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Multi-year analysis of the fish colonisation dynamic in three newly installed fishways in medium sized Belgian rivers

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Abstract – The temporal dynamic use of newly installed fishways after a reopening event is not well known as most studies are not performed just after the opening and are generally limited to a single season or year. We carried out monitoring of three fishways for several consecutive years on three rivers in Belgium from the date of their opening. To identify the colonisation dynamics of fish species, we analysed temporal patterns in specific diversity, abundance, biomass, and associated environmental conditions. We detected different capture peaks and the appearance of new species several years after opening the migratory axis (up to 8 years post-opening). The dynamic of colonization showed that the same species may migrate earlier or later depending on the river. The analysis of the periodicity of capture indicated that some species made movements throughout the year while others at more precise periods. Moreover, the periodicity of movements was either stable or fluctuating over the year of monitoring, depending on the species. Our results highlight the importance of long-term monitoring to detect temporal dynamics in fish colonisation, allowing to improve our understanding of the opening effect of a migratory axis.

Keywords: Monitoring / fishes / river / restored connectivity / temporal trend / migratory axis

1 Introduction

Freshwater ecosystem fragmentation is recognised as one of the most impactful on the aquatic resources, affecting habitat connectivity on multiple spatial and temporal scales and leading to reduced species geographical distribution and/or communities and populations isolation (Carpenter *et al.*, 2011; Romão *et al.*, 2018; Legrand *et al.*, 2020; Ovidio *et al.*, 2020; Consuegra *et al.*, 2021). As freshwater fish must disperse or migrate throughout the year to access breeding, feeding and refuge habitats, populations are largely impacted in terms of their structure, migration, recruitment or spawning success by physical obstructions (Weibel and Peter, 2013; Mameri *et al.*, 2019; Ovidio *et al.*, 2021; Benitez *et al.*, 2022; Grimardias *et al.*, 2022). Spawning activity is one of the most common motivators for long-distance migration, but other movements may occur outside the spawning period for ontogenetic and trophic reasons (Benitez *et al.*, 2015, 2018). Therefore, the restoration of river longitudinal connectivity is a management restoration action that has to be associated with the presence of qualitative functional habitats and a sufficient physicochemical water quality (Bernhardt and Palmer, 2007; Fullerton *et al.*, 2010; Tummers *et al.*, 2016; Ovidio *et al.*, 2020: 2023).

Scientists and river managers have succeeded in facilitating the passage of fish around or through obstructions using fishways, bypass channels and fish elevators. The ability to use fishways depends on the species and their life stage but also their ability to swim; consequently, fishways designs may vary depending on the target species (Noonan *et al.*, 2012; Silva *et al.*, 2018; Grimardias *et al.*, 2022). Over the last years, progress has been made to improve fishway access and performance, combining knowledges of hydraulics and fish ecology. Fishways design tend to become predominantly adapted to different species, sizes and migratory strategies (Benitez *et al.*, 2015; Ovidio *et al.*, 2017, 2020; Romão *et al.*, 2019; Grimardias *et al.*, 2022).

When new fishways are installed in rivers, there is also a real interest to perform a monitoring programme to evaluate their seasonal use by different species and to quantitatively evaluate the extent to which fish will have access to newly opened river sections. As humanely and/or logistically costly, very few studies on the use of fishways have been done during several consecutive years (Tummers *et al.*, 2016; Legrand *et al.*, 2020; Benitez *et al.*, 2022; Grimardias *et al.*, 2022). Such long-term monitoring is, however, interesting to highlight the between years variability in the use of the fishways for

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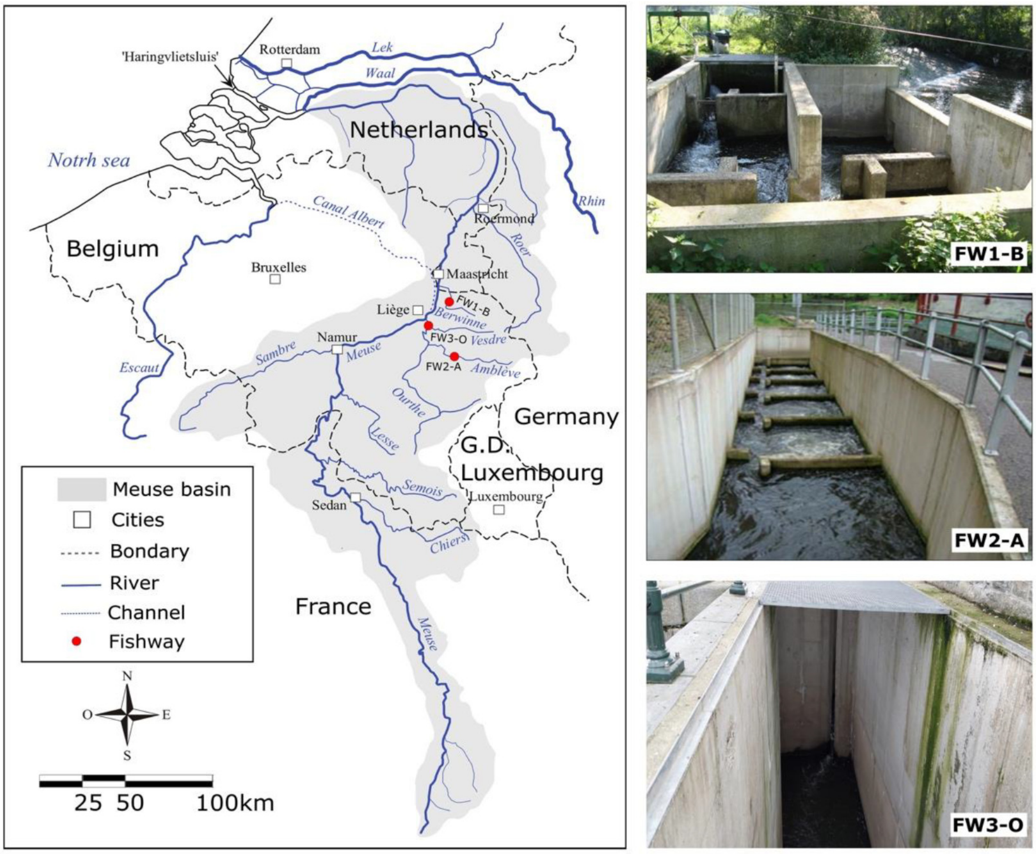

Fig. 1. Locations of the Berneau fishway in the Berwinne (FW1-B), the Lorcé fishway in the Amblève (FW2-A) and the Grosses-Battes fishway in the Ourthe River (FW3-O) and pictures showing fishway configurations.

different species under fluctuating environmental conditions (Belliard *et al.*, 2018; Benitez *et al.*, 2022). The use of capture traps as a monitoring method is relatively fastidious because it requires regular human passage. However, this method makes it possible to obtain precise and qualitative information on fish such as species taxonomic determination, individuals weight, size or sex, and to employ tagging for different scientific purposes (Prchalová *et al.*, 2011; Benitez *et al.*, 2022). Moreover, monitoring during several consecutive years since the opening of the migratory axis allows to analyse the temporal processes of colonisation of newly re-opened habitats by fish communities, which is an important, but yet purely informed, scientific key-point for following restoration of longitudinal continuity.

