

Life history traits and timing of elvers moving over a River Meuse dam after recent glass eel restocking

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ABSTRACT

This study describes for the first time some aspects of the life history traits and movement behaviour of young eels during the first year following their capture on the French Atlantic coasts that were released as glass eels into a large river with a vast catchment area. The restocked individuals have small size, exhibit discrete, cryptic, and benthic life habits, and have nocturnal activity. These make capturing individuals and studying this stage very challenging. Taking advantage of its positive thigmotactic behaviour, we used a fishway adapted for eels to collect samples using eel traps and trap pools lined with freshwater mussel shells. Results revealed that the restocked eels' abundance has positively impacted the eel local stock, growth rate was good, catch periodicity followed that of older eel individuals, and composition of the associated fish species was indicative of the fish fauna that ascends the River Meuse through this fishway. These findings would open prospects for restocking using glass eels as a viable strategy to boost declining local stocks and, probably in the long term, increase the future escapement rate to the sea of silver eel spawners from the catchment, but the question of survival in large rivers still needs more research.

1. Introduction

The European eel *Anguilla anguilla* exhibits great plasticity about habitat use, with either residence in a freshwater, brackish, or marine habitat, or engage in migrations between functional habitats (Tesch, 2003, Daverat et al., 2006). The species reproduces in a single spawning area located in the well-known Sargasso Sea off Bermuda, where the eel larvae, the leptocephali, use the oceanic currents to reach the mainland coasts of Europe and North Africa as glass eels (Righton et al., 2021). These young eels grow in a wide range of habitats, such as lagoons, estuaries, marshes, rivers, streams and lakes, and become yellow eels for about 5–20 years (Daverat et al., 2006, Righton et al., 2021). After which they undergo metamorphosis and migrate back to spawn in the spawning area as mature silver eels (van den Thillart et al., 2004, van Ginneken and Maes, 2005). However, due to global warming, pollution, diseases, parasites, barriers to up- and down-stream migration, and watershed management practices leading to the loss of habitat carrying capacity and quality, as well as overfishing at its all life stages, the state of eel stocks is very concerning (Feunteun, 2002, Bonhommeau et al.,

2008, Belpaire et al., 2009, Drouineau et al., 2018, Delrez et al., 2021). The species is listed on the Red List of the International Union for Conservation of Nature and is classified as critically endangered (Pike et al., 2020, CITES, 2024).

In Belgium, the eel stocks that ascend the River Meuse at Lixhe dam, 323 kilometres upstream from the North Sea through the Dutch Meuse, have been monitored annually since 1992 using a historical pool-and-weir fishway (Nzau Matondo and Ovidio, 2016, Belpaire et al., 2021, Benitez et al., 2025). This specific infrastructure serves as a critical scientific observatory; previous long-term monitoring based on the annual capture, measurement, and counting of eels from this same fish pass revealed a drastic decline in stock levels after 2003 (Nzau Matondo and Ovidio, 2016, Nzau Matondo et al., 2024). Specifically, previous studies demonstrated that the number of ascending eels dropped by about 4.2% per year from 1992 to 2014 (Nzau Matondo and Ovidio, 2016), collapsing to just 2.3% of historical record levels by 2024 (Benitez et al., 2025). These prior evaluations established that natural recruitment through the river network had become insufficient to supply or colonize the entire Belgian Meuse catchment area, which represents

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nearly one-third of the international Meuse catchment area (Baras et al., 1996, Nzau Matondo and Ovidio, 2018). The species, once widespread and abundant in this important basin (Philippart et al., 2001), is now in an alarming and catastrophic situation requiring urgent conservation actions. Consequently, while early fishway monitoring at this dam documented the collapse of natural upstream migration (Nzau Matondo and Ovidio, 2016), it also highlighted the urgent need for experimental management actions, leading to the implementation of localized glass eel restocking programs below the obstacle to artificially restore the depleted local stock. In accordance with the implementation of the European Union's 2007 Eel Regulation (UE-Council of the European Communities, 2007), the Belgian Eel Management Plan, established at the end of 2008 and accepted in January 2010 (Vlietinck et al., 2010), practises restocking using glass eels to restore and safeguard local stocks that have been depleted. Restocking for scientific purposes has also been initially undertaken in shallow aquatic ecosystems, including the headwater streams and the Meuse tributaries. These shallow aquatic environments have enabled continuous and accurate monitoring of restocked eels using the combined application of electrofishing and telemetry techniques. These techniques have highlighted high growth rates (Ovidio et al., 2015, Nzau Matondo et al., 2021) and survival rates (Nzau Matondo et al., 2020, Nzau Matondo et al., 2023a), and the optimal approach for glass eel release involving the dispersal of individuals across the longitudinal river profile, targeting suitable refuge habitats to maximize local stock restoration (Nzau Matondo et al., 2020). They have also demonstrated the eel density improvement in streams (Nzau Matondo et al., 2023a) and revealed the initiation of biological processes related to sedentarization and silvering, and the dynamics of dispersal and continental habitat exploitation (Nzau Matondo et al., 2019, Nzau Matondo et al., 2023b). Other studies have shown the high quality of restored eel stocks, which were attributed to their high lipid content, a low prevalence and load of pathogens and chemical contaminants (Nzau Matondo et al., 2022), and a predominance of females (Nzau Matondo et al., 2023a). However, in an aquatic ecosystem consisting of large and deep rivers, little is currently known about the early biology and ecology of glass eels after restocking (Nzau Matondo et al., 2024). They have been less studied partially due to the great depth and the difficulty in carrying out effective sampling using efficient capture equipment in wide, deep riverine ecosystems. This difficulty is even greater for the small eels, particularly glass eels, exhibiting nocturnal activity and discrete, benthic and cryptic life habits (Baras et al., 1998), during the first year of life after their release. And yet, this model type offers vast areas for the species to grow and therefore it can have a significant contribution for boosting local stocks. Additionally, enhanced knowledge could facilitate the implementation of more efficient management strategies for this endangered species. To monitor cryptic young eels in deep waters, our previous studies successfully validated a collection system that exploits the species' positive thigmotactic behaviour. Prior research conducted from 2010 to 2015 demonstrated that lining fishway resting pools with structured substrates, provides effective artificial shelters to trap small individuals efficiently (Nzau Matondo and Ovidio, 2018). Consequently, this study applies this pre-validated trapping framework to the Lixhe dam, ensuring a reliable sampling method to accurately evaluate the outcomes of the restocking program in a deep river environment. The ultimate goal of this study was to accurately assess the possible restocked eels' abundance in the area of restocking based on how many eels attempted to go over the Lixhe dam in comparison to previous years when no restocking was done below the dam, the growth and catch periodicity, as well as the composition of the associated fish species diversity, during the first year after they were released as glass eels. This was done so that we could better predict and understand how the restocking would affect a large, deep riverine ecosystem.

