Received: 7 June 2018 | Revised: 2 October 2018 | Accepted: 14 January 2019
DOI: 10.1002/aqc.3062

RESEARCH ARTICLE

WILEY

What happens to glass eels after restocking in upland rivers? A long-term study on their dispersal and behavioural traits

Billy Nzau Matondo[1] | **Emilie Séleck**[1] | **Arnaud Dierckx**[1] | **Jean-Philippe Benitez**[1] | **Xavier Rollin**[2] | **Michaël Ovidio**[1]

[1] Department of Biology, Ecology, and Evolution, University of Liège, Liège, Belgium

[2] DGO3-DNF-Fisheries Service, Public Service of Wallonia, Jambes, Belgium

Correspondence
Billy Nzau Matondo, Laboratory of Fish Demography and Hydroecology, Biology of Behaviour Unit, Freshwater and Oceanic Science Unit of Research – FOCUS, University of Liège, 22 Quai E. Van Beneden, B-4020 Liège, Belgium.
Email: bnmatondo@uliege.be

Funding information
European Fisheries Fund and the Wallonia Public Service, Grant/Award Number: 44-1604-008

Abstract

1. The European eel *Anguilla anguilla* is a critically endangered fish species as a result of human activities and climate change in river and oceanic ecosystems. Restocking using glass eels in continental freshwater areas is a potential conservation measure for enhancing local eel stocks and for conserving the species in aquatic habitats, where it may otherwise disappear. However, little is known about the fate of these restocked individuals and the early ecological behaviour of the young eels translocated in rivers.
2. A portable radio-frequency identification (RFID) telemetry system and 12-mm tags were used to track restocked eels for a duration of 4 years. The aim was to understand the early movement, behavioural traits, dispersal, and habitat use of elvers after restocking performed in 2013 with glass eels in a shallow riverine environment.
3. From the 241 tagged eels (total length, Q_{50} = 152 mm), 85% were detected in 1968 positions during a period of 4 years, beginning in 2014. Clear seasonality in eel activity was observed, with higher mobility in summer when the water temperature was high (above 12°C). Dispersal was slowed by numerous artificial obstacles and the high carrying capacity of habitats. There was a negative relationship between the body size of eels at tagging and their mobility. Five behavioural categories of mobility patterns were identified: ascending, descending, oscillating with an upstream trend, oscillating with a downstream trend, and stationary. The first four categories depleted with time, in favour of stationary individuals that displayed a highly sedentary lifestyle.
4. This study provides new knowledge of the long-term dispersal behaviour of restocked eels and the influence of seasons, barriers, and habitats on their colonization strategy changing with time. The results contribute to a better understanding of the issue of uncommon restocking practices in upland rivers.

KEYWORDS

Anguilla anguilla, behaviour, conservation measure, detection telemetry, endangered species, mobility, portable antenna, restocking

1 | INTRODUCTION

During recent years, the abundance of the European eel, *Anguilla anguilla*, has drastically declined throughout its distributional range as a result of physical barriers, habitat loss, pollution, diseases, overfishing, and changes in oceanic currents (Belpaire et al., 2009; Dekker, 2003; Friedland, Miller, & Knights, 2007). This eel species is considered to be outside its safe biological limits, and since 2008 it has been listed as Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Dekker & Beaulaton, 2016; ICES, 2013; Jacoby & Gollock, 2014).

Unlike most fish species, eels spawn once in their lifetime in the Sargasso Sea, where they die after breeding (van Ginneken & Maes, 2005). At the early developmental stage leptocephalus larvae, which are transparent and leaf shaped, drift through the Atlantic Ocean on an oceanic current from their breeding ground to the coasts of Europe and North Africa, travelling more than 4000 km in 2–3 years (Bonhommeau, Castonguay, Rivot, Sabatié, & Le Pape, 2010). At the continental shelf, leptocephalus larvae metamorphose into glass eels that are minute, transparent, young eels. The glass eels gather in very large shoals that migrate into estuaries and, depending upon the density, colonize inland fresh waters as pigmented elvers. By feeding on invertebrates, the elvers become yellow eels and remain in fresh waters for 10–15 years until they are ready to return to their birthplace as silver eels to give rise to the next generation. Spawning migration can last for more than 6 months (Righton et al., 2016), and the silver eels use high fat stores for sexual maturation and the journey to reach the spawning ground (Tesch & Thorpe, 2003).

For a successful life cycle, yellow eels, in a growth phase with a highly sedentary lifestyle, must have access to suitable habitats and substantial food resources to store fat for reproduction (Belpaire et al., 2009; Laffaille, Acou, & Guillouet, 2005; Ovidio, Seredynski, Philippart, & Nzau Matondo, 2013). In the Meuse basin, such habitats are available in the upper parts of inland waters, but they are continually emptied of eels because of the progressive departure of the oldest individuals at the silver eel stage, which is not compensated for by the return of young yellow eels (Nzau Matondo & Ovidio, 2016). The estimated eel stock in the lower part of the Meuse River in Belgium, more than 320 km upstream from the North Sea, dropped from 445 000 individuals in 1993 (Baras, Philippart, & Salmon, 1996) to 7200 in 2013 (Nzau Matondo, Benitez, Dierckx, Philippart, & Ovidio, 2017). Similarly, the number of new eels entering the Belgian Meuse River has drastically declined by 95.5% in 23 years, and their body size has increased by 4 mm per year since 1992, with the inhibition of colonization linked to density (Nzau Matondo & Ovidio, 2016; Nzau Matondo & Ovidio, 2018). In the Meuse basin, the reason for this drastic decline in the local stock of eels is clearly riverine recruitment failure from the North Sea.

Under such conditions, restocking using young life stages remains a solution to enhance the local stocks of eels and to conserve the species in the upper parts of rivers, and probably over the long term to meet the silver eel escapement target in the Eel Recovery Plan of the European Union (Council of the European Communities, 2007). Restocking using glass eels and elvers is one of the recovery options identified by the European Commission for habitats with low or no natural immigration (Ovidio, Tarrago-Bès, & Nzau Matondo, 2015; Simon, Dörner, & Richter, 2009; Simon, Dörner, Scott, Schreckenbach, & Knösche, 2013). As artificial reproduction of the European eel is not yet possible, the only source of restocking material is the translocation of wild-caught glass eels or elvers (Pedersen & Rasmussen, 2016). Many studies have reported encouraging outcomes, such as the restocked young eels surviving (with a survival rate of 3.5–20% reported by Shiao, Lozys, Iizuka, & Tzeng, 2006; with a survival rate of 5–45% reported by Simon & Dörner, 2014) and growing (with growth in streams of 0.5–10.5 cm year^{-1} reported by Ovidio et al., 2015; with growth in lakes of 0.9–9.3 cm year^{-1} reported by Pedersen, 2000 and Simon et al., 2013; and with growth in lagoons of 5.5–8.3 cm year^{-1} reported by Lin, Lozys, Shiao, Iizuka, & Tzeng, 2007) in their novel environments. Most of these studies were conducted in the short term, dealing with restocking efficiency in growth and survival (Andersson, Sandström, & Hansen, 1991; Bisgaard & Pedersen, 1991; Lin et al., 2007; Pedersen, 2009; Simon & Dörner, 2014). Little is known, however, about the early movement behavioural traits, dispersal, and habitats of young eels restocked as glass eels in the field. This lack of knowledge arises from the difficulties in studying the early developmental stages of species exhibiting cryptic behaviour and nocturnal activity (Baras, Jeandrain, Serouge, & Philippart, 1998; Ovidio et al., 2013), combined with the very small size of the individuals. Such knowledge might be useful for better understanding the adaptive capacity of the young eels translocated in the upper parts of rivers, and therefore improving the outcomes of restocking practices.

To bridge this gap in knowledge, a mobile radio-frequency identification (RFID) telemetry system was used to track small restocked eels in a shallow upland river that has a high carrying capacity (available food and shelter) and no natural immigration owing to the failure in riverine recruitment at the site (absence of catches of naturally recruited eels). This portable telemetry system has been used recently for small-bodied tagged fish in shallow waters (Cucherousset et al., 2010; Cucherousset, Roussel, Keeler, Cunjak, & Stump, 2005). As the RFID passive integrated transponder (PIT) tags used are small, inexpensive, and very resilient, with a very long life, this system is widely used and has already contributed to a better understanding of the ecology, behaviour, and management of small-bodied fishes belonging to various families (Cottidae: Keeler, Breton, Peterson, & Cunjak, 2007; Gobiidae: Breen, Ruetz, Thompson, & Kohler, 2009; Petromyzontidae: Quintella, Andrade, Espanhol, & Almeida, 2005; Salmonidae: Roussel, Cunjak, Newbury, Caissie, & Haro, 2004; Esocidae: Cucherousset, Paillisson, & Roussel, 2007; Cucherousset, Paillisson, Cuzol, & Roussel, 2009). To date, however, this system has not been used widely for young eels in small- and medium-sized rivers, owing to their natural absence at this stage and the limited read range of the tags, restricting their functionality. The present study aimed to clarify further the early movement behavioural traits, dispersal, and habitats of young eels translocated as glass eels in a shallow river environment. During a 4-year study involving intensive telemetry monitoring following restocking, tests were carried out at the individual scale: (i) on the space and time use of the restocked eels, in terms of home-range use, net distance travelled, dispersal, and habitat use; (ii) on the types of movement behavioural patterns displayed; and (iii) on the relationships between the date of tagging, body size, and behavioural groups of the eels.

