Characteristics of the fishways and antennae arrays installed on the upper Rhine River between Lauterbourg and Basel, from downstream to upstream

Characteristics	Iffezheim (IFF)	Gambsheim (GAM)	Strasbourg (STR)	Gerstheim (GER)	Brisach (BRI)	Kembs (KBS)
HPP discharge ($m^3.s^{-1}$)	1500	1100	1400	1400	60	90
River section	Rhine	Rhine	Rhine	Rhine	Old Rhine	Old Rhine
Total height (m)	12.5	11.4	13.25	11.7	5.25	11.75
Distance from IFF (river km)	0	25	46	61	109	160
Fishway type	Pool type, vertical slot	Pool type, vertical slot	Pool type, vertical slot + bypass channel	Pool type, vertical slot + bypass channel	Pool type, vertical slot	Pool type, vertical slot
Construction year	2000 and 2013 *	2006	2016	2018	2008	2016
Nature-like channel length	/	/	500 m	394 m	/	/
Total length (m)	283	290	748	750	120.5	2 × 200
Nb of entrances	3	2	2	2	2	3
Fishway discharge ($m^3.s^{-1}$)	1.2	1.2	1.1–1.25	1.2	0.8	2 × 0.9
Attraction flow ($m^3.s^{-1}$)	11–16	9.8–13.8	8.8–13.8	9.2–13.8	-	1.2–2.2
Pool sizes of fishway (m)	4.5 long x 3.3 wide	4 long x 3.3 wide	3.5 long x 3 wide	3.5 long x 3 wide	3.6 long x 2.4 wide	3.5 long x 3 wide
Pool number	47	48	43	38	21	46
Water drops between pools (m)	0.2–0.3	0.1–0.25	0.2	0.2	0.25	0.25
Year of RFID installation	2013	2010	2016	2019	2021	2017
Number of antennae	14	10	11	7	3	8
1st downstream detection zone	Entrances	Attraction flow pool	Entrances	Entrances	Entrances	Entrances
Last upstream detection zone	Last slot	Last slot	Last slot	Last slot	Last slot	Last slot

*Iffezheim's fishway was modified in 2013 (construction of a third entrance) following HPP modification (addition of a 5th turbine)

Appendix B

Table B
Qualitative movement metrics considered in the MCA. The 2nd line indicates the status of the variable in the MCA (active or illustrative)

Common name (*latin name*)	**% Detected**	**Passage occurence**			**Activity index**				**River reaches Travelled**			**Outside migration**		**Navigation lock use**		**Site downs. Mov.**		**Reach down. Mov.**		**Mean detection duration during mig. period**		
Illustrative		*Illustrative*			*Active*				*Active*			*Active*		*Illustrative.*		*Active*		*Active*		*Active*		
Modalities		**No**	**1 site**	**> 1 site**	**VLF**	**LF**	**MF**	**HF**	**0**	**1 reach**	**2 reaches+**	**yes**	**no**	**yes**	**no**	**yes**	**no**	**yes**	**no**	**Short**	**Medium**	**Long**
Asp (*Leuciscus aspius*)	52.6 % (82/156)	70	11	1	40	35	7	0	74	7	1	16	66	0	82	1	81	5	77	32	31	10
Barbel (*Barbus barbus*)	91 % (233/257)	62	148	23	143	48	26	16	166	44	23	74	159	13	220	25	208	8	225	44	92	87
Common bream (*Abramis brama*)	75.6 % (264/349)	87	167	9	172	69	20	3	216	42	6	21	242	2	262	17	247	13	251	46	166	47
Chub (Squalius cephalus)	73.9 % (34/46)	12	19	3	17	6	6	5	25	6	3	13	21	2	32	6	28	0	34	13	12	9
Nase (Chondrostoma nasus)	57.7 % (195/338)	86	101	8	95	75	23	2	166	23	6	52	143	2	193	14	181	37	158	52	85	38
TOTAL	70.5 % (808/1146)	317 (39 %)	446 (55 %)	44 (6 %)	467 (58 %)	233 (29 %)	82 (10 %)	26 (3 %)	647 (80 %)	122 (15 %)	39 (5 %)	176 (22 %)	631 (78 %)	19 (2 %)	789 (98 %)	63 (8 %)	745 (92 %)	63 (8 %)	745 (92 %)	187 (25 %)	386 (50 %)	191 (25 %)