To contextualize this work within the broader, multi-year framework of regional eel conservation, we formulated the following large, long-term hypotheses that extend beyond the immediate scope of this

single-year sampling: (1) the ascending eel stock over the Lixhe dam would be increased through the glass eel restocking, as a very young stage was introduced to the area where it is naturally absent and old eel stocks are declining, which would enhance the local stock, with probable positive long-term impact on silver eel escapement from river basins; (2) the restocked eels in the River Meuse would experience a substantial increase in their growth rate, resulting from its higher temperatures compared to its colder tributaries where growth performance is typically depressed; (3) the restocking would increase overall eel population density, resulting in an early seasonal capture of older eels, as high upstream migration rates at dams are known to coincide with high density pressures of riverine eels, potentially shifting environmental thresholds (period, water temperature, and river flow) at the time of catch compared to younger cohorts; and (4) the composition of the associated species that ascends the fishway with very young eels undergoes modification due to potential piscivorous attraction, or remains merely indicative of the site's historical fish composition.

To gather information about these subjects, we used the species' behaviour of seeking contact with structures (Russon et al., 2010, Russon and Kemp, 2011, Piper et al., 2015, Nzau Matondo et al., 2024) to trap and catch the eels in the fishway using eel traps and pool traps lined with freshwater mussel shells as shelters for eels. This fishway operates at low water velocity and depth, which are conducive to the eel movements and habitats (Jellyman and Arai, 2016, Laffaille et al., 2004).

2. Materials and methods

2.1. Study area

This study was done at the first dam on the Belgian Meuse near the border with the Netherlands (Fig. 1). It is in Lixhe, 323 kilometres upstream from the North Sea, on a section of the river that can't be used for navigation. The Meuse is 925-km long, and its catchment area cover is 36,000-km². This area includes parts of France, Luxembourg, Belgium, Germany and the Netherlands. However, over a third of the river's area is in Wallonia, Belgium (Baras et al., 1996, Nzau Matondo and Ovidio, 2018). A lock is located downstream from Lixhe, ensuring the connection to the Albert Canal, which links the upper reaches of the Meuse at Liège and the Antwerp harbour (the Schelde estuary). In the study site, the river is 424-m long, 262-m wide and 6–8-m deep. Glass eel restocking has been done successfully over the last ten years, with the most recent event occurring on March 31, 2022. The success of this has been demonstrated by an increase in eel count migrating upstream through the fish pass and a decrease in their size, observed in the second year after restocking efforts (Nzau Matondo and Ovidio, unpublished data). The most recent release of glass eels occurred on 26 February 2025. It involved 48 kg ($n = 106,667$) individuals with mean total length of 78 mm and mean weight of 0.45 g. Caught on the French Atlantic coast, they were released on both banks of the Meuse, with a density of 1 individual per m². The release was carried out beyond 56 m of concrete banks downstream of the Lixhe dam (Supplementary figure 1), and over 368 m of natural banks suitable for eels to shelter between roots of riverside trees and in crevices of large stone and block assemblages (Nzau Matondo et al., 2021). The study site was chosen due to its strategic geographical location as an entry point for diadromous fish entering Belgium/Wallonia from the North Sea via the Netherlands, secure sampling infrastructure (two fishways), and recent restocking using glass eels. From 26 February to 21 October 2025, fish in the site experienced a mean daily of water temperatures of 19.4 (range 8.9–26.8) °C and flows of 69.6 (11.4–312.1) m³s⁻¹. This would suggest that since being released, glass eels have benefited from a moderate temperature that is conducive to growth (> 8 °C: Sadler, 1979, Morin et al., 1999).

The Lixhe dam, built in 1980, was equipped on the right bank of the river with a 23.2 MW hydropower station (catching 340 m³s⁻¹) and two fishways. A pool-and-vertical slot fishway operates at high discharge

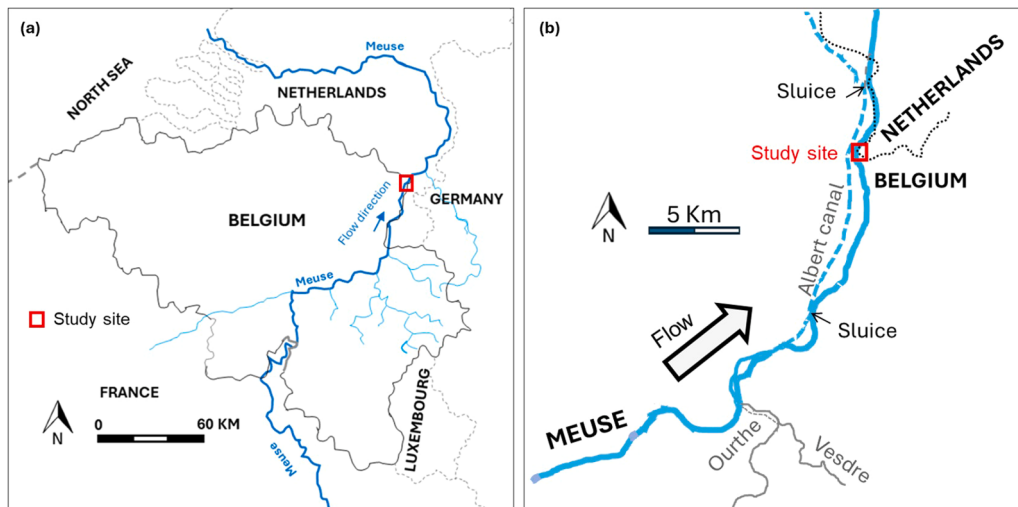


Fig. 1. Map of catch site location in Belgium (a) and the Belgian Meuse (b).

($1 \text{ m}^3\text{s}^{-1}$), high attractive flow ($1.5 \text{ m}^3\text{s}^{-1}$), large pools (4.7–9.7-m long $\times$ 2.5-m wide $\times$ 1.5-m deep) and deep slots (1.3 m) with a selective cage trap for large fish (Benitez et al., 2022). Built in 1998, it is 165-m long, located on the right bank of the river and has 26 large pools to ensure the upstream migration for spawners of large migratory fish species such as Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. Another fishway built in 1980, is 48-m long and located between the power station and the spillway. It is a pool-and-weir pool configuration equipped with 56 pools (1.5–2.5-m long $\times$ 1.2-m wide $\times$ 1.0-m deep). At the inlet of pool no. 53, there is a non-selective cone trap (grid mesh 5-mm $\times$ 5-mm) for the size of fish caught. This cone has a central opening which allows fish to enter and be trapped, without being able to leave the basin through the same opening. The system works with low discharge ($0.3 \text{ m}^3\text{s}^{-1}$), low attractive flow ($0.2 \text{ m}^3\text{s}^{-1}$), shallow deep slots (0.3 m) and low height difference between pools (0.15 m). There is a steel grid (mesh 10-mm $\times$ 10-mm) at the outlet of the further upstream basin, the pool no. 56, to keep fish from leaving the fishway.

