Article

Assessment of Fish Abundance, Biodiversity and Movement Periodicity Changes in a Large River over a 20-Year Period

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Abstract: A river is an ecosystem where fish fauna represents an important structural element. To re-establish connectivity, it is imperative to allow movement between functional habitats. Due to the hydromorphological complexity of large anthropized rivers and the lack of study techniques that can be used in such environments, relevant data with regard to fish ecology are scarce. On the River Meuse, Belgium, at a point 323 km upstream from the North Sea, the Lixhe hydroelectric dam is equipped with two fishways. Both were continuously monitored using capture traps for 20 consecutive years (from 1999 to 2018), representing 4151 monitoring events. The objectives of the present study were to describe the overall abundance and movement indicators of mainly holobiotic potamodromous fish species and to analyse their temporal evolution. We captured 388,631 individuals (*n* = 35 fish species) during the 20 years of fishway monitoring; 22.7% were adults (>75% of which were cyprinids), and 83.3% juveniles (>90% cyprinids). From 1999 to 2018, the results showed a drastic reduction in yearly captures for some native species as well as the apparent emergence of non-native (e.g., *Silurus glanis*) and reintroduced species (e.g., *Salmo salar*). The annual capture periodicities associated with environmental factors were clearly defined and were mostly related to the spring spawning migration of the adult stage. This long-term monitoring demonstrated how the fishways are used by the whole fish community and allowed a better understanding of their movement ecology in a large lowland anthropized river. The appearance of non-native species and the drastic decline in abundance of some common and widespread European fish should prompt river managers to adopt conservation measures.

Keywords: anthropized; fishway; free movement; mobility pattern; monitoring; potamodromous; River Meuse; temporal trend

1. Introduction

Rivers are fragmented by many obstacles for the purposes of hydropower, navigation, flow control, or water supply [1]. River fragmentation by dams causes physicochemical and hydromorphological modifications of upstream and downstream habitats, hydropeaking, alterations to the river's natural flow, and obstruction to sediment and biological organisms such as fish and invertebrates [2–4]. In an ecosystem where fish fauna represents an important functional element, it is imperative to re-establish connectivity to allow each species to complete its life cycle [5–7], because these barriers fragment previously natural rivers and can thus preclude movement between functional habitats [8,9]. The complete

removal of obstacles would constitute the ideal scenario, but this is typically complicated to implement due to the presence of numerous social and usage constraints [4,10]. A mitigation solution for the restoration of free movement is the development of a fishway, which must be multi-species and allow the circumvention of the obstacle in question by both diadromous (highly migratory) and potamodromous species [5,9,11,12]. The latter are important because they constitute sentinel species in terms of the ecological conditions of river environments due to their abundance and their ecological requirements.

Anthropogenic pressures such as migration barriers can affect global freshwater biodiversity [13]. Temporal surveys offer a useful means to detect potential effects, including the identification of endangered species [14]. Nevertheless, long-term comparisons of fish assemblages in rivers are rarely possible because of the scarcity of historical data [15]. Consequently, few studies have attempted to highlight multi-species temporal evolutions in complex environments such as lowland rivers using point-electrofishing data [16–18], or partial count data from fishways [19], where the data are not collected using the same method in the same place within a historical context. Electrofishing in small units of a habitat is frequently performed in large rivers where extensive fish surveys are impossible, but inevitably provides uncertain estimates of fish community characteristics [20]. Moreover, presence and absence data do not reflect the majority of changes in biota, given that such changes are more complex than the simple disappearance or appearance of particular species; a more nuanced understanding can only be obtained from a quantitative analysis [15]. Indeed, the International Union for Conservation of Nature (IUCN) uses the rate of abundance decrease as a criterion for building its Red List. Furthermore, surveys of fish populations provide crucial information on the population dynamics of invasive species, thereby allowing identification of those species for which control operations are required [14]. Finally, climate change, habitat degradation, and artificial connections between river basins can enable the establishment of invasive species, which present an ecological risk through affecting community structure and ecosystem functions [19,21].

Studies of potamodromous fish species' mobility patterns tended to use radio telemetry, e.g., [22–25], Passive Integrated Transponder (PIT) telemetry [11,26] and, more recently, acoustic telemetry, e.g., [27–30]. Fish movements have rarely been studied in large lowland hydrosystems, as noted by Radinger and Wolter [31] in their review, finding that 80% of studies involved small rivers (<15 m^3/s) with a narrow stream width (<10 m). This situation can be explained by both practical and environmental constraints. Indeed, although the data collected by active telemetry (radio and acoustic) tend to be very accurate, these methods require significant financial (transmitters, detection systems) and human resources (e.g., fish capture, tagging, fish tracking, data processing). Another limitation of such studies is the duration as demonstrated by Radinger and Wolter [31], who noted a median duration of 150 days, mainly due to the short life span of the transmitters used and the small number of species and individuals studied.

New methods of fish-passage inventories have appeared with the development of video [32], but their operation has proved limited owing to the turbidity that exists in lowland rivers and the difficulty of distinguishing between close species. A fishway combined with a capture trap with a real and continuous counting may be an alternative tool for studying fish abundance and fish movements at a multi-species level in such environments, considering that a fishway in the upstream direction is necessary to enable movement towards upstream habitats [11]. The use of a capture trap at large time scales allows one to collect complementary information on the local fish fauna, such as changes in species diversity, abundance, and seasonality of migration patterns, at different developmental stages [5,19]. The simultaneous and continuous recording of environmental factors allows the identification of thresholds (triggers or inhibitors) affecting fish movements, such as spawning migration and dispersal movement outside the spawning season [33,34]. Indeed, it is imperative to study fish behavioural ecology more precisely at large time scales in order to improve our understanding of their biological responses, particularly when environmental changes (both climatic and anthropogenic) are so prevalent.

In the lowland Belgian Meuse River, two fishways (an old pool-type and a new vertical-slot pool-type) equipping a hydroelectric dam have been monitored by capture traps, using the same methodology for 20 consecutive years. Such long-term monitoring can be regarded as a useful tool to understand changes in an aquatic environment, using fish as biological sentinel species. The aims of this study were to study the overall and temporal evolution of fish abundance as well as fish movement indicators of holobiotic potamodromous and diadromous fish species in the River Meuse at multi-species and multi-stage scales. We analysed: (i) fishway utilisation (fish biodiversity, headcount, biomass and proportion of different life-stage and ecological groups); (ii) the difference in fish biodiversity between the old and new fishways; (iii) the evolution of fish communities, using abundance and fish biodiversity indices over time; and (iv) mobility patterns at annual scales for adult and juvenile stages using fish movement indicators and their changes over time.

2. Materials and Methods

2.1. Study Site

The Meuse River basin drains a catchment area of 36,000 km^2. The Belgian downstream part of the Meuse has an average annual discharge of 400 m^3/s and is, therefore, classified as a bream fish zone [35]. This study was conducted at the first dam of the Belgian part of the Meuse (at Lixhe), 323 km upstream from the North Sea, on a non-navigable part of the river. Built in 1980, the Lixhe dam, which measures 8 m high (Figure 1), was built to facilitate navigation and to produce hydroelectricity via its four Kaplan turbines on the right bank of the river (a 23,200 kW hydroelectric plant). Since its construction, a first fishway F1 (Table 1) working at low discharge (maximum 0.3 m^3/s) has been located in the middle of the dam between the turbines and the valves. F1 is equipped with a cone trap in the most upstream pool and a fine grid in the upstream slot, retaining all the fish that use it, including eels and small fish (minimum capture size: 10 mm). A second fishway F2 (Table 1) was built in 1998 to cater more specifically for the migration of large fish species such as Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. It operates at high flow (1 m^3/s) and includes an attraction flow of 2.5 m^3/s. F2 is located on the right bank and is equipped with a cage trap and a lift in the upper pool, which retains large fish, but not eels and small fish (minimum capture size: 150 mm).

2.2. Fishway Monitoring and Environmental Factors

From January 1999 to December 2018 (20 years), fishways and capture traps were in continuous operation and were each equipped with an upstream grid preventing the capture of individuals from upstream. Any fish (>150 mm for F2) that arrived upstream of the pass was therefore present in the trap while waiting to be monitored. A total of 4,151 fishway monitoring events of capture traps were performed (*n* = 1704 for F1, and *n* = 2447 for F2). The monitoring frequency of capture traps varied from one to five times per week (mean times = 2.3/week), according to the intensity of fish capture. From 2011, for safety reasons during winter conditions, F1 was monitored only between April and October, although only 1.3% of captures were observed in F1 from 1999 to 2010. During monitoring, the upstream part of F1 was completely closed to drastically reduce the flow within the five first pools, and fish were caught with a dip net in the upper pool. During the monitoring of F2, a grid was manually placed downstream of the cage just before the ascent, preventing other fish from passing during the monitoring. The cage was lifted partially out of the water. On each monitoring date, captured individuals were: (i) taken out of the upstream pool of F1 or the cage of F2 with a hand net; (ii) placed in a tank containing river water; (iii) anaesthetised in a solution of 4-allyl-2-methoxyphenol (Eugenol: 0.1 mL/L); (iv) identified to the species level, counted, measured (±1 mm, fork length), and weighed (±1 g); they were then (v) released upstream of the dam after a 10-minute recuperation period.
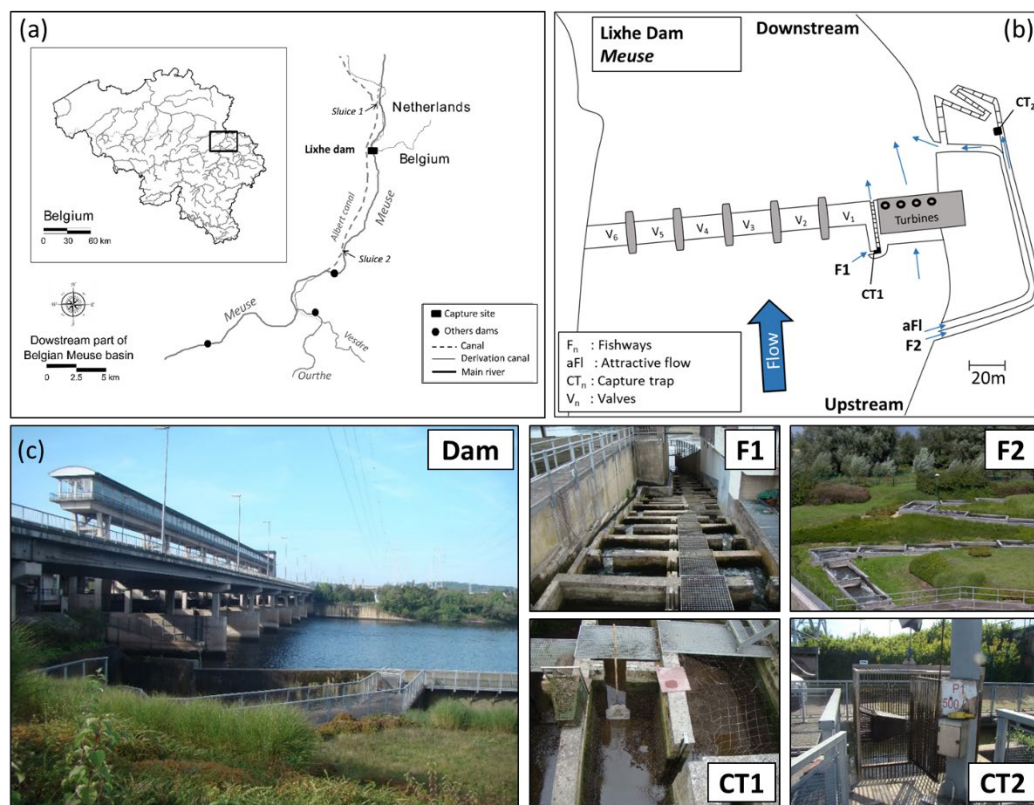
Figure 1. Location of the study site at the Belgian scale (**a**); schematic representation of the study site (**b**); pictures of the dam, the fishways (F1 and F2) and the capture traps (CT1 and CT2) (**c**).