Appendix C

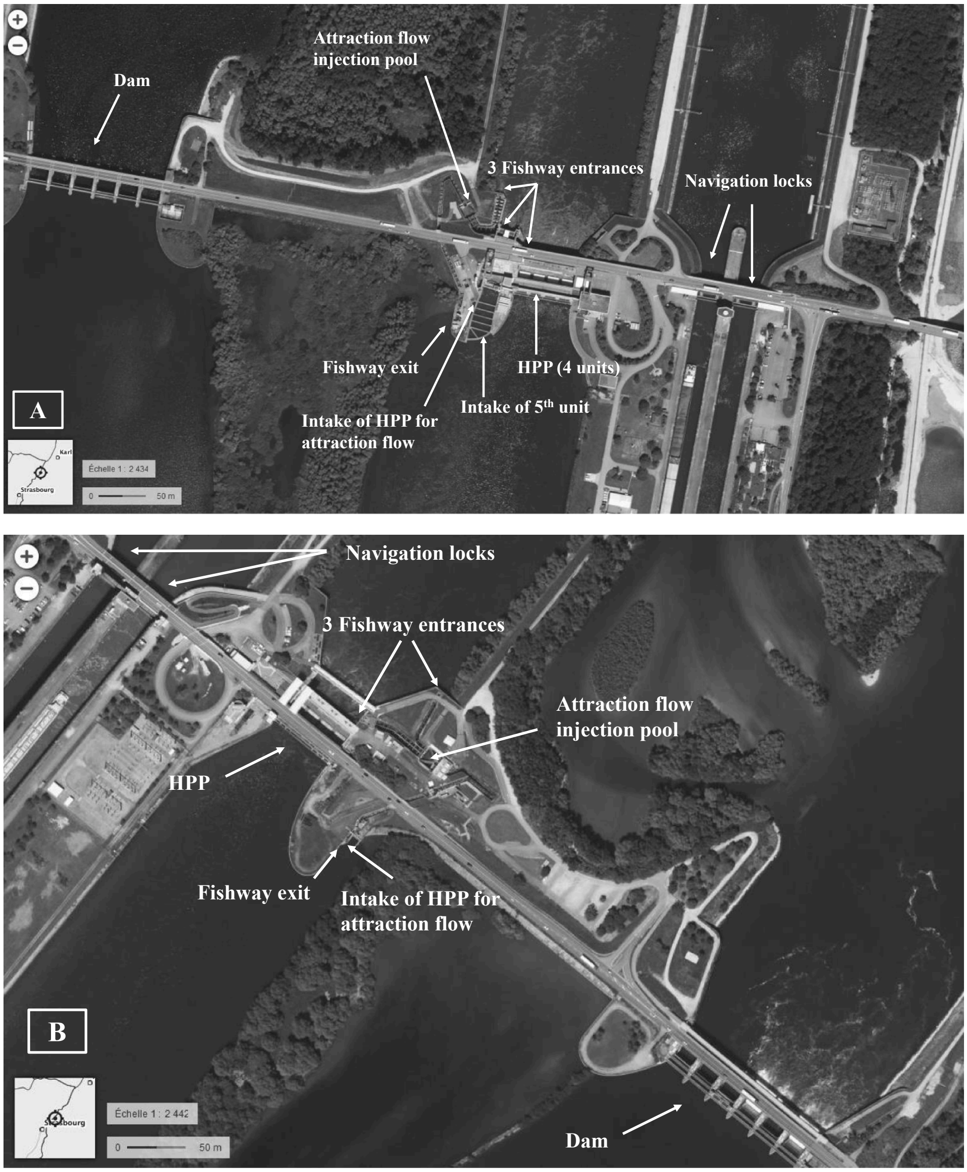

Fig. C. Aerial pictures of hydropower complexes within the study site equipped with upstream fishways: A. Iffezheim, B. Gambsheim, C. Strasbourg, D. Gerstheim, E. Brisach, F. Kembs K