2.2. Fish capture and biometric measurements

From 5 May to 21 October 2025, fishway was checked one to three times per week depending on site accessibility, as result of maintenance work at the hydropower station. During each monitoring, the two most downstream eel traps located in the resting basin, the pool no. 8, were checked first (Supplementary figure 2). They were followed by checking of the two other eel traps located upstream in another resting basin, the pool no. 19. We also used five most upstream basins as trap pools, the pools no. 52–56, which were lined with freshwater mussel shells as shelters for eels. This was done by obstructing the water from the Meuse to enter the fishway through outlet of basin no. 56 thanks to a wooden board and installing two successive dipnets, each 47-cm long $\times$ 40-cm wide, at the inlet of basin no. 52. The first dipnet had mesh 3 $\times$ 3 mm diameter followed immediately by the second with 1 $\times$ 1 mm to catch small fish leaving the first dipnet as well the trap pools. This one was added because the first dipnet did not retain the small eels.

The eel trap was made of rigid plastic, cylindrical and elongated, measuring 420-mm in diameter $\times$ 1060-mm in length (Aquaculture France Eurl, La Trinité-Surzur, France). It was divided into two compartments, the second of which was an internal chute that permitted eels to enter but impeded their exit. This final trap compartment was 720-mm in length $\times$ 250 mm and 115 mm in diameter at its entrance and end, respectively. It featured a single entrance that was 140-mm in length and had a diameter that decreased from 65 mm at the entrance to 10 mm at the exit. Each trap was anchored to the bottom with a 10 kg

weight. Two types of traps were used. The first included eel traps 1 and 1', which had only mesh 25–30-mm long $\times$ 5-mm wide. The second included eel traps 2 and 2', which had these mesh openings reinforced with mesh 5-mm $\times$ 5-mm. In each trapping pool, two eel traps were placed side by side along the right wall of the pool, in order of traps 1 – 2 in the furthest downstream trapping basin, the pool no. 8, and traps 2' – 1' pool no. 19. Their entrances were oriented away from the current to guide fish swimming upstream through the fishway into the eel trap (Nzau Matondo et al., 2024).

The trapped fish in eel traps and pool traps were anesthetized with clove oil (10%, $0.2 \text{ mL}\cdot\text{L}^{-1}$). They were identified and counted by species. Biometric measurements focused on measuring the total length (TL, with a precision of $\pm 1 \text{ mm}$) in eels and the fork length (FL, $\pm 1 \text{ mm}$) in other fish species. The weights (W, $\pm 1 \text{ g}$) were taken exclusively from eels. After recovering from anaesthesia, fish were released upstream of the fishway where they were caught to continue their upstream migration. We categorized the eels into two major groups: "the 2025 Cohort", which included the young eels from the glass eel restocking carried out on 26 February 2025, and "the Cohorts prior to 2025", which comprised all the older eels that did not belong to the 2025 Cohort (Fig. 2). This last group sized TL > 200 mm.

2.3. Data analysis

Fisher's exact test (FET) was used to compare relative abundances of fish between catch pools and between device meshes in eel traps as well as between species caught. Pearson's Chi-squared (χ^2) test was applied to compare the catch per unit effort (CPUE) expressed as the number of eels catch daily between the two trapping devices. The total length (TL) and weight (W) relationships were described by the equation $W = a \times \text{TL}^b$ and estimated by linear regression on log-transformed data [$\log_{10}(W) = b \times \log_{10}(\text{TL}) + \log_{10}(a)$]. In this linear regression, W is the weight (g), TL is total length (cm), a is the intercept or coefficient referring to body shape, and b is the slope or growth coefficient. The coefficient b allows to identify the type of growth with $b = 3$ signifying isometric growth, $b < 3$ negative allometric growth and $b > 3$ positive allometric growth (Froese, 2006; Nzau Matondo et al., 2023a; Pachla et al., 2026). Since the TL data did not meet a normal distribution (Kolmogorov-Smirnov test, $p < 0.001$), the non-parametric Kruskal–Wallis (KW) test, followed by Dunn's post-hoc (DU) test with Bonferroni correction, was performed to make multiple pairwise comparisons of the sums of mean TL ranks between the capture tools. The Wilcoxon (W) signed-rank test for paired samples with normal continuity correction was run to compare catch data of temperature and flow between the two



Fig. 2. Pictures of two major cohort groups (a), the Cohorts prior to 2025 (b) and the Cohort 2025 (c).

cohort groups. The statistical analyses were conducted using the Rcmdr 2.3.–2, Hmisc, and dunn.test packages of the R statistical software version 3.3.2 (R Development Core Team, 2016; Fox, 2017; Harrell, 2018). The results were classified as statistically significant when the estimated probability of error (p) was less than 0.05.

3. Results

3.1. Fish species assemblage

N = 1256 fish were caught belonging to 12 species at sizes 37 mm

(*Alburnus alburnus*) to 1200 mm (in *Silurus glanis*) (Table 1). Most fish caught (abundance relative = 91.5%), were in basins no. 52–56 as trap pools (FET, odds ratio = 124.73, p < 0.001), where all the 12 species were caught. We also caught 7.5% (length range = 45 mm in *N. melanostomus* to 440 mm in *A. anguilla*) of fish belonging to 9 species in basin no. 8 (eel traps 1 and 2), which was higher than 1.0% (90 mm in *N. melanostomus* to 330 mm in *A. anguilla*) fish and 2 species caught in basin no. 19 (eel traps 1' and 2') (FET, odds ratio = 8.020, p < 0.05). *Abramis brama*, *Aspius aspius* and *Silurus glanis* were not caught in the four eel traps. The device with only plastic trap openings, the eel traps 1 and 1', accounting for 6.8% (70 mm in *Rutilus rutilus* to 440 mm in

Table 1 Abundance and body length of fish species according to capture tools and their location in fishway. Length is the TL for eel and the FL for non-eel species.