2 | METHODS

2.1 | Study site

The Mosbeux River, in southern Belgium, has a catchment of 19.16 km^2 and is 6.36 km in length, flowing directly into the Vesdre River, a tributary of the Ourthe River, which drains into the Meuse River (Figure 1a, b). The study site was located 359.3 km upstream from the Meuse River estuary in the Netherlands. The site included 2.380 km of the Mosbeux River, beginning at its mouth, located in the Vesdre River (Figure 1c), as well as 0.584 km of the Vesdre River downstream of its confluence with the Mosbeux River. The Mosbeux River is a typical trout zone, and the Vesdre River is a barbel zone (Huet, 1949). This study site was selected because it was subjected to the restocking of glass eels (n = 4155) in 2013, which were released at a single point in the Mosbeux River, 0.040 km upstream of its mouth (Ovidio et al., 2015). During the study period (from 2014 to 2017), the observed mean width and depth of the Mosbeux River were 2.40 and 0.18 m, respectively, compared with 14.90 and 0.44 m, respectively, for the Vesdre River. In each river, the water temperature was continuously recorded using TidbiT v2 data loggers (Onset Computer Corporation, Bourne, MA). The substrate of the two river bottoms consisted mainly of large stones and blocks. The stretch monitored (2.964 km long) was highly fragmented by several artificial obstacles (n = 49; cumulative waterfall height, WC = 13.86 m) (Figure 1d). The fish biodiversity, analysed by electrofishing surveys in the study site, comprised 11 species, of which the most abundant were the bullhead *Cottus rhenanus* and the brown trout *Salmo trutta*. Old resident eels (total length, TL: mean = 666 mm; range = 515–910 mm) were present, but their quantity was very low (density: Mosbeux = 0.003 eels m^{-1}; Vesdre = 0.005 eels m^{-1}). Similarly, these eels disappeared with time and were not replaced by new naturally recruited eels because of the shutdown of the natural immigration of wild eels from the Meuse River (Nzau Matondo & Ovidio, 2016; Nzau Matondo & Ovidio, 2018).

2.2 | Eel capture and tagging procedure

Electrofishing (EFKO, 3.0 kVA) using hand nets with a 40 × 40 cm diameter and 2 × 2 mm mesh was used to capture the small restocked eels, following the technique used by Ovidio et al. (2015). From November 2014 to September 2016, nine electrofishing sessions (S_1–S_9) were performed (Table 1). The captured eels were

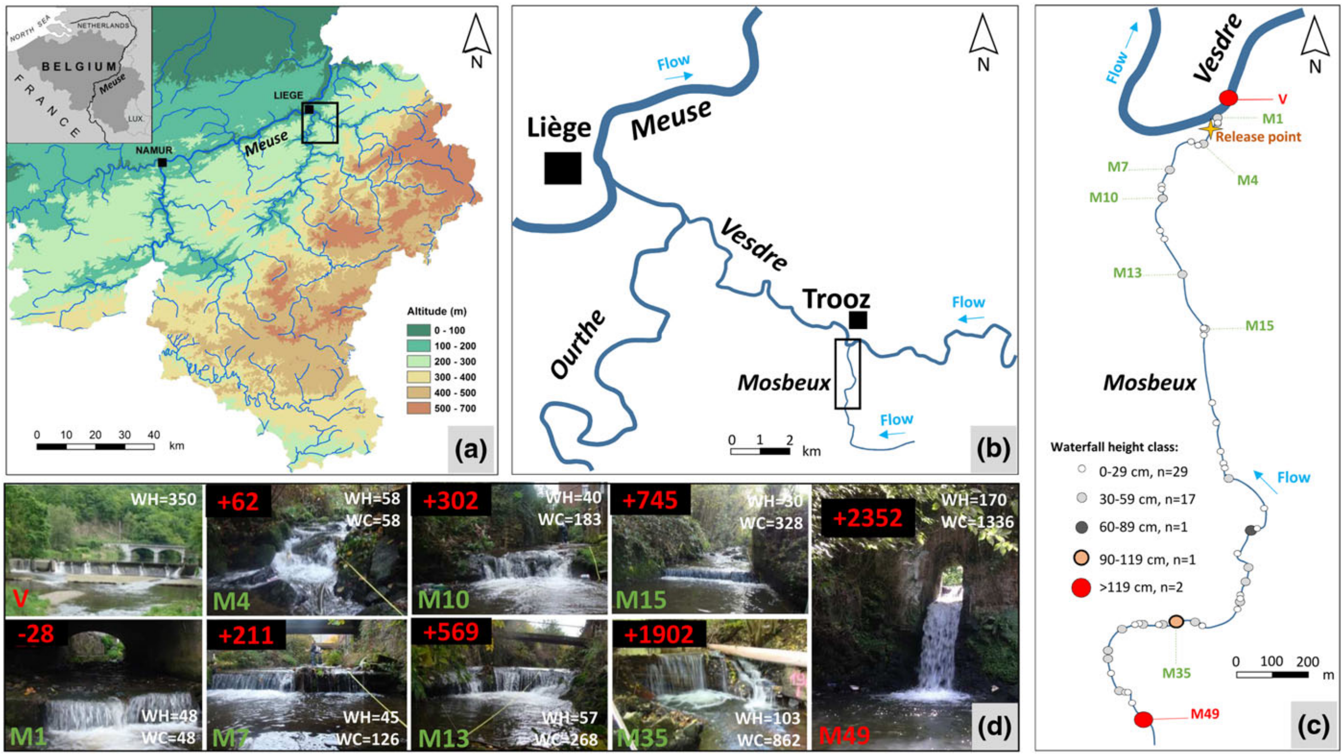

FIGURE 1 (a, b) Location of the study area in the Belgian Meuse River basin, (c) the physical obstacles, and (d) pictures of the major obstacles in the Vesdre (V) and Mosbeux (M) rivers. Mean values of the waterfall height (WH) and cumulative waterfall height from the release point (WC) are given in cm. M or V accompanied by a number indicates the river and the number of obstacles from the release point of glass eels in May 2013, respectively. The number preceded by – or + shows the distance in metres downstream or upstream of the release point

TABLE 1 Detailed information about the capture, tagging, and tracking of restocked eels. Brackets indicate the most upstream position of the captured eel as observed during the S_7 fishing session. Length, weight, home range, and distance travelled are expressed as the means ± SDs. M, Mosbeux; V, Vesdre; *b*, allometric growth coefficient. Range positions are given in metres upstream (+) and downstream (−) of the release point of the glass eels in May 2013

Tagged eels		Body			Capture			Tracking						
Fishing session	*n*	Length (mm)	Weight (g)	*b*	River	Date	Range positions and no. of eels	From	To	No. of days	No. of positions	Eel detection (%)	Linear home range (m)	Distance travelled (m)
S_1	25	138 ± 30	4.9 ± 4.2	2.84	M	18 Nov. 2014	−30 to +55; *n* = 25	17 Dec. 2014	3 May 2017	53	246	96	292 ± 436	370 ± 465
S_2	13	169 ± 36	9.4 ± 7.4	3.31	M	19 Nov. 2014	+135 to +290; *n* = 13	17 Dec. 2014	3 May 2017	53	113	85	606 ± 587	718 ± 640
S_3	45	134 ± 32	4.3 ± 3.7	2.99	M V	19 May 2015 19 May 2015	−30 to +95; *n* = 43 −37; *n* = 2	27 May 2015	3 May 2017	43	616	96	251 ± 255	341 ± 317
S_4	42	142 ± 44	6.4 ± 10.4	2.43	M V	27 May 2015 27 May 2015	−30 to +100; *n* = 27 −58 to −33; *n* = 15	3 Jun. 2015	3 May 2017	42	411	95	210 ± 233	293 ± 322
S_5	31	140 ± 40	5.4 ± 5.2	3.01	M V	9 Jun. 2015 9 Jun. 2015	−23 to +87; *n* = 22 −57 to −37; *n* = 9	6 Jul. 2015	3 May 2017	40	242	84	190 ± 439	205 ± 439
S_6	20	165 ± 51	10.2 ± 11.0	2.95	M V	25 May 2016 25 May 2016	−15 to +110; *n* = 17 −61 to −45; *n* = 3	22 Jun. 2016	3 May 2017	24	109	85	214 ± 195	245 ± 227
S_7	19	189 ± 42	13.6 ± 11.7	3.37	M	6 Jul. 2016	+204 to +326 (+2282); *n* = 19	26 Jul. 2016	3 May 2017	21	93	79	529 ± 482	573 ± 488
S_8	31	313 ± 69	66.6 ± 44.5	2.84	V	12 Jul. 2016	−383 to −220; *n* = 31	26 Jul. 2016	3 May 2017	20	104	71	300 ± 52	324 ± 98
S_9	15	307 ± 98	60.1 ± 53.2	3.06	M V	22 Sep. 2016 22 Sep. 2016	−30 to −29; *n* = 2 −348 to −66; *n* = 13	5 Oct. 2016	3 May 2017	15	34	47	222 ± 120	225 ± 121
All data	241	180 ± 82	17.6 ± 30.9	3.15	M V	18 Nov. 2014 to 22 Sep. 2016 19 May 2015 to 22 Sep. 2016	−30 to +326 (+2282); *n* = 168 −383 to −33; *n* = 73	17 Dec. 2014	3 May 2017	53	1968	85	304 ± 230	371 ± 275

anaesthetised with eugenol 1/10 in alcohol (0.5 mL L^{-1}), measured (TL, to nearest 1 mm), weighed (to nearest 0.01 g), and tagged using small biocompatible RFID tags (half duplex, with a resonance frequency of 134.2 kHz, powered from a battery-less reader signal, with a typical read time of 70 ms; Texas Instruments Inc., Dallas, TX) if their mass exceeded 0.8 g. These tags (size/weight in air: 12 × 2 mm/0.095 g) were inserted in the eel visceral cavity using a small incision (2 mm long) made with a scalpel in the pre-anal position. The inserted tags weighed, on average, 2.31% (range = 0.06–10.56%, Q_{95} = 6.8%) of the eel's body mass. Tagged eels were placed in a basin with river water to fully recover from the anaesthetic before being released into the river at their precise capture point. The capture–mark–recapture (CMR) method was used in the Mosbeux River in May and June 2015 by tagging 87 small-bodied eels to assess the tag retention rate and the recapture rate. The TL of these tagged eels was between 88 and 330 mm (mean = 135 mm), and the RFID tag weight to eel body weight (T/B) ratio varied between 0.48 and 10.56%. During three electrofishing episodes of CMR, 23% (TL, range = 103–192 mm, mean = 128 mm, n = 20) of the tagged eels were recaptured (T/B ratio at tagging: range = 0.84–8.64%, mean = 3.76%) over 1 month after tagging with perfect tag retention (100% of the recaptured eels), and with incisions fully closed in 2–3 weeks. Similarly, the nine fishing sessions provided estimates of the mean annual growth of the tagged eels that were recaptured.

