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RESEARCH ARTICLE

Decreased stock entering the Belgian Meuse is associated with the loss of colonisation behaviour in yellow-phase European eels

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Abstract – The upstream migratory behaviour of yellow-phase European eels was investigated in regulated inland rivers (>320 km upstream the sea), where the stock is in drastic decline. From 2010 to 2015, eels entering the Belgian Meuse River ($n = 1357$; total length, 231–755 mm) were caught in fish passes, tagged with a pit-tag and released. Their upstream movements were tracked during the next six consecutive years, using three detection stations installed in vertical-slot fish passes of the Meuse and its Ourthe tributary. Among the 1357 eels tagged, 27.6% ($n = 374$ individuals) were detected at one or more of the three upstream detection stations. Only 6.6% ($n = 89$) of tagged eels were detected at the two subsequent stations. In this last group, most of the detected eels continued to move upstream through the Meuse rather than leaving it for the Ourthe. Water temperature >13 °C, river flow 24–226 m^3/s, dark time 00:00–05:00 h and the spring–summer seasons were the most important cues for upstream migration. Temperatures and flows at detection did not differ between size classes of ascending eels, while the detection period was earlier and daily speed was faster in large (>450 mm) eels. However, small (≤300 mm) eels moved further upstream at slow speeds because they alternated between short periods of movement and long stationary periods. This behaviour suggests the existence of a few nomad individuals and probably more home range dwellers in the entering population. Small eels were better suited to colonise upper rivers.

Keywords: Upstream movement / behaviour / body size / speed / yellow-phase eels / freshwater

1 Introduction

Many fish species in the world are either or both overexploited and suffer from habitat degradation, and many stocks have collapsed (Zhou et al., 2010). Among them, the emblematic migratory European eel *Anguilla anguilla* is considered to be outside safe biological limits (ICES, 2013; Dekker and Beaulaton, 2016), and since 2008, the species has been listed as critically endangered on the IUCN Red List of Threatened Species (Jacoby and Gollock, 2014).

The causes of the eel decline include human activities and climate changes in riverine and oceanic ecosystems. The human activities involve physical barriers (hydropower dams, navigation weirs, turbines, pumps) that prevent upstream and downstream migration, habitat loss by river canalisation and wetland drainage, overexploitation and poaching at all life stages, pollution by contaminants and transfer of diseases (Belpaire et al., 2009; Dekker and Beaulaton, 2016). The climate changes have influenced the fluctuations in oceanic currents, reproduction success and larval drift (Knights, 2003; Friedland et al., 2007).

The European eel is a diadromous fish species, which spawn in the Sargasso Sea. The transparent, leaf-like larvae, called leptocephali, are transported by oceanic currents and leave after metamorphosing into glass eels and, then, migrate upstream and enter the inland freshwaters and estuarine environments of Europe and North Africa as pigmented elvers (Daverat et al., 2005). In growth zones, these elvers become yellow eels that metamorphose into silver eels, which migrate back downstream, utilising high-fat reserves, through the ocean to the Sargasso Sea, where they reproduce and die (Tesch, 2003).

Yellow eels are found in all water types, from coastal marine waters through to brackish estuaries, in eutrophic and oligotrophic, shallow and deep waters, and throughout rivers, to their upland headwaters (Daverat et al., 2006). During the growth phase, the yellow eel must have access to suitable

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*Corresponding author: bnmatondo@uliege.be habitats and substantial food resources, for an accumulation of energy reserves useful to complete the eel's reproductive cycle to the Sargasso Sea (Maes et al., 2005; Belpaire et al., 2009). Yellow eels were abundant in many parts of the Belgian Meuse River basin, from low- to upland areas (Baras et al., 1996; Philippart, 2006; Philippart et al., 2010). However, in the Meuse River at Lixhe in Belgium, a drastic decline of upstream migrant yellow eels has been demonstrated. It has been reported that the number of ascending eels in a fishway decreased by 95.5% in 23 years (Nzau Matondo and Ovidio, 2016). Similarly, the estimated eel stock in the lower part of the Belgian Meuse has dropped from 4 45 000 individuals in 1993 (Baras et al., 1996) to 7184 in 2013 (Nzau Matondo et al., 2017). Concomitantly with declining abundance, the entering migrant eels have increased in body size by 4.1 mm per year, since 1992 (Nzau Matondo and Ovidio, 2016).