Trap location from downstream (Pool number)	Capture tool	Species	Length (mm)		Abundance	
			Mean ± SE	Range	n	%
8	Eel trap 1	<i>Anguilla anguilla</i>	116 ± 60	85–440	74	100.0
		<i>Alburnoides bipunctatus</i>	80 ± 0	80–80	49	66.2
		<i>Barbus barbus</i>	130 ± 0	130–130	1	1.4
		<i>Rutilus rutilus</i>	90 ± 40	70–150	1	1.4
		<i>Neogobius melanostomus</i>	113 ± 26	75–140	4	5.4
		<i>Perca fluviatilis</i>	78 ± 4	75–80	16	21.6
		<i>Leuciscus leuciscus</i>	100 ± 0	100–100	2	2.7
					1	1.4
8	Eel trap 2	<i>A. anguilla</i>	94 ± 8	80–105	20	100.0
		<i>Alburnus alburnus</i>	70 ± 28	50–90	9	45.0
		<i>Leuciscus cephalus</i>	52 ± 0	52–52	2	10.0
		<i>N. melanostomus</i>	94 ± 38	45–130	1	5.0
		<i>L. leuciscus</i>	100 ± 0	100–100	6	30.0
					2	10.0
19	Eel trap 1'	<i>A. anguilla</i>	330 ± 0	330–330	11	100.0
		<i>N. melanostomus</i>	103 ± 13	90–130	1	9.1
19	Eel trap 2'				10	90.9
		<i>A. anguilla</i>	129 ± 5	125–132	2	100.0
52–56	Pool trap				2	100.0
		<i>A. anguilla</i>	171 ± 111	85–812	1149	100.0
		<i>A. alburnus</i>	93 ± 45	37–250	407	35.4
		<i>A. bipunctatus</i>	90 ± 20	45–130	440	38.3
		<i>Aspius aspius</i>	124 ± 13	90–140	41	3.6
		<i>B. barbus</i>	102 ± 8	95–120	13	1.1
		<i>Abramis brama</i>	204 ± 129	100–500	3	0.3
		<i>L. cephalus</i>	130 ± 16	110–150	38	3.3
		<i>R. rutilus</i>	71 ± 19	50–87	4	0.3
		<i>N. melanostomus</i>	83 ± 24	45–160	3	0.3
		<i>P. fluviatilis</i>	100 ± 0	100–100	191	16.6
		<i>Silurus glanis</i>	1200 ± 0	1200–1200	1	0.1
		<i>L. leuciscus</i>	102 ± 12	90–120	1	0.1
					7	0.6

A. anguilla) of the total fish caught, did not significantly differ from the device with plastic trap openings and additional meshes, the eel traps 2 and 2', 1.7% (45 mm in *N. melanostomus* to 132 mm in *A. anguilla*) (FET, odds ratio = 3.667, $p > 0.05$).

Of the 12 species identified, *A. anguilla* (37.3%, 85–812 mm), *A. alburnus* (35.2%, 37–250 mm), and *N. melanostomus* (17.8%, 45–160 mm) were the most-caught species (FET, range, odds ratio = 6.567–18.747, $p < 0.05$). *Alburnoides bipunctatus* (3.3%, 45–130 mm), *Abramis brama* (3.0%, 100–500 mm), and *Aspius aspius* (1.0%, 45–130 mm) each represented less than 4%, while the other six species each represented less than 1% of the total fish caught. The fish species targeted by this study, eels ($n = 468$), were more frequently captured in the basins no. 52–56 as pool traps (87.0%, 85–812 mm) than in basin no. 8 (12.4%, 80–440 mm) and basin no. 19 (0.6%, 125–330 mm) (FET, range, odds ratio = 4.740–618.912, $p < 0.001$). Captures in eel traps with manufactured mesh represented 10.7% (85–440 mm) and were more abundant than captures in traps with additional mesh (2.3%, 80–132 mm) (FET, range, odds ratio = 58.072–308.251, $p < 0.001$).

3.2. Abundance and growth in eel cohorts

During our study period, 468 eels (median = 120 mm, mean = 163.7, 90%CI = 95–413 mm, range = 80–812 mm) were caught. Of which 372 eels (79.5%, median = 115 mm, 90%CI = 95–135 mm, range = 80–170 mm) belonged to the 2025 Cohort and 96 eels (20.5%, median = 335 mm, 90% CI = 235–503 mm, range = 210–812 mm) to the cohorts prior to 2025 (Fig. 3). Eels were caught in all trap types except for the additional mesh traps, which failed to catch individuals from the cohorts prior to 2025. The catch in pool traps was more prevalent in the

2025 Cohort, accounting for 84.4% of the eel total number (FET, range, odds ratio = 26.863, $p < 0.001$). These individuals were larger than those in other trap types except for the two eels caught in the trap 2' having additional mesh (KW test: $df = 3$, $\chi^2 = 56.720$, $p < 0.001$ and DU test, $p < 0.01$). In the cohorts before 2025, eels were mostly caught in pool traps, accounting for 96.9% (FET, range, odds ratio = 865.687, $p < 0.001$), while no individual was captured in the traps with additional mesh. The three (3.1%) eels caught in the traps without additional mesh had TLs that were not very different to those caught in pool traps.

In both groups, there was a positive relationship between total length and weight (Fig. 2). The total length explained 81.4% and 96.5% of the variance in weight in the 2025 Cohort and the cohorts prior to 2025, respectively (adjusted R^2 , $p < 0.001$) (Fig. 4). The coefficient 'a' was -3.399 in the first cohort group and -3.013 in the second group. The coefficient 'b' showed positive allometric growth ($b > 3.0$) in both cohorts and fell within the theoretical range expected for teleosts ($2.5 < b < 3.5$; Froese, 2006; Pachla et al., 2026) indicating thick-bodied eels and good trophic condition resulting from optimal environmental conditions for growth in this fish species with an elongated body shape.

3.3. Catch per unit effort, periodicity and environmental factors

From 5 May to 21 October 2025, we conducted 36 days of trap monitoring. Catches per unit effort (CPUEs) when the two trapping devices and the two cohort groups were pooled ranged from 0 to 47 eels per day (on 22 July) and 94% of eels were caught between 3 June and 12 September, with the median of the catch distribution observed on 1 August. The similar CPUE distribution was observed in pool traps with CPUEs ranging from 0 to 34 eels per day (on 4 August) and 93% between