In order to restore connectivity, multi-species vertical slot fishways were installed in three medium size rivers in the south of Belgium. Theses fishways were intensively monitored by capture traps during several consecutive years after setup to obtain data on their use by different fish species and on the evolution and changes of fish species using the fishways over time. Such long-term monitoring is particularly adapted to analyse the colonization dynamic of migratory axes, just after the reestablishment of rivers longitudinal connectivity. In order to meet these objectives, we analysed: (1) the diversity, abundance, biomass and size of species captured in the three fishways; (2) the evolution of the dynamic pattern of capture over consecutive years, at species and ecological guild levels; (3) the periodicity of capture and its variation over years of monitoring; and (4) the environmental conditions (water temperature and flow conditions) associated with species capture.

2 Material and methods

2.1 Study site and fishways characteristics

The study was conducted on three rivers belonging to the Belgian Meuse River basin: the Berwinne, a tributary of the Meuse; the Amblève a tributary of the Ourthe; and the Ourthe (Fig. 1). Each of these rivers have a fishway (FW) built in 2002 (Berwinne River: FW1-B), 2007 (Ambleve River: FW2-A) and 2009 (Ourthe River: FW3-O) to restore connectivity. Before that, no device was present at these physical barriers (concrete ramp dam at FW1-B and FW3-O and hydropower dam at FW2-A). The average annual discharge is 1.9 m^3/s for the Berwinne, 19.3 m^3/s for the Amblève and 67.4 m^3/s for the Ourthe. The ecological status of rivers as defined by biological, physicochemical and hydro morphological indicators is medium for the Berwinne and good for the Amblève and Ourthe Rivers (*i.e.* Public Service of Wallonia – DEE). According to Huet (1949), the downstream parts of the Berwinne and Amblève Rivers belong to the grayling/barbel

Table 1. Characteristics of the Berneau (FW1-B), Lorcé (FW2-A) and Grosses-Battes (FW3-O) fishways.

Characteristics	Berneau (FW1-B)	Lorcé (FW2-A)	Grosse-Battes (FW3-O)
Fishway type	Pool type, vertical slot	Pool type, vertical slot	Pool type, vertical slot
Construction year	2002	2007	2009
Period of monitoring	October 2002–October 2008	October 2007–October 2015	September 2009–September 2012
Delta height of dam (m)	1.4	3.3	4
Attraction flow (m^3/s)	–	–	1.5
Total length of fishway (m)	16	67	73
Number of pools	4	15	16
Pool size of fishway (m)	4.2–3 long × 3–1.8 wide	2.8–5.2 long × 2.7 wide	3.5–5.6 long × 2 wide
Height between pools (m)	0.3	0.25	0.25
Water depth of slot (m)	0.7	1	1.2
Slot width (m)	0.2	0.25	0.3

fish zone and the Ourthe river is characterised as a barbel fish zone (Huet, 1949). In total, 23 species are potentially present in the Berwinne and Amblève Rivers and 24 species in the Ourthe River (Electrofishing data, University of Liège). All fishways are vertical-slot pool multi-specific types (height between pools ≤0.3 m) equipped with 4 (FW1-B), 15 (FW2-A) and 16 (FW3-O) pools. The three fishways have a constant operating flow and are not influenced significantly by river flow fluctuations. In addition, a capture trap was installed in the three fishways. The first one (FW1-B) was equipped with a grid located in the upper pool with 3 cm of space in the upstream opening and a cone in the downstream opening. The second (FW2-A) and the last one (FW3-O) had a cage in the upstream pool with a grid of 1 × 1 × 1 cm and 5 × 5 × 5 cm, respectively (Tab. 1). The minimum capture size is 50 mm (FW1-B), 25 mm (FW2-A) and 150 mm (FW3-O).

2.2 Fish capture and environmental variables

The three fishways (FW) were monitored for several consecutive years: from October 2002 to October 2008 for FW1-B, from October 2007 to October 2015 for FW2-A and from September 2009 to September 2012 for FW3-O. The monitoring period ranged from 2 to 5 times per week, depending on the capture intensity with a total of 730 monitoring events at FW1-B, 1311 at FW2-A and 286 at FW3-O. Individuals in the capture trap were caught with a dip net after placing a grid just downstream, which prevents the passage of other individuals during the monitoring.

Captured fishes were anesthetised in a solution of 4-allyl-2-methoxyphenol (Eugenol: 0.1 ml/L), identified at the species level, counted, measured (±1 mm, fork length) and weighed (±1 g). Following biometric analyses, fish were released upstream of the dam after a recuperation period of a few minutes. Fish caught were grouped into different guilds according to their ecological preferences (Benitez *et al.*, 2022):

- Rheophilic species: trout (*Salmo trutta)*, sea trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), barbel (*Barbus barbus*), chub (*Squalius cephalus*), nase (*Chondrostoma nasus*), spirlin (*Alburnoides bipunctatus*), asp (*Aspius aspius*), dace (*Leuciscus leuciscus*), grayling (*Thymallus thymallus*), loach (*Barbatula barbatula*) and bullhead (*Cottus rhenanus*).
- Eurytopic species: common bleak (*Alburnus alburnus*), common bream (*Abramis brama*), silver bream (*Blicca bjoerkna*), roach (*Rutilus rutilus*), gudgeon (*Gobio gobio*), european catfish (*Silurus glanis*), minnow (*Phoxinus phoxinus*), European eel (*Anguilla Anguilla*) and three-spined stickleback (*Gasterosteus aculeatus*).
- Limnophilic species: pike (*Esox lucius*), perch (*Perca fluviatilis*), tench (*Tinca tinca*), ide (*Leuciscus idus*), common rudd (*Scardinius erythrophthalmus*), koi (*Cyprinus rubrofuscus*), common carp (*Cyprinus carpio*) and leather carp (*Cyprinus carpio nudus*).

This separation in ecological guilds allows to have a more synthetic view of the colonisation process for species having closer habitat preference.

Environmental variables were continuously recorded (every hour) during the monitoring of the fishways. Data on water temperature (°C) were recorded by data loggers (Tidbit Onset) installed at the inlet of the fishways, and the flow data (m^3/s) were granted by SETHY (Wallonia Public Service of Hydrological Studies) located 3 km downstream of the FW1-B, 16 km downstream of the FW2-A and 0.2 km of the FW3-O.

2.3 Data and statistical analysis

Firstly, we produced a global view of the fish diversity (*i.e.* by species and by ecological guild and in terms of abundance, biomass and size) observed in each FW. We presented the results by year of monitoring in order to take in account the reproductive periods. It should be noted that some species were not present every year in the different fishways. For species with at least 5 individuals captured per year of monitoring, we compared the sizes of individuals between the different monitoring years for the three FW with non-parametric Kruskal-Wallis test.