2.3 | Mobile RFID telemetry system

The eels were tracked using a mobile RFID detection telemetry system in combination with recapture during the nine fishing sessions. The RFID tracking system consisted of an array with a backpack electronic recorder connected to a hand-held oval antenna (48.0 × 58.6 cm diameter) with half-duplex RFID tags and a handy reader using BLUETERM software. This portable reader was connected to an electronic box via Bluetooth. From December 2014 to May 2017, 53 tracking sessions were carried out. The sessions were conducted during the day approximately one to three times per month by wading upstream of the monitored stretch (Cucherousset et al., 2005; Cucherousset et al., 2010), which was marked every 5 m.

Before this mobile telemetry system was used, a range test was conducted to verify the detection range and efficiency, in order to determine the most appropriate field technique for this study. By moving the tag to various distances inside and outside the oval antenna, the maximum distance of detection was determined to be 33 cm. In the field, the detection efficiency was higher in shallower areas (detection rate ± SD: Mosbeux River = 88.3 ± 4.0%, linear distance = 181 m, n = 38 eels) than in deeper areas (Vesdre River = 60.8 ± 19.2%, linear distance = 405 m, n = 43 eels). Using a sweeping technique, the same operator moved the antenna submerged near the river bottom to scan all habitats.

To test whether the detection of a tag corresponded to the presence of a live eel, three experiments (with the first experiment conducted on 27 May 2015, the second experiment conducted on 9 June 2015, and the third experiment conducted on 25 May 2016) were performed at the same site (linear distance = 130 m) located in the Mosbeux River. For each experiment, on the same day, a tracking session preceded an electrofishing session with two passages, performed with the same protocol as that used for the nine fishing sessions to capture the eels for tagging.

Each detected eel was associated with the date, the identification of the substratum of the physical habitat, the eel individual code, and its precise location in the study site. The identification of substratum was made using the Wentworth particle size classification system (diameter perpendicular to the largest axis: blocks = 26–102 cm; large stones = 13–25 cm; Wentworth, 1922). This identification also included other habitat categories such as submerged roots and below river banks (Baras et al., 1998; Ovidio et al., 2013).

2.4 | Data analysis and statistics

The mobility of the tagged restocked eels was analysed using several indicators following Ovidio et al. (2013). The linear home range (HR) was defined as the distance between the most upstream and downstream positions of the tagged eel. The net distance travelled (ND) was expressed as the straight-line distance between two consecutively detected positions, and the total distance travelled (TD) was defined as the sum of the NDs. These indicators were calculated for every month and season, and for the entire study period. The exploitation index of the home range (EI) was the ratio calculated by dividing the TD by the HR. The longitudinal dispersal of the tracked eels and the influence of physical obstacles on their mobility were described during each survey period throughout the stretch monitored.

To assess the types of colonization behaviour, the fine-scale movements of the individual restocked eels were analysed, beginning at the time of tagging. From this analysis, the tracked eels were categorized into five behavioural groups (G_1–G_5). The ascending individuals, G_1, showed only upstream movements. The descending individuals, G_2, displayed only downstream movements. The oscillating individuals with an upstream trend, G_3, moved upstream as well as in the downstream direction, but the overall assessment of the movements showed a progression towards upstream. The oscillating individuals with a downstream trend, G_4, moved upstream as well as downstream, but the overall assessment of the movements showed a progression towards downstream. The stationary individuals, G_5, performed upstream and downstream movements of less than 50 m from the tagging position.

All statistical analyses were performed using the R statistical software package RCMDR 3.3.2 (R Development Core Team, 2016), and results were considered significant when P < 0.05. The relationship between the monthly activity and the water temperature was assessed using a generalized linear model (GLM), which included temperature as a fixed effect and the individual as a random effect. In these analyses, the number of detection positions (Poisson distribution and log-link function) and the total and maximum distance travelled (gamma distribution and log-link function) were the dependent variables. The HR, TD, EI, and TL data, as well as the number of detected position data, did not follow a normal distribution (Kolmogorov–Smirnov test, $P < 0.001$). For these parameters, comparisons between the four seasons (winter, spring, summer, and autumn), between the nine fishing sessions (S_1–S_9), and between the five behavioural groups (G_1–G_5) were performed using the Kruskal–Wallis (*H*) test, followed by the Wilcoxon (*W*) signed rank test for multiple pairwise comparisons. A GLM (gamma distribution and log-link function) was used to test the relationship between length at tagging (TL) and the various mobility parameters (HR, TD, and EI).

3 | RESULTS

3.1 | Capture, tagging, and tracking details

In total, 241 eels were tagged in the nine fishing sessions and ranged from 87 to 461 mm in size, with Q_{50} = 152 mm and Q_{95} = 376 mm (Table 1). The relationship between length (TL) and weight (B) was described as $\log B(g) = -6.13 + 3.15 \times \log TL(\mathrm{mm})$ (R^2 = 0.986 and $P < 0.0001$). The eels in the S_2 and S_7 fishing sessions showed the highest values of the allometric coefficient. The eels were mainly captured in the Mosbeux River (Mosbeux/Vesdre ratio = 2.3 : 1; $\chi^2 = 74.896$; $P < 2.2 \times 10^{-16}$). They were all successfully released at their capture site after tagging.

During the nine fishing sessions, 47 eels were recaptured 1–3 years after tagging. At tagging, these eels were 91–387 mm (mean = 142 mm) in size, with an RFID tag weight to eel body weight (T/B) ratio ranging from 0.1 to 10.6% (mean = 3.3%). Their observed growth was between 2 and 119 mm yr^{-1} (mean ± SD = 30.7 ± 17.3 mm yr^{-1}) (Figure 2).

Of the eels tagged, 85% (n = 205) were detected (n = 1968 positions) over 53 tracking days from 17 December 2014 to 3 May 2017. The detection rates, the number of tracking days, and the number of detected positions varied among the nine fishing sessions. The detections were lower for eels tagged during the S_8 and S_9 fishing sessions (the later sessions), in which the eels were mainly tagged in the Vesdre River. The detection rates varied among the five initial survey periods of tracking, from 46% in the first survey period (from November 2014 to May 2015) to 87% in the second survey period (from June 2015 to November 2015) (Table 2). The number of tracking days was higher for eels originating from the earlier (S_1 and S_2) fishing sessions than for those from the later sessions. The number of detected positions varied among individuals between 1 and 29 detections per eel (Q_{50} = 6 detections and Q_{95} = 22 detections), and the fishing sessions with the highest detection rates were S_3 and S_4.

The relationship between eel capture and detection varied among the three experiments, from 40.9% of the eels captured for n = 22 detected eels in the first experiment to 69.2% of the eels captured for n = 13 detected eels in the third experiment. In the second experiment, 43.2% of the eels were captured for n = 37 detected eels. In these three experiments, the eels captured had been previously detected.

Most habitats used by the detected eels were interstices between blocks (47% of the eels detected for 52% of the detection positions) or interstices between large stones (44% of the eels detected for 46% of the detection positions). The least occupied habitats were under river banks and submerged roots, which accounted for 1 and 8% of the detected eels for 0.8 and 1.2% of the detection positions, respectively.

3.2 | Dispersal

The longitudinal dispersal of the eels increased with time (Figure 3; Table 2). The maximum dispersal was observed during the fifth survey period (the last tracking survey period); however, a higher increase in dispersal between two subsequent survey periods occurred in the third and fourth survey periods. The fourth survey period had the maximum linear distance of eel tagging. The second and fourth survey periods included the summer months and showed higher water temperatures. The extreme positions of the detected eels were −484 m and +2345 m (100% of eels, linear distance = 2829 m), which showed a dispersal of eels over almost the entire stretch monitored.

The eels were mostly detected in the Mosbeux River during each survey period, with an abundance that was 2.5–6.1 times that found in the Vesdre River. The abundance of eels detected in a river other than the river in which they were tagged varied among the five survey

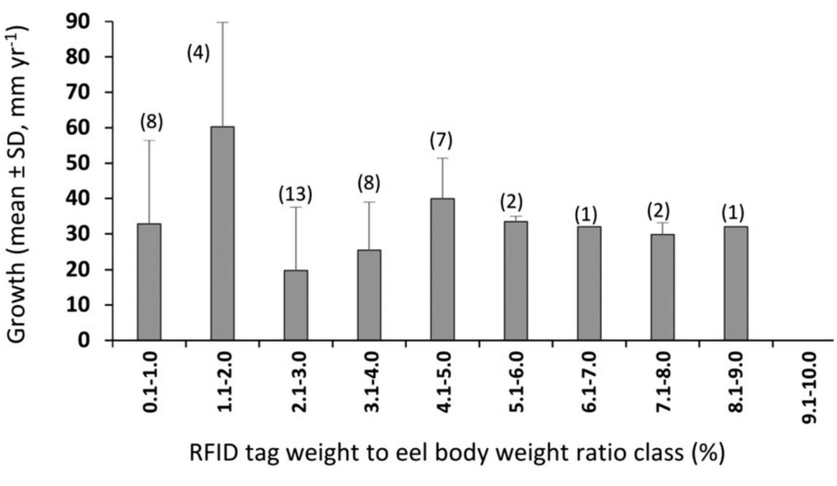

FIGURE 2 Mean growth of the tagged eels from 2014 to 2016, according to the ratio of the radio-frequency identification (RFID) tag weight to the eel's body weight. Numbers in brackets indicate sample sizes

TABLE 2 Longitudinal dispersal of the tagged eels and water temperature. The detected range positions and linear distance are given in metres. In survey periods 4 and 5, the most upstream position of the eel tagged is +2282 m

	Vesdre				Mosbeux				All rivers						
			Range of positions of detections and (linear distance)				Range of positions of detections and (linear distance)				Range of positions of detection and (linear distance)				
Survey period	*n*	Water temp. °C	90%	100%	*n*	Water temp. °C	90%	100%	*n*	Water temp. °C	90%	100%	Cumulative tagging *n*	Detection %	Cumulative range of positions of tagging
1. Nov. 2014 to May 2015	8	8.5	−60 to −30 (30)	−60 to −30 (30)	49	8.6	−28 to +290 (318)	−29 to +309 (338)	57	8.5	−30 to +285 (158)	−60 to +309 (369)	125	45.6	−58 to +290
2. Jun. 2015 to Nov. 2015	36	14.7	−64 to −30 (34)	−250 to −30 (220)	99	12.0	−25 to +660 (685)	−29 to +747 (776)	135	13.3	−60 to +560 (620)	−250 to +747 (997)	156	86.5	−58 to +290
3. Dec. 2015 to May 2016	15	8.4	−67 to −32 (35)	−78 to −30 (48)	77	8.7	−29 to +670 (699)	−29 to +742 (771)	92	8.6	−57 to +637 (694)	−78 to +749 (827)	176	52.3	−58 to +290
4. Jun. 2016 to Nov. 2016	40	13.8	−360 to −47 (313)	−386 to −30 (416)	101	11.6	−19 to +1297 (1316)	−29 to +2345 (2374)	141	12.7	−306 to +747 (1053)	−386 to +2345 (2731)	241	58.5	−383 to +326
5. Dec. 2016 to May 2017	24	7.9	−382 to −34 (416)	−30 to −484 (514)	97	8.0	−10 to +1090 (1100)	−28 to +2344 (2380)	121	8.0	−330 to +745 (1075)	−484 to +2344 (2828)	241	50.2	−383 to +326

periods, from 2.9% (n = 7) in the fifth survey period to 10.2% (n = 18) in the third survey period. The proportion of eels detected in the Vesdre River but tagged in the Mosbeux River ranged from 7.5% in the fourth survey period to 66.7% in the third survey period (mean = 24.3%).