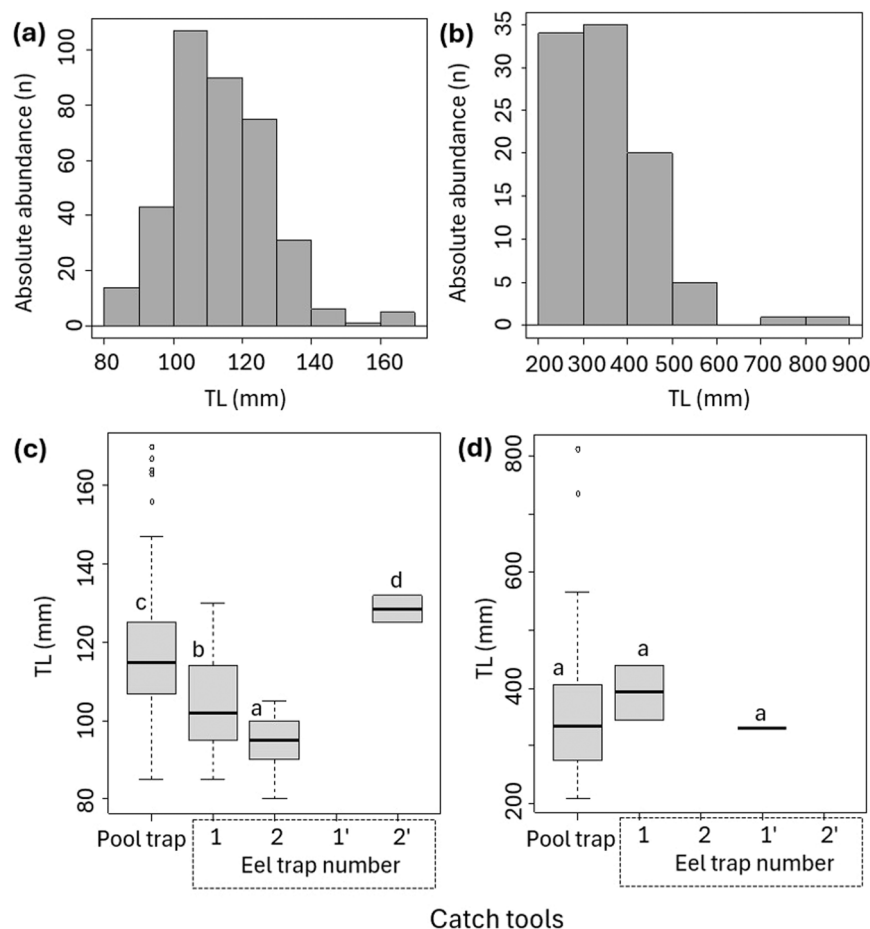


Fig. 3. TL-frequency distribution with 10- and 100-mm class intervals in the cohort 2025 (a) and the cohorts prior to 2025 (b), and TL according to catch tools for the cohort 2025 (c) and the cohorts before 2025 (d). Catch tools sharing at least one common letter did not differ significantly (KW and DU tests, $p < 0.05$).

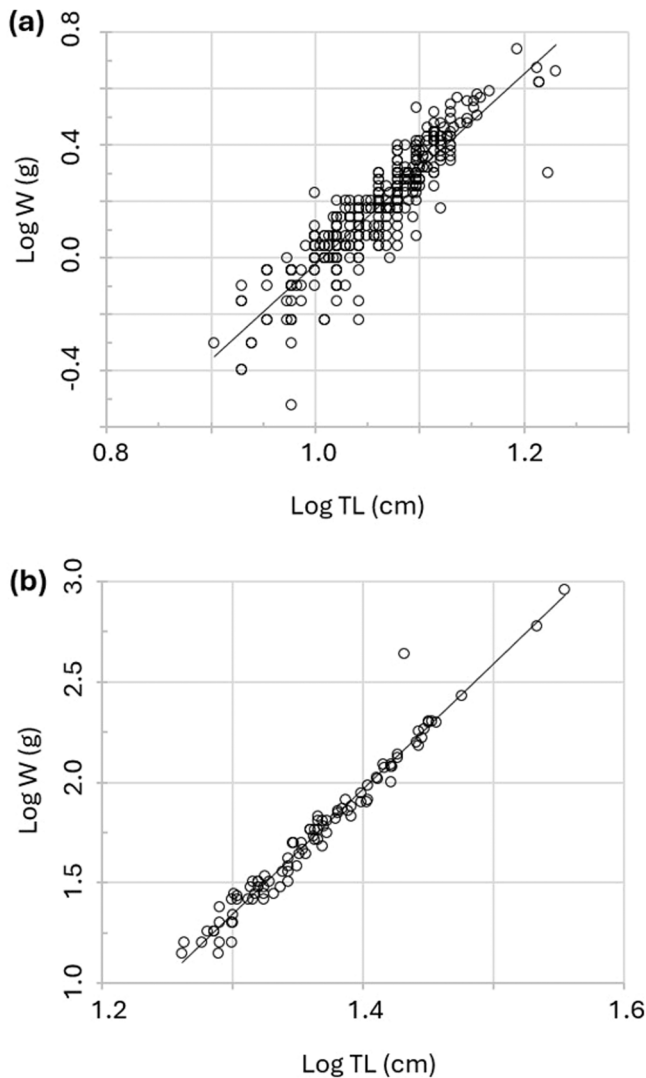


Fig. 4. Total length (TL) to weight (W) relationship in the cohort 2025 (a) and the cohorts before 2025 (b).

3 June and 12 September and the median on 1 August (Fig. 5; Table 2). In the eel traps, the CPUEs varied from 0 to 20 eels per day (22 July); 94% were made between 16 July and 1 August, with the median on 22 July. Mean and maximum CPUEs for all cohorts pooled were 13 and 47 eels per day, respectively. They were higher in the 2025 Cohort (values, mean = 9 and 11 ind., and maximum = 20 and 34 ind. in eel traps and pool traps, respectively) than in the cohorts before 2025 (2 and 3 ind., and 2 and 23 ind.) regardless of the catch tool (Pearson's Chi-squared χ^2 -test: df = 1, $\chi^2 = 4.246$ –33.333, $p < 0.05$) (Table 2).

Catch season of all eels ranged from 5 May to 10 October (duration 158 days) and 90% between 3 June and 12 September (100 days). In both cohorts, catch seasons of 90% and 100% eels were shorter in the eel traps than in the pool traps (χ^2 -test: df = 1, $\chi^2 = 34.105$ –130.060, $p < 0.001$). The catch seasons in pool traps started early and ended early in the cohorts prior to 2025, while they began late in eel traps. In the eel traps, the first individual caught in the cohorts prior to 2025 represented 33% of the total catch and was observed on 29 July, a date which coincided with the 46th individual (82%) caught in the 2025 Cohort. However, for the same catch device, the catch seasons did not differ significantly between the two cohort groups.

