Limnologica 99 (2023) 126061

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Movement behaviour and fishway performance for endemic and exotic species in a large anthropized river

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ARTICLE INFO

Keywords:
Telemetry
Ecological continuity
Migration
Dam
River restoration

ABSTRACT

Studies of fishway performance, at the multi-species level in large rivers, are scarce and this raises the question of the passage success of both endemic and exotic species in anthropised environments. The study was conducted in the downstream part of the River Meuse (average annual discharge = 400 $m^3.s^{-1}$) on a 13 km transect between two successive fishways (M_0 and M_1). From 2015–2021, a total of 1065 adult individuals, representing 14 large potamodromous (including asp *Aspius aspius* and catfish *Silurus glanis* as exotics) and diadromous species, were captured at the trap of the Lixhe fishway (M_0), individually tagged (using biocompatible RFID tags-Radio Frequency Identification), and released upstream of M_0. To analyse the performance of the M_1 vertical slot fishway using standardised metrics, a RFID detection station was placed with one antenna at the entrance and one antenna at the most upstream pool of the M_1 fishway (5.7 m height 18 pools). With 456 individuals detected in the M_1 fishway, the ascending rate from M_0 to M_1 was 42.8% (the common bream, *Abramis brama* achieving the best performance with 85.7%); the exotic species (catfish and asp) reached 21.5% and 30.5%, respectively. The adjusted passage performance was the best for the exotic asp (94.9%) followed by the trout, *Salmo trutta* (90.0%). The median time to cross the M_1 fishway was shorter for the trout (median = 01h08) and longer for the eel *Anguilla anguilla* (median = 21h17); the exotic asp was also very fast (median = 1h31). The hourly passage time at M_1 was variable, with some species migrating during daylight, dark periods or the entire 24 h cycle. The multispecies vertical slot fishway studied presented the best performance, in terms of passage success, at an international level, associated with good transit times. It also allows the passage of exotic species, which will increase their expansion area.

1. Introduction

Rivers are considered to be the quintessence of connectivity (Wiens, 2002), corresponding to the extent to which a species or population can move among landscape elements in a mosaic of habitat types (Hilty et al., 2012). The mobility, spatial distribution and temporal variations of fish are major elements of fish biology and can influence their population dynamics and productivity (Fredrich et al., 2003; Gardner et al., 2013; Radinger and Wolter, 2014). Most fish species develop movement behaviours in order to complete their biological activities such as feeding, resting and breeding, in various functional habitats within their home range (Benitez et al., 2015). River connectivity is essential for river dynamics and for the resilience of fish assemblages and populations; reaching good ecological status for river systems is a priority (Ovidio and Philippart, 2008; Sánchez-Pérez et al., 2022). However, the omnipresence of physical barriers reduces watershed longitudinal connectivity in, both upstream and downstream. As the removal of barriers is not often possible, the use of different fishway models represents a measure for countering the inaccessibility of functional habitats and increasing the ecological connectivity of rivers (Silva et al., 2018). The re-establishment of the longitudinal connectivity, using fishways, will enhance biodiversity by facilitating metapopulation processes, restoring gene flow among populations and allowing access to tributaries (Lake and Bond Reich, 2007; Pelicice and Agostinho, 2008; Benitez et al., 2018; Ovidio et al., 2020).

Recent studies on the patrimonial holobiotic potamodromous fish species showed that a wide diversity of these species develop migratory movement behaviour, in various life stages and sizes (Benitez et al., 2015, 2018; Ovidio et al., 2020). These movements/migrations occur during the four seasons of the year, their timing depending on the species and life stage (Lucas and Baras, 2001; Crook, 2004; Benitez et al., 2015). Capra et al. (2018) suggested that the home-range of

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https://doi.org/10.1016/j.limno.2023.126061
Received 17 October 2022; Received in revised form 22 December 2022; Accepted 12 January 2023
Available online 17 January 2023

potamodromous species in a lowland river is not river size-dependent but more certainly river continuity-dependent (the length of the river section without obstacles), which underlines the importance of good fishway efficiency for potamodromous species (to allow individuals to exploit an adapted home range size). This means that, ideally, the fishways have to be efficient for both diadromous and potamodromous species throughout the seasons, for species of different sizes and with various swimming and leaping capabilities. Taking into account the wide diversity of species with different biological requirements and strategies to deal with passage facilities, successful fishway design and implementation requires a multidisciplinary approach that involves ecohydraulics, fish behaviour, policy and socioeconomics (Silva et al., 2018).

It is, therefore, crucial to improve fishway design and to collect data from a wide range of structural typologies on different fish species in a wide variety of rivers and regions, in order to find more successful, integrative solutions for the future (Cook and Hinch, 2013; Kemp, 2012; Ovidio et al., 2017). Studies on passage efficiency (the percentage of the fish present which entered and successfully moved through a fishway) have increased in the past 10 years and more recent efforts have been made to focus on non-commercial species (Alexandre et al., 2013; Branco et al., 2013; Sanz-Ronda et al., 2016; Silva et al., 2010, 2012; Ovidio et al., 2017; Grimmardias et al., 2022; Sánchez-Pérez et al., 2022). In the course of these studies, additional efforts were made to quantify fishway performance at the multispecies level, including the entire fish community, to be as representative as possible (Castro-Santos et al., 2009; Bunt et al., 2012, 2016).