We investigated dynamic patterns of capture per year of monitoring for each FW, using cumulative curves for the three ecological groups (including all individuals) and for species with a minimum of 10 captured individuals. The number of captures was computed as a percentage, with 100%

corresponding to the total number of individuals captured during the entire monitoring, namely during 6 years at FW1-B, 8 years at FW2-A and 3 years at FW3-O. We used the chi^2 test to determine if the observed distribution of captures during each year of monitoring for each FW was homogeneous or heterogeneous compared to a theoretical number of captures (corresponding to the total capture divided by the number of years of monitoring). We also used chi^2 test to compare (i) the number of captures between rheophilic and eurytopic guilds during the first three years of monitoring for each fishways and between the three fishways since the lowest monitoring time is 3 years at FW1-B; (ii) the number of captures of rheophilic and eurytopic guilds during the first year compared to the sum of captures in the second and third year. Only species with at least 5 individuals captured per year were considered for these tests. This last constrain excluded the limnophilic guild from these tests.

We analysed the periodicity of capture (by month) per year of monitoring for species with at least 5 individuals captured for each year of monitoring using violinplots. We compared temporal trends in capture periodicity between the years of monitoring with non-parametric Kruskal-Wallis tests. The post hoc pairwise comparison of the Mann-Whitney (U) test was used when the Kruskal-Wallis test was significant.

The environmental values were transformed into daily data, and each fish captured was linked with the environmental data of the previous day's capture (Benitez *et al.*, 2015). The temperature and flow data were analysed by species with a minimum of 3 individuals for each fishway. Since the rivers have different sizes, the flow values were divided by the average flow of each river. We calculated the 25 and 75 percentiles of index flow values during capture (*i.e.* river flow the day before the capture divided by the average annual flow) to determine 3 migration flow categories:

- Low flow migration: < percentile 25.
- Mean flow migration: between percentile 25 and percentile 75.
- High flow migration: > percentile 75.

The proportion of individuals (%) per species captured for each category was further calculated at the three FW.

The significance level was set at $p < 0.05$ for all statistical tests (chi^2 test, Kruskal-Wallis and Mann-Whitney) and was performed using a R statistical program.

3 Results

3.1 Capture diversity (abundance, biomass and size)

A total of $n = 1504$ individuals from 13 different fish species were captured in the FW1-B from October 2002 to October 2008. In the FW2-A, $n = 4507$ individuals belonging to 23 species were monitored from October 2007 to October 2015. In the FW3-O, $n = 1403$ fish from 21 species were captured from September 2009 to September 2012 (Tab. 2).

The most abundant ecological guild at the FW1-B and FW2-A in terms of number of individuals was the rheophilic guild with 82% and 53% of individuals captured, respectively, and the eurytopic guild in FW3-O with 63% of individuals captured. At FW2-A and FW1-B, eurytopic species were the second most abundant guild with 47% and 18% of individuals captured, respectively, and the rheophilic guild with 35% in FW3-O (Tab. 2).

During the first year of monitoring, 397 individuals were captured at FW1-B, 540 at FW2-A and 898 at FW3-O. The number of individuals over the monitoring time varied from 163 to 397 in the FW1-B, from 161 to 1333 in the FW2-A and from 117 to 898 in the FW3-O. This represents 5–10 species, 11–17 species and 11–18 species, respectively. At FW1-B, the greatest number of species was captured between 2004 and 2005 with 10 species, between 2012 and 2013 at FW2-A with 17 species, between 2009–2010 and 2011–2012 at FW3-O with 18 species captured. New species were still captured during the fourth and fifth years of monitoring at FW1-B, during the second, fifth, sixth and eight years at FW2-A and during the second year of monitoring at FW3-O (Fig. 2). In terms of number of individuals per species, the spirlin (rheophilic) was the most abundant at FW1-B ($n = 548$ individuals), the minnow (eurytopic) at FW2-A ($n = 1837$) and the bream (eurytopic) at FW3-O ($n = 833$) (Tab. 2).

Regarding the biomass, rheophilic species were dominant at FW1-B and FW2-A, representing 95% (139 kg) and 96% (608 kg), respectively, of the total biomass and eurytopic species at the FW3-O with 52% (1275 kg) of the total biomass. The most represented species in terms of biomass was the trout at FW1-B (97 kg), the barbel at FW2-A (276 kg) and the bream at FW3-O (1038 kg). The biomass over year of monitoring varied from 14 to 53 kg at FW1-B, from 32 to 161 kg at FW2-A and from 197 to 1778 kg at FW3-O (Tab. 2).

The largest and smallest individuals captured at FW1-B were an eel (765 mm) during the first year and a minnow (31 mm) during the fourth year of monitoring, respectively; a barbel (640 mm) during the last year and a minnow (39 mm) during the first year of monitoring at FW2-A; an European catfish (1160 mm) during the last year and a spirlin (46 mm) during the first year of monitoring at FW3-O (Tab. 2). The KW statistical test showed no trend between the different monitoring year regarding the size of individuals captured in the three FW (KW test, all $p > 0.05$).

3.2 Dynamic pattern of capture over consecutive years

The rheophilic species were the first to be captured in the three fishways. Species of this guild were captured regularly throughout the year of monitoring at FW1-B and FW2-A, with 50% of individuals captured during the third and fourth years of monitoring, respectively. At FW3-O, rheophilic species showed an earlier capture with 50% of the capture rate during the first year of monitoring; the same trend was observed for the eurytopic species. At FW1-B, the eurytopic species reached 50% of capture rate during the fourth year of monitoring, and during the third year at FW2-A. We observed 50% of capture rate of limnophilic species during the first year of monitoring at FW1-B and FW3-O, and during year sixth at FW2-A (Fig. 3a).

The cumulative frequency of fish capture during years of monitoring changed according to the species (Fig. 3b). The grayling at FW2-A and the trout at FW3-O showed a homogeneous distribution of captures throughout the entire monitoring period (Chi^2 test, $p > 0.05$). The trout at FW1-B

Table 2. Number of individuals (n), biomass (g) and range size (mm) of captured fishes for the Berneau (FW1-B), Lorcé (FW2-A) and Grosse-Battes (FW3-O) fishways.

Species	FW1-B																	
	2002-2003			2003-2004			2004-2005			2005-2006			2006-2007			2007-2008		
	n	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm
Rheophilic species	336	48236	–	167	22250	–	168	22258	–	203	12124	–	217	19052	–	149	15163	–
Trout	74	30305	225-575	53	18152	96-590	43	15177	129-458	31	9463	109-382	40	13088	75-472	23	10868	130-510
Rainbow trout	–	–	–	1	229	283	–	–	–	–	–	–	1	320	294	2	504	270–317
Barbel	7	13697	370–606	–	–	–	1	1150	458	1	353	312	1	1248	467	1	8	87
Chub	52	2670	64–362	93	3591	60–410	111	5776	78–415	43	1606	49–288	73	3389	57–370	38	2683	70–414
Nase	–	–	–	–	–	–	–	–	–	1	4	72	–	–	–	–	–	–
Spirlin	201	1564	62–116	20	278	83–102	13	155	78–108	127	698	57–740	102	1007	71–129	85	1100	71–129
Eurytopic species	62	2516	–	13	186	–	7	40	–	165	1733	–	3	11	–	14	50	–
Roach	2	152	135–192	1	129	96	–	–	–	–	–	–	–	–	–	–	–	–
Gudgeon	–	–	–	–	–	–	–	–	–	3	65	108–130	–	–	–	–	–	–
Minnow	57	177	50–80	12	57	55–80	7	40	61–92	160	348	31–84	2	10	64–77	11	47	57–83
Eel	3	2187	720–765	–	–	–	–	–	–	2	1320	686–740	–	–	–	–	–	–
T.S stickleback	–	–	–	–	–	–	–	–	–	–	–	–	1	1	41	3	3	40–46
Limnophilic species	1	2498	–	–	–	–	–	–	–	–	–	–	1	15	–	–	–	–
Perch	–	–	–	–	–	–	–	–	–	–	–	–	1	15	105	–	–	–
Carp	1	2498	427	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	397	53250	–	180	22436	–	175	22298	–	368	13857	–	221	19078	–	163	15213	–