During the trap monitoring period, daily mean temperature and flow at sampling site varied between 15.6 and 26.8 °C (median = 21.8 °C, 90% CI = 16.1–25.0 °C) and 12.0–131.8 m²s⁻¹ (median = 49.9 m²s⁻¹,

90% CI = 20.5–88.5 m²s⁻¹), respectively (Fig. 6). Eels were caught at a temperature range of 15.8–26.8 °C (median = 23.6 °C, 90% CI = 20.1–25.0 °C) and river flow of 12.0–131.8 m²s⁻¹ (median = 40.6 m²s⁻¹, 90% CI = 12.0–90.4 m²s⁻¹). The 2025 Cohort (median = 23.7 °C, 90% CI = 20.5–25.0 °C, 100% = 15.8–25.0 °C) was caught at higher temperature than the cohorts prior to 2025 (median = 23.1 °C, 90% CI = 19.1–25.5 °C, 100% = 19.1–26.8 °C) (W test, V = 3268, $p < 0.001$). However, the flows at the eel catch did not differ significantly between the 2025 Cohort (median = 40.6 m²s⁻¹, 90% CI = 12.0–90.4 m²s⁻¹, 100% = 12.0–131.8 m²s⁻¹) and the cohorts before 2025 (median = 39.4 m²s⁻¹, 90% CI = 34.4–58.4 m²s⁻¹, 100% = 23.0–103.1 m²s⁻¹) (W test, V = 3268, $p > 0.05$).

4. Discussion

This study's eel abundance was low, accounting for 8.3% of the record level observed in 1992, a trend that reflects the long-term depletion of the Meuse local stock. From 1992–2003, total catches at the Lixhe dam using the same continuously monitored fish pass ranged from 1787 to 5614 eels, with maximum CPUEs reaching up to 1335 eels per day (Nzau Matondo and Ovidio, 2016). These historical data provide a crucial baseline, as they represent a period before the drastic stock decline where natural recruitment from the North Sea was still functional. In comparison, our excessively low catch levels in 2025, despite recent restocking efforts, must be interpreted with caution. First, this monitoring represents an assessment of the possible restocked eels' abundance in the immediate area of restocking, based on how many individuals attempted to ascend a dam located just above their release site. Second, this low number could reflect the technical inefficiency of the trapping tools used for the small-sized '2025 Cohort'. The grid and mesh sizes were too large to fully prevent small glass eels from escaping the pool traps or the fishway. This methodological constraint partially obscures the positive impact of glass eel restocking on local stock levels. However, the success of the operation is revealed by a high ratio of approximately 3.9 between the restocked 2025 Cohort and the older cohorts. Furthermore, the total ascent at Lixhe dam rose to 8.3% of the 1992 level in 2025, compared to only 2.3% in 2024, leading to a reduction in the annual stock decline rate (from 3.1% to 2.8%). In the context of previous research in shallow tributaries, where electrofishing and telemetry demonstrated high survival and rapid dispersal into refuge habitats (Nzau Matondo et al., 2019, 2020, 2021, 2023a,b), these new observations at the dam confirm that restocked glass eels can also successfully survive, adapt, and initiate upstream migration within large, deep riverine ecosystems. This strengthens the hypothesis 1 that when natural recruitment via the Dutch Meuse is insufficient, localized glass eel restocking below obstacles is a viable strategy to boost declining local stocks.

With a mean length of 163.7 mm (median, 120 mm), the eels in this study exhibited length never recorded in a 33-year-monitoring period of this fishway since 1992 (Nzau Matondo and Ovidio, 2016, Benitez et al., 2025). The predominance of individuals from the 2025 Cohort compared to those from previous cohorts would explain this observation. The 2025 Cohort measured between 80 and 170 mm (mean, 115.1 mm). Similar sizes were very rare (<1%: Baras et al., 1996, Nzau Matondo and Ovidio, 2016) before the Belgian Eel Management Plan implementation in 2011, which used the glass eel restocking as management measures to restore eel local stocks in Wallonia, Belgium (ICES, 2018, Belpaire et al., 2021). During this period, the smallest eel caught in the Meuse was 114 mm in 1993 (Baras et al., 1996) and 140 mm in 1992 and 2001 (Nzau Matondo and Ovidio, 2016). In an 8-month period since February 2025 in the Meuse, the 2025 Cohort exhibited a mean length increment increase of 37 mm (range, 2–92 mm) with body shape coefficient a of -3.4 and growth coefficient b value of 3.4. It was 51 mm (4–107 mm) with a values ranging from -3.3 to -1.9 and b values varying from 2.1 to 3.5 during a 7-month period since March 2017 in glass eels caught on the French Atlantic coast and restocked in five

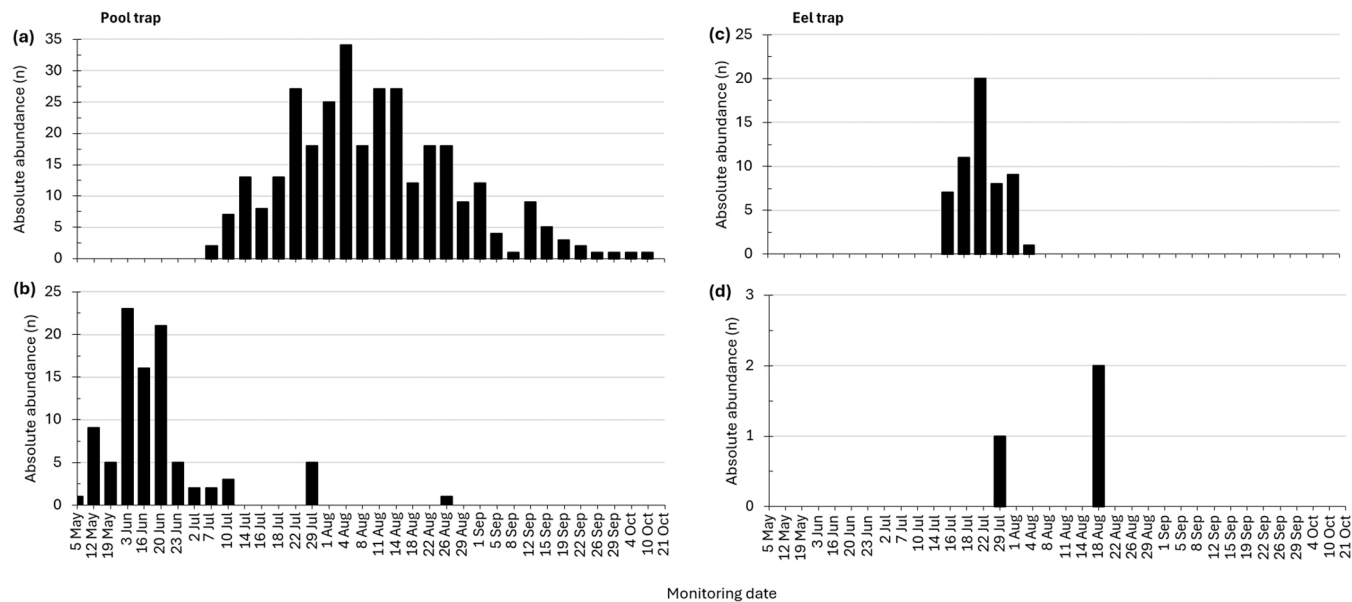


Fig. 5. Periodicity of eels in trap pools and net traps for the cohort 2025 (a and c) and the cohorts prior to 2025 (b and d).