Such a significant reduction in the entering eel stock has raised serious concerns about whether incoming yellow eels will continue to colonise upstream rivers into the Belgian Meuse Basin, far beyond their entry point into Belgium. Similarly, in the context of the stock decline, it is not known whether those larger eels have changed their upstream migration rate. Earlier field works performed outside the framework of the stock decrease, revealed that the upstream migration speeds of eels unaided by tidal transport, were dependent on river current gradient (Aprahamian, 1988), population density pressure (Moriarty, 1986; Ibbotson et al., 2002) and body size of the eels (Clough et al., 2004). For these authors, the low upstream migration rates coincided with the high river current gradient and low density of riverine eels, and the swimming performance increased with increasing eel length. However, such field investigations were rare. Therefore, the longitudinal colonisation behaviour of yellow eels in continental freshwaters remains poorly understood (Feunteun et al., 2003; Laffaille et al., 2004). Analysis involving long-term monitoring at a place where the eel density is very low will help to gain insight on the behaviours guiding the colonisation of the upstream riverine habitats by large eels. A better understanding of the colonisation process of upland rivers is valuable for the development of better, adequate eel management plans, aiming to preserve and restore the stock, particularly in regions distant from the sea, and to meet the silver eel escapement target in the European Commission Eel Recovery Plan (EU, 2007).

Here, we used radio frequency identification (RFID) to track the long-term individual upstream movements of the yellow eels, using automatic transponder detection stations installed in vertical slot fishways. The aim was to investigate the longitudinal colonisation behaviour and activity of the incoming eels in the Belgian Meuse river basin, in an area where the flows are regulated for navigation and hydropower production, and the fishing and consumption of eels are prohibited. Considering the distant location of the study site from estuaries (>320 km upstream from the North Sea) and the stock decline, our study analysed the upstream migratory movement behaviour of various sized eel classes. This analysis involved the percentage of upstream migrants, the colonisation speed, the influence of environmental factors, particularly, the water temperature and flow, period of migration and hour of movement, and the choice of migratory route.

2 Methods

2.1 Study area

The study was performed in the Meuse River basin (Belgium), 323 km upstream from the North Sea (Fig. 1). The International Meuse River basin drains a 36 000 km^2 catchment area, of which a major proportion (nearly a third) is located in Belgium. The source of the Meuse [total length (TL), 925 km] lies in France and flows into the North Sea in The Netherlands. A large part of the Meuse is highly artificial, with several dams ($n = 46$) for navigation and hydropower, bank rectification, flow regulation and physicochemical pollution. The Meuse biodiversity is characterised by the presence of nearly 40 fish species, such as the non-native European catfish *Silurus glanis*, a potential predator for eel and its competitor for resources (Wysujack and Mehner, 2005; Gualtieri et al., 2006; Bevacqua et al., 2011). In this study area, eel has not been subject to effective management measures, such as restocking practices for over two decades (Belpaire et al., 2016).