Nonetheless, enhanced connectivity with multispecies fishway can be a disadvantage in some situations, allowing the invasion, dispersal and increased recruitment of unwanted and/or exotic species; facilitating the spread of diseases; and providing access to degraded habitats that act as ecological sinks (Franklin et al., 2021). There is an increased interest in focussing some research on both endemic and exotic/non indigenous species. Such challenging studies imply the tagging of numerous individuals of different fish species in the field and monitoring over a mid or long-term period, in order to obtain enough data to allow the evaluation of the fish pass performance. The use of automatic tagging detection systems allows the collection of quantitative data on the temporal use of the fishway, which, associated with the use of standardised metrics, would allow inter-site comparisons (Ovidio et al., 2017). Such studies on fish-pass performance in large anthropised rivers are rarer, due to the increased difficulty in installing large detection telemetry systems (but, see Nzau Matondo et al., 2017 and Grimmardias et al., 2022).

In the lower course of the Meuse in Belgium, large fishways have been progressively installed over the last 20 years, strongly stimulated by the Salmon program, aiming to reintroduce this flagship species into Belgium after its extinction in the beginning of the 20th century (Renardy et al., 2022). These fishways were primarily designed for large rheophilic species but it transpires that they are also intensively used by eel, eurytopic and limnophilic species, as well as by exotic species at different times of the year and day (Nzau Matondo et al., 2017; Benitez et al., 2018, 2022). However, since their installation, the passage performance of the fishway of the main course of the Meuse was never quantified at the multispecies level. The objective of this paper is to use pit-telemetry at one of the fishways of the Meuse as a prototype site, in order to quantify: 1) the ascending rate and progression time from the capture site in the main course of the Meuse; 2) the performance of the fishway, in terms of passage efficiencies and transit time; and 3) the temporal use of the fishway at a seasonal and daily scale. The study extends over seven consecutive years, using endemic and exotic species of the Meuse River as biological models.

2. Material and methods

2.1. Study area

The study was conducted in the downstream part of the River Meuse (average annual discharge = 400 $m^3.s^{-1}$, catchment area = 36,000 km^2, bream zonation) on a 13 km transect between two successive fishways (M_0 and M_1, Fig. 1). The lower course of the River Meuse is canalised and fragmented by obstacles for navigation, water regulation and hydroelectricity production (Fig. 1). The habitat is deep (an average depth of 5 m) and homogeneous (muddy bottom with some blocks), with an absence of gravel bed and very sparse bank vegetation. According to physicochemical requirements, the water quality is good in the Meuse

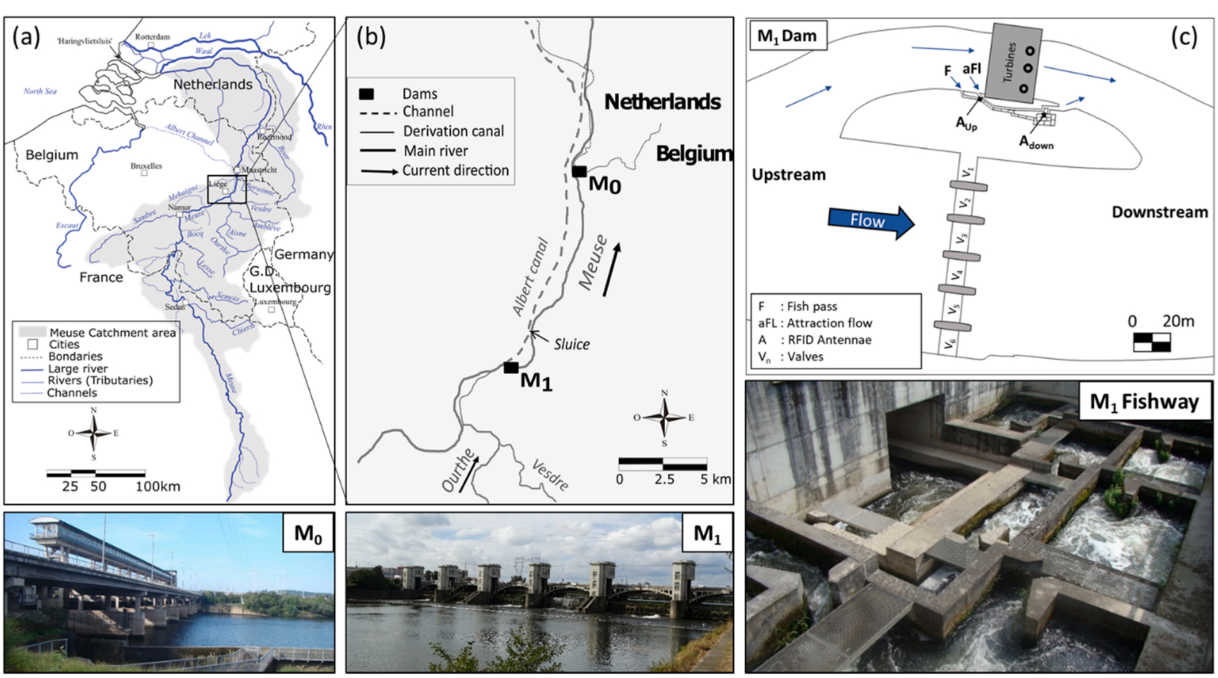

Fig. 1. Location of the study site at countrywide scale (1a) and in the Meuse catchment area (1b). Schematic representation of the M_1 hydroelectric site showing the positioning of the RFID antennas and the fishway (1c). Photographs of the M_0 and M_1 sites. Photograph of the M_1 fishway.