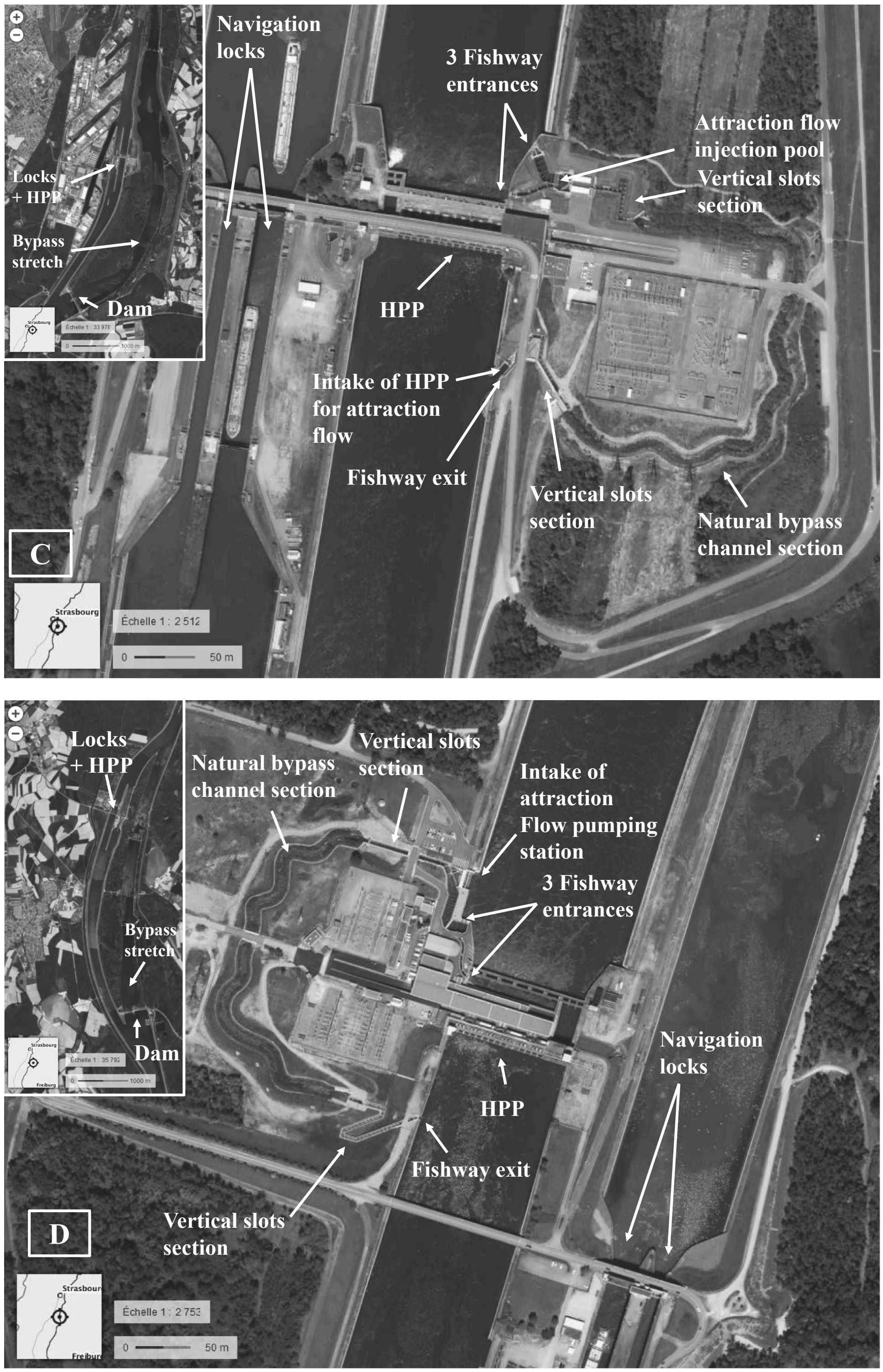

Fig. C. (*continued*).