Species	FW2-A																							
	2007–2008			2008–2009			2009–2010			2010–2011			2011–2012			2012–2013			2013–2014			2014–2015		
	n	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm
Rheophilic species	392	153722	–	121	40343	–	199	70013	–	666	64733	–	152	88110	–	113	26822	–	324	57634	–	420	107103	–
Trout	219	40285	62–439	72	11101	78–379	79	15362	11–343	63	12966	41–354	59	25635	83–417	51	8246	92–453	138	26098	84–606	179	33860	84–505
Rainbow trout	3	391	133–256	13	5098	210–478	25	12650	276–499	21	11123	235–540	8	14567	180–464	12	4304	202–394	14	10835	307–464	54	22839	187–492
Brook trout	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1272	319–335
Barbel	62	97910	131–595	6	9532	259–554	30	39345	54–575	23	27579	55–620	6	35464	54–544	5	8634	418–558	9	15036	427–580	32	42366	52–640
Chub	12	6166	106–465	9	10572	123–510	3	1374	85–463	35	7475	115–510	8	7641	72–140	11	2976	83–506	2	171	119–220	4	190	136–186
Nase	2	3269	490–500	–	–	–	–	–	–	1	13	108	–	–	–	1	27	125	–	–	–	–	–	–
Spirlin	56	565	74–102	3	34	92–99	49	291	53–105	472	3137	61–121	52	1206	61–115	22	129	66–98	117	2145	58–115	125	2909	54–112
Dace	8	243	103–177	–	–	–	4	42	82–127	33	451	78–188	6	488	76–97	1	76	184	16	333	83–210	5	303	66–250
Grayling	26	4880	173–425	13	3987	179–438	8	945	176–296	10	1934	168–349	11	3041	178–282	10	2430	176–305	25	2991	154–338	16	3340	110–375
Loach	2	2	55–59	3	11	63–90	1	4	80	5	24	42–86	1	26	79	–	–	–	3	25	98–105	1	5	89
Bullhead	2	11	77–85	2	8	62–63	–	–	–	3	31	36–81	1	42	69	–	–	–	–	–	–	1	19	106
Eurytopic species	147	3926	–	145	1108	–	1134	2707	–	535	2019	–	8	561	–	47	452	–	28	631	–	68	3410	–
Common bleak	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	15	72–94	–	–	–	–	–	–
Bream	1	1528	456	–	–	–	1	6	69	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Silver bream	–	–	–	1	58	144	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Roach	–	–	–	2	61	110–140	–	–	–	3	43	74–109	–	–	–	1	80	171	4	79	103–114	7	164	84–180

Table 2. (continued).

Species	FW2-A																							
	2007–2008			2008–2009			2009–2010			2010–2011			2011–2012			2012–2013			2013–2014			2014–2015		
	n	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm	*n*	g	mm
Gudgeon	118	2175	88–150	23	561	100–138	12	271	76–141	34	390	71–124	8	561	94–136	16	276	93–231	23	516	101–145	14	288	100–140
Minnow	26	79	39–74	118	426	52–69	1121	2430	44–87	497	1585	55–82	–	–	–	28	81	56–78	–	–	–	47	2958	52–86
Eel	1	143	469	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	36	296	–	–	–
T.S stickleback	1	1	50	1	2	52	–	–	–	1	1	46	–	–	–	–	–	–	–	–	–	–	–	–
Limnophilic species	1	3828	–	–	–	–	–	–	–	–	–	–	1	2006	–	3	4376	–	3	301	–	–	–	–
Pike	–	–	–	–	–	–	–	–	–	–	–	–	1	2006	612	–	–	–	–	–	–	–	–	–
Perch	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	226	170–220	3	301	158–216	–	–	–
Carp	1	3828	570	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leather carp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	4150	560	–	–	–	–	–	–
Total	540	161476	–	266	41451	–	1333	72720	–	1201	66752	–	161	90677	–	163	31650	–	355	58566	–	488	110513	–

Species	FW3-O								
	2009–2010			2010–2011			2011–2012		
	n	g	mm	*n*	g	mm	*n*	g	mm
Rheophilic species	381	769401	–	47	72186	–	66	159982	–
Trout	8	12301	249–624	5	4388	254–536	6	6298	362–578
Sea trout	5	10287	499–640	3	4907	472–571	2	6302	561–760
Rainbow trout	4	7688	492–581	1	2206	580	8	20991	492–635
Barbel	170	481573	102–704	13	35380	175–681	29	83956	440–689
Chub	41	60924	184–528	12	14965	373–503	16	35308	421–529
Nase	138	195456	138–512	11	7099	109–422	5	7127	364–479
Spirlin	13	66	46–91	–	–	–	–	–	–
Asp	–	–	–	1	2228	601	–	–	–
Grayling	2	1106	327–398	1	1013	451	–	–	–
Eurytopic species	497	926536,6	–	69	121606	–	313	227274	–
Common bleak	–	–	–	3	97	133–147	–	–	–
Bream	479	903047	315–575	58	107943	401–550	296	27168	373–590
Silver bream	4	1587	241–276	1	261	237	–	–	–
Roach	9	3095	168–328	5	1809	177–300	8	1856	180–275
Gudgeon	1	24	121	–	–	–	–	–	–
European catfish	4	18784	880–950	2	11496	876–1070	9	198250	920–1160
Limnophilic species	20	82480	–	1	2975	–	11	89717	–
Pike	5	12542	590–761	–	–	–	1	1377	555
Tench	3	4810	432–475	–	–	–	–	–	–
Ide	1	426	295	–	–	–	1	1220	398
Common rudd	1	1528	389	–	–	–	–	–	–
Koï	2	9361	521–671	–	–	–	–	–	–
Carp	8	53813	540–723	1	2975	505	9	87120	674–858
Total	898	1778418	–	117	196767	–	390	476973	–