Table 1
Characteristics of the M_0 and M_1 fishways on the Meuse River.

Characteristics	M_0 Fishway	M_1 Fishway
River	Meuse	Meuse
Located	Lixhe	Monsin
Height of dam (m)	8	5.7
Distance from the sea (km)	323	336
Distance from M_0 (km)	-	13.1
Presence of sluice gate(s)	No	No
Fishway type	Pool type, vertical slot	Pool type, vertical slot
Construction year	1998	2000
Discarge of fishway (m^3/s)	1	0.8
Range of dissiped energy (Wm^3)	50–140	48 – 168
Attraction flow (m^3/s)	2.5	4
Pool size (m)	Variable from 4.7 to 9.7 × 2.5	Variable from 3.5 to 7.4 × 2.5
Pool number	26	18
Height between pools (m)	0.3	0.3
Water depth of slot (m)	1.3	1.3
Slot width (m)	0.5	0.4

(Public Service of Wallonia – AQUABIO). The total number of fish species in the Belgian Meuse is 36 (75% are cyprinids), they belong to different ecological categories: eurytopic, limnophilic and rheophilic species (Schiemer and Spindler, 1989; Benitez et al., 2022). The exotic species (the Asp and the catfish) are represented by the suffix 'exo' (Table 1).

2.2. Fish capture and tagging

The study period was 2015–2021, during which time the furthest downstream fishway (Lixhe fishway in Meuse) was equipped in the upstream pool with a capture cage which has cubic shape of 2 m with a mesh of 5 cm. The entrance of the cage is equipped with a cone to retain fish and the capture limit of fish was ± 150 mm. Over the study period, the trap was monitored 2–5 times a week, depending on the capture intensity. Captured fish were anesthetised in a solution of 4-allyl-2-methoxyphenol (Eugenol 0.1 ml L−1), identified, measured (± 1 mm fork length) and weighed (± 1 g) (Benitez et al., 2022). A total of 1065 adult individuals (representing 14 large species, including cyprinidae, salmonidae, esocidae, percidae, siluridae and anguillidae) were individually tagged (Table 2) using biocompatible RFID tags (Radio Frequency Identification, Texas Instruments, HDX, 134.2 kHz; 32 × 3 mm and 0.9 g in weight). These tags were inserted in a 5 mm-long incision in the intraperitoneal cavity of the fish, using a scalpel (Ovidio et al., 2017). Tagged fish were released upstream of the capture trap after a recuperation period of a few minutes.

2.3. System for fish detection and behavioural metrics used

To analyse the behaviour of fish coming from M_0 in the M_1 fishway, a RFID detection station was placed (CIPAM®-France) with one antenna at the entrance and one antenna at the most upstream pool of the M_1 fishway (Fig. 1). The antenna dimensions were 0.8 × 1.8 m with a detection area of 1.5 m^2. The RFID station listens to the presence of tagged fish every day, 24 h/24 h. Fish passing by the antennae were recorded by the RFID stations, with associated information on the individual code, calendar date and specific time. These detection data allowed us to determine several behavioural metrics of the fish passing (Ovidio et al., 2017; Benitez et al., 2018):

1. *the ascending rate* up to M_1: the percentage of the number of individuals detected at M_1 out of the total number of individuals tagged at M_0, per species
2. *the progression times* M_0-M_1: the distance (km) per day (km/d) between the release time in M_0 and the first detection time in M_1, per species.
3. *the fishway use time*: the number of detections within the M1 fishway per individual and per hour, on a daily scale per species.
4. *The full-passage transit time*: travel time (in hours) from the last detection by the down- antenna at the entrance to the last detection by the up-antenna at the last pool.
5. *DH transit time*: transit time as a function of the topographic difference in height between both antennas, in hours per metre (hours/meter).
6. *the adjusted passage efficiency*: percentage of individual fish that made a complete fishway passage, out of the total number of individuals detected at the entrance.

2.4. Environmental factors and statistical analysis

Water temperature (°C) was recorded every hour during fishway monitoring periods, using Tidbit Onset data loggers installed at the inlet of the M_0 fishway. Mean daily flow data ($m^3.s^{-1}$) were provided by the Wallonia Public Service of Hydrological Studies (SETHY, Public Service

Table 2
The ecological guild (Rheo. =rheophilic; Eury. =eurytopic, Limno. = Limnophilic and exo. = exotic species), the numbers of fish tagged and biometric characteristics per species.

Species	Ecological gild	N tagged 2015–2021	Median FL (mm)	Min. FL (mm)	Max. FL (mm)
Salmonidae					
Trout, *Salmo trutta*	Rheo.	21	482	346	542
Cyprinidae					
Barbel, *Barbus barbus*	Rheo.	56	593	300	748
Chub, *Squalius cephalus*	Rheo.	164	408	290	641
Nase, *Chondrostoma nasus*	Rheo.	101	372	265	463
Ide, *Leuciscus idus*	Rheo.	13	446	386	591
Asp, *Aspius aspius*	Rheo.-Exo	128	470	198	598
Roach, *Rutilus rutilus*	Eury.	32	252	180	357
Common carp, *Cyprinus carpio*	Eury.	4	680	500	725
Common bream, *Abramis brama*	Limno.	14	434	412	482
Tench, *Tinca tinca*	Limno.	5	440	408	465
Esocidae					
Pike, *Esox lucius*	Limno.	3	664	655	698
Percidae					
Common perch, *Perca fluviatilis*	Limno.	2	415	409	422
Siluridae					
Catfish, *Silurus glanis*	Eury.-Exo	79	1037	780	1650
Anguillidae					
European eel, *Anguilla anguilla*	Eury.	443	371	131	4460

Table 3
Overview of the fish species tagged. Summarised results per species, in terms of detections and passage within the M_1 fishway and progression times M_0-M_1 between 2015 and 2021.