The study area (Fig. 1) included the Belgian Meuse River, from the hydroelectric dam of Lixhe (323 km from the North Sea) to the hydropower and navigation dam of Yvoz–Ramet (31.2 km upstream from Lixhe). It also included the lower regulated course of the Ourthe tributary (TL, 165 km; catchment area, 3624 km^2), from its confluence with the Meuse (18.9 km from Lixhe) to the hydropower dam of Angleur (2.3 km from the confluence). The Ourthe is a primary tributary, providing a substantial amount (nearly a third) of the catchment area of the Belgian Meuse and potential growing habitats for the eel. In this study area, free movement of eels and other fish is ensured by new vertical slot fishways (Fig. 1; Tab. 1). There are also three canals (Albert Canal, Liège Canal, Ourthe Canal) and two sluices that offered potential alternate migration routes for the eels (Fig. 1). Several alternative passages can deviate eel from the main route and cause loss of detection (Fig. 1). (i) From the release site, eel can travel upstream to reach the Albert Canal, through the sluice located downstream the first detection station A, (ii) Station B can be bypassed by the ship lock at the Yvoz-Ramet Dam, and (iii) the eels can enter the Ourthe tributary by the Ourthe Canal, without being detected at station C.

The fishways at each hydropower dam had a similar configuration (vertical slot type, Tab. 1). The physicochemical characteristics of the water were similar in the Meuse and the Ourthe, regarding pH and dissolved oxygen saturation. The Ourthe tributary had a smaller width, colder water and lower flow than the Meuse (Wilcoxon test, $p < 0.0001$). Within the Meuse, water temperature was significantly higher and flow lower at the upstream station B than at station A (Tab. 1).

2.2 Tagging, release and monitoring

A total of 1371 eels (TL: mean ± SD, 415 ± 62 mm; range, 231–882 mm) were collected during their upstream migration, by trapping at the Lixhe fish passes (Fig. 1) from 2010 to 2015 (range, 90–540 eels per year). After capture, the eels were anaesthetised with eugenol 1/10 in alcohol (0.5 mL L^{-1}), measured (±1 mm), weighed (±1 g) and individually tagged using biocompatible RFID tags (Texas Instruments, HDX,

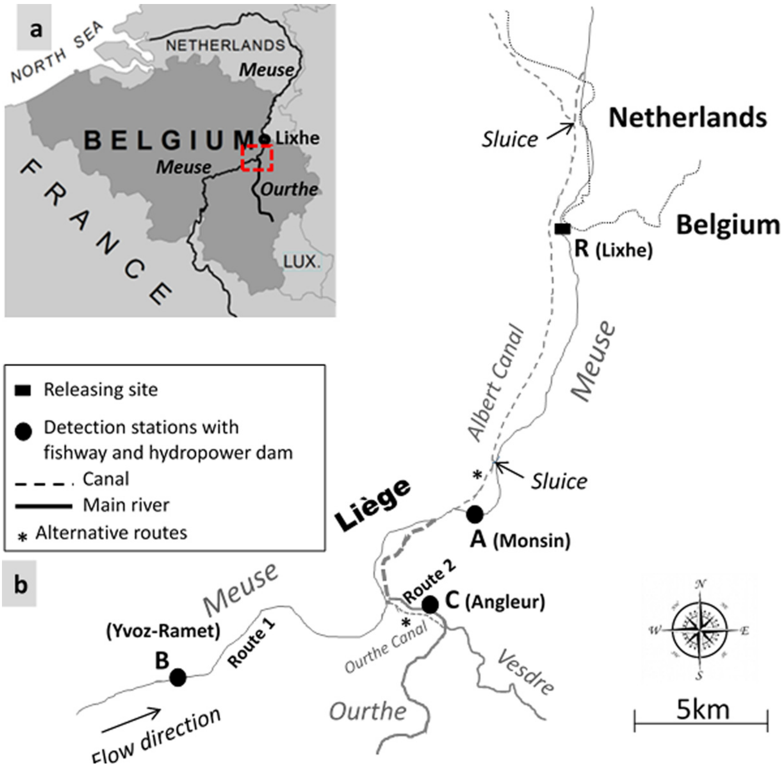

Fig. 1. Map of the study area in the International and Belgian Meuse River basins (a), and location of the catch and release site in the Meuse (at **R**–Lixhe), the first upstream detection station in the Meuse (**A**–Monsin), the upstream migration route 1 in the upper Meuse (**B**–Yvoz-Ramet), the upstream migration route 2 in the Ourthe tributary (**C**–Angleur), and the alternative migration routes of yellow-phase eels (the navigable canals of Albert and Ourthe, and the non-navigable Liège Canal) (b).