Table 1. Characteristics of the fishways at Lixhe dam on the Meuse River.

Characteristics	Fishway F1	Fishway F2
Fishway type	Pool and weir	Alterne vertical slot
Construction year	1980	1998
Discharge of fishway (m^3/s)	0.3	1
Attraction flow (m^3/s)	0.2	2.5
Length (m)	48	165
Pool number	56	26
Pool size, length $\times$ width (m)	1.5 to 2.5 $\times$ 1.2	4.7 to 9.7 $\times$ 2.5
Pool water depth (m)	1	1.5
Height between pools (m)	0.15	0.3
Water depth of slot (m)	0.3	1.3
Slot width (m)	0.35	0.4

Fish were categorised into the ecological groups (eurytopic, limnophilic and rheophilic species) proposed by Schiemer and Spindler [36] according to their preferred habitat. We used Philippart and Vrancken's [37] research on the Meuse River basin to delineate the size limit (maturity size) between adult and juvenile stages for each fish individual of all species. Water temperature (°C) was recorded continuously every hour using data loggers (Tidbit Onset) installed at the inlet of F1. Hourly flow data (m^3/s) and hourly dissolved oxygen (mg/L) were provided by the Wallonia Public Service of Hydrological Studies (SETHY, Walloon Region) of a station installed just upstream of the Lixhe dam. The environmental data were then transformed into daily average values. During each monitoring event, each fish capture was linked with the environmental data of the previous day's capture [5].

2.3. Data and Statistical Analysis

We analysed environmental factors during the study period (1999 to 2018) using boxplots. To detect any monotonic temporal trend, non-parametric Mann–Kendall tests (MK test) [38,39] were applied to the median annual values for water temperature, water flow, and dissolved oxygen. The relative abundance of captured fish for both fishways was described at the ecological group level and at the species level for both stages. The distribution of proportions of adult and juvenile stages was compared between the fishways using the parametric chi-square test. We studied temporal trends in: (i) proportions by year of headcount and biomass (total and by ecological group), and (ii) capture headcount by year for the most abundant species for both stages, using the MK test (positive trend = increase in capture by year; negative trend = decrease in capture by year). The mobility patterns were defined by annual capture periodicities through the date of capture within fishways. To investigate the characteristics of capture periodicities by capture peak, for adult and juvenile stages, environmental values (temperature and flow) and fish-size data were assigned to the 10th, 50th, and 90th percentiles for fish species with a total abundance of more than 10 individuals over the 20 years of monitoring. Finally, we analysed temporal trends (MK test) in migration phenology for the adult stage of the most abundant species (reaching a minimum of five individuals over 10 years) and used a simple linear regression analysis to identify relationships between migration indicators by year, the capture headcount per year, and the mean spring temperature. For all statistical tests, the significance level was set at $p < 0.05$ and performed using the R statistical programme (The R Foundation for Statistical Computing, Vienna, Austria, version 3.1.1.).

3. Results

3.1. Fluctuations in Environmental Factors

The median annual water temperature between 1999 and 2018 (median annual value ± IQR) varied between 13.6 ± 11.7 °C (2012) and 17.0 ± 11.0 °C (2007, Figure 2). The median annual water flow between 1999 and 2018 varied between 41.8 ± 158.6 m³/s (2005) and 358.4 ± 441.4 °C (2001). No significant positive or negative temporal trend was observed in median annual water temperatures or median annual water flows (MK test, $p > 0.05$). The median annual dissolved oxygen showed a significant positive temporal trend (MK test, tau = 0.35, $p = 0.03$), with values ranging from 6.6 mg/L to 10.1 mg/L.
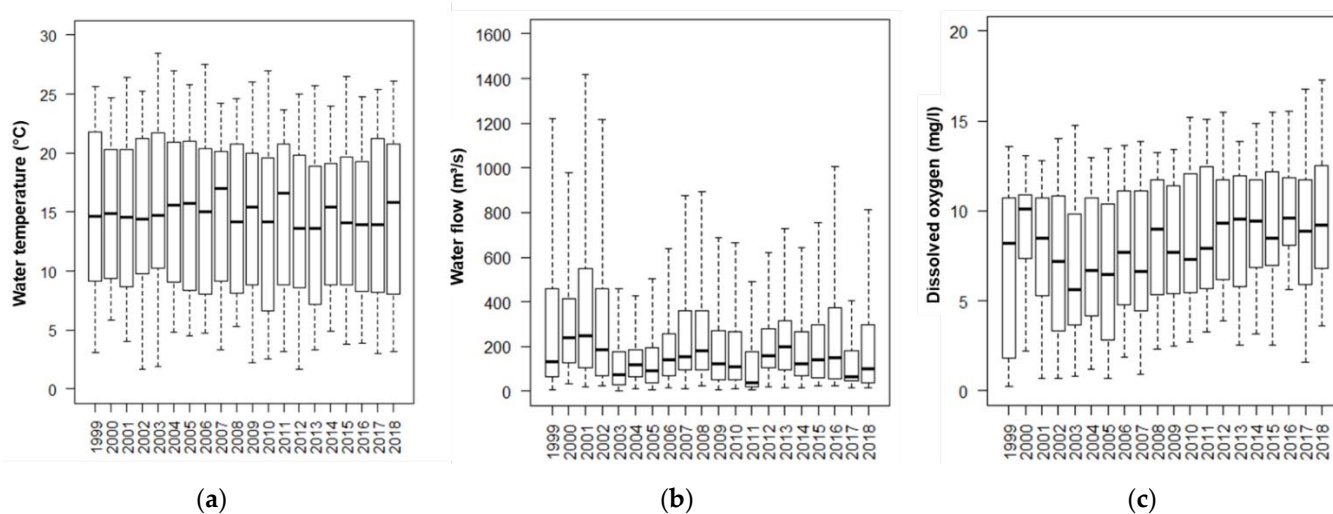

Figure 2. Global values per year from 1999 to 2018 of mean daily water temperature (**a**), mean daily water flow (**b**), and mean daily dissolved oxygen (**c**).

3.2. Overall Biodiversity and Change over Time

From January 1999 to December 2018, 388,631 fish belonging to 35 species were captured in the fishways of the Lixhe dam (93.6% in F1, 6.4% in F2; Table 2), with a total biomass of 30,229 kg. Juveniles accounted for 83.3% of total captures in terms of the number of individuals and for 2.5% of the total biomass. The proportions of adults and juveniles differed significantly between F1 (16.3% vs. 83.7%, respectively) and F2 (99.4% vs. 0.6%, respectively) (chi-square test, $p < 0.001$). Combining the data from F1 and F2, the most represented fish families were Cyprinidae (85.4%), Aercidae (9.3%) and Anguillidae (4.9%). By ecological group, eurytopic species were in the majority (88.4%), far exceeding limnophilic (9.5%) and rheophilic species (2.1%). At the specific level, roach *Rutilus rutilus* (67.6%), common bleak, *Alburnus alburnus* (17.9%) and perch *Perca fluviatilis* (11.7%) were the most frequently captured species in the juvenile stage. In the adult stage, the most common species were common bleak (28.4%), common bream *Abramis brama* (23.2%), European eel *Anguilla anguilla* (22.8%), and roach (19.2%).

Table 2. Overall results (i.e., total for F1 and F2) of fish capture numbers from 1999 to 2018 differentiating between adult and juvenile results and ecological group information (Eury. = eurytopic; Rheo. = rheophilic and Limno. = limnophilic).