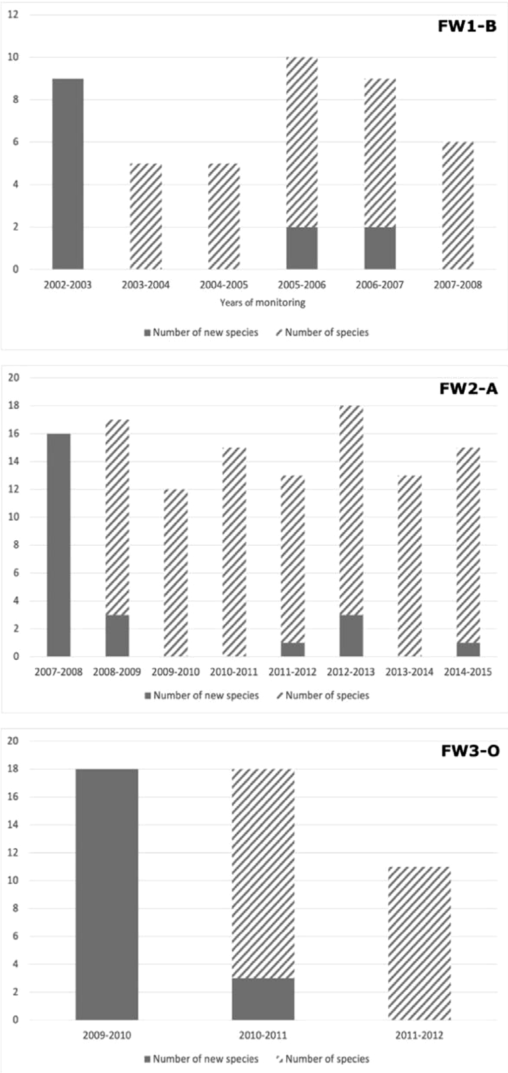

Fig. 2. Histograms of the number of species and new species in the Berwinne (FW1-B), the Amblève (FW2-A) and the Ourthe River (FW3-O), depending on the year of monitoring.

and FW2-A; the chub at FW1-B and FW3-O; the barbel at FW2-A and FW3-O; the spirlin at FW1-B; the gudgeon at FW2-A; and the nase and the bream at FW3-O had heterogeneous capture frequencies (Chi^2 test, all $p < 0.05$). The distribution of the number of captures of rheophilic and eurytopic guilds is significantly different between the first 3 years for the three fishways (Chi^2 test, all $p < 0.05$). The number of captures of rheophilic species in the first year was significantly greater than the number of captures of eurytopic species at FW1-B and FW2-A and the reverse trend was observed at FW3-O (Chi^2 test, $p < 0.05$). Moreover, the number of captures of rheophilic species during the first year was significantly greater than the sum of the second and third year captures at FW2-A and FW3-O. The same trend was observed for the eurytopic species at FW1-B and FW3-O (Chi^2 test, $p < 0.05$) (Fig. 3a). Some species were quickly captured: the barbel at FW1-B and FW3-O, for which 54% and 50% of individuals were captured after 30 and 34 days of monitoring respectively, the sea trout (50% of individuals after 60 days), the chub (51% of individuals after 57 days), the nase (72% of individuals after 24 days), the spirlin (69% of individuals after 6 days) and the bream (51% of individuals after 46 days) at FW3-O (Fig. 3b).

3.3 Periodicity of capture

The periodicity of capture for the trout at FW1-B, the barbel and the chub at FW3-O showed no significant difference between years of monitoring (KW test, $p > 0.05$). The periodicity was significantly different between years for the other species: the chub and the spirlin at FW1-B, the trout at FW2-A and FW3-O, the barbel, the gudgeon and the grayling at FW2-A, and the bream, the roach and the nase at FW3-O (KW test, all $p < 0.05$). The bream at FW3-O showed a significant difference in the periodicity of capture between all the years of monitoring. Some species had only two years with a different periodicity: the barbel at FW2-A (2007–2008 and 2014–2015) and the trout and the nase at FW3-O (2009–2010 and 2011–2012). The chub and the spirlin at FW1-B had a similar periodicity between years 2005–2006 and 2006–2007 and between years 2005–2006 and 2007–2008. The trout, the gudgeon and the grayling at FW2-A had at least 3 years of similar capture periodicity (Fig. 4).

3.4 Environmental factors

Temperature and flow values during individuals captures varied by species and by FW. The median capture temperature varied from 10 °C (trout) to 22.1 °C (minnow) for the FW1-B, from 7.4 °C (stickleback) to 25.8 °C (minnow) for FW2-A and from 7.9 °C (grayling) to 19.2 °C (common carp) for FW3-O. The river median index flow at which individuals were captured varied from 0.26 (gudgeon) to 1.3 (eel) for FW1-B, from 0.16 (spirlin) to 2.03 (stickleback) for FW2-A and from 0.15 (spirlin) to 1.08 (nase) for FW3-O. The trout was the species captured at the highest water flow index value for the three fishways, with 6 at FW1-B, 5.1 at FW2-A and 3.4 at FW3-O. The minimum water flow index value was 0.10 (minnow) at FW1-B, 0.08 (spirlin) at FW2-A and 0.13 (trout) at FW3-O (Tab. 3).

Most of captures took place at mean flow (flow index values between 0.17 and 0.64) for all FW with 53% of captures at FW1-B, 58% at FW2-A and 73% at FW3-O. The spirlin was the only species that had most of its individuals captured at low flow index values (flow index <0.17) at FW2-A (63.4%) and FW3-O (92.3%). However, at FW1-B 54.7 % of individuals were captured at mean flow index value. The gudgeon at FW1-B, the brook trout at FW2-A, the common bleak and the European catfish at FW2-0 had 100 % of their capture at mean flow index. Other species had most individuals that were captured under different flow index conditions depending on the river (Tab. 4).

4 Discussion

Measures to restore the free movement of fish at physical barriers are generally based on the installation of fishways, as the full removal of these barriers is most often not possible