Table 2
CPUE and periodicity of both cohort groups according to trap tools. Catch periods refer to the dates when 50% (median), 90%, and 100% of eels were caught, as shown by the catch date distribution. Parentheses denote the catch period duration.

Catch tool	Cohort	N total	CPUE		Catch period		
			Mean ± SE	Maximum	Median	90% (days)	100% (days)
Pool traps	2025	316	11 ± 10	34 on 4 August	8 August	14 July–12 September (60 d)	2 July–10 October (100 d)
	Prior to 2025	93	3 ± 8	23 on 3 June	16 July	12 May–7 September (56 d)	5 May–26 August (113 d)
Eel net traps	2025	56	9 ± 6	20 on 22 July	22 July	16 July–1 August (16 d)	16 July–4 August (19 d)
	Prior to 2025	3	2 ± 1	2 on 18 August	18 August	29 July–31 August (20 d)	29 July–18 August (20 d)

tributaries of the Meuse (Nzau Matondo et al., 2021). This has fallen to 28 mm in colder oligotrophic tributary of the Meuse (Nzau Matondo et al., 2021). The 2025 Cohort in this study was also caught on the French Atlantic coast. In small coastal catchments and estuaries along the French coast of the Eastern English Channel, Denis et al. (2022) have recorded mean TL increments of 76–115 mm per year at one-year-old age in glass eels, as well as 3–115 mm per year with the a values ranging from −17.2 to −11.7 and the b values varying from 2.7 to 3.6, irrespective of eel sex and age. The published annual TL increments of eels were 14–41 mm per year in Irish rivers (Poole and Reynolds, 1996, Moriarty, 1973,1983), 16–66 mm per year in British rivers (Naismith and Knights, 1993, Mann and Blackburn 1991, Naismith and Knights, 1990, 1993, Aprahamian, 2000, Champkin et al., 2024), 55 mm per year in Alsatian Rhine in Germany (Meunier, 1994), 50–75 mm per year in Camargue in France and 37–152 mm per year in Spain rivers (Fernández-Gelgado et al., 1989). Despite the lack of results for eels at their first-year age, we can state that the growth performance of the 2025 Cohort falls within the range of growth values recorded across Europe. Our results are therefore within acceptable limits and tend to show that eel growth is good even after restocking as glass eels in freshwaters. This growth is greater than that of oligotrophic, colder and nutrient-poor rivers that are located further north (Poole and Reynolds, 1996, Moriarty, 1983). Conversely, it is lower than that of countries in southern Europe that have estuaries (Fernández-Gelgado et al., 1989), which are brackish ecosystems much more productive than rivers and enable a longer season of high temperatures, highlighting that eel growth performance is increased under high temperature conditions (hypothesis 2). This emphasizes the importance of estuaries as crucial

habitats for eel growth and, consequently, for the species' conservation. Eels grow faster in ideal, warmer aquatic environments. The observed positive allometric growth in eels within our study suggests optimal growth conditions and abundant prey in the Meuse habitats. This means that the density of eels would be far much lower than their carrying capacity, which is the highest density that these habitats can support under normal conditions. Furthermore, this is supported by the fact that the total catch and maximum CPUE values were very low in 2025, reaching levels that had never been seen before the sharp drop in eel stocks at this site in 2004 (Nzau Matondo and Ovidio, 2016). An eel catch season and duration, from 5 May to 10 October for 158 days, was observed in this study. These were in the range of catch seasons and durations reported at Lixhe dam during the period preceding the drastic decline in stocks, which occurred from 3 April (in 2003) to 10 October (in 1999) for durations that ranged from 130 (in 1992) to 174 (in 1999) days (Nzau Matondo and Ovidio, 2016). However, the cohorts prior to 2025 tended to start and end migration earlier than the 2025 Cohort. It is highly likely that the increased population density pressure after restocking is involved in this upstream migration and catch phenology (Ibbotson et al., 2002), leading to a shift towards a late catch season for small eels (hypothesis 3). Eel capture occurred primarily during periods of low flow and when water temperature increased in the Meuse. During this period, water temperature, more than river flow, was an important factor influencing eel movements. An increase in catches in spring and summer, as well as a peak in late autumn, have also been observed in a Spanish river, indicating that temperature plays a role in eel capture (Lobón-Cervia et al. 1995). The cohorts prior to 2025 had a relatively lower average capture temperature (22.8°C) than the 2025

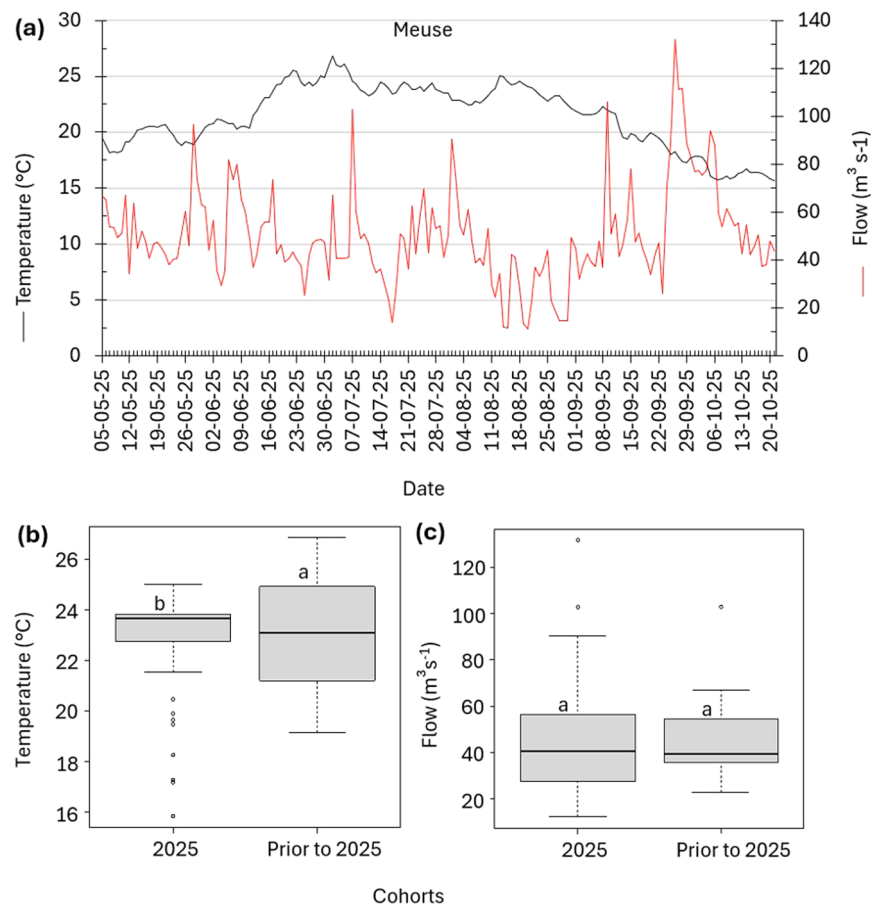


Fig. 6. Daily mean temperatures and flow in the Meuse with 1-day class intervals during the trap monitoring period and comparison of temperature and flow at catch between the cohort 2025 ($n = 372$) and the cohorts prior to 2025 ($n = 96$). Boxplots are shown with median bars. Hinges indicate first and third quartiles and circles mark outliers. Cohorts sharing the same letter did not differ significantly (W test, $p < 0.05$).