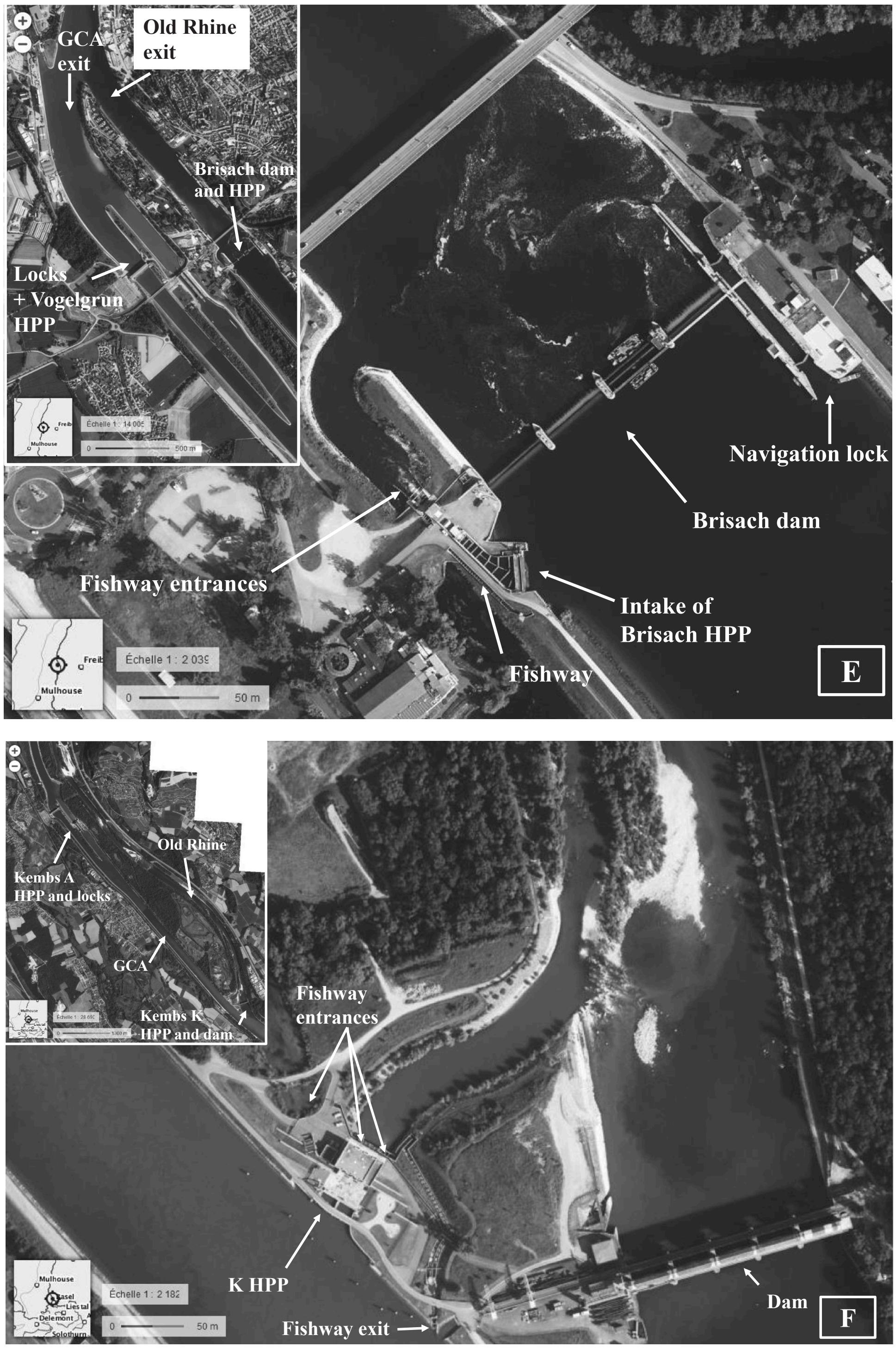

Fig. C. (*continued*).