Table 1. Fishways and daily water physicochemical characteristics at the detection stations from 2010 to 2015.

	Meuse River		Ourthe tributary
Parameters	**A-Monsin**	**B-Yvoz-Ramet**	**C-Angleur**
a. Pool and vertical slot fishway			
Discharge, (m^3 s^{-1})	0.8	0.8	0.5
Attraction flow, (m^3 s^{-1})	4.0	3.0	1.5
Delta height, (m)	4.5	4.5	4.0
Pool size, (length×width, in m)	variable size×2.5	3.5×2.0	3.5×2.4
Pool water depth, (m)	1.5	1.5	1.5-1.7
Pool number	18.0	17.0	16.0
Slot width, (m)	0.30	0.25	0.25
Slot water depth, (m)	1.3	1.3	1.2
b. Physicochemical conditions (mean, range)			
Locations	50°39´N-5°37´E	50°35´N-5°27´E	50°36´N-5°36´E
Temperature, (°C)	14.4, 1.8-27.6	15.4, 1.8-28.8	11.5, 0.2-26.0
Flow, (m^3 s^{-1})	256.3, 37.8-2370.1	204.4, 31.1-1792.7	51.9, 6.3-625.8
pH	8.1, 7.5-9.2	8.1, 7.2-8.7	8.3, 7.4-9.5
Range dissolved oxygen, (%)	92.8, 22.0-125.0	93.9, 38.0-125.0	97.8, 50.0-113.0

134.2 kHz; size/weight in air: 23 × 3 mm/0.6 g). These tags were inserted into a 2–3 mm-long incision, made using a scalpel in the visceral cavity of the eels (Nzau Matondo et al., 2017). The inserted tags weighed, on average, 0.72% (range, 0.02–2.14%) of the eel's body weight, to meet the best requirement (Jepsen et al., 2002), that is, 2%. This tagging method was previously tested, by holding 26 eels (TL, 215−441 mm) in 1.04 × 1.04 × 0.41 m basins, to evaluate the tag rejection and the induced fish mortality. A perfect retention of the tag (100% of the tagged eels), without mortality, was observed at 20 days after tagging, with the incision fully healed.

After tagging, the eels were released into the Meuse River, at a single site located 0.2 km upstream from the Lixhe Dam, to allow the eels to continue their upstream migration. The eel movements were tracked using RFID detection stations (Cipam®, Clermont-Ferrand, France). A rectangular antenna (0.8 m wide × 1.8 m deep) was placed in front of the vertical slot upstream from the upper pool of the fishway, at each hydroelectric dam. Eels passing through the antenna were recorded by the station, with associated information on the individual code, date and hour. Two detection stations were placed in the Meuse River, at the first upstream station [**A**, Monsin (upstream distance from the release site: 13 km)] and in the upper Meuse [**B**, Yvoz-Ramet, route 1 (upstream distance from the release site: 31 km)]. There was also one station located in the Ourthe tributary [**C**, Angleur, route 2 (upstream distance from the release site: 21 km)]. Considering the fundamental role of temperature on upstream movements of the eels in regulated rivers, particularly in our study area (Nzau Matondo and Ovidio, 2016), water temperature was continuously recorded at each station, using data loggers (Onset Hobo TidbiT® version 2). Flow data were provided by the Wallonia Public Service of Hydrological Studies.