Conversely, the proportion of eels detected in the Mosbeux River but tagged in the Vesdre River varied between 1.0% in the second survey period and 10.4% in the third survey period (mean = 6.3%).

Many tracked and captured eels were located downstream of physical obstacles, and few (n = 5) moved successfully upstream of obstacle M15 (waterfall height, WH = 30 cm; cumulative waterfall height, WC = 325 cm), located at +745 m (Figure 2). The detected eels decreased in the upstream direction with an increased cumulative crest height of obstacles from point 0 (Figures 2 and 3). During the last tracking survey period, 26% of the 121 eels detected were located between −484 m and point 0; 34% of the detected eels were located between 0 and obstacle M7 at +211 m (WH = 45 cm; WC = 126 cm). This percentage of eels decreased to 24% between M7 and M13 at +569 m (WH = 57 cm; WC = 268 cm), and 12% between M13 and M15 at +745 m (WH = 30 cm; WC = 328 cm). This fell to 3% between M15 and M35 at +1902 m (WH = 103 cm; WC = 862 cm) and 1% at the foot of the impassable obstacle, M49, located at +2352 m (WH = 170 cm; WC = 1336 cm).

3.3 | Home range, distance travelled, and exploitation index

The HR, TD, and EI values varied widely among the tracked individuals (Figure 4). The HR of the detected eels ranged from 2 to 2288 m, with Q_{50} = 67 m and Q_{95} = 718 m. The TD was slightly longer than the HR, and ranged from 2 to 2294 m, with Q_{50} = 85 m and Q_{95} = 832 m. The EI varied from 1.00 to 7.14, with Q_{50} = 1.30 and Q_{95} = 3.08. At tagging, the detected eels were 87–461 mm in size, with Q_{50} = 141 mm and Q_{95} = 286 mm. The size of the eels was negatively correlated with the TD (GLM gamma: coefficient ± SE = $-16.890 \times 10^{-5} \pm 7.723 \times 10^{-5}$, $z = -2.187$, $P = 0.030$) and EI (coefficient ± SE = -0.133 ± 0.039, $z = -3.442$, $P = 7.010 \times 10^{-4}$). In contrast, no significant correlation was found between the size of the eels and their HR (coefficient ± SE = $-15.590 \times 10^{-5} \pm 8.975 \times 10^{-5}$, $z = -1.737$, $P = 0.084$).

3.4 | Seasonal activity

The number of detected positions by eel, the HR, and the TD differed significantly among the four seasons (Figure 5). The number of detected positions was greater in autumn than in the other seasons (H test, df = 3, $H = 39.716$, $P = 1.224 \times 10^{-8}$; range, W = 16266–22225, $P = 2.376 \times 10^{-4}$–8.346×10^{-4}); however, the HR and TD values were higher in the summer than in the other seasons (H test, HR, df = 3, $H = 20.224$, $P = 1.525 \times 10^{-4}$; range, W = 1679–3805, $P = 3.035 \times 10^{-5}$–1.121×10^{-7}) (total distance, df = 3, $H = 20.411$, $P = 1.395 \times 10^{-4}$; range, W = 1838–3704, $P = 4.946 \times 10^{-5}$–3.566×10^{-7}).

The monthly activity of the tagged eels showed that the eels were detected throughout the year, and the number of detected positions

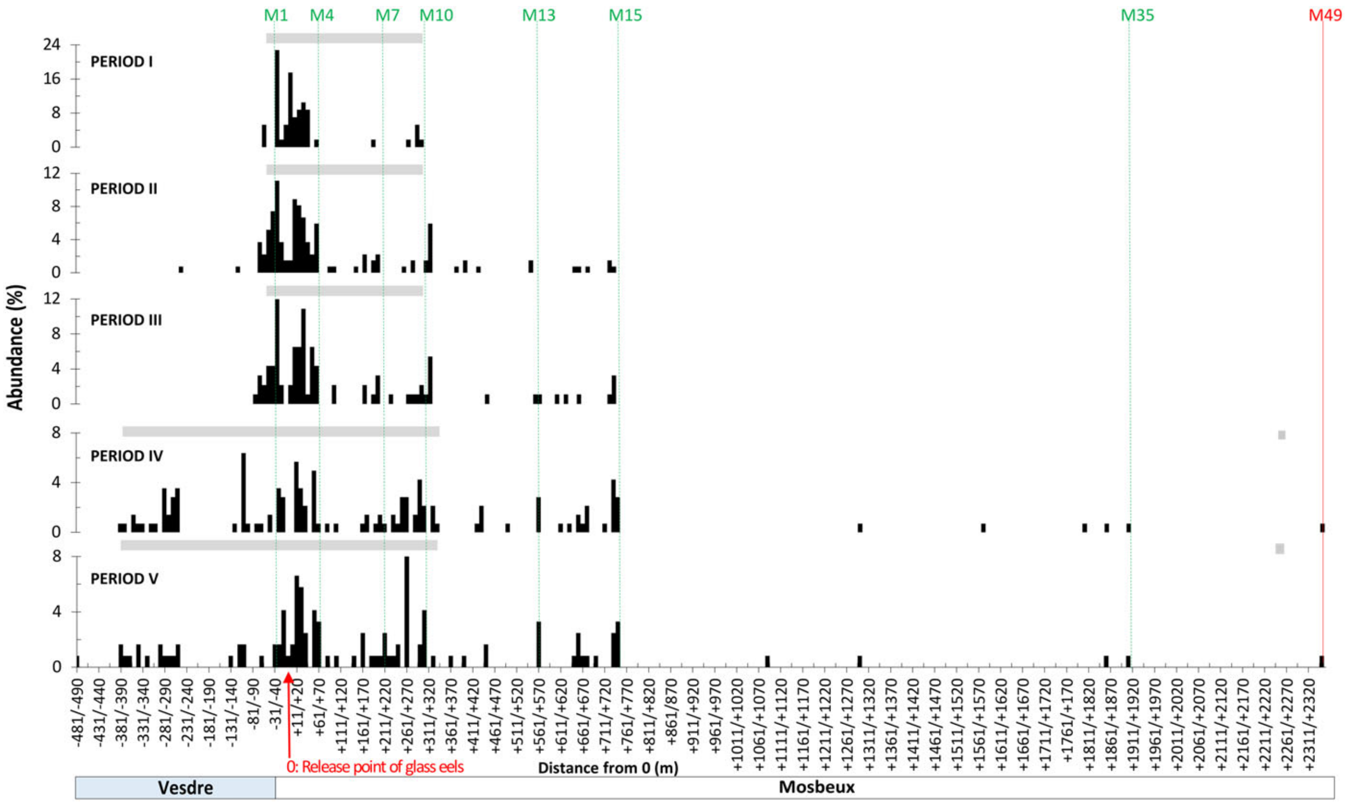

FIGURE 3 Dispersal of the tagged eels during the period of the survey. The cumulative catch area is indicated in grey. The obstacles in the Mosbeux River are labelled with M and marked with green dashed lines for passable barriers and a red line for impassable barriers

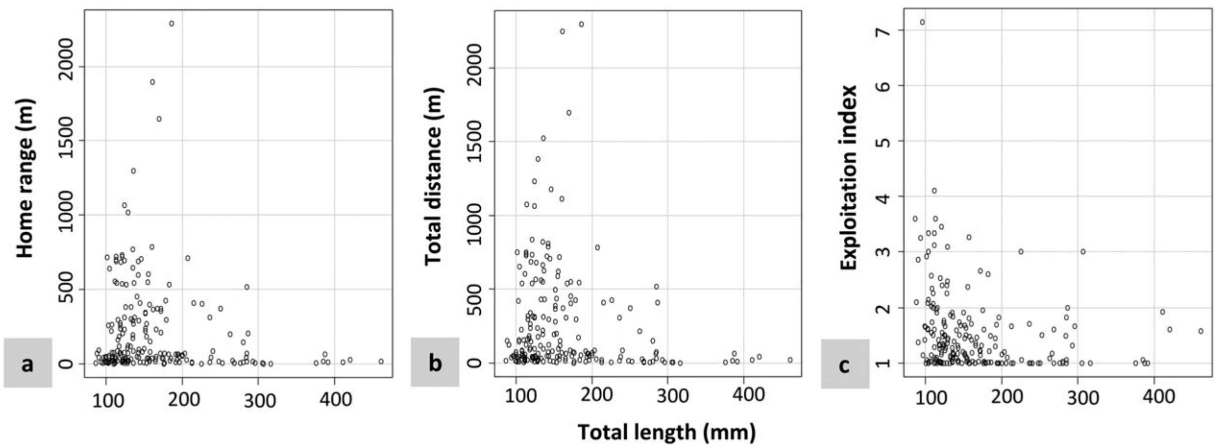

FIGURE 4 Home range, total distance travelled, and exploitation index of the home range according to body length of the detected eels (a–c, n = 205), from 2014 to 2017

was greater in autumn, particularly in October and November, without being correlated with water temperature (GLM Poisson: coefficient ± SE = $8.576 \times 10^{-10} \pm 1.853 \times 10^{5}$, z = 0, P = 1) (Figure 6). The TD and maximum distance travelled varied monthly, but no significant relationships were found between water temperature and TD (GLM gamma: coefficient ± SE = $-1.104 \times 10^{-6} \pm 1.853 \times 10^{5}$, z = 0, P = 1) or between water temperature and maximum distance travelled (GLM gamma: coefficient ± SE = $3.682 \times 10^{-8} \pm 3.580 \times 10^{4}$, z = 0, P = 1). The total and maximum distances were greater during the warm months in summer (from July to September, with a monthly mean temperature range of 13.5–15.4°C) than during the cold months of the other seasons (Figure 6).