Species		Ecol. Group	N Total	N F1	N F2
Common Name	**Latin Name**		(N Adult—N Juvenile)	(N Adult—N Juvenile)	(N Adult—N Juvenile)
Anguillidae					
European eel	*Anguilla anguilla*	Eury.	19,163 (19,163–0)	19,163 (19,163–0)	0
Cyprinidae					
Asp [†]	*Aspius aspius*	Rheo.	752 (283–469)	470 (1–469)	282 (282–0)
Barbel	*Barbus barbus*	Rheo.	464 (351–113)	127 (24–103)	337 (327–10)
Chub	*Leuciscus cephalus*	Rheo.	1309 (709–600)	642 (45–597)	667 (664–3)
Common bleak	*Alburnus alburnus*	Eury.	78,342 (23,866–54,476)	77,358 (22,882–54,476)	984 (984–0)
Common bream	*Abramis brama*	Eury.	21,944 (19,504–2440)	6352 (3921–2431)	15,592 (15,583–9)
Common Carp [†]	*Cyprinus carpio*	Eury.	198 (197–1)	3 (2–1)	195 (195–0)
Crucian carp	*Carassius carassius*	Limno.	11 (11–0)	6 (6–0)	5 (5–0)
Dace	*Leuciscus leuciscus*	Rheo.	77 (45–32)	76 (44–32)	1 (1–0)
Grass carp [†]	*Ctenopharyngodon idella*		2 (2–0)	0	2 (2–0)
Gudgeon	*Gobio gobio*	Rheo.	69 (68–1)	64 (63–1)	5 (5–0)
Ide	*Leuciscus idus*	Rheo	3209 (68–3141)	3148 (12–3136)	61 (56v5)
Koi [†]	*Cyprinus carpio*	Limno.	6 (6–0)	0	6 (6–0)
Minnow	*Phoxinus phoxinus*	Rheo.	53 (31–22)	53 (31–22)	0
Nase	*Chondrostoma nasus*	Rheo.	676 (308–368)	369 (3–366)	307 (305v2)
Prussian carp [†]	*Carassius gibelio*	Limno.	10 (10–0)	9 (9–0)	1 (1–0)
Roach	*Rutilus rutilus*	Eury.	222,256 (16,136–206,120)	217,767 (11,700–206,067)	4489 (4436–53)
Rudd	*Scardinius erythrophthalmus*	Eury.	73 (72–1)	52 (51–1)	21 (21–0)
Silver bream	*Blicca bjoerkna*	Eury.	1482 (1477–5)	461 (456–5)	1021 (1021–0)
Spirlin	*Alburnoides bipunctatus*	Rheo.	780 (278–502)	777 (275–502)	3 (3–0)
Tench	*Tinca tinca*	Limno.	249 (248–1)	57 (57–0)	192 (191–1)
Percidae					
Perch	*Perca fluviatilis*	Limno.	36,107 (237–35,870)	35,985 (192–35,793)	122 (45–77)
Ruffe	*Gymnocephalus cernua*	Limno.	5 (4–1)	5 (4–1)	0
Zander	*Sander lucioperca*	Limno.	4 (3–1)	2 (2–0)	2 (1–1)
Salmonidae					

Table 2. *Cont.*

Species		Ecol. Group	N Total	N F1	N F2
Common Name	Latin Name		(N Adult—N Juvenile)	(N Adult—N Juvenile)	(N Adult—N Juvenile)
Brook trout [†]	*Salvelinus fontinalis*	Rheo.	3 (3–0)	2 (2-0)	1 (1–0)
Rainbow trout [†]	*Oncorhynchus mykiss*	Rheo.	14 (14–0)	7 (7-0)	7 (7–0)
Salmon [‡]	*Salmo salar*	Rheo.	180 (180–0)	1 (1-0)	179 (179–0)
Trout	*Salmo trutta*	Rheo.	353 (346–7)	37 (31-6)	316 (315–1)
Other species					
Pike	*Esox lucius*	Limno.	8 (8–0)	0	8 (8–0)
Pumpkinseed [†]	*Lepomis gibbosus*	Limno.	1 (1–0)	0	0
Catfish [†]	*Silurus glanis*	Eury.	173 (173–0)	0	173 (173–0)
Tilapia [†]	*Oreochromis niloticus*	Limno.	1 (1–0)	0	0
Round goby [†]	*Neogobius melanostomus*	Limno.	655 (100–555)	653 (98-555)	2 (2–0)
Kessler's goby [†]	*Ponticola kessleri*	Limno.	1 (1–0)	0	1 (1–0)
Stickleback	*Gasterosteus aculeatus*	Eury.	1 (1–0)	0	0
Total			388,631 (83,905–304,726)	363,648 (59,084–304,564)	24,983 (24,821–162)

[†] non-native species; [‡] reintroduced species.

Over the 20-year period, in the case of the adult stage of all species, we observed a significant negative temporal trend with regard to the proportions of all individuals captured per year (MK test, tau = −0.72, $p < 0.001$) (Figure 3). In terms of ecological groups, there were significant temporal trends (negative) only for proportions of eurytopic individuals at adult stage (MK test, tau= −0.74, $p < 0.001$). Furthermore, in the adult stage, there were significant negative temporal trends (MK test, $p < 0.05$) with regard to the total biomass captured per year (tau = −0.54) and the proportions of eurytopic (tau= −0.55) and limnophilic biomass (tau = −0.54). On the other hand, we observed a significant positive temporal trend with regard to the proportion of rheophilic biomass per year (MK test, tau = 0.50, $p = 0.002$). The number of adults per year (Figure 4a) significantly decreased over time (MK tests, $p < 0.05$) for nine species: bream (tau = −0.81), yellow eel (tau = −0.74), tench (tau = −0.63), silver bream (tau = −0.62), gudgeon (tau = −0.60), bleak (tau = −0.44), perch (tau = −0.41), roach (tau = −0.41), and rudd (tau = −0.37). Conversely, we observed a significant increasing trend between 1999 and 2018 with regard to the number of adults (MK test, $p < 0.05$) of six species: catfish (tau = 0.70), asp (tau = 0.69), spirlin (tau = 0.67), goby (tau = 0.64), Atlantic salmon (tau = 0.62), and trout (tau = 0.41). The species showing no significant temporal trend in number in the adult stage (MK test, $p > 0.05$) were chub, dace, nase, carp, barbel, ide, and minnow.