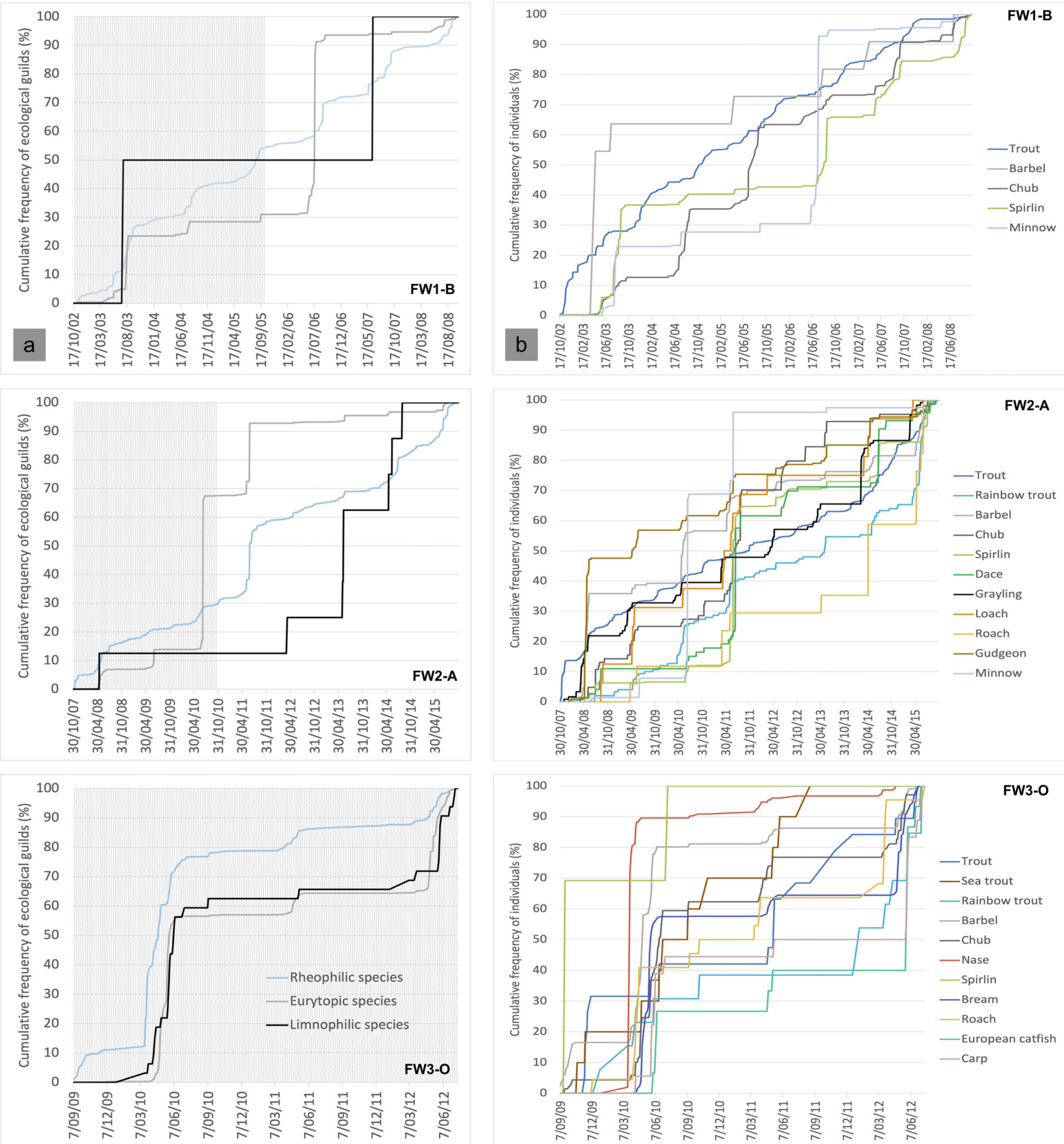

Fig. 3. (a) Cumulative frequency of the three ecological guilds with the shaded area corresponding to the first three years of monitoring common to the three FW and (b) cumulative frequency of captured individuals per species (belonging to the three guilds only) in the Berwinne (FW1-B), Amblève (FW2-A) and Ourthe River (FW3-O) according to the monitoring days.

(Silva *et al.*, 2018). Long-term scientific monitoring of fishways is not frequent, and most studies focus on the reproductive period of a few target species or during a limited time period (synthesis in Noonan *et al.*, 2012 and Benitez *et al.*, 2022). In this study, we performed long-term manual monitoring of three multi-species fishways equipped with capture devices as soon as they were installed in order to analyse their progressive use by fish and to perform analysis on the dynamic of colonisation of the re-opened migratory axis, at a multi-species level and over a long period of time.

Our results show that the three fishways were used by a wide diversity of fish species, as the number of species captured represents 58% of the species potentially present in the Berwinne (species absent: the grayling, the dace, the stone loach, the bullhead, the common bleak, the bream, the pike, the tench and the common rudd), 100% of species in the Amblève and 70% in the Ourthe River (species absent: the

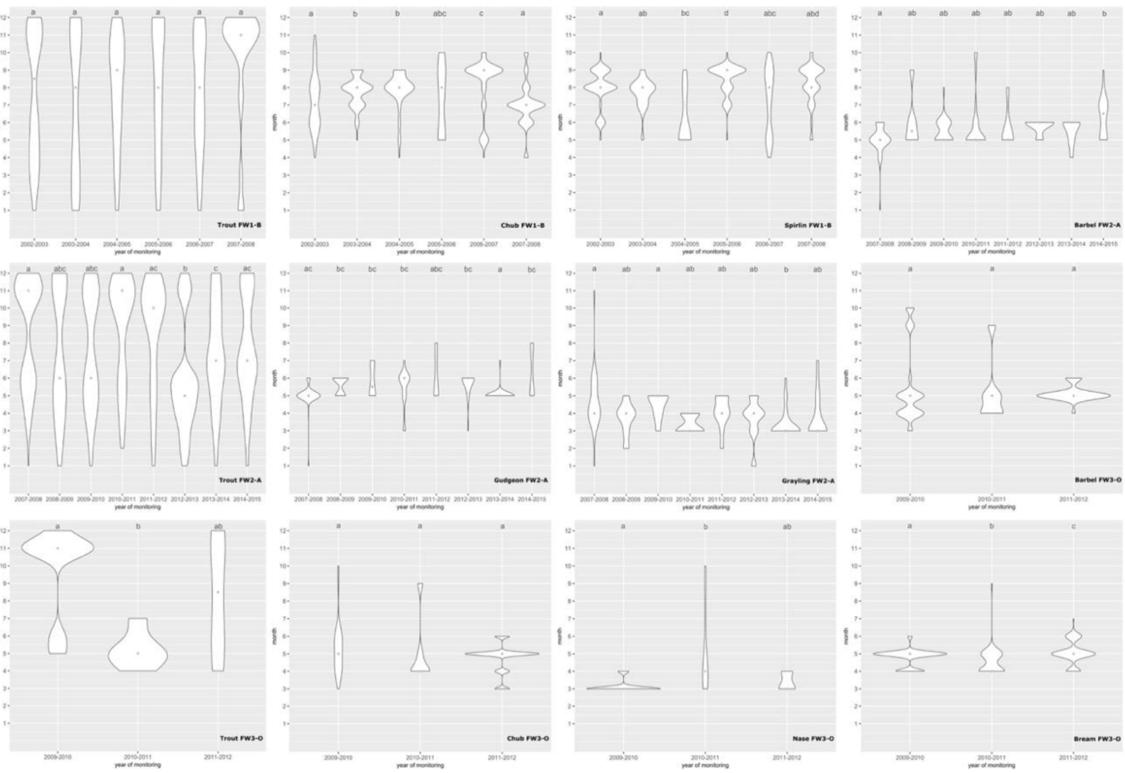

Fig. 4. Violin plots of the periodicity of capture (month) by year of monitoring, and the median represented by a point in the Berwinne (FW1-B), the Amblève (FW2-A) and the Ourthe (FW3-O) River. Species sharing at least one common letter (above each violin plot) did not differ at the 0.05 level of significance.

loach, the bullhead and the minnow). In terms of representativeness of captures in the fishways, the dominant ecological guild was the rheophilic guild in the Berwinne (FW1-B) and in the Amblève (FW2-A) Rivers. These rivers have low mean annual temperatures, coarse substrate and a high current velocity which correspond to rheophilic preferences in terms of habitats (Huet, 1949). The captures in the lower Ourthe River (FW3-O), with higher mean temperature, higher flow and finer substrate, were dominated by the eurytopic species. The important fish diversity sampled in the three fishways attests of their proper functioning through their use by fish species presenting different ecological exigences (Epler *et al.*, 2004; Thiem *et al.*, 2013; Benitez *et al.*, 2015) and swimming capacities (Baudoin *et al.*, 2015). We observed that the number of new fish species captured in the three fishways was variable and gradual from the beginning (axis opening) to the end of the monitoring. Indeed, new species were still captured after 5 years of monitoring at FW1-B, 8 years at FW2-A and 2 years at FW3-O. To obtain 100% of the species captured in the fishways, it took 220 days of monitoring at FW1-B, 935 days at FW2-A and 87 days at FW3-O. Therefore, while lengthening the monitoring time, we succeeded in detecting species which would have been considered absent on a shorter timescale. This underlines the pertinence of long-term monitoring to have a complete view of the fishway use after the opening of a migratory axis as the migratory impulse may vary depending on the species, their functional habitat requirements, or the environment. Lamouroux *et al.* (2006) observed in a fishway of the Rhône River that the number of species varied from 16 to 26 over the 9 years of monitoring while 32 species were counted in total. The variations in terms of species presence over time between the different rivers could originate from potential seasonal biotic and abiotic variations such as environmental factors that may or may not trigger movements, or pressures present in the rivers that will impact movements in fish populations (Veiga *et al.*, 2006; Costa *et al.*, 2007; De Leeuw and Winter, 2008). As the main goal of installing a fishway is to allow species to move through newly opened habitats, our results underline that the colonisation may be a long process in some instances for some species. But, the important point is that in the long term, the connectivity between river stretches is restored.