3.5 | Movement behavioural traits

From the fine individual movement analysis, five behavioural groups were identified in the eels that were tracked. In decreasing abundance,

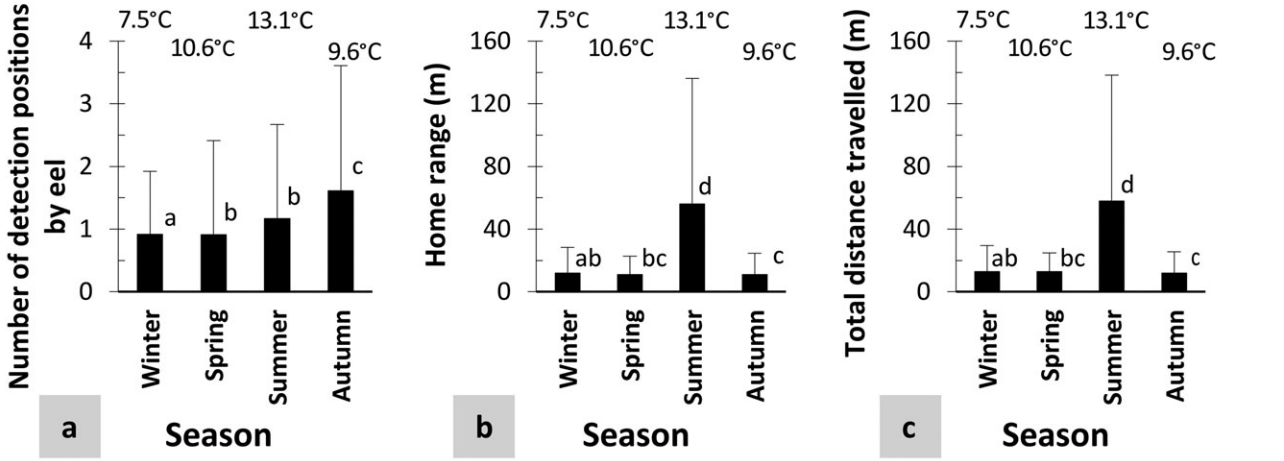

FIGURE 5 Seasonal variation in (a) the number of detected positions, (b) the linear home range, and (c) the total distance travelled for the tagged eels, from 2014 to 2017. *H* and *W* tests: $P < 0.05$. Winter $n = 72$, spring $n = 109$, summer $n = 112$, autumn $n = 124$. Values are expressed as the means ± SDs

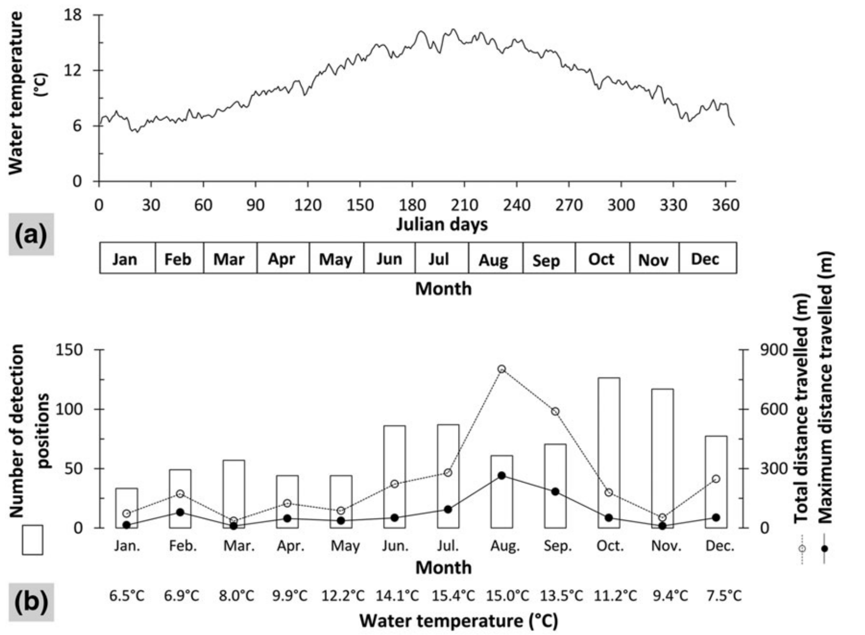

FIGURE 6 Monthly variations in (a) water temperature in the study area and (b) activities of the tagged eels, from 2014 to 2017

there were: (i) stationary individuals, G_5 ($n = 97$; 47%); (ii) oscillating individuals with an upstream trend, G_3 ($n = 47$; 23%); (iii) ascending individuals, G_1 ($n = 44$; 22%); (iv) descending individuals, G_2 ($n = 9$; 4%); and (v) oscillating individuals with a downstream trend, G_4 ($n = 8$; 4%) (Figure 7a). The number of behavioural groups decreased with the date of the fishing session of tagging, from four to five groups in the earlier S_1–S_4 fishing sessions to two or three groups in the later S_8–S_9 sessions. G_5 occurred in each session, and its highest abundance was observed in S_8 and S_9 (Figure 7b).

The five behavioural groups differed significantly in HR, TD, EI, and body size. G_1 showed a greater HR than all of the other groups (*H* test: df = 4, $H = 152.620$, $P < 2.2 \times 10^{-16}$; range, $W = 36–990$, $P < 0.05$) (Figure 7c); however, the TD in G_1 was only higher than that in G_2 and G_5 ($H = 143.420$, $P < 2.2 \times 10^{-16}$; $W = 42–985$, $P < 0.05$) (Figure 7d). A higher EI was found in G_3–G_5 ($H = 48.260$, $P = 8.330 \times 10^{-10}$; $W = 0–130$, $P < 0.05$) (Figure 7e). G_2 eels were significantly larger than those in the other groups, except G_5 ($H = 14.759$, $P = 5.228 \times 10^{-3}$; $W = 0–45$, $P < 0.01$) (Figure 7f).

4 | DISCUSSION

Using a mobile RFID detection system and electrofishing, this study described the individual behavioural traits, the dispersal, and the habitats of young eels restocked as glass eels in upland rivers, where this developmental stage is naturally absent. This system succeeded in detecting the mobile individuals as well as the non-catchable immobile eels buried under shelters. As the tags applied are very resilient and

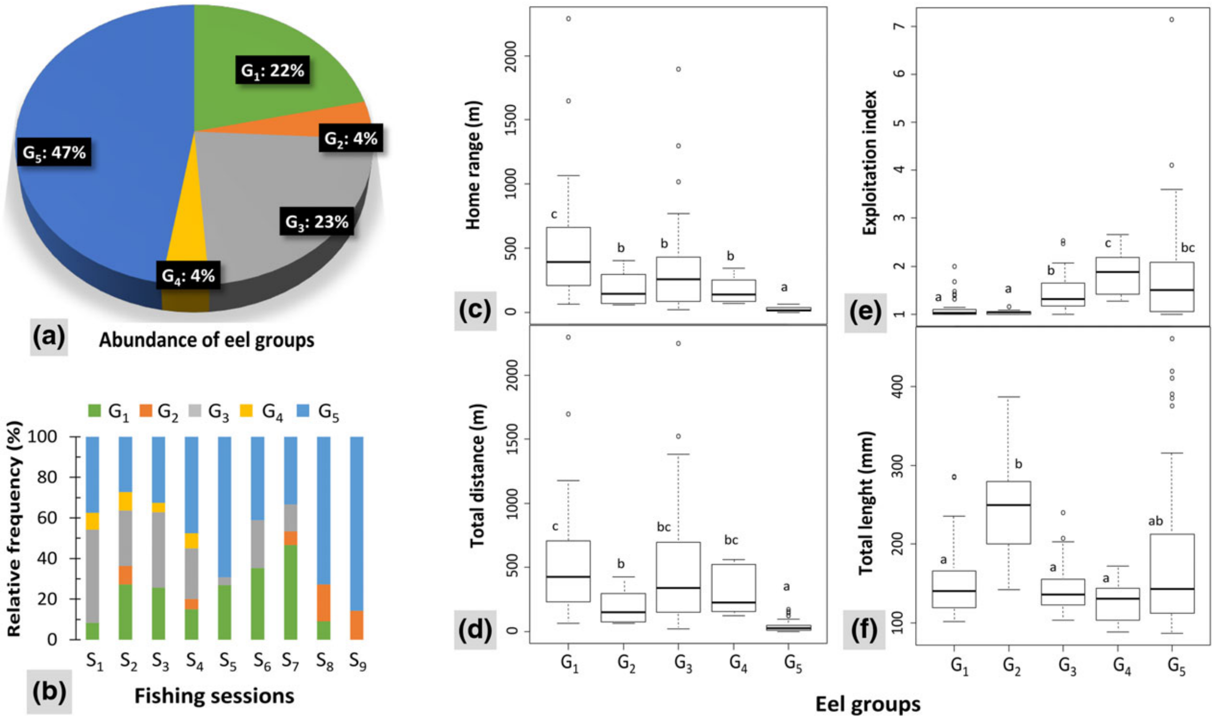

FIGURE 7 Comparison of (a) abundance, (b) fishing session composition, (c) home range, (d) total distance travelled, (e) exploitation index of the home range, and (f) total length of the behavioural profile groups of eels (G_1, n = 44; G_2, n = 9; G_3, n = 47; G_4, n = 8; and G_5, n = 97), from 2014 to 2017. Values are medians and the 5th, 25th, 75th, and 95th percentiles; bars mark the medians, and circles indicate outliers. Eel groups marked with the same letter are not significantly different (H and W tests: P < 0.05)

have a very long life, this system offered the advantage of monitoring the eels and studying their behavioural traits over a period of 4 years, regardless of season, eel activity, and water temperature.