Over the 20-year period, in the case of the juvenile stage of all species, we observed a significant negative temporal trend (MK test, $p < 0.001$) with regard to the proportions of all individuals captured per year (tau = −0.46, $p < 0.001$) and for the total proportions of biomass captured per year (tau = −0.39) (Figure 3). In terms of ecological groups, there were significant negative temporal trends (MK test, $p < 0.05$) only for the proportions of eurytopic individuals (tau = −0.47) and eurytopic biomass (tau = −0.48). Six species showed a significant decreasing trend (MK test, $p < 0.05$; Figure 4b) in number over time: chub (tau = −0.62), bream (tau = −0.60), roach (tau = −0.59), bleak (tau = −0.55), dace (tau = −0.40), and nase (tau = −0.39). Two species significantly increased in number between 1999 and 2018 (MK test, $p < 0.05$): goby (tau = 0.64) and asp (tau = 0.50). The other four species represented in the juvenile stage (roach, ide, spirlin, barbel and perch) showed no significant temporal trend in number (MK test, $p > 0.05$).
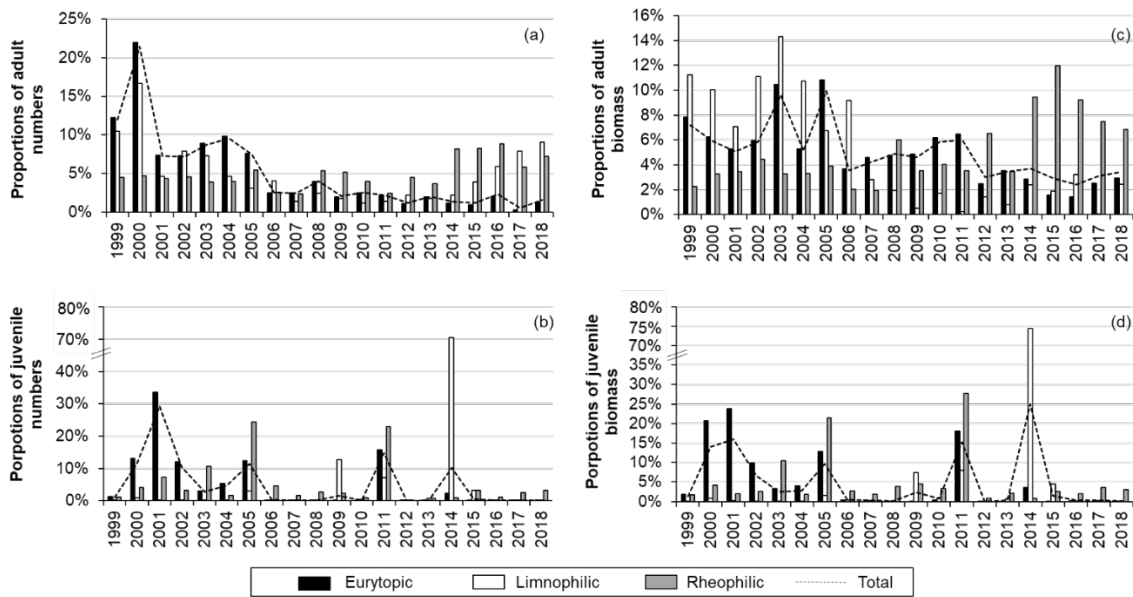
Figure 3. Temporal evolution of proportions of individuals captured as adults (**a**) and as juveniles (**b**); and proportions of biomass for adults (**c**) and for juveniles (**d**) both according to their ecological group (bar charts) and in total (black dotted lines).
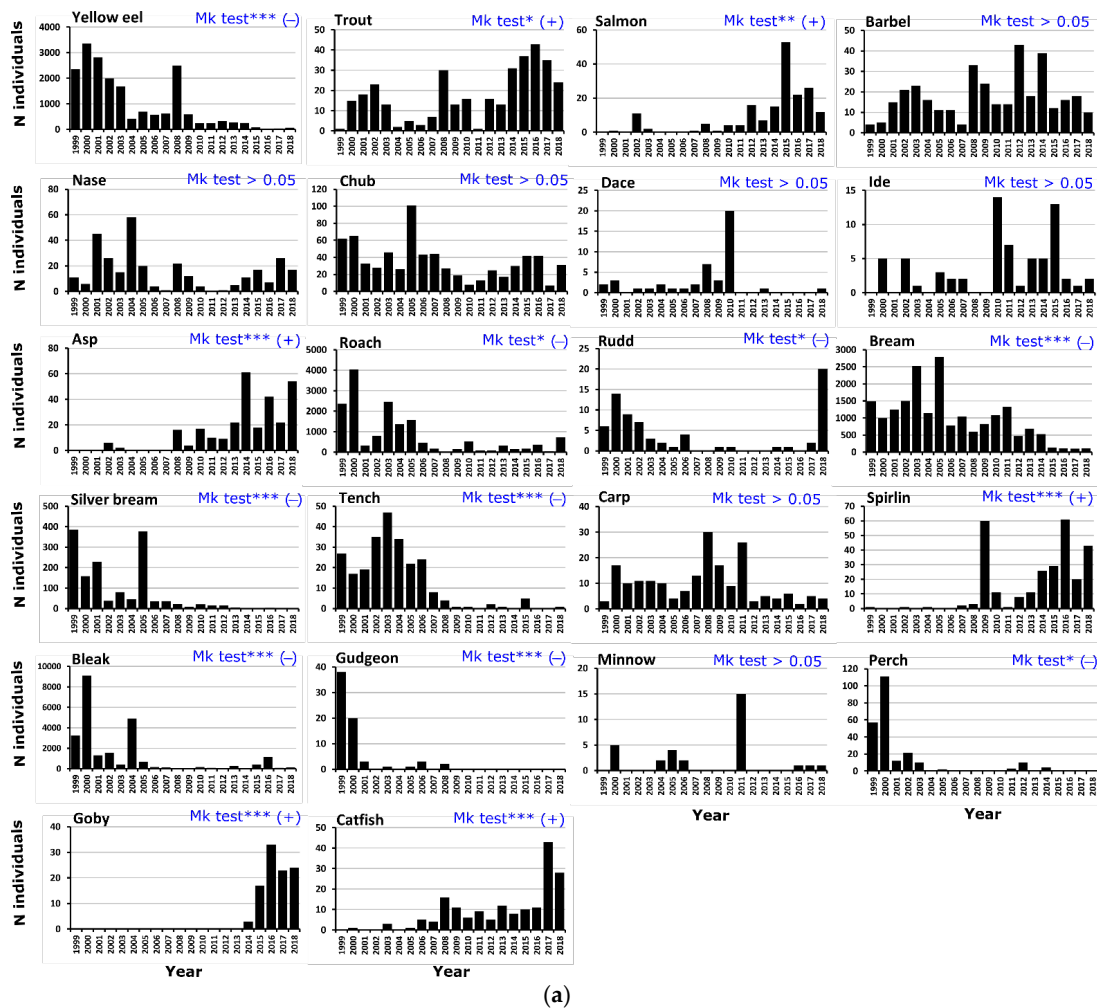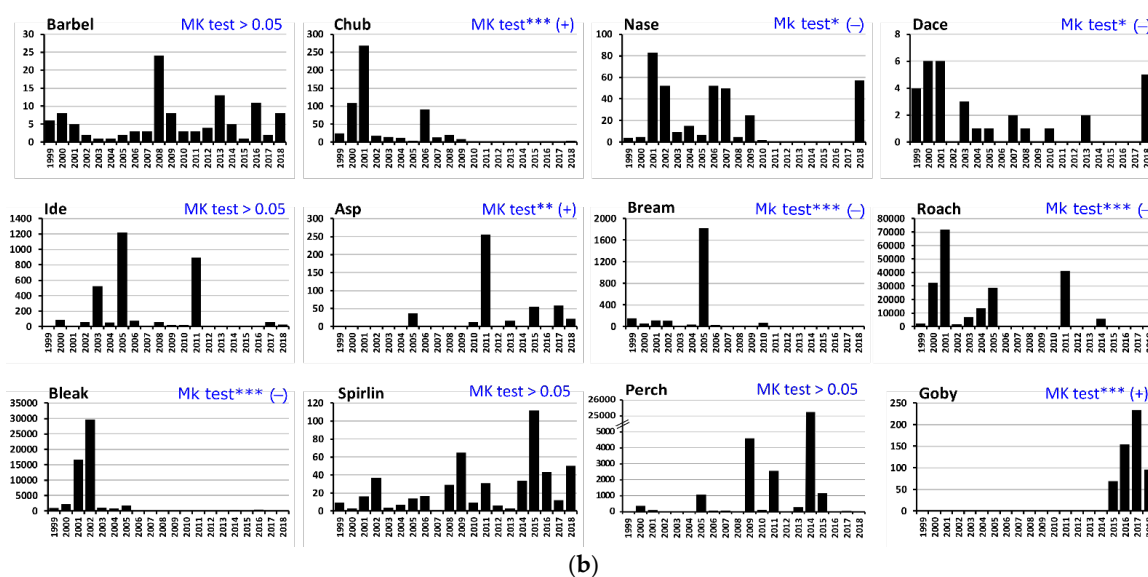

Figure 4. *Cont.*

Figure 4. Temporal evolution of the headcount (number of individuals captured per year) by species (**a**) in the adult stage from 1999 to 2018 and (**b**) in the juvenile stage from 1999 to 2018; in blue, the results of the Mann–Kendall test (positive temporal evolution of the headcount: +; negative temporal evolution: −; level of significance: (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

3.3. Overall Fish Movement Indicators and Their Changes over Time

3.3.1. Annual Capture Periodicities by Species

Among the 35 species captured, a degree of seasonality was observed in the adult stage in 24 species (Figure 5a–c). Some species were captured mainly during the spring: nase (97.7%), bream (97.1%), silver bream (97.1%), bleak (89.3%), chub (85.6%), roach (85.2%), gudgeon (83.8%), and carp (83.7%). One species (spirlin) was captured mainly during the summer (90.3%). Several species were captured in the trap during the spring and the summer: asp (79.9% in spring, 19.8% in summer), catfish (78.0%, 20.8%), goby (75.0%, 23.0%), tench (74.2%, 25.4%), minnow (64.5%, 35.5%), eel (60.9%, 38.9%), rudd (55.6%, 38.9%), Prussian carp (50%, 50%), and crucian carp (36.4%, 63.6%). Three other species were observed during the spring and the autumn: barbel (69.8% in spring, 25.6% in autumn), dace (51.1%, 46.7%), and ide (45.6%, 45.7%). Finally, some species used the fishway during the spring, the summer, and the autumn: perch (75.5% in spring, 13.9% in summer, 9.7% in autumn), trout (40.7%, 25.4%, 28.6%), and salmon (36.1%, 11.1%, 51.1%).

During the study period, the seasonality of capture in the juvenile stage was calculated for 13 species (Figure 5a–c). Juveniles were mainly captured during the summer: asp (99.6%), perch (99.4%), ide (97.2%), roach (96.2%), chub (92.7%), and bleak (92.2%). Six species were captured during the summer but also during the spring and the autumn: barbel (15.9% in spring, 72.6% in summer, 11.5% in autumn), bream (5.0%, 69.9%, 25.1%), dace (15.6%, 62.5%, 18.7%), nase (17.7%, 57.1%, 24.2%), goby (54.9%, 42.8%, 2.2%), and spirlin (56.6%, 42.3%, 1.2%). Minnow juveniles were captured only in the spring.