Species	Ecological guild	N tagged 2015–2021	N detected	N passage
Salmonidae				
Trout, *Salmo trutta*	Rheo.	21	10	9
Cyprinidae				
Barbel, *Barbus barbus*	Rheo.	56	19	16
Chub, *Squalius cephalus*	Rheo.	164	136	119
Nase, *Chondrostoma nasus*	Rheo.	101	47	27
Ide, *Leuciscus idus*	Rheo.	13	5	2
Asp, *Aspius aspius*	Rheo. - exo.	128	39	37
Roach, *Rutilus rutilus*	Eury.	32	2	0
Common carp, *Cyprinus carpio*	Eury.	4	1	0
Common bream, *Abramis brama*	Limno.	14	12	7
Tench, *Tinca tinca*	Limno.	5	0	0
Esocidae				
Pike, *Esox lucius*	Limno.	3	2	0
Percidae				
Common perch, *Perca fluviatilis*	Limno.	2	1	0
Siluridae				
Catfish, *Silurus glanis*	Eury. - exo.	79	17	9
Anguillidae				
European eel, *Anguilla anguilla*	Eury.	443	165	82

of Wallonia), at a frequency of one measurement every hour. Ascending rates were compared between ecological fish groups, using the chi^2 test and the fish characteristics of a species (size and tagging period) between the individuals detected and individuals undetected in M1, using the Wilcoxon test for species with $n > 8$ for each group. Because data violated the assumptions of normality (Kolmogorov-Smirnov, $p < 0.05$), non-parametric tests were used. The progression time M_0-M_1 and transit time between species ($n > 8$ individuals) was compared using the non-parametric test of Kruskall–Wallis. When the Kruskal–Wallis test was significant, the *post hoc* pairwise comparison of the Dunn test with Bonferroni–Holm correction was compared. For all statistical tests, the significance level was set at $p < 0.05$ and these were performed using the R statistical program (The R Foundation for Statistical Computing, Vienna, Austria, version 3.1.1.).

3. Results

3.1. Ascending rate

During the seven years study period (2015–2021), 456 individuals were detected at the M_1 fishway, leading to a global ascending rate of 42.8% (Table 3, Fig. 2). This rate varies at the species level, from 6.3% for roach, *Rutilus rutilus* to 85.7% for common bream, *Abramis brama* and it was significantly greater for rheophilic species (53.0%) than for non-rheophilic (16.8%) species (chi^2 test, $p < 0.001$). Comparison of the tagging characteristics between fish detected at M_1 and non-detected fish showed that there was a significant difference (Wilcoxon tests, all $p < 0.05$) in the tagging period for eels (detected = a median of the 24th week of the year; non-detected = a median of the 26th week), asp (detected = median of 19th week; non-detected = median of 20th week), barbel, *Barbus barbus* (detected = median of 19th week; non-detected = median of 20th week) and catfish (detected = 22nd week; non-detected = 23rd week) and a significant difference in the size of eels (detected = median of 391 mm; non-detected = median of 356 mm), barbel (detected = median of 614 mm; non-detected = median of 582 mm) and chub, *Squalius cephalus* (detected = median of 415 mm; non-detected = median of 371 mm).

3.2. Progression time M_0 to M_1

The specific median progression time M_0-M_1 (Fig. 3) varied between 0.48 km/d for the nase, *Chondrostoma nasus* (min. = 0.01 km/d; max. = 24.4 km/d) and 5.20 km/d for the trout (min. = 0.83 km/d; max. = 17.55 km/d); the fastest individual recorded was a chub, with a progression time of 52.11 km/d. This was significantly different between most abundant species (KW test: χ^2=28.63, df=7, $p < 0.001$): trout, barbel, chub, nase, asp, common bream, catfish and eel. The pairwise comparison (Dunn test, all $p < 0.05$) showed that trout (median value = 5.20 km/d, IQR = 7.90 km/d) took significantly less time than nase (median value = 0.48 km/d, IQR = 4.37 km/d), asp (median value = 0.03 km/d, IQR = 0.91 km/d) and catfish (median value = 0.19 km/d, IQR = 1.06 km/d) to arrive at M_1 and asp took significantly more time than eel (median value = 0.01 km/d, IQR = 3.09 km/d) and chub (median value = 1.16 km/d, IQR = 4.51 km/d).