The results indicated that approximately 85% of the tagged eels were detected in five tracking survey periods beginning in November 2014 (survey period detections: mean = 59%, range = 46–87%). This detection success exceeded that of detections reported in many studies using conventional mark–recapture methods (0–18.5%, Naismith & Knights, 1988; White & Knights, 1997; 2.1%, Baras et al., 1996; 6.8%, Nzau Matondo et al., 2017). The detection rate was also higher than that of RFID telemetry studies of wild yellow eels using fixed detection stations (37.5%, Nzau Matondo et al., 2017; 27.6%, Nzau Matondo & Ovidio, 2018). The high detection performance in this study could be attributed to the portability of the system, which allowed active searching for individuals during the seasons when the species is more active (from spring to summer) and less active (from autumn to winter), and to the shallow environment of the selected study area that facilitated detections. In contrast, mark–recapture methods require the handling of eels, which are difficult to capture because of their cryptic habit in the daytime and their trophic and migratory activities at night (Baras et al., 1998). This behaviour makes the redetection rate of mobile RFID telemetry more efficient than the recapture rate with electric fishing. Based on the high eel capture and detection relationships of up to 69.2% observed during the three experiments, and the rapid dispersal of certain eels that were detected upstream outside the 130 m of linear distance sampled, we can confirm that most eels detected were probably alive. The detected eels that were not captured were located hiding in more cryptic habitats, such as in the crevices between blocks or large stones, under river banks, and among submerged roots, thus making any accurate mortality assessment difficult. The mark–recapture methods used during the nine fishing sessions in this study provided estimates of the annual growth (mean = 30.7 mm yr^{-1}) of the restocked eels, which was higher than that of PIT-tagged naturally recruited eels (24.1 mm yr^{-1}), but lower than that of untagged naturally recruited eels (61.5 mm yr^{-1}) (Mazel, Charrier, Legault, & Laffaille, 2013). The difference in annual growth rates for the tagged eels could result from a difference in both size at tagging (mean for this study, 142 mm; 316 mm in Mazel et al., 2013) and study area location (Belgian rivers in this study; a French river in Mazel et al., 2013); however, Pedersen (2009) observed no growth, or very little growth, in the restocked eels because water temperatures were too low and the habitat offered too little shelter. All these results demonstrated that the PIT tagging of elvers did not stop their growth, suggesting that the restocked glass eels were of good quality and that the study area is a better growth habitat and, therefore, the restocked eels have the potential to produce silver eels.

With a median HR estimated to be approximately 67 m, a median TD travelled of 85 m, and a median EI of the home range of 1.30 in the five tracking survey periods of this study, the eels originating from restocking (total length, Q_{50} = 141 mm) showed quite limited mobility. Individual dispersal was variable, however, with some more extended extreme values observed in the tagged eels (from −484 m to

+2345 m from the release point of glass eels in 2013, linear distance = 2829 m). As this study is the first on this early life stage, it cannot be compared with other studies, but the findings contrast with the long distances that the species travels during its upstream and downstream migration phases in rivers and during its spawning migration in the ocean. In the Meuse River, Nzau Matondo and Ovidio (2018) reported a daily ascending distance of 0.317 km (41.5 km annually) in yellow eels (mean TL = 412 mm). White and Knights (1997) estimated the daily distance travelled by elvers and juvenile eels of 80–320 mm to be approximately 0.64 km in the non-tidal Severn and Avon rivers; however, our observation is consistent with the restricted mobility reported for wild yellow eels during mark–recapture (eels, mean TL = 313 mm: Laffaille et al., 2005) or tracking studies (mean TL = 591 mm: Baras et al., 1998; 689 mm: Ovidio et al., 2013). The low mobility in this study may have been strongly influenced by the high carrying capacity of the rivers, offering burrow and food availabilities. The discharges of organic effluents from domestic sources and the high mean daily temperatures (>9°C) may have favoured dietary diversity, through the development of several live prey resources. The low mobility may also be influenced by the low eel density because of the shutdown of natural migration and the effect of man-made barriers making upstream movement more arduous; however, this estimated mobility does not include the eels that emigrated outside the monitored area and were no longer redetected. In addition, tracking occurred only during the daytime, and the eels are discreet animals that generally move at night and display cryptic habits in the daytime (Baras et al., 1998; Ovidio et al., 2013). These factors might lead to an underestimation of mobility.

Several hypotheses can be envisaged to explain why 15% of the tagged eels were never detected: (i) some eels might leave the study area after release; (ii) as discrete animals moving at night (Baras et al., 1998; Ovidio et al., 2013), the eels might be deeply buried in shelters and thereby outside the detection field of the mobile RFID system for the tracking performed during the day; (iii) mortality caused by handling, illegal fishing (Laffaille et al., 2005), and predation is likely, with predation by piscivorous fish (the trout *Salmo trutta*, Kennedy & Fitzmaurice, 1971) and birds (the heron *Ardea cinerea*, Zydelis & Kontautas, 2008; the great cormorant *Phalacrocorax carbo sinensis*, Oehm, Thalinger, Eisenkölbl, & Traugott, 2017); (iv) the RFID tag might be rejected (Baisez, 2001; Feunteun, Acou, Laffaille, & Legault, 2000) and deposited out of the detection range of the antenna; and (v) there are possible biases related to the use of the mobile RFID detection system that depended on people's availability to use it and on environmental conditions that might lead to a lack of data during the night or when the rivers were inaccessible as a result of flooding. This system operated only two days per month in the daytime and did not allow the continuous recording of data over a 24-hour cycle.

The seasonal activity of the detected eels peaked during the summer (from July to September), when the water temperature was high (above 12°C). Greater activity in summer might also be associated with the increased availability of prey such as young fish (De Nie, 1987), crustaceans (Lévêque & Daget, 1984), molluscs (Lammens, de Nie, Vijverberg, & van Densen, 1985), insect larvae (Kangur, Kangur, & Kangur, 1999), and aquatic oligochaetes (Deelder, 1985). Activity was reduced from autumn to spring (from October to June) because the water temperature became too low for eel activity. This observation is consistent with previous findings on yellow eels, in which the eels had little or no activity at low temperatures (Baras et al., 1998; Itakura, Miyake, Kitagawa, & Kimura, 2017; Ovidio et al., 2013). During the study period (from 28 November 2014 to 31 May 2017), the daily water temperature ranged from 3.1 to 16.0°C (mean: 9.7°C) in the Mosbeux River, and from 1.7 to 23.4°C (mean: 10.6°C) in the Vesdre River. In these two rivers, the minimum and maximum temperatures occurred on 31 December 2016 and 4 July 2015, respectively. The higher abundance of eels (up to 66.7% in a tracking survey period) detected in the Vesdre River after leaving the Mosbeux River (the river in which they were tagged) than of those making the inverse journey (maximum of 10.4% for eels detected in the Mosbeux River after being tagged in the Vesdre River) might be explained by the higher water temperature of the Vesdre River. This result also demonstrated that glass eels, naturally adapted to move upstream once they reach continental inland water, might move in the downstream direction after translocation for restocking purposes.

Negative relationships were observed between body size at tagging and mobility parameters, even though this relationship was not significant for the home range; this clearly indicates that the smaller-sized eels were more mobile. Nzau Matondo and Ovidio (2018) reported similar observations during the colonization phase of yellow eels, showing that small eels (≤300 mm) moved further upstream by alternating short periods of movement with long stationary periods. The ability of eels to breathe outside the water, and their forward and backward undulatory swimming could contribute to the greater movement performance of the small eels travelling further and climbing numerous physical obstacles in the study area (Baudoin et al., 2015; D'Août & Aerts, 1999). A role of both body size and tagging date was also detected in the behavioural profiles of the eels. The later tagging (S_8 and S_9) sessions yielded larger eels, but the number of behavioural groups during these two fishing sessions was low and was dominated by the G_5 individuals that displayed stationary behaviour (73–86% of the eels). In contrast, eels originating from the S_1 and S_2 tagging sessions, with smaller sizes, expressed a larger number of behavioural groups dominated by a higher rate of ascending movement and included both the G_1 and G_3 groups (54–55% of the eels). This finding highlighted the importance of the timing of tagging because the species show high behavioural plasticity, with strategies such as 'founder' and 'pioneer' prevailing in the youngest stages (glass eels and elvers) during their first year in rivers (Feunteun et al., 2003; Laffaille et al., 2005). In this study, the earlier fishing and tracking sessions of eel tagging occurred during their second year in the rivers.

Most eels detected belonged to G_5 (stationary individuals), which had the lowest home range and total distance travelled. This G_5 group as well as the G_3 and G_4 oscillating individuals showed a better use of the river, evidenced by a greater exploitation index of the home range. These three groups accounted for 74% (n = 152) of the eels detected that combined upstream and downstream movements during their mobility. The G_5 group exploited a home range with restricted movements, showing a low total distance travelled. The G_3 and G_4 groups exhibited significantly greater displacements, as shown by a longer total distance travelled. Such behavioural strategies could explain the better use of the river and translate into groups G_3–G_5 being 'home range dwellers' that adopt a highly sedentary lifestyle (Feunteun et al., 2003; Laffaille et al., 2005; Ovidio et al., 2013). The lowest exploitation index of the home range, observed in the G_1 and G_2 groups, resulted from the proactivity of the eels. The G_1 ascending eels showed only upstream movements, with a higher proportion of 'nomad' (or emigrant) eels (n = 42; 21% of the detected eels) that continued upstream migration, whereas two individuals (1%) were established in habitats in the upper boundaries of the river. G_2, the least abundant group, accounted for only nine (4%) of the eels detected, which performed large leaps downstream. Despite their extreme scarcity, G_2 was the eel group with the largest body size, and some of the eels in this group appeared to be slowly beginning the silvering process. This finding suggested that the G_2 individuals grew faster and could mature and migrate earlier than those in the other eel groups, leading us to question whether the G_2 group will have the energy to migrate successfully to the sea once arriving at the silver eel stage, compared with eels dwelling for a long time in rivers to reach larger sizes before maturing and undergoing seaward migration. According to Stacey, Pratt, Verreault, and Fox (2015), a substantially earlier maturation age associated with faster annual growth in eels may eliminate the benefit of conservation restocking because of the long migration that eels must undertake from the study area to the Sargasso Sea. In this study, the eels were in the fifth year of their lives in fresh water, after being restocked as glass eels in May 2013, and G_2 was the least abundant group. In addition, in Western Europe, the sexual maturity and associated metamorphosis of silver eels were reached later (in 6–10 year olds; 30–45 cm), depending on the sex (Cattrijsse & Hampel, 2000). These patterns may suggest that the restocked eels in this study were not yet globally ready to migrate to their spawning grounds. The high use of the interstices between blocks and between large stones as refuges observed in the detected eels could be related to the high abundance of these types of refuges in the study area. These microhabitats are more concealed, thereby providing more protection to the members of this species that exhibit a highly sedentary lifestyle (Cucherousset et al., 2010; Ovidio et al., 2015).