3.3.2. Fish Size and Environmental Factors Associated with Captures

During the monitoring period 1999–2018, water temperature and flow were associated with the capture peaks of 22 species in the adult stage (Table 3). The median size by species in the adult stage and by capture peak ranged from 66 mm (goby) to 1033 mm (catfish) for the capture size. Nase was the species with the lowest median capture temperature (11 °C) and the highest median capture flow (263.3 m^3/s) during the spring between the 78th and the 108th days of the year (from 19 March to 18 April). Bleak was the species with the highest median capture temperature (23 °C) during the summer between the 183rd and the 239th days of the year (from 2 July to 27 August).
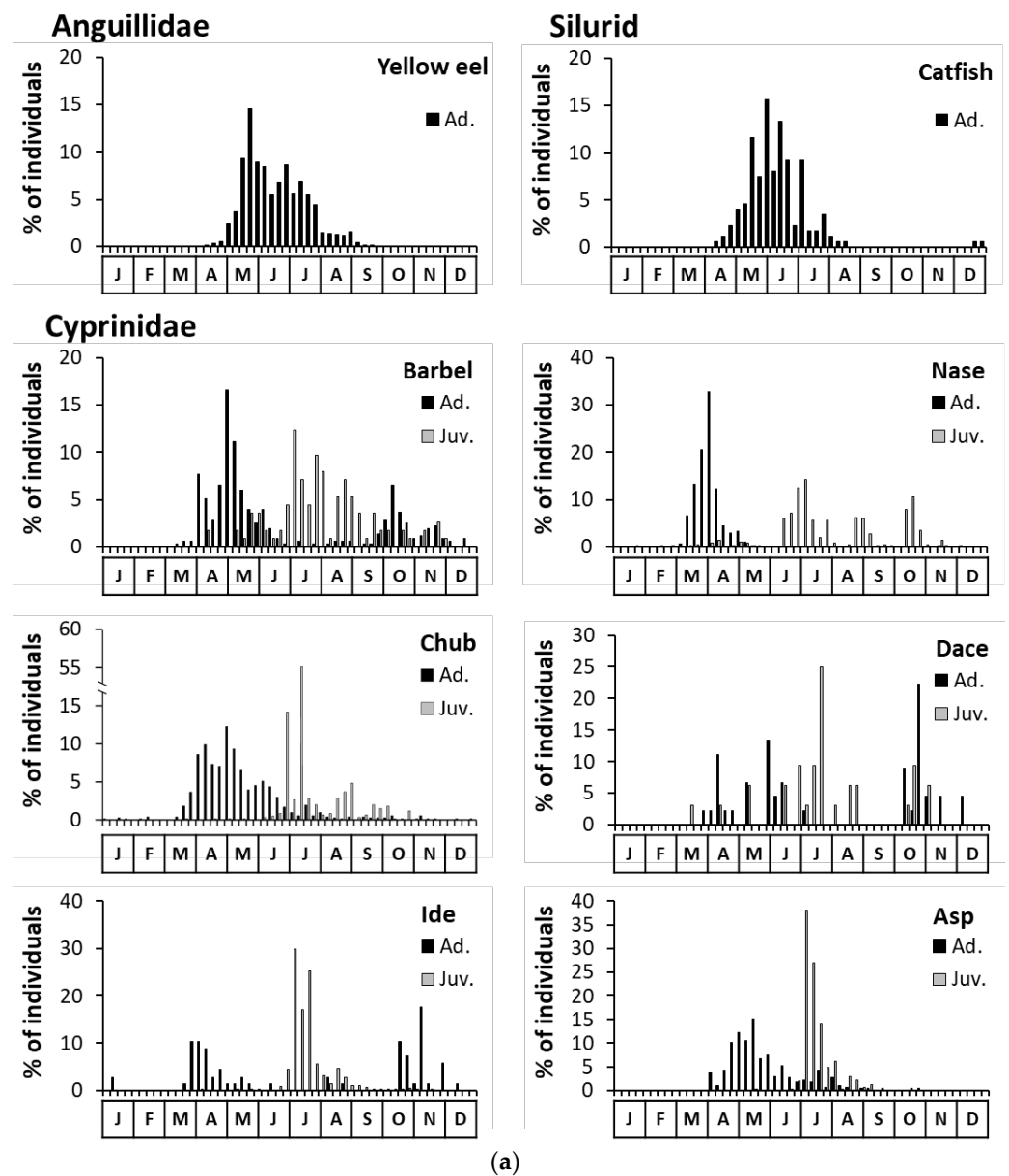
Figure 5. *Cont.*
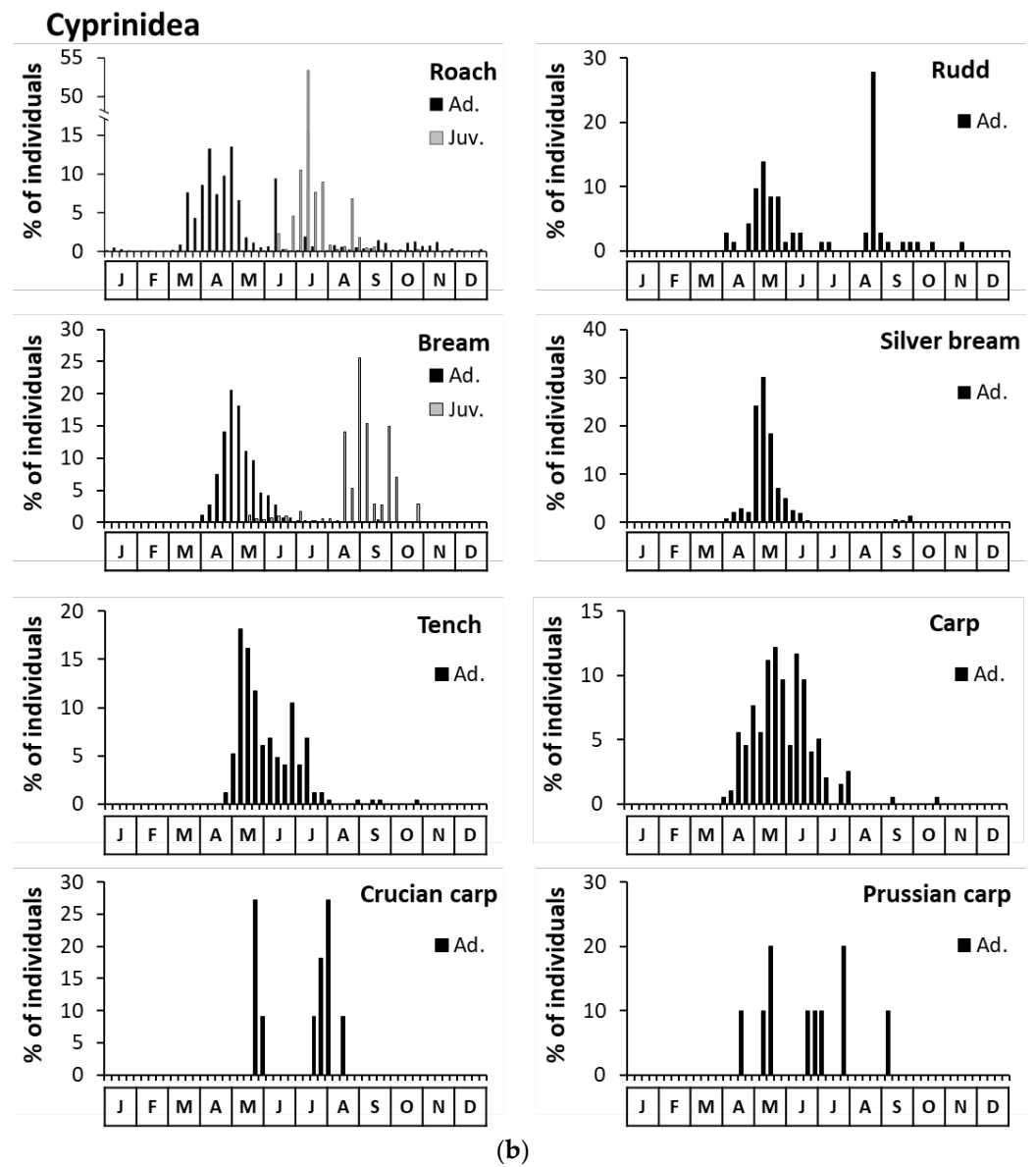
Figure 5. *Cont.*
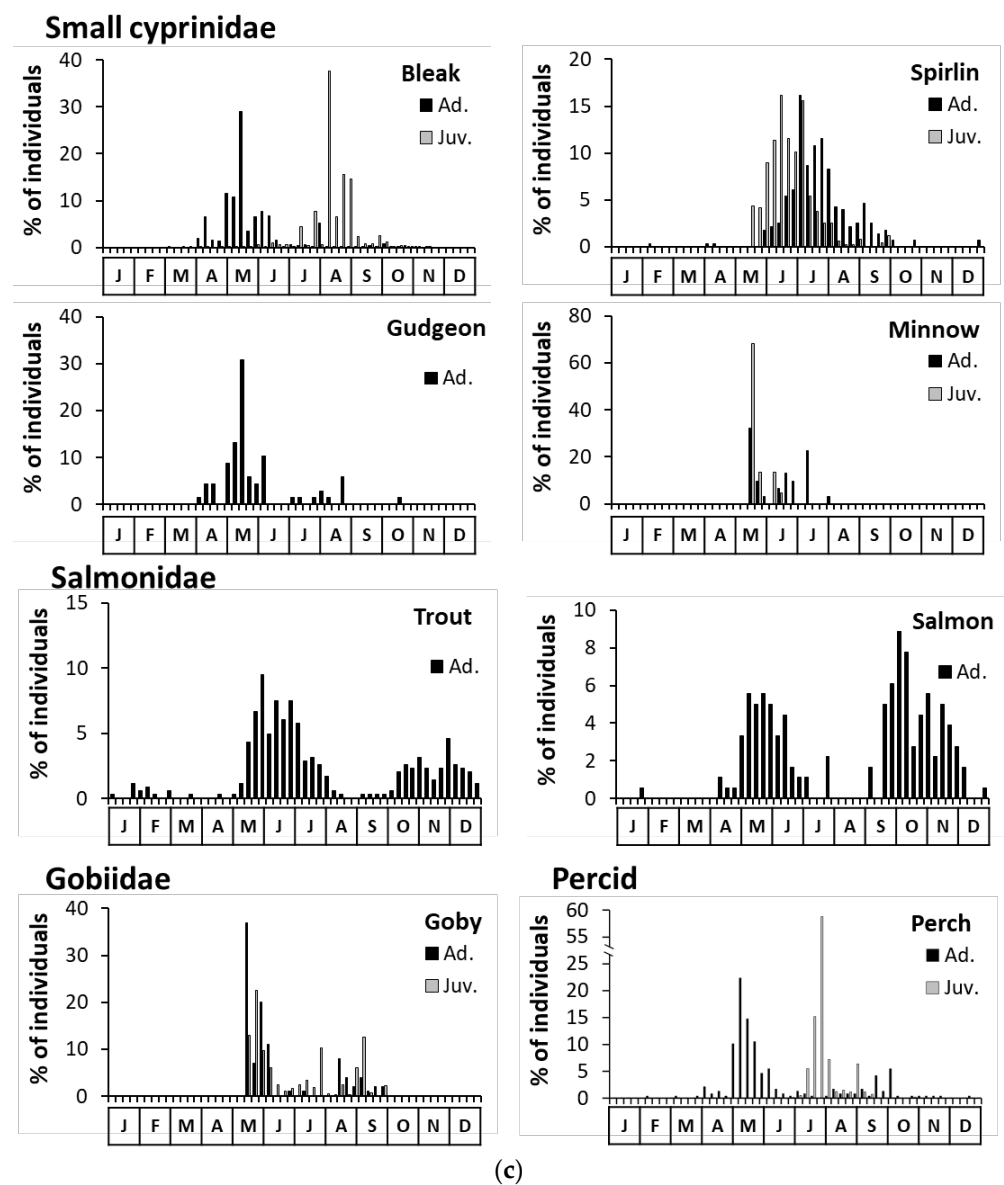
Figure 5. Overall capture periodicity (1999–2018) by species in terms of percentages of individuals (**a**) of yellow eel, catfish, and rheophilic Cyprinidae (barbel, nase, chub, dace, ide and asp), (**b**) of eurytopic and limnophilic Cyprinidae (roach, rudd, bream, silver bream, tench, carp, crucian carp, and Prussian carp) and (**c**) of small Cyprinidae (bleak, spirlin, gudgeon and minnow), Salmonidae (trout and salmon) and other families (perch for percid and goby for Gobiidae), distinguishing between adult (black) and juvenile (white) stages.