The greatest number of individuals were captured during the first year of monitoring at FW1-B ($n = 399$ individuals) and FW3-O ($n = 897$ individuals), and during the third year at FW2-A ($n = 1333$ individuals). Results at FW2-A suggest that even if the fishway was used by fishes just after its opening, the fish capture peaks take some time to appear. Sun *et al.* (2022) showed a marked increase in trout abundance 4 years after restoration of a migratory axis in the river Deerness in England. The maximum fish biomass was observed during the first year of monitoring for the three fishways. During the first year of monitoring, larger species identified as roach, barbel, grayling or common carp, increased the biomass despite a small number of individuals. Concerning the Ourthe River, a

Table 3. Temperature and flow index (*i.e.* river flow the day before the capture divided by the average annual flow) values (median, minimum and maximum values) per species having at least 3 individuals captured, at the Bewinne (FW1-B), the Amblève (FW2-A) and the Ourthe (FW3-O) rivers.

Species	Temperature (°C)			Flow index		
	FW1–B Median (Min.–Max.)	FW2–A Median (Min.–Max.)	FW3-O Median (Min.–Max.)	FW1-B Median (Min.–Max.)	FW2-A Median (Min.–Max.)	FW3-O Median (Min.–Max.)
Trout	10.0 (4.5–23.3)	10.3 (1.4–25.9)	11.0 (6.9–18.3)	0.82 (0.14–7.99)	0.60 (0.10–6.89)	0.40 (0.13–3.37)
Sea trout	–	–	16.2 (9.5–24.1)	–	–	0.27 (0.13–0.47)
Rainbow trout	12.0 (9.7–16.6)	14.3 (3.3–25.9)	10.4 (5.6–19.8)	0.50 (0.14–4.61)	0.33 (0.10–2.86)	0.38 (0.30–2.07)
Brook trout	–	14.2 (12.6–16.5)	–	–	0.24 (0.23–0.46)	–
Barbel	12.6 (12.6–19.5)	17.0 (6.4–25.9)	14.4 (7.8–20.4)	1.33 (0.26–1.38)	0.33 (0.10–2.36)	0.40 (0.14–1.55)
Chub	17.4 (11.4–23.3)	18.7 (6.6–20.9)	15.3 (8.1–24.1)	0.57 (0.14–4.39)	0.30 (0.11–3.73)	0.39 (0.13–1.20)
Nase	–	10.5 (7.3–18.0)	10.2 (7.5–17.6)	–	1.24 (0.21–2.20)	1.08 (0.13–1.55)
Spirlin	17.9 (11.9–23.3)	20.9 (8.1–25.9)	18.0 (16.0–25.6)	0.37 (0.11–2.44)	0.16 (0.09–1.68)	0.15 (0.14–0.79)
Dace	–	18.0 (5.8–23.4)	–	–	0.21 (0.12–3.73)	–
Grayling	–	8.9 (2.6–25.9)	7.9 (7.5–25.6)	–	0.46 (0.11–2.40)	0.44 (0.14–0.79)
Loach	–	13.9 (7.8–20.1)	–	–	0.32 (0.16–1.37)	–
Bullhead	–	13.0 (5.8–13.9)	–	–	1.21 (0.26–3.46)	–
Common bleak	–	–	17.6 (17.6–17.6)	–	–	0.22 (0.22–0.22)
Bream	–	–	14.8 (8.4–20.4)	–	–	0.37 (0.16–1.08)
Silver bream	–	–	16.7 (12.7–24.1)	–	–	0.30 (0.13–0.37)
Roach	16.0 (14.3–16.0)	14.4 (8.4–25.9)	10.5 (7.4–18.3)	0.95 (0.29–1.21)	0.22 (0.11–1.32)	0.45 (0.19–1.53)
Gudgeon	19.3 (15.7–20.5)	16.3 (4.6–25.9)	–	0.26 (0.22–0.45)	0.31 (0.09–1.74)	–
Minnow	22.1 (12.8–23.3)	25.8 (11.5–25.9)	–	0.37 (0.11–1.27)	0.17 (0.15–1.75)	–
Eel	14.3 (10.0–20.5)	–	–	1.22 (0.45–4.37)	–	–
Stickleback	13.7 (12.0–16.3)	7.4 (7.3–18.1)	–	0.47 (0.25–1.27)	2.03 (0.31–2.20)	–
European catfish	–	–	18.9 (14.9–20.7)	–	–	0.35 (0.17–0.49)
Pike	–	–	10.2 (7.9–11.9)	–	–	0.70 (0.39–1.20)
Tench	–	–	16.4 (12.0–19.1)	–	–	0.28 (0.25–0.40)
Common carp	–	–	19.2 (15.4–22.8)	–	–	0.35 (0.16–0.77)
Perch	–	14.3 (11.5–25.9)	–	–	0.47 (0.28–1.62)	–

larger number of bream ($n = 479$) were captured during the first year for a weight of 903 kg with a strong influence on the repartition of the biomass. When assessing the effect of the reopening of a migratory axis by means of fishway monitoring, it is, therefore, important not to extrapolate trends of a single year of monitoring. The size diversity of individuals captured showed that the three fishways are used by individuals of different age classes, both juveniles and adults (Prchalová *et al.*, 2011; Benitez *et al.*, 2015).

Our results on the dynamic pattern showed that the rheophilic species were the first to be captured at the three fishways. These species are very exigent in terms of habitats suggesting that they migrate first in order to find new suitable habitats for their needs (De Leeuw and Winter, 2008; Pander *et al.*, 2013; Benitez and Ovidio, 2017). In addition, as rheophilic species tend to be attracted by higher flows, it is possible that they found the input of fishways more easily (Britton and Pegg, 2011; Benitez and Ovidio, 2017; Benitez *et al.*, 2018). Rheophilic species were regularly captured at FW1-B and FW2-A throughout the year of monitoring and had an early capture peak at FW3-O, while the eurytopic species showed later peaks for the first two fishways and an earlier peak for FW3-O. In addition, our results showed that the number of captures during the first year of opening of the migratory axis was overall higher than the total captures during the second and third years after opening suggesting post-opening effect of migratory axis. We observed that the same species may colonise fishways at different time steps, depending on the river. For example, the barbel migrated at FW1-B and FW3-O (with 50% of the individuals captured during the first year after opening), while much later at FW2-A (50% of the individuals having been captured during the third year of monitoring). This species is known for its important mobility, moving regularly between its resting and feeding habitats but also at the time of the spawning period (Baras *et al.*, 1994; Ovidio *et al.*, 2007; Le Pichon *et al.*, 2016). The sea trout, the chub, the nase, the spirling and the bream at FW3-O migrated early at FW3-O (with 50% of the individuals captured during the first year of monitoring). This tendency may be associated with a quick colonisation process of the migratory axis since, subsequently, the number and biomass of individuals captured for these species decreased (Benitez *et al.*, 2015). Other species reached 50% of capture rate after more than two years of monitoring like the minnow at FW1-B and FW2-A or the roach and the dace at FW2-A with strong variations between years, as previously shown in the Elbe River in Czech Republic (medium flow conditions = 160 m^3/s) where the abundance of captures varied from one year to

Table 4. Proportion of capture per species (%) by index flow category; low flow migration (< percentile 25), mean flow migration (between percentile 25 and percentile 75), high flow migration (> percentile 75) with percentile 25 = 0.17 and percentile 75 = 0.64.