4.1 | Implications for conservation

In this study, the tracked eels progressively exploited a larger area of the river over the years, showed mobility influenced by seasons and physical obstacles, and expressed a diversity of individual behavioural patterns. Most glass eel restocking practices are performed in deep lowland rivers and lakes, which makes the monitoring of the efficiency of this practice difficult (Pedersen, 2009; Simon et al., 2013). The high recapture and redetection rate compared with the low numbers of restocked glass eels observed in the study suggests that the uncommon small upland river selected for the restocking has a good carrying capacity, and that this type of aquatic environment may be a promising location for restocking. Once the young eels become silver eels, however, restocking in the upstream part of the rivers would increase the distance and the cumulative number of hydroelectric obstacles to pass to reach the sea. Such restocking practices may thus need to be accompanied by measures to allow the safe downstream migration of silver eels. The results suggest that the best method for restocking would be to scatter the glass eels in available habitats throughout multiple release sites. Such a method should help to minimize the eel density and promote higher rates of dispersal. The young eels dispersed in both the upstream and the downstream directions, indicating the plasticity of glass eel movement behaviour after the translocation and restocking events. Small barriers slowed the dispersal in upstream directions, and hence increased the accumulation of eels downstream of the physical obstacles. Glass eels have an important capacity to pass through obstacles by crawling (Baudoin et al., 2015), but barriers without a crawling zone cause problems because of the poor swimming capacity of eels. Therefore, for the dispersal of the restocked young eels, actions such as barrier removal and specific fish passage should help improve upstream dispersal.

Habitat destruction is one of the causes of eel population decline, but habitat restoration or conservation is rarely used to restore eel stocks because it requires a deep knowledge of the habitat preference of eels (Laffaille et al., 2003). Restoring habitat through increasing the supply of available, more concealed microhabitats in altered or impoverished environments could be a particularly beneficial and promising way to restore local eel stocks from controlled upstream restocking. As the crevices between blocks and between large stones were found to be important habitats for eels, it is also necessary to protect these bottom substrates of the rivers from human impacts. These crevices translate into a key feature of the carrying capacity of the habitat, in terms of the availability of both shelter and food resources that can be used during the selection of rivers for restocking.

A well-implemented restocking programme should be regarded as a valuable management measure for reducing the risk of collapse of local eel stocks in upstream river catchments and, probably in the long term, meeting the silver eel escapement target in rivers with a shutdown of natural immigration. Given the lack of behavioural data in the first year of an eel's life in fresh water after restocking, as well as the lack of nocturnal data, we recommend that early tagging methods should be used, together with a mobile RFID detection system and an extended network of fixed RFID detection antennas, to provide continuous recordings of data over a larger area.

ACKNOWLEDGEMENTS

The authors express thanks to G. Rimbaud for his help during the electrofishing sessions. We also thank the Editor in Chief and the two anonymous referees for their helpful comments. This study was funded by the 'Definition of the scientific and technical bases for an optimisation and evaluation of the efficiency of European glass eel (*Anguilla anguilla*) restocking practices' project funded by the European Fisheries Fund and the Wallonia Public Service (FEAMP No. 44-1604-008).

ORCID

Billy Nzau Matondo https://orcid.org/0000-0002-7098-9972
Jean-Philippe Benitez https://orcid.org/0000-0002-5643-070X
Xavier Rollin https://orcid.org/0000-0001-7197-7829
Michaël Ovidio https://orcid.org/0000-0002-0136-5840

REFERENCES

Andersson, J., Sandström, O., & Hansen, H. J. M. (1991). Elver (*Anguilla anguilla* L.) restockings in a Swedish thermal effluent – recaptures, growth and body conditions. *Journal of Applied Ichthyology*, *7*, 78–89. https://doi.org/10.1111/j.1439-0426.1991.tb00513.x

Baisez, A. (2001). Optimisation des suivis des indices d'abondances et des Structure de taille de l'anguille européenne (*Anguilla anguilla*, L.) dans un marais endigué de la côte atlantique: relations espèce habitat, PhD thesis, University of Toulouse, Toulouse, France.

Baras, E., Jeandrain, D., Serouge, B., & Philippart, J. C. (1998). Seasonal variations in time and space utilization by radio-tagged yellow eels *Anguilla anguilla* (L.) in a small stream. *Hydrobiologia*, *371*, 187–198. https://doi.org/10.1007/978-94-011-5090-3_22

Baras, E., Philippart, J. C., & Salmon, B. (1996). Estimation of migrant yellow eels stock in large rivers through the survey of fish passes: A preliminary investigation in the River Meuse (Belgium). In I. G. Cowx (Ed.), *Stock assessment in inland fisheries* (pp. 314–325). London, UK: Oxford fishing news books (Blackwell).

Baudoin, J. M., Burgun, V., Chanseau, M., Larinie, R. M., Ovidio, M., Sremski, W., … Voegtle, B. (2015). *Assessing the passage of obstacles by fish. Concepts, design and application, The ICE protocol for ecological continuity*. France: Onema.

Belpaire, C. G. J., Goemans, G., Geeraerts, C., Quataert, P., Parmentier, K., Hagel, P., & De Boer, J. (2009). Decreasing eel stocks: Survival of the fattest? *Ecology Freshwater Fish*, *18*, 197–214. https://doi.org/10.1111/j.1600-0633.2008.00337.x

Bisgaard, J., & Pedersen, M. I. (1991). Mortality and growth of wild and introduced cultured eels *Anguilla anguilla* (L.) in a Danish stream, with special reference to a new tagging technique. *Dana*, *9*, 57–69.

Bonhommeau, S., Castonguay, M., Rivot, E., Sabatié, R., & Le Pape, O. (2010). The duration of migration of Atlantic *Anguilla anguilla* larvae. *Fish and Fisheries*, *11*, 289–306. https://doi.org/10.1111/j.1467-2979.2010.00362.x

Breen, M. J., Ruetz, C. R., Thompson, K. J., & Kohler, S. L. (2009). Movements of mottled sculpins (*Cottus bairdii*) in a Michigan stream: How restricted are they? *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 31–41. https://doi.org/10.1139/F08-189

Cattrijsse, A., & Hampel, H. (2000). Life history and habitat use tables. Final Report. Subproject 1 – 'Nursery Function Westerschelde'. University of Gent, Department of Biology, Marine Biology Section.

Council of the European Communities (2007). Council regulation (EC) no 1100/207 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union*, *L248*, 17–23.

Cucherousset, J., Britton, J. R., Beaumont, W. R. C., Nyqvist, M., Sievers, K., & Gozlan, R. E. (2010). Determining the effects of species, environmental conditions and tracking method on the detection efficiency of portable PIT telemetry. *Journal of Fish Biology*, *7*, 1039–1045. https://doi.org/10.1111/j.1095-8649.2010.02543.x

Cucherousset, J., Paillisson, J. M., Cuzol, A., & Roussel, J. M. (2009). Spatial behaviour of young-of-the-year northern pike (*Esox lucius*) in a temporarily flooded nursery area. *Ecology of Freshwater Fish*, *18*, 314–322. https://doi.org/10.1111/j.1600-0633.2008.00349.x

Cucherousset, J., Paillisson, J. M., & Roussel, J. M. (2007). Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. *Fisheries Research*, *85*, 159–164. https://doi.org/10.1016/j.fishres.2007.01.011

Cucherousset, J., Roussel, J. M., Keeler, R., Cunjak, R. A., & Stump, R. (2005). The use of two new portable 12-mm PIT tag detectors to track small fish in shallow streams. *North American Journal of Fisheries Management*, *25*, 270–274. https://doi.org/10.1577/M04-053.1

D'Août, K., & Aerts, P. (1999). A kinematic comparison of forward and backward swimming in the eel *Anguilla anguilla*. *The Journal of Experimental Biology*, *202*, 1511–1521.

De Nie, H. W. (1987). Food, feeding periodicity and consumption of the eel *Anguilla anguilla* (L.) in the shallow eutrophic Tjeukemeer (The Netherlands). *Archiv für Hydrobiologie*, *109*, 421–443.

Deelder, C. L. (1985). Exposé synoptique des données biologiques sur l'anguille, *Anguilla anguilla* (Linnaeus, 1758). FAO Synopsis Sur Les Pêches, N°8O (Révision 1).

Dekker, W. (2003). Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? *Fisheries Management and Ecology*, *10*, 365–376. https://doi.org/10.1111/j.1365-2400.2003.00352.x

Dekker, W., & Beaulaton, L. (2016). Climbing back up what slippery slope? Dynamics of the European eel stock and its management in historical perspective. *ICES Journal of Marine Science*, *73*, 5–13. https://doi.org/10.1093/icesjms/fsv132

Feunteun, E., Acou, A., Laffaille, P., & Legault, A. (2000). European eel (*Anguilla anguilla*): Prediction of spawner escapement from continental population parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 1627–1635. https://doi.org/10.1139/f00-096

Feunteun, E., Laffaille, P., Robinet, T., Briand, C., Baisez, A., Olivier, J. M., & Acou, A. (2003). A review of upstream migration and movements in inland waters by anguillid eels: Toward a general theory. In K. Aida, K. Tsukamoto, & K. Yamauchi (Eds.), *Eel biology* (pp. 191–213). Tokyo, Japan: Springer- Verlag. https://doi.org/10.1007/978-4-431-65907-5_14

Friedland, K. D., Miller, M. J., & Knights, B. (2007). Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. *ICES Journal of Marine Science*, *64*, 519–530. https://doi.org/10.1093/icesjms/fsm022

Huet, M. (1949). Aperçu de la relation entre la pente et les populations piscicoles des eaux courantes. *Schweizerische Zeitschrift für Hydrologie - Swiss Journal of Hydrology*, *11*, 332–351. https://doi.org/10.1007/bf02503356

ICES. (2013). Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL), 3–9 September 2012, Copenhagen, Denmark, Ices Cm 2013/ACOM:18, 824224.