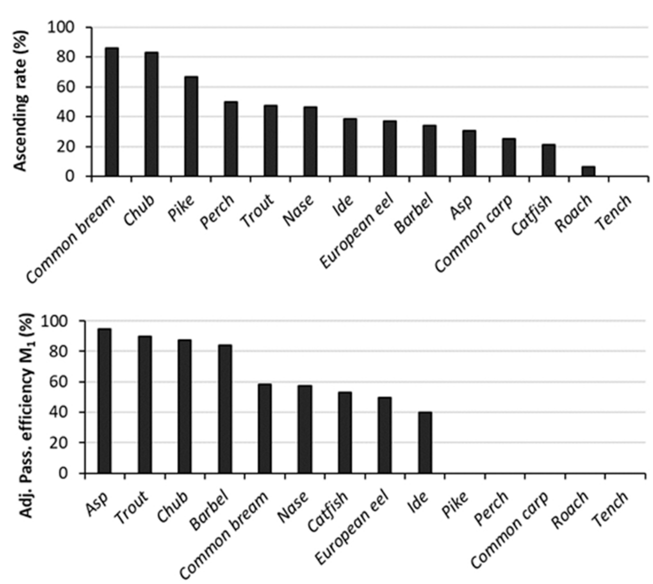

Fig. 2. Ascending rate (up graph) from M_0 to M_1 and adjusted passage efficiency in M_1 fishway (bottom) per species equipped with RFID tags.

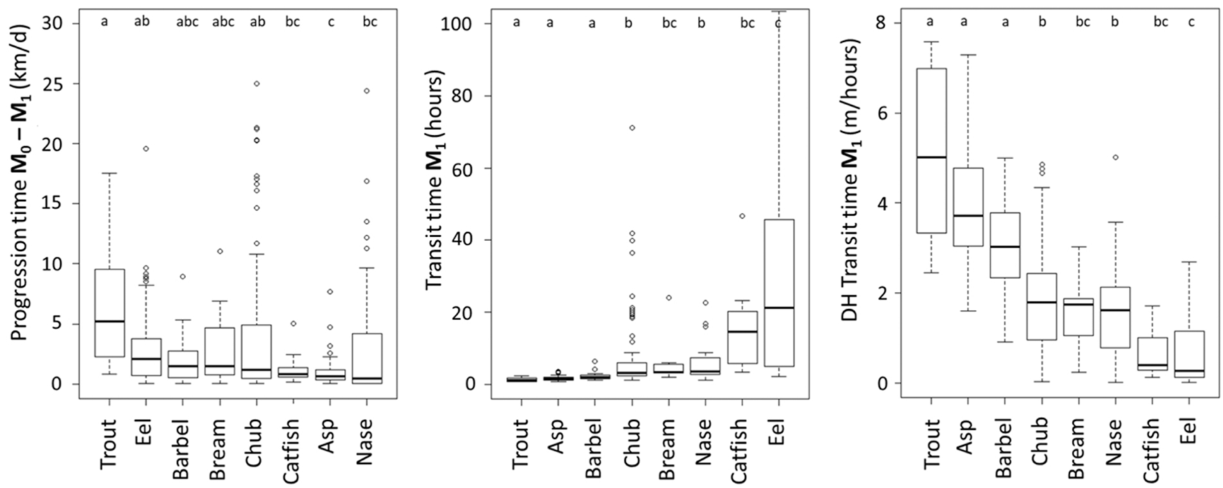

Fig. 3. Distribution of data by species for progression time M_0-M_1 in km per day (left), transit time M_1 in hours (middle) and DH transit time M_1 in meters per hour (right). Quartile 1 and 3: lower and upper box border, median: solid horizontal line, whiskers: smallest and largest value and circles: outliers values. Species sharing at least one common letter (above each boxplot) did not differ at the 0.05 level of significance.