Species	FW1–B			FW2–A			FW3–O		
	<P25	[P25–P75]	>P75	<P25	[P25-P75]	>P75	<P25	[P25-P75]	>P75
Trout	1.5	37.7	60.8	9.4	44	46.6	14.3	66.7	19
Sea trout	–	–	–	–	–	–	10	90	0
Rainbow trout	25	25	50	24.3	53.1	22.6	0	64.3	35.7
Brook trout	–	–	–	0	100	0	–	–	–
Barbel	0	27.3	72.7	13.8	77.6	8.6	2.4	78.8	18.9
Chub	2.2	52.9	44.9	7.1	64.3	28.6	9.6	75.3	15.1
Nase	–	–	–	0	50	50	0.6	12.2	87.2
Spirlin	4.9	54.7	40.3	63.4	29	7.6	92.3	7.7	0
Dace	–	–	–	14.9	77	8.1	–	–	–
Grayling	–	–	–	2.5	61.5	36.1	33.3	33.3	33.3
Loach	–	–	–	5.9	70.6	23.5	–	–	–
Bullhead	–	–	–	0	20	80	–	–	–
Common bleak	–	–	–	–	–	–	0	100	0
Bream	–	–	–	–	–	–	0.2	84.3	15.5
Silver bream	–	–	–	–	–	–	20	80	0
Roach	0	33.3	66.7	27.8	61.1	11.1	0	65.2	34.8
Gudgeon	0	100	0	10.9	85.9	3.2	–	–	–
Minnow	11.2	68.3	20.5	5.8	92.7	1.5	–	–	–
Eel	0	20	80	–	–	–	–	–	–
Stickleback	0	75	25	0	33.3	66.7	–	–	–
European catfish	–	–	–	–	–	–	0	100	0
Pike	–	–	–	–	–	–	0	33.3	66.7
Tench	–	–	–	–	–	–	0	100	0
Common carp	–	–	–	–	–	–	5.6	88.9	5.6
Perch	–	–	–	0	80	20	–	–	–

another depending on temperature and flow conditions (Prchalová *et al.*, 2011). These results underline that the temporal dynamic of colonisation of a newly opened river stretch is quite variable between species but also for the same species living in different habitats, and that a complete vision of the process requires multi-year monitoring from the opening.

In terms of periodicity of movements between monitoring periods, we observed that the majority of species (except the trout at FW1-B, the barbel and the dace at FW3-O) had a trend of periodicity that varied over time. Variations of recruitment rates and differences in terms of environmental conditions over monitoring time are important factors that influence movement periodicity over time (Ovidio and Philippart, 2008; Tummers *et al.*, 2016; Pachla *et al.*, 2022). In addition, it could also be expected that movement of individuals from downstream areas to the newly open upstream river stretch may influence the population dynamic and define new biological exchanges that influence mobility patterns of the different size classes in the river (Roscoe and Hinch, 2010). Despite variations of movement periodicity over time, the main peaks were observed during spawning periods for the barbel, the gudgeon, the nase, the grayling, the chub and the bream, which is consistent with the literature (Philippart, 1989; Lucas and Batley, 1996; Fredrich *et al.*, 2003; Epler *et al.*, 2004; Ovidio *et al.*, 2007; Ovidio and Philippart, 2008; Benitez *et al.*, 2015; Romão *et al.*, 2019; Winter *et al.*, 2021). The spirlin at FW1-B showed main peaks outside of its migration period, as also observed by Benitez *et al.* (2015).

Most of the captures were observed above 8 degrees for the three fishways, although some captures of individuals took place at lower temperatures (*e.g.* trout captures between 5 and 7 °C or the grayling captures at FW2-A and FW3-O between 6 and 7 °C). In the Odra River in Poland (mean annual flow = 168 m^3/s), similar results were obtained with fish captures starting/increasing when temperature reached 8 °C (Kotusz *et al.*, 2006). Temperature ranges of captures for a single species was variable between fishways but with close median values. Some species had wide temperature capture ranges in some fishways and limited in others like the roach with temperatures ranging from 14 to 16 °C at FW1-B (median = 16), 8 to 26 °C at FW2-A (median = 14) and 7 to 18 °C at FW3-O (median = 10.5). The spawning period strongly influenced the temperatures at which individuals of most species were captured (Prchalová *et al.*, 2011; Benitez and Ovidio, 2017). In addition, movement of individuals of a species can vary not only with temperature but also with flow, and sometimes both together (Ovidio *et al.*, 1998; Slavík *et al.*, 2009; Boavida *et al.*, 2018). As for temperature, the flow rate at capture was very variable from one fishway to another as observed by Benitez and Ovidio (2018). The trout was captured at both low and high flow index values. Salmonids are known for their great swimming ability to cope with higher flow conditions (Slavík *et al.*, 2009). The large difference in flow at which trout were captured could be explained by different types of movements (reproduction, habitat change). We observed that during some peaks of flow index values, large rheophilic species were captured (trout, rainbow trout, barbel, chub and nase) while small species were preferentially captured at relatively lower flow values like the minnow and the spirlin (Prchalová *et al.*, 2011). Since the ability to swim against current velocity is related to the size of the individuals, large species would be more adapted to move during important flows, contrary to smaller individuals (Rasmussen and Belk, 2017; Mameri *et al.*, 2019; Stoffers *et al.*, 2022). These differences in the influence of environmental factors on the period of movement must be considered when assessing the effect of river connectivity restoration.

Our study based on multi-annual multi-species analysis of the dynamics of fish colonisation of three fishways in three rivers in Belgium showed a wide temporal diversity of species moving upstream through the devices. We detected the presence of different capture peaks and the arrival of new species, sometimes long time after the opening of the migratory axis. The dynamic of captures varied according to the year of monitoring showing that periodicity may fluctuate over time and depending on the river for some species. In the future, to determine the ecological benefit of the opening of new axis for fish populations, it would be interesting to (i) realize an exhaustive fish sampling downstream of the obstacle (before the opening of the migratory axis) in order to obtain information on the species likely to migrate; (ii) incorporate active telemetry monitoring data of individuals that crossed fishways to analyse their capacity to reproduce and to develop adapted behavioural tactics to exploit new habitats.

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