The size, temperature, and water flow ranges for juvenile captures were defined for 13 species (Table 4). The median capture size values per species in juvenile stage and per peak capture ranged from 36 mm (nase) to 105 mm (bream). Bleak was the species with the highest median capture temperature (24.2 °C) as a juvenile during the summer between the 207th and the 240th days of the year (from 27 July to 28 August). Roach juveniles captured during the spring exhibited the lowest median capture flow (25.4 m³/s).

Table 3. Characteristics of capture (number of individuals, capture size, capture periodicity, capture temperature and capture flow) by species and capture peak for adults.

Species	Peak Period	N	Capture Size (mm)			Capture Periodicity (Capture Date)			Capture Temperature (°C)			Capture Flow (m³/s)		
			P10	P50	P90	P10	P50	P90	P10	P50	P90	P10	P50	P90
Yellow eel	*Spr + Sum + Aut*	19,163	253	316	405	133	160	202	18.3	22.1	24.8	49.3	121.2	219.7
Trout	*Spr + Sum*	226	371	500	648	137	164	198	17.5	20.1	22.7	50.1	98.3	248.4
	Aut	99	454	562	690	284	316	344	9.4	11.9	18.2	40.9	151.1	411.7
Salmon	Spr	63	667	780	921	119	140	163	14.3	18.1	21.2	44.3	95.3	222.4
	Aut	95	655	754	900	267	287	326	10.3	14.8	17.0	43.6	94.2	287.6
Barbel	*Spr*	244	438	568	648	94	124	150	12.3	14.9	19.4	60.7	175.4	382.2
	Aut	90	312	435	604	273	287	325	12.1	15.2	18.0	30.9	98.6	304.9
Nase	*Spr*	303	335	382	440	78	91	108	9.4	11.3	13.8	130.4	236.3	829.7
Chub	*Spr + Sum*	673	327	395	462	90	120	167	13.3	16.0	2.9	80.7	165.0	366.4
	Aut	17	172	362	483	261	279	325	10.2	16.9	20.1	16.0	117.3	486.6
Dace	*Spr*	23	105	125	173	93	128	157	9.3	17.9	21.3	71.1	160.2	454.4
	Aut	21	108	120	175	281	291	334	10.5	14.6	15.0	65.3	65.3	277.6
Ide	*Spr*	32	199	414	501	82	97	135	9.2	13.4	17.1	167.5	208.3	409.8
	Aut	32	256	342	415	287	305	330	11.1	14.7	18.2	23.9	40.9	165.4
Asp	*Spr*	233	436	498	548	108	130	157	15.2	17.2	21.1	55.6	102.6	214.6
	Sum	48	415	449	525	176	193	221	19.8	22.0	24.1	52.4	122.2	277.7
Roach	*Spr*	13,035	114	167	242	87	110	157	12.0	15.4	20.8	120.1	187.4	306.9
	Sum	984	103	117	192	187	216	255	19.2	20.7	22.9	36.6	47.6	135.4
	Aut	1191	115	172	290	265	291	316	11.6	15.0	20.3	15.7	57.7	331.1
Rudd	*Spr*	40	188	275	337	111	125	155	15.1	17.8	20.6	115.4	193.3	328.8
	Sum	29	110	124	288	229	232	248	19.1	22.6	23.1	32.8	35.73	86.76
Bream	*Spr*	18,940	314	366	411	107	123	147	13.9	17.1	20.0	69.9	141.9	301
	Sum	464	159	370	419	173	187	260	17.8	21.0	23.6	40.8	88.2	278.2
	Aut	87	154	180	381	263	267	304	14.2	19.0	20.3	49.7	68.6	174.9
Silver bream	*Spr*	1434	132	222	271	115	124	145	14.4	17.1	18.9	130.8	174.5	346.8
	Aut	30	112	123	159	263	267	291	14.9	20.1	20.4	65.3	174.9	174.9
Tench	*Spr + Sum*	244	374	420	468	124	142	185	17.3	18.8	24.1	51.3	115.3	238.8
Carp	*Spr + Sum*	196	487	641	762	113	145	182	16.9	19.7	23.8	43.7	113.6	229.5
Crucian carp	*Spr + Sum*	11	172	278	374	136	202	221	15.1	22.2	24.1	74.4	141.6	654.1
Prussian carp	*Spr + Sum*	10	160	245	326	109	174	240	17.7	20.0	23.8	68.4	129.0	188.2
Bleak	Spr	21,327	95	110	136	101	131	156	14.1	19.0	21.4	91.5	154.5	239.3
	Sum	2084	90	90	117	183	210	238	20.6	22.7	23.2	41.5	52.1	136.1
	Aut	411	83	90	122	273	274	291	15.0	17.1	20.3	57.8	84.6	165.6
Sprilin	*Spr + Sum*	502	66	70	82	170	197	244	18.6	22.9	24.7	22.2	64.1	149.3
Gudgeon	*Spr*	57	92	104	132	102	129	151	15.1	18.9	20.7	129.2	163.2	310.9
Perch	*Spr*	179	174	229	332	118	129	151	15.3	18.1	20.8	95.8	171.3	241.0
	Aut	22	158	185	317	267	273	318	11.0	19.6	20.2	19.5	57.7	323.9
	Sum	34	152	172	321	187	238	260	17.7	22.0	24.1	36.2	82.5	200.2
Catfish	*Spr + Sum*	171	851	1033	1340	128	155	189	17.1	21.3	23.8	26.7	84.5	211.1
Goby	*Spr*	75	61	75	106	130	140	153	16.9	19.1	21.3	52.31	108.4	558.5
	Sum	23	60	66	115	202	232	256	18.7	23.1	24.1	17.8	35.7	84.9

Table 4. Characteristics of capture (number of individuals, capture size, capture periodicity, capture temperature and capture flow) by species and capture peak for juveniles.

Species	Peak Period	N	Capture Size (mm)			Capture Periodicity (Day of the Year)			Capture Temperature (°C)			Capture Flow (m³/s)		
			P10	P50	P90	P10	P50	P90	P10	P50	P90	P10	P50	P90
Barbel	*Spr*	18	56	74	154	102	145	168	14.4	19.7	22.8	36.1	61.9	169.1
	Sum	86	48	97	157	181	207	251	18.7	22.1	24.2	34.1	78.8	257.7
Nase	*Sum*	259	30	36	69	168	186	239	19.8	22.6	25.4	22.5	76.2	217.2
	Aut	89	40	47	61	281	289	298	17.3	17.5	17.9	91.5	92.1	263.1
Chub	*Sum*	557	40	50	69	181	190	232	22.3	23.6	25.1	51.5	86.4	97.3
Dace	*Sum*	20	47	66	80	176	197	227	21.1	23.9	24.6	23.2	50.3	96.4
Ide	*Sum*	3059	60	66	75	181	190	220	21.8	22.9	24.3	35.5	56.5	78.3

Species	Peak Period	N	Capture Size (mm)			Capture Periodicity (Day of the Year)			Capture Temperature (°C)			Capture Flow (m³/s)		
			P10	**P50**	**P90**	**P10**	**P50**	**P90**	**P10**	**P50**	**P90**	**P10**	**P50**	**P90**
Asp	*Sum*	467	74	78	88	181	185	211	22.0	22.9	23.9	21.5	51.1	61.3
Roach	*Spr*	6011	49	49	84	140	161	162	20.2	22.2	22.2	25.4	25.4	147.0
	Sum	198,460	41	49	60	181	190	228	21.8	23.6	25.1	40.0	70.0	97.3
	Aut	1649	51	57	88	268	289	302	13.3	17.7	19.5	44.2	109.9	193.6
Bream	*Spr*	118	69	105	124	133	149	165	14.2	20.7	22.1	69.5	161.6	498.5
	Sum	1723	50	60	70	224	237	244	20.7	21.8	23.0	20.2	38.5	71.2
	Aut	599	65	65	97	265	265	291	15.3	19.4	19.4	18.2	28.9	65.3
Bleak	*Spr*	1664	50	70	78	135	160	171	19.2	22.1	24.5	53.0	99.5	156.5
	Sum	50,299	50	51	60	207	221	240	21.9	24.2	25.9	51.5	82.0	84.9
	Aut	2513	58	67	72	266	269	287	16.0	18.2	21.3	33.0	64.9	165.6
Spirlin	*Spr + Sum*	502	47	55	63	149	168	196	19.2	21.1	23.5	45.7	84.3	137.2
Minnow	*Spr*	22	38	42	44	129	129	155	19.6	19.6	21.7	27.3	47.0	145.9
Perch	*Spr*	92	43	102	127	142	164	171	16.4	20.6	22.7	30.3	121.0	163.0
	Sum	35,665	68	73	76	197	203	223	19.3	23.0	23.7	50.8	64.9	96.4
	Aut	92	92	101	121	275	291	291	15.3	15.3	17.8	61.4	65.3	102.6
Goby	*Spr*	301	38	47	56	139	142	156	17.6	19.2	22.5	52.3	58.9	97.3
	Sum	254	27	36	52	186	229	245	21.3	23.9	25.4	17.0	48.0	74.6

3.3.3. Temporal Trends in Fish Movement Indicators and Fish Size

The temporal trends in migration indicators over the study period were analysed with respect to nine species in the adult stage during their spawning migration (Figure 6), reaching a minimum of five individuals over 10 years. The start migration showed a positive temporal trend only for eel (from 134th to the 152th day of the year), nase (from 78th to 89th day of the year), and bleak (from 97th to 150th day of the year) (MK tests, $p < 0.05$). Bleak also showed a significant positive temporal trend of the migration peak (from 127th to 150th day of the year) (MK test, $p = 0.03$). These temporal trends in the timing of migration were not significantly associated with the numbers captured (linear regressions, $p > 0.05$), but they were associated with the mean spring temperature (linear regressions, $p < 0.05$) for eel (migration start) and bleak (migration peak). Other species without a significant temporal trend showed migration indicators significantly negatively related to the mean spring temperature (linear regression, $p < 0.05$): eel (migration peak), barbel (migration start, peak, and end), chub (migration start and peak), asp (migration start and peak), bream (migration start, peak, and end), and carp (migration start and peak). The median size of four species (eel, barbel, bream, and carp) exhibited a significant positive temporal evolution (MK test, $p < 0.05$), with increases ranging from 46 mm (barbel) to 113 mm (carp). The increase in size of eel and bream were significantly associated with decreased numbers of annual captures (Table 5).