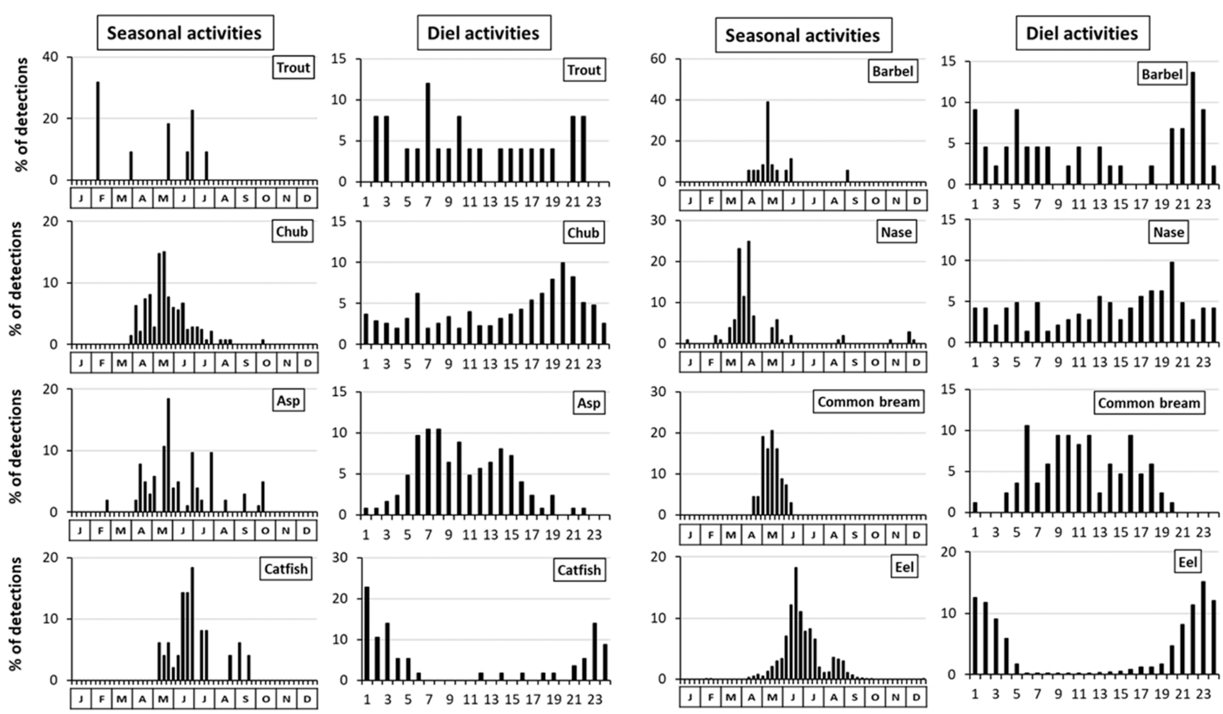

Fig. 4. Diel and seasonal mobility recorded by the RFID antennae during the passage of fish within the M_1 fishway at a seasonal and daily period time scales.

3.3. Adjusted passage efficiency and transit time of the M_1 fishway

Of the 456 individuals detected at the fishway entrance of M_1, 308 were detected at the upstream antenna, representing 67.5% of global adjusted passage efficiency (Fig. 2). Pike, roach, tench and perch did not pass the fishway. The interspecific values of adjusted passage efficiencies ranged between 0.0% and 94.9%. The rheophilic species had higher efficiency (> 80%, including all rheophilic species but with the best efficiencies for asp (94.9%) and trout (90%)) than the limnophilic species (46.7%) and the eurytopic species (49.2%) (chi^2 tests, all $p < 0.001$). The median full-passage transit time (Dh transit time) in M_1 (Fig. 3) was 3h25 min (1.65 m/h) and lasted between 1h08 min (5.01 m/h) for the trout and 21h17 min (0.27 m/h) for the eel and it was significantly different between species (KW test, χ^2=159.57, df=7, $p < 0.001$). Rheophilic species such as trout (median value = 1h08 min, IQR = 1h06 min), asp (median value = 1h32 min, IQR = 42 min) and barbel (median value = 1h52 min, IQR = 56 min) had a transit time M_1 significantly faster than other species, while eel (median value = 21h17 min, IQR = 40h43 min) showed a significantly slower transit time than catfish (median value = 14h37 min, IQR = 16h54 min) and common bream (median value = 3h16 min, IQR = 2h59 min) (Dunn test, all $p < 0.05$).

3.4. Seasonal and diel mobility pattern

The movement activity period at the seasonal scale (Fig. 4) occurred in late winter (March 1st–March 21st) and in spring for two species: nase, with a median date of April 4th, and a median date of May 18th for trout. Two species showed seasonal activity, mainly in spring, and a unimodal pattern with a median date of May 10th, for the common bream, and May 11th for the barbel. Other species showed seasonal activity, mainly in spring and summer: the chub (median value of May 12th), the asp (May 21st), the eel (June 21st) and the catfish (June 22th). Diel activities of fish within fishways varied according to species (Fig. 4). Among cyprinids, three species were detected in all diel periods and at all hours of the day, with more detection being recorded at dusk and early night time: the barbel (38.6% of diel activity: 17h00–23h00), the chub (51.8%: 17h00–23h00) and the nase (44.0%: 17h00–23h00). Individuals of common bream (83.5%: 6h00–17h00), asp (84.7%: 6h00–17h00) and trout (60%: 5h00–17h00) presented a maximum detection activity during dawn and daytime periods. The catfish (89.4%: 20h00–5h00) and the eel (92.2%: 20h00–5h00) were mainly detected during night and dawn periods.

4. Discussion

The main contribution of this study is to present quantitative results of fishway performance in real conditions in a large river and for a great variety of fish species, mainly potamadromous but also diadromous (European eel and trout) and exotics (catfish and asp). The use of radio frequency identification technology (RFID) was particularly adapted to increase the number of fishes tagged and to work continually at a long-term multi-annual time scale. Pit-tags have an infinite lifespan, which is particularly interesting and increases detection rates for fish with long life expectancy (>15 years for some species studied), and that may sometimes alternate high and low individual mobility patterns between years (Benitez et al., 2018; Nzau Matondo and Ovidio, 2018; Alexandre et al., 2023). The likelihood that the tagging procedure or the presence of the transponder could have interfered with fish swimming performance and survival cannot be systematically excluded. Nevertheless, because of their low weight ratio (< 0.5%), it is presumed to be minimal, in comparison with the 2% rate recommended (Ficke et al., 2012; Lucas, 2000). Furthermore, tags were inserted using a procedure that has been successfully used and validated in previous studies in the Meuse basin (Ovidio et al., 2017; Nzau Matondo and Ovidio, 2018; Benitez et al., 2018).