Appendix D

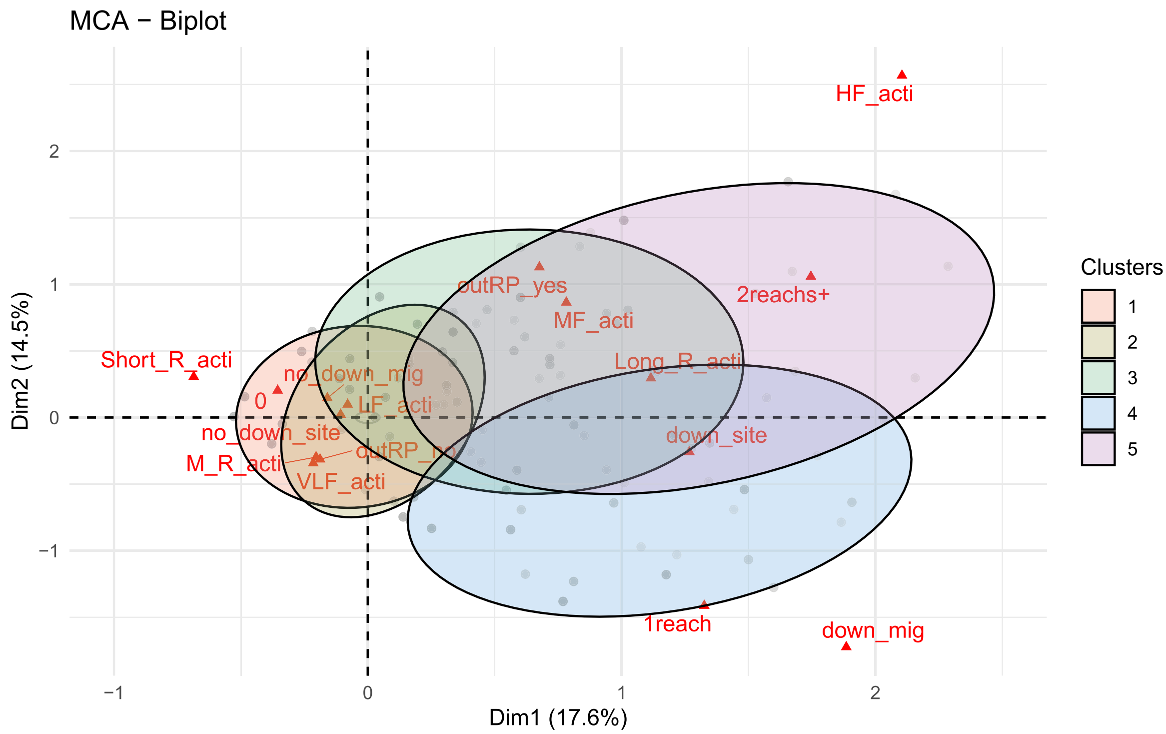

Fig. D. Biplot of individuals (light grey) and active categories (red) on the two most prominent MCA dimensions. Smallest possible ellipses that enclose all points of each cluster are also drawn

Appendix E

Table E
Contingency table of all individuals of the RFID dataset detected at least once according to their classifications based either on visual assessment (patterns A-G) or on HCPC (clusters 1–5)

Cluster\Pattern	A	B	C	D	E	F	G
1	272	69	36	3	0	0	0
2	124	11	21	5	0	0	0
3	10	33	41	7	0	0	0
4	6	4	5	72	21	0	10
5	6	2	15	3	6	26	3

Data availability

Data will be made available on request.

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