Table 5. Results by species in the adult stage with regard to temporal trends in migration phenology (Mann–Kendall test) and the relationships (simple linear regression) between the migration indicators by year and both the capture headcount per year and the mean spring temperature (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

| Species	N Years	Indicators	Temporal Trend		Headcount			Mean Spring Temperature		
			Tau	*p*-Value	t-Value	*p*-Value	R^2	t-Value	*p*-Value	R^2
Eel	20	Migration start	0.34	0.04 *	−1.84	0.08	0.16	−3.82	0.001 **	0.45
		Migration peak	0.03	0.87	−1.45	0.16	0.10	−2.54	0.02 *	0.26
		Migration end	−0.12	0.47	−0.40	0.70	0.001	−0.70	0.49	0.03
		Fish size	0.86	<0.001 ***	−4.69	<0.001 ***	0.55	−0.53	0.61	0.02
Barbel	16	Migration start	0.19	0.30	−0.37	0.72	0.01	−3.98	0.001 **	0.51
		Migration peak	0.07	0.71	−1.06	0.31	0.07	−2.95	0.001 **	0.37
		Migration end	0.05	0.80	−1.54	0.15	0.14	−4.42	<0.001 ***	0.56
		Fish size	0.48	0.01 *	1.68	0.11	0.16	−0.06	0.95	0.00
Nase	15	Migration start	0.40	0.04 *	0.35	0.73	0.01	−0.25	0.80	0.00
		Migration peak	0.01	1.00	−1.64	0.12	0.17	−0.28	0.78	0.01
		Migration end	−0.32	0.10	−0.32	0.75	0.01	−0.19	0.85	0.00
		Fish size	−0.28	0.17	−0.32	0.75	0.01	1.50	0.16	0.15
Chub	20	Migration start	0.04	0.39	−0.98	0.34	0.05	−2.66	0.02 *	0.28
		Migration peak	−0.09	0.60	−1.19	0.25	0.07	−2.46	0.02 *	0.25
		Migration end	0.06	0.69	−0.37	0.72	0.01	−1.16	0.26	0.07
		Fish size	−0.14	0.39	0.40	0.69	0.01	0.40	0.69	0.01
Asp	12	Migration start	−0.18	0.45	−2.67	0.02 *	0.41	−2.47	0.03 *	0.38
		Migration peak	0.00	1	−1.54	0.15	0.19	−3.89	0.003 **	0.60
		Migration end	−0.12	0.62	−0.37	0.72	0.01	−1.93	0.08	0.27
		Fish size	0.10	0.73	0.88	0.4	0.07	1.99	0.07	0.28
Roach	19	Migration start	0.21	0.23	−1.19	0.28	0.07	0.60	0.56	0.02
		Migration peak	−0.11	0.53	0.72	0.48	0.03	−0.01	0.97	0.00
		Migration end	−0.12	0.48	0.55	0.59	0.02	0.01	0.99	0.00
		Fish size	0.23	0.18	−0.97	0.35	0.05	−0.90	0.38	0.05
Bream	20	Migration start	−0.02	0.92	−1.67	0.11	0.13	−7.41	<0.001 ***	0.75
		Migration peak	−0.09	0.58	−1.43	0.17	0.10	−5.07	<0.001 ***	0.59
		Migration end	−0.06	0.74	−1.52	0.14	0.11	−5.33	<0.001 ***	0.61
		Fish size	0.44	0.01 *	−4.50	<0.001 ***	0.53	0.25	0.81	0.00
Carp	14	Migration start	0.08	0.74	−1.27	0.23	0.12	−3.09	0.01 *	0.44
		Migration peak	0.28	0.19	−1.29	0.22	0.12	−2.68	0.02 *	0.37
		Migration end	−0.26	0.21	0.88	0.39	0.06	−1.01	0.33	0.08
		Fish size	0.49	0.02 *	0.04	0.97	0.00	−1.79	0.10	0.21
Bleak	20	Migration start	0.52	0.002 **	−1.22	0.24	0.08	−1.02	0.32	0.05
		Migration peak	0.35	0.03 *	−0.87	0.40	0.04	−2.25	0.04 *	0.22
		Migration end	−0.07	0.67	0.75	0.46	0.03	−1.59	0.13	0.12
		Fish size	0.11	0.51	−0.70	0.49	0.03	2.60	0.02 *	0.27
Catfish	12	Migration start	0	1	0.02	0.98	0.00	−1.71	0.12	0.23
		Migration peak	0.03	0.94	−0.39	0.7	0.02	−1.33	0.21	0.15
		Migration end	0.41	0.07	0.57	0.58	0.03	−0.24	0.81	0.01
		Fish size	−0.36	0.12	−0.67	0.52	0.04	−0.07	0.94	0.00
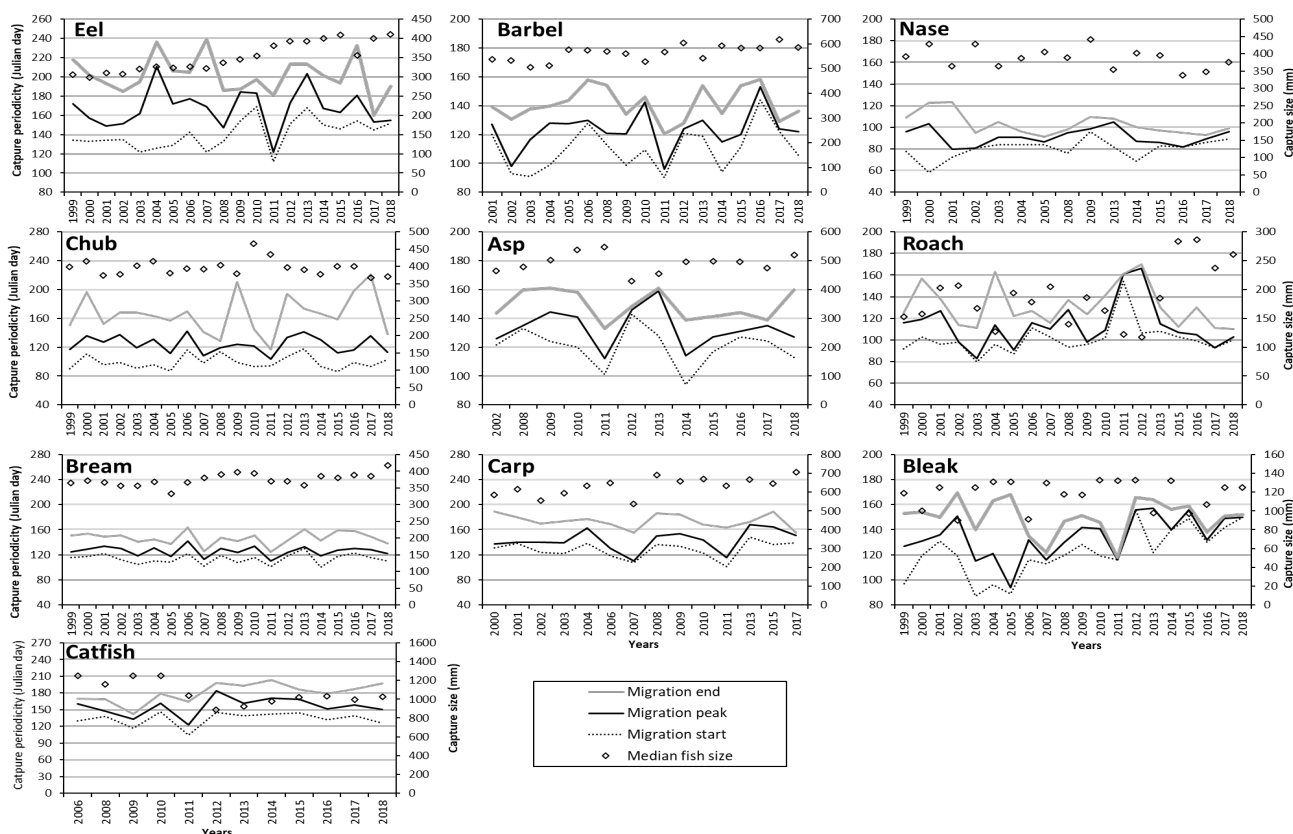
Figure 6. Annual temporal trends in the migration phenology (migration start, migration peak, migration end, and median fish size) of species in the adult stage during their spawning migration period.

4. Discussion

Prior to this study, a continuous manual monitoring of fishways over a 20-year period using capture traps at a multispecies level had never been undertaken. However, it proved to be an efficient method for the acquisition of data on fish ecology in a large lowland river. The presence of two distinct meso-habitats (the river banks and the main river channel) in large rivers has far-reaching implications for assessments of fish populations in such large ecosystems [40]; a combination of sampling methods would be required to capture more species and to complete the species inventory [40,41]. Although the analysis of fishway use is an indirect and selective fish inventory method which provides no information on resident individuals, it is still a useful tool for riverine management. In particular, it is useful for analysing the evolution and migration dynamics of fish populations over long periods of time [5,12,42]. Biodiversity measures enhance our understanding of the complex components driving ecosystems [43], but data may be biased, because the abundance of species and the densities of fish can vary in identical habitats during ontogeny [44], from season to season, and even from day to night [45]. Continuous, multi-annual monitoring helps to counter these difficulties in ecosystems where fragmentation causes freshwater biodiversity to decline [8]. In addition to the potential selectivity of the fishway, which is contingent on its multi-species efficiency [9,46], another potential source of bias is the fact that many fish species are either largely stationary or largely mobile throughout their life cycle [31], meaning that the data collected via fish passage monitoring only cover the mobile fraction of the population. Furthermore, it is essential to assess fish migration dynamics after the restoration of longitudinal connectivity with fishways and the most efficient post-evaluation studies in this regard involve long-term monitoring [46].