Despite the distance (13.1 km) between the tagging site and the M_1 fishway, the re-detection level was quite important and a global multi-species mean detection rate of 42.8% was achieved. We observed interesting differences between the ecological guilds. The rheophilic species were the most detected species, with a mean rate of 53.0% and chub presenting the highest rate of 82.9%. Rheophilic species are known for their seasonal migrations between functional habitats, their medium size and need for large rivers (Fredrich et al., 2003; Ovidio and Philippart, 2008; Prchalová et al., 2011; Ovidio et al., 2016, 2017; Benitez et al., 2018; Capra et al., 2018). As the main course of the River Meuse does not have a gravel bed substrate adapted for the spawning of these species, they have to actively search for access to tributaries in order to spawn; they are forced to use the fishway of the Meuse to enter the Ourthe sub-basin, 19.2 km upstream form the tagging site. The mean detection rate of the eurytopic species is globally lower (33.2%). These more ubiquitous species (e.g. roach) have less constraints to find functional habitats in the main course of the Meuse and do not need to imperatively cross barriers to complete their biological cycle; this may explain their lowest detection rate. The European eel have time to colonise freshwater growth residence areas, especially since the reduction of their population which, by the biological mechanism of density dependence, decreases their need to move upstream due to a lack of competition for the habitat (Nzau Matondo and Ovidio, 2018). The mean detection rate of limnophilic species reaches a high rate of 62.5%. Among this category of species, the phytophilic fish (represented by bream and pike, with a detection rate of 85.7% and 66.7%, respectively) probably strain to search for vegetation to spawn. As the banks of the lower River Meuse have mostly been concreted, vegetation is absent which force them to move further upstream. Some authors already observed long distance movements for fish species like bream (Donnely et al., 1998; Gardner et al., 2013), tench (Donnely et al., 1998) and pike (Ovidio and Philippart, 2005), demonstrating the ability of the species of this guild to move long distances. The two exotic species, the asp and the silurus, demonstrated their ability to colonise the upper Meuse as their detection level was 30.5% and 21.6%, respectively. As a rheophilic species, the asp is known to have a strong capacity to move long distances (Horky and Slavik, 2016; Benitez et al., 2018), especially during the spawning period. Catfish are rather known to be quite resident with high site fidelity, with movements focussed during the summer period (Capra et al., 2018). The detection rates observed in this study over a 13 km stretch, for these two exotic species, is, however, not anecdotal and underlines their potential capacity to progressively colonise the upper parts of the Meuse basin using a multi-specific fishway. The non-detection of some individuals in M_1, after tagging in M_0, may be related to the absence of RFID antennae below M_1 (Bunt et al., 2012; Ovidio et al., 2017; Silva et al., 2018). The fish have to enter M_1 to be detected, which has certainly minimised the ascending rate. The size of the individuals may also represent a selective criterion in the non-detection. Indeed, for 3 species (eel, barbel and chub), we observed that the size of the individuals detected at M_1 was significantly greater than those of non-detected individuals. Size may influence a better swimming ability (for the larger individuals) (Baudoin et al., 2015) or a larger home range (Woolnough et al., 2009). The marking period also influences the ascending rate for eel, asp, barbel and catfish, where later marking results in a lower detection rate. The advancement of the reproduction period may explain this result because of a need to reproduce more quickly after tagging. In fact, the progression time taken can sometimes be important, travelling 13 km can lead to an inability to find an optimal spawning site upstream of M_1 in time. The interspecific variability of progression time shows that rheophilic species tend to migrate faster, especially trout. In contrast, intraspecific variability indicates that the need to migrate quickly may depend on the individual.

The *adjusted passage efficiency* of the fishway was variable depending on species and their ecological group. The rheophilic Salmonidae, represented by the trout, reach an excellent rate of 90%. Salmonids are generally known to have better passage efficiency than other species due to their good swimming capacity and ability to jump (Baudoin et al., 2015). The passage success observed in our study is higher than that evaluated by Noonan et al. (2011) in their meta-analysis review (an average of 61.7% for salmonids with a range from 30% to 80%) and higher than most of the rates mentioned in a recent literature review by Ovidio, (Table 5) et al. (2020). More recently, Grimmardias et al. (2022) estimated the adjusted passage efficiency at 68% for salmonids in a vertical slot fishway of the Rhone River. The rheophilic cyprinidae reach a rate of 87.15% with a value of 87.5% for chub and 84.2% for barbel. Those results are much higher than the mean international average rates (Noonan et al., 2011) for non-salmonid fish (21,1% average, 19–45% range). More recent studies on rheophic cyprinids in vertical slot or pool and weir fishways showed adjusted passage efficiency from 7.1% to 66.7% for barbel (Ovidio et al., 2017; Grimmardias et al., 2022) and 25% for the Northern Straight Mouth Nase (*Pseudochondrostoma duriense*) (Pedescoll et al., 2019). Among the eurytopic and the limnophilic species, roach, pike, *Esox lucius*, perch, *Perca fluviatilis*, tench, *Tinca tinca* and carp, *Cyprinus carpio* did not cross the fishway, but only a few were tagged and/or approached M_1. These species were already captured in M_0 during a long-term monitoring period (Benitez et al., 2022), suggesting their ability to use a vertical slot fishway. The eel reached a passage efficiency of 49.7%. A rate of 29% was observed for the roach in a pool and weir fishway by Knaepkens et al. (2016). Eels have poor swimming capacities (Baudoin et al., 2015) and may sometimes have difficulties passing the slot between basins where the current speed increases. The relationship between the cost and the ecological benefit is an important consideration for fishway projects, but the key question is: what percentage of each species need to get through a fishway to meet ecological objectives and to ensure population viability? The very good passage quantified for rheophilic cyprinidae and salmonidae will allow them to reach the main Ourthe tributary to reproduce with positive repercussions in terms of demographic gains for their populations. We can reasonably think that the passage performances observed for eurytopic and limnophilic species, even if they are lower, also constitute an improvement in terms of gene flow effect, metapopulation reconnection and access to functional habitats (Ovidio et al., 2020). However, it is still complicated to assess the demographic gain for a population from fish passage improvement or restoration and there is a need to perform behavioural and demographic studies to evaluate the ecological gain of fish passage for indigenous species. The exotic catfish and asp demonstrated a very good capacity to cross the fish pass (53% and 95% of adjusted passage efficiency, respectively). Three species of exotic gobies are also present in the Meuse and already use a fishway located further downstream (Benitez et al., 2022). Unfortunately, selectively blocking exotic species in a multi-species fishway is very difficult to set up, especially if their size range and swimming capacities contrast. This creates a 'connectivity conundrum' (Zielinski et al., 2020), whereby restoring connectivity runs counter to decreasing or eliminating the further spread of invasive or undesirable species. The very good passage success of exotic species in the fishway of the Meuse constitutes a collateral adverse effect of the reopening of the migration route that will increase expansion areas, with potential negative impacts for indigenous species (Leuven et al., 2009; McLaughlin et al., 2013). In an experimental approach in a baffle fish-ramp, Franklin et al. (2021) observed that passage efficiency was, on average, lower for the exotic species, suggesting that the use of such a selective structure may, in some instances, slow down the progression of invasive species.