Cohort (23.3°C) due to their earlier capture period. All these cohorts were caught in 2025 at an average catch temperature of 23.1°C (range, $15.8\text{--}26.8^{\circ}\text{C}$), and flow rate of $44.8\text{ m}^3/\text{s}$ (range, $12.0\text{--}131.8\text{ m}^3/\text{s}$). These values would show higher temperatures and lower flows in 2025 compared to years with abundant eel catches. During these years, eels were caught at average temperature of 20.2°C (range, $10.5\text{--}29.1^{\circ}\text{C}$ and flow rate of $113\text{ m}^3/\text{s}$ (range, $6.2\text{--}712\text{ m}^3/\text{s}$ at Lixhe (Nzau Matondo and Ovidio., 2016). Literature reported the accepted thresholds of $10\text{--}15^{\circ}\text{C}$ for eels to start migration (Naismith and Knights, 1988, White and Knights, 1997, Nzau Matondo and Ovidio, 2016). Our observed temperatures can be interpreted as an upward shift in the minimum temperature thresholds for migratory activity, confirming the thermophilic nature of the species. The catch of all cohorts in 2025, especially the small eels like the 2025 Cohort at Lixhe was also facilitated by the low stable flow rate ($0.3\text{ m}^3/\text{s}$) in the fish pass compared to the variable flows in the Meuse, which reach very high values.

From May to October 2025, we captured a total of 12 fish species in our combined trapping devices, compared to 9 species in the eel traps. The River Meuse at Lixhe is known to have hosted 35 species from 1999 to 2018 (Benitez et al., 2022) and 25 species in 2024 (Benitez et al., 2025). Before the periods of drastic decline of the ascending eel stocks (from 1992 to 2003) at this site as well as before the Belgian Eel Management Plan implementation in 2011, (Philippart et al., 2001) have inventoried 21 fish species migrating upriver via the two fishways and 17 species via the same fish pass used in the present study. Nzau Matondo et al. (2024) observed 11 species through sampling using fyke nets placed upstream of the Lixhe dam. Benitez et al. (2025) reported also 11 species in 2024 using at the same fishway as our study.

These results would suggest a relatively constant number of species ascending the Meuse via this fishway in 2024–2025, but also an erosion of biodiversity since 2001. It's possible that these results are due to global warming, expansion of predators like *S. glanis*, and the spread of invasive mollusks that reduce phyto and zooplankton production through intense water filtration activity (Daufresne et al., 2015, Otjacques et al., 2016). All these considerations could mean that glass eel restocking did not have a significant impact on shifts in the assemblage of fish species (hypothesis 4). This observation is fully consistent with the findings of Félix et al. (2020), who reported that glass eel restocking events did not cause short-term disruptions or significant changes to local fish biological communities and their ecological status. Furthermore, although it was hypothesized that the morphology of young eels might attract a broader range of ascending piscivorous predators (Mann, 1982), our trapping data confirms that the restocking program did not artificially inflate the abundance or diversity of predatory species within the fishway. The fishway also exhibited selectivity towards certain species, which was explained by the low number of species moving through it compared to the overall biodiversity present at Lixhe. It is therefore justified that a new fish pass was built eighteen years later in the same site to ensure the river's upstream continuity for large migratory fish species. Certain species like *A. brama*, *A. aspius* and *S. glanis* were not caught in the eel traps probably because of their low abundance as well as their high body length. This sampling tool also exhibited within the same species selectivity towards the fish size, favouring the capture of small individuals and the species with bodies that are longer than they are tall. This was supported by the maximum lengths of $330\text{--}440\text{ mm}$ found in three eels caught belonging to the

cohorts prior to 2025. The narrow entrance and short length of the trap compartment could explain this selectivity, which could prevent larger individuals of *A. brama* and *S. glanis* to be trapped. This should therefore be considered when selecting capture tools targeting larger individuals.

While the results of this study provide highly precise insights into the early juvenile traits and movement dynamics of restocked glass eels, certain management implications must be interpreted with caution, as they are based on a dataset restricted to a single site and a single annual cycle. In riverine ecosystems, European eel recruitment, growth performance, and migratory phenology are typically subject to substantial interannual variations driven by fluctuating meteorological conditions, biological cycles, and broad-scale environmental shifts (Bonhommeau et al., 2008, Drouineau et al., 2018). Consequently, the trends observed at the Lixhe dam in 2025 offer a valuable snapshot of post-restocking ecology in large deep rivers, but they may not fully capture the long-term, multi-cohort dynamics or the spatial heterogeneity across the entire Meuse catchment. To build more robust and scalable management strategies for this critically endangered species, further multi-year monitoring programs spanning multiple river sections are required to validate these preliminary findings and confirm the large-scale viability of glass eel restocking.

5. Conclusion

For the first time in the Belgian River Meuse, we have described the life history traits of young eels during the first year of restocking as glass eels. As a discrete, cryptic, benthic, and nocturnal species, eels are difficult to capture and to study, particularly in a large river (Baras et al., 1998). Taking advantage of its positive thigmotactic nature, we were able to characterize the abundance, growth, and migration periodicity of the first life stage of elvers, as well as composition of the associated fish species. Growth was good, abundance impacted positively the local stock, and migration occurred with other fish species. However, within eels, older individuals moved before the young eels due to probably to population density pressure after glass eel restocking (Ibbotson et al., 2002). These findings provide new insights into glass eel restocking in large rivers and as an effective measure to boost declining local stocks, and probably in the long term, to increase the escapement rates of silver eels that reproduce at sea. However, the issue of their survival in such a vast and deep ecosystem still needs to be investigated (Nzau Matondo et al., 2020).

CRedit authorship contribution statement

Billy Nzau Matondo: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michaël Ovidio:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2026.105285.

Data Availability

Data will be made available on request.

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