Itakura, H., Miyake, Y., Kitagawa, T., & Kimura, S. (2017). Site fidelity, diel and seasonal activities of yellow-phase Japanese eels (*Anguilla japonica*) in a freshwater habitat as inferred from acoustic telemetry. *Ecology of Freshwater Fish*, *27*, 737–751. https://doi.org/10.1111/eff.12389

Jacoby, D., & Gollock, M. (2014). *Anguilla anguilla*. In: IUCN2014.IUCNRed List of Threatened Species. Version 2014.1. www.iucnredlist.org

Kangur, K., Kangur, A., & Kangur, P. (1999). A comparative study on the feeding of eel, *Anguilla anguilla* (L.), bream. *Abramis brama* (L.) and ruffle, *Gymnocephalus cernuus* (L.) in Lake Võrtjärv, Estonia. *Hydrobiologia*, *408*(409), 65–72. https://doi.org/10.1007/978-94-017-2986-4_7

Keeler, R. A., Breton, A., Peterson, D. P., & Cunjak, R. A. (2007). Apparent survival and detection estimates for PIT-tagged slimy sculpin in five small New Brunswick streams. *Transactions of the American Fisheries Society*, *136*, 281–292. https://doi.org/10.1577/T05-131.1

Kennedy, M., & Fitzmaurice, P. (1971). Growth and food of brown Trout *Salmo trutta* (L.) in Irish waters. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, *71*, 269–352.

Laffaille, P., Acou, A., & Guillouet, J. (2005). The yellow European eel (*Anguilla anguilla* L.) may adopt a sedentary lifestyle in inland freshwaters. *Ecology of Freshwater Fish*, *14*, 191–196. https://doi.org/10.1111/j.1600-0633.2005.00092.x

Laffaille, P., Feunteun, E., Baisez, A., Robinet, T., Acou, A., Legault, A., & Lek, S. (2003). Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment. *Ecology of Freshwater Fish*, *12*, 254–264. https://doi.org/10.1046/j.1600-0633.2003.00021.x

Lammens, E. H. R. R., de Nie, H. W., Vijverberg, J., & van Densen, W. L. T. (1985). Resource partitioning and niche shifts of bream (*Abramis brama*) and eel (*Anguilla anguilla*) mediated by predation of smelt (*Osmerus eperlanus*) on *Daphnia hyalina*. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1342–1351. https://doi.org/10.1139/f85-169

Lévêque, C., & Daget, J. (1984). Cyprinidae. In J. Daget, J.-P. Gosse, & D. F. E. T. van den Audenaerde (Eds.), *Check-list of the freshwater fishes of Africa (CLOFFA)* (ed., Vol. 1) (pp. 217–342). Paris and Tervuren: ORSTOM and MRAC.

Lin, Y. J., Lozys, L., Shiao, J. C., Iizuka, Y., & Tzeng, W. N. (2007). Growth differences between naturally recruited and stocked European eel *Anguilla anguilla* from different habitats in Lithuania. *Journal of Fish Biology*, *71*, 1773–1787. https://doi.org/10.1111/j.1095-8649.2007.01642.x

Mazel, V., Charrier, F., Legault, A., & Laffaille, P. (2013). Long-term effects of passive integrated transponder tagging (PIT tags) on the growth of the yellow eel (*Anguilla anguilla* (Linnaeus, 1758)). *Journal of Applied Ichthyology*, *29*, 906–908. https://doi.org/10.1111/jai.12111

Naismith, I. A., & Knights, B. (1988). Migrations of elvers and juvenile European eels, *Anguilla anguilla* L., in the River Thames. *Journal of Fish Biology*, *33*, 161–175. https://doi.org/10.1111/j.1095-8649.1988.tb05570.x

Nzau Matondo, B., Benitez, J. P., Dierckx, A., Philippart, J. C., & Ovidio, M. (2017). Assessment of the entering stock, migration dynamics and fish pass fidelity of European eel in the Belgian Meuse River. *River Research and Applications*, *33*, 292–301. https://doi.org/10.1002/rra.3034

Nzau Matondo, B., & Ovidio, M. (2016). Dynamics of upstream movements of the European eel *Anguilla anguilla* in an inland area of the River Meuse over the last 20 years. *Environmental Biology of Fish*, *99*, 223–235. https://doi.org/10.1007/s10641-016-0469-x

Nzau Matondo, B., & Ovidio, M. (2018). Decreased stock entering the Belgian Meuse is associated with the loss of colonisation behaviour in yellow-phase European eels. *Aquatic Living Resources*, *31*, 7. https://doi.org/10.1051/alr/2017047

Oehm, J., Thalinger, B., Eisenkölbl, S., & Traugott, M. (2017). Diet analysis in piscivorous birds: What can the addition of molecular tools offer? *Ecology and Evolution*, *7*, 1984–1995. https://doi.org/10.1002/ece3.2790

Ovidio, M., Seredynski, A., Philippart, J. C., & Nzau Matondo, B. (2013). A bit of quiet between the migrations: The resting life of the European eel during their freshwater growth phase in a small stream. *Aquatic Ecology*, *47*, 291–301. https://doi.org/10.1007/s10452-013-9444-1

Ovidio, M., Tarrago-Bès, F., & Nzau Matondo, B. (2015). Short-term responses of glass eels transported from UK to small Belgian streams. *Annales de Limnologie - International Journal of Limnology*, *51*, 219–226. https://doi.org/10.1051/limn/2015016

Pedersen, M., & Rasmussen, G. H. (2016). Yield per recruit from stocking two different sizes of eel (*Anguilla anguilla*) in the brackish Roskilde Fjord. *ICES Journal of Marine Science*, *73*, 158–164. https://doi.org/10.1093/icesjms/fsv167

Pedersen, M. I. (2000). Long-term survival and growth of stocked eel, *Anguilla anguilla* (L.), in a small eutrophic lake. *Dana*, *12*, 71–76.

Pedersen, M. I. (2009). Does stocking of Danish lowland streams with elvers increase European eel populations? *American Fisheries Society Symposium*, *58*, 149–156. https://doi.org/10.1002/rra.1232

Quintella, B. R., Andrade, N. O., Espanhol, R., & Almeida, P. R. (2005). The use of PIT telemetry to study movements of ammocetes and metamorphosing sea lampreys in river beds. *Journal of Fish Biology*, *66*, 97–106. https://doi.org/10.1111/j.0022-1112.2005.00584.x

R Development Core Team, (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org

Righton, D., Westerberg, H., Feunteun, E., Økland, F., Gargan, P., Amilhat, E., … Aarestrup, K. (2016). Empirical observations of the spawning migration of European eels: The long and dangerous road to the Sargasso Sea. *Science Advances*, *2*, e1501694. https://doi.org/10.1038/srep21817

Roussel, J. M., Cunjak, R. A., Newbury, R., Caissie, D., & Haro, A. (2004). Movements and habitat use by PIT-tagged Atlantic salmon parr in early winter: The influence of anchor ice. *Freshwater Biology*, *49*, 1026–1035. https://doi.org/10.1111/j.1365-2427.2004.01246.x

Shiao, J. C., Lozys, L., Iizuka, Y., & Tzeng, W. N. (2006). Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios. *Journal of Fish Biology*, *69*, 749–769. https://doi.org/10.1111/j.1095-8649.2006.01147.x

Simon, J., Dörner, H., & Richter, C. (2009). Growth and mortality of European glass eel *Anguilla anguilla* marked with oxytetracycline and alizarin red. *Journal of Fish Biology*, *74*, 289–295. https://doi.org/10.1111/j.1095-8649.2008.02117.x

Simon, J., & Dörner, H. (2014). Survival and growth of European eels stocked as glass and farm sourced eels in five lakes in the first years after stocking. *Ecology of Freshwater Fish*, *23*, 40–48. https://doi.org/10.1111/eff.12050

Simon, J., Dörner, H., Scott, R. D., Schreckenbach, K., & Knösche, R. (2013). Comparison of growth and condition of European eels stocked as glass and farm sourced eels in lakes in the first four years after stocking. *Journal of Applied Ichthyology*, *29*, 323–330. https://doi.org/10.1111/jai.12078

Stacey, J. A., Pratt, T. C., Verreault, G., & Fox, M. G. (2015). A caution for conservation stocking as an approach for recovering Atlantic eels. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*, 569–580. https://doi.org/10.1002/aqc.2498

Tesch, F. W., & Thorpe, J. E. (Eds.) (2003). *The eel* (Third ed.). Oxford, UK: Blackwell Science. https://doi.org/10.1002/9780470995389

van Ginneken, V. J. T., & Maes, G. E. (2005). The European eel (*Anguilla anguilla*, Linnaeus), its lifecycle, evolution and reproduction: A literature review. *Reviews in Fish Biology and Fisheries*, *15*, 367–398. https://doi.org/10.1007/s11160-006-0005-8

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *Journal of Geology*, *30*, 377–392. https://doi.org/10.1086/622910

White, E. M., & Knights, B. (1997). Environmental factors affecting migration of the European eel in the Rivers Severn and Avon, England. *Journal of Fish Biology*, *50*, 1104–1116. https://doi.org/10.1111/j.1095-8649.1997.tb01634.x

Zydelis, R., & Kontautas, A. (2008). Piscivorous birds as top predators and fishery competitors in the lagoon ecosystem. *Hydrobiologia*, *611*, 45–54. https://doi.org/10.1007/s10750-008-9460-7

How to cite this article: Nzau Matondo B, Séleck E, Dierckx A, Benitez J-P, Rollin X, Ovidio M. What happens to glass eels after restocking in upland rivers? A long-term study on their dispersal and behavioural traits. *Aquatic Conserv: Mar Freshw Ecosyst*. 2019;1–15. https://doi.org/10.1002/aqc.3062