The fishway transit and DH transit time are interesting metrics and rapid passages are a sign of best performance, as fish have to spend as little time as possible in a fishway during their movements in rivers (Baudoin et al., 2015). With a global median transit time of 3h25 min (1.65 m/h), the performance of the studied fishway is relatively good at the multispecies level. The rheophilic salmonid logically demonstrates the best transit time, with an excellent median time of 1h8 min (5.01 m/h). Among the rheophilic cyprinids, the exotic asp was the fastest (median 1h32 min, 3.72 m/h) followed by the barbel, chub and nase (1.62–3.03 m/h). The European eel spends more time (median 5h59) but this is not ecologically detrimental as they have time to reach their growth habitats for their long stay in freshwater at the yellow stage (Nzau Matondo and Ovidio, 2018). The exotic catfish was the slowest species observed (median time: 14h36 min; 0.39 m/h) but still manages to pass through.

Considering these results, we can reasonably assume that the transit times are in line with the ecological needs of indigenous species and allow them to reach the functional habitats located upstream of the fishway in good time, with very reasonable delays. Comparing transit times between the studies is not relevant due to the contrasting typology and length of fishways, but the use of the delta height transit time is a more adapted standardised metric (Ovidio et al., 2017). The barbel reaches a delta-height transit time of 4.0–4.8 m/h in two huge vertical fishways in France (Grimmardias et al., 2022). The trout and the grayling (*Thymallus thymallus*) achieved 1.5 m/h and 1.36 m/h in a small vertical slot fishway in Belgium, respectively (Ovidio et al., 2017). Tétard et al. (2014) measured a median delta height transit speed of 2.28 for all the species studied in a huge (187 m long) fishway in France.

The use of RFID technology provided significant accuracy for recording the timing of movements within fishways. It showed that, when considering all the species, the fishways are used at any time of the day or night during a large part of the annual cycle. At species level, barbel, nase and chub used the fishway during the entire diel cycle. For other species, such as trout, asp, and common bream, movements were mainly detected during the crepuscular periods, although with eel and catfish, movements mainly occurred during the night. Few data concerning diel behaviour patterns are available for potamodromous species (but see Benitez et al., 2018). Some results were obtained by the radio tracking of trout, barbel and chub within less degraded environments and, unlike our results, these demonstrated greater movement activities during the night, dawn and dusk (Baras et al., 1994; Lucas, 2000; Ovidio et al., 2002). These results show that it is essential to keep fishways functioning over the entire year and at any time of the day or night. Otherwise, there is a risk that some species will be prevented from reproducing or reaching functional habitats at the right time.

5. Conclusions

The restoration of ecological continuity in a river is imperative for both diadromous and potamodromous species of fish in highly disturbed river systems. Within highly fragmented river ecosystems, the cumulative effects of barriers to fish movement can significantly limit the performance of restoration of local connectivity (Tummers et al., 2016). This strongly underlines the need for fully performing fishways, especially in the lower parts and/or the highly altered parts of river basins, where a deficit of functional habitat is frequent for exigent potamodromous species and which correspond to the starting of the migration for the diadromous species moving upstream. The multispecies vertical slot fishway studied was one of the best performing in terms of passages success at an international level, associated with good transit times. But in return, it also allowed the passage of exotic species that will increase their expansion area. The next step would be to undertake complementary behavioural studies by active telemetry in order to follow the fish after their passage, to better understand and quantify the ecological gain (access to new functional habitats, spawning success) provided by the installation of fishways.

CRediT authorship contribution statement

Michaël Ovidio: Funding acquisition, Conceptualization, Investigation, Project administration, Supervision, Writing - original draft, Writing - review & editing. **Arnaud Dierckx:** Methodology, Resources. **Jean-Philippe Benitez:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Michael Ovidio reports financial support was provided by Public Service of Wallonia.

Data Availability

Data will be made available on request.

Acknowledgments

The study was financed by the Public Service of Wallonia through the "Meuse Salmon" scientific program. We thank LUMINUS for providing access to the fishways, and we thank SPW-SETHY-MET for the river flow data. We thank all the students and members of UGERAA-ULIEGE who participated in collecting field data.

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