During the 20 years of monitoring, 388,631 individuals representing 35 species were recorded. The proportions of juveniles and small species were higher in the pool-and-weir fishway, F1. This is partly because F2 cannot capture fish less than 150 mm in length, which

leads to underestimates of juveniles and small species in the latter. Although juveniles were frequently observed in F1, it was not possible to assess the fishway preferences of juveniles, eels, and small species. However, it was clear from the comparison of ecological categories between fishways that large rheophilic species preferred the modern fishway, as already observed by Stuart and Berghuis [47]. With regard to both fishways, the families most represented in the adult stage were Cyprinidae (85.4%) and the ecological group of eurytopic species (88.4%). As previously observed for the annual headcount of the diadromous eel in the River Meuse [48], the annual headcount of many eurytopic and limnophilic species (roach, rudd, bream, silver bream, tench, bleak, and perch) decreased drastically, despite several years of improvement in the physicochemical water quality of the River Meuse. Although temperature and flow trigger the movement of most fish species, we did not observe a mutual trend between temperature and flow and the annual quantity of mobile individuals captured in the studied fishways. On the contrary, we observed a significant increase in dissolved oxygen in the river, following the construction of numerous sewage treatment plants [49], whereas populations of eurytopic and limnophilic species showed a significant decrease in headcount over time. Declining fish abundance is thought to owe to the effects of the reported drastic decline in phytoplankton biomass simultaneously with the sufficient presence of nutrients for plankton growth [19], prompted by the large-scale invasion of Asian clams, *Corbicula* spp. [50]. Unlike rheophilic species, which showed an increasing temporal trend in their proportion of biomass, limnophilic and eurytopic fish species clearly preferred eutrophic water bodies inversely correlated to water quality [51] and were probably affected by this decrease in resources at the base of the food pyramid [16,30]. Other hypotheses include a possible increase in predation by the great cormorant *Phalacrocorax carbo* [52] and the appearance of piscivorous fish species. One study has suggested that the emergence of catfish in a new setting had little impact on the composition of the ichthyofauna present [53], but counts of catfish and asp both significantly increased over the period investigated. These noted increases will likely have implied a new predation pressure on the largest native fish species (which previously were rarely consumed by native predatory fish), resulting in potentially different trophic interactions [54,55] as have been reported for salmon [56]. Moreover, the decreases in captures in the adult stage were accompanied by significant decreases in the juvenile stage in some species, especially eurytopic species such as roach, bream, and bleak, suggesting a possible overall decrease in the recruitment of these species into the Meuse basin. Nevertheless, inter-annual fluctuations in the number of captured juveniles appear to be related to shoal effects [5], as captures were generally found to be clumped in time and counts might have been underestimated from 2011, when the F1 monitoring period was shortened.

The construction of F2 in 1998 at Lixhe dam was a part of the 'Meuse salmon programme' that aims to restore the complete life cycle of migratory salmonids in the River Meuse basin, improving free movement (upstream and downstream) via the installation of modern fishways adapted to diadromous salmonids [57]. The continuous monitoring revealed the first beneficial outcome of the restoration project: a significant upward trend in the number of adult salmon and sea trout in reproductive migration caught in the lower Belgian Meuse. A low number of returning Atlantic salmon in the lower Belgian Meuse currently remains, supported by a stocking management strategy [58] aimed at maintaining a naturally sustainable population. Indeed, the River Meuse is equipped with several no fish-friendly hydropower plants which have a negative impact on the survival of downstream migratory fish. Supplementary efforts must be undertaken in the future, especially to evaluate the efficiency of fishways [4] and thereby support smolts' downstream migration and escapement success as well as to optimise restocking practices [59,60]. Furthermore, the continuous monitoring of fishways is a good tool for identifying and quantifying invasion of non-native species. Indeed, in the Belgian Meuse, the emergence of the piscivorous species asp and catfish (as already mentioned) was identified in the early 2000s, while goby was first seen in the early 2010s. All three species increased during the study period, while another six non-native species were seen more occasionally. The

addition of invasive species further impairs the functions and services of such already fragile ecosystems [13]. Moreover, the artificialisation of ecosystems appears to be a key driver of non-native species' colonisation around the world [16], and the connection of large hydrographic basins for navigation facilitates these invasions [61]. Selective fish passage technologies that allow the passage of native species without aiding the dispersal of non-natives would increase the management options available both to protect vulnerable species and to meet legislative obligations [62].

Our analysis of the seasonal variations in captured adult abundances revealed that fishway use was distributed throughout the year, with a clear periodicity of movements indicating that populations of potamodromous species carry out migratory movements. Three main seasonal peaks of fish mobility (spring, summer, and autumn) were clearly observed, as already recorded in the Meuse [11] and other medium-sized rivers [5]. The spring peaks mostly comprised cyprinid species (barbel, nase, chub, bream, silver bream, roach, gudgeon, tench and bleak) and occurred when water temperatures ranged from 10 °C to 20 °C, depending on the species. These coincided with the circum-reproduction period and were clearly associated with spawning activity (further indicated by the capture of a large number of sexually mature fish). The other peaks of cyprinid mobility occurred in the autumn (barbel, dace, ide, roach, bream, and bleak) and the summer (chub, asp, roach, bream, carp, and tench), corresponding to exploratory movements towards thermal refuges or research of wintering habitats [5,11]. In the case of salmonids (trout and salmon), the capture peak during autumn represents a spawning migration [24], but the spring peak may represent pre-spawning movements during a period characterized by comfortable temperatures or possibly the exploration of fresh tributaries before the summer, during which temperatures in the Meuse are often high. In the case of catfish, a set of upstream movements was observed in the spring and early summer when water temperatures were between 17 °C and 23 °C; this is in line with other studies [28,29] and possibly related to reproduction [53]. Moreover, when all the juveniles combined are considered, we observed three peaks of movement (spring, summer, and autumn) when the water flow was low (<100 m^3/s) and the water temperature was above 20 °C. The juvenile capture peaks in the spring (spirlin, roach, bleak, and bream) and the autumn (nase, barbel, roach, chub, and bream) involved smaller numbers of individuals than in the summer, but they took place under environmental conditions close to the summer peak, specifically temperatures near 20 °C for the spring peak and near 17 °C for the autumn peak. This certainly suggests ontogenetic movement, with individuals taking advantage of low flow conditions and a thermal threshold sufficiently high for their relatively poor swimming capacity [63]. In addition, these juvenile capture data indicate that: (i) juveniles can explore their environment via upstream movements, not just downstream drifting [64]; (ii) suitable spawning habitats exist downstream for species counted in the juvenile stage (no salmonids); and (iii) reproductive success clearly varies greatly given the wide range of numbers recorded over the years.

Radinger and Wolter [31] have noted that the duration of movement behaviour studies rarely exceeds 200 days, rendering multi-year comparisons impossible. In this study, we were able to assess the evolution over the years of spawning migration indicators for nine species in the adult stage, thanks to our use of a continuous monitoring methodology. Only three species (eel, nase, and bleak) demonstrated a significant temporal trend in any of their migration indicators; in these specific cases generally, there was a later migration start. These trends were not associated with the annual numbers captured; in the case of eel and bleak, they were negatively associated with the mean spring temperature. Eel, barbel and bream showed a temporal trend of increasing size. For the eel, this resulted from a drastic decrease in numbers caught and a loss in colonisation behaviour as already explained by Nzau Matondo and Ovidio [65]. Although not measured in this study, explanations for variations in migration indicators include predation risk, the proportion of mobile and stationary individuals, downstream recruitment, and environmental and anthropic influences [31,66]. Our results demonstrated that the migration period is flexible and that

the triggering environmental factors, such as the contribution of the temperature, also vary slightly from year to year. This corroborates Benitez and Ovidio's [33] finding showing flexibility in the responses of barbel to environmental variables and an optimisation of the starting date of migration to spawning grounds depending on the fish's position in the river basin.

5. Conclusions

Over the 20 years of monitoring, we observed that fishways in a large anthropized river were used by diverse fish species across a wide variety of stages and size ranges. Moreover, a previous study of the mobility patterns of fish from the Lixhe fishways in the upstream part had already demonstrated the value of restoring the river's connectivity for the whole fish community, so that optimal habitats can be exploited [11]. More specifically, the significant proportion of young fish observed indicates the prominent role of fishways in the context of the ontogenic dispersal of juveniles and sub-adults. This implies that when passage devices represent the only solution, they must be adapted to their swimming capacity. We observed changes in fish assemblages with a decreasing overall abundance of fish. The drastic decline in abundance of some common and widespread European fish (eurytopic and limnophilic cyprinids as well as eels) and the appearance of invasive species (asp, catfish, and goby) allowed us to detect major ecological changes in the Meuse and should prompt the adoption of active conservation measures in the future [67,68]. Doing so would enable a decision to be made to support some fish populations through restocking programmes, as has already proved successful for eels [69], or to develop specific artificial spawning grounds [70] for species in serious decline. Furthermore, the studied fishways were most heavily used in the spring, during the circum-spawning period, although movements occurred throughout the year, confirming the importance of maintaining ecological continuity in a lowland river year-round [5,71]. These results highlight the usefulness of fishway monitoring in contributing to the management of river environments and in conserving the functionality of fishways over time. Despite the quantity of data collected, some questions remain unanswered, particularly concerning the temporal evolution of the number of captured fish but also patterns of mobility. It would be interesting, for example, to obtain fish abundance data in upstream and downstream parts of the dam, whether by traditional methods (nets and electrofishing) or new methods such as environmental DNA [72,73]. Finally, the Anthropocene has ushered in innumerable direct and indirect anthropogenic effects on all freshwater taxa, and there exists considerable potential for ecosystem-level changes through bottom-up and top-down responses [74]. These must be studied and monitored in order to most effectively guide management decisions for river ecosystems.

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