2.3 Size classes of the yellow eels

The captured eels (TL, 231–882 mm) were categorised into silver ($n = 14$) and yellow ($n = 1357$) eels. All the silver eels (TL: mean ± SD, 770 ± 49 mm; range, 708–882 mm) were excluded from the analysis. The yellow eels were identified by three morphological descriptors (Pankhurst, 1982; Durif et al., 2005; Nzau Matondo et al., 2017), including the yellow colour of the belly, the absence of a well-defined lateral line and the ocular index (OI) < 6.5. The eels were also designated as a yellow eel, if only two of the descriptors (most often no lateral line and the OI value) were met. Silver eels had a blackish-brown back and silvery-white belly, a well-defined lateral line and an OI ≥ 6.5, according to Pankhurst's silvering threshold value (Pankhurst, 1982). Yellow eels (TL: mean ± SD, 412 ± 62 mm; range, 231–755 mm; Fig. 2) were divided into six class sizes ($S_1 – S_6$) (Tab. 2). Eels > 450 mm are considered females, while <450 mm may mature to male or female. The median date of tagging was similar for both S_5 and S_6, which occurred earlier than S_3 and later than S_1, S_2 and S_4. The relationship of length (Lt) to weight (W) of the 1357 yellow eels tagged was described by log W (g) = −6.04 + 3.07 × log Lt (mm) ($R^2 = 0.905$ and $p < 0.0001$).

2.4 Colonisation indicators

The colonisation behaviour of eels was analysed using several indicators. The rate of ascending eels is defined as the proportion (%) between the number of eels detected and the total number of eels tagged at each detection station. The rate of detections per year is the proportion (%) between the number of eels detected and the total number of eels tagged each year. The diel activity rhythm is the proportion (%) between the number of eels detected at a specific hour and the total number of the eels detected over 24 h, at each detection station.

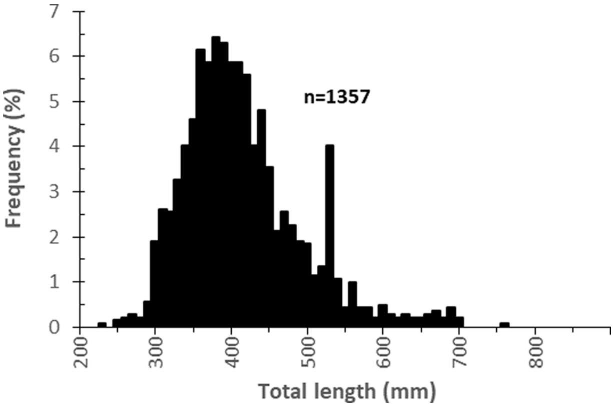

Fig. 2. Length-frequency distribution (10 mm class interval) of yellow eels tagged during the study period from 2010 to 2015.

The preferred migration route for the ascending eels was determined, by comparing between the proportion of eels migrating upstream through route 1 at **B** in the Meuse River (larger width, higher flow and higher temperature) and the proportion of eels migrating by route 2 at **C** in the Ourthe tributary (smaller width, lower flow and lower temperature). For route 1, this was expressed as the number of eels detected at the downstream station **A** in the Meuse and then redetected on route 1 at **B** in the upper Meuse, divided by the total number of eels detected at **A** and then redetected at **B** and **C** in the Ourthe (×100%). For route 2, this was expressed as the number of eels detected at **A** in the Meuse and redetected on route 2 at **C** in the Ourthe tributary, divided by the total number of eels detected at **A** and redetected at **B** and **C** (×100%).

For determining the size class of the ascending eels that was the most detected, we used the D/T index, representing the ratio of the number of detected eels divided by the number of tagged eels. We also calculated the O/A index, defined as the ratio of the number of eels detected in their tagging year divided by the number of eels detected after the tagging year.

The relationship between size and water temperature during migration, between size and period and between size and flow were analysed, to understand the effect of the body size of the eel on upstream colonisation behaviour. Similarly, the relation between size and migration speed was tested. The temperature and the flow at detection, the period and the hour of movement, and the migration speed were also described, according to the cumulated seasonal migration percentage of 50% (P50), 90% (P90), and the last eels. For the detection period, the maximum duration was also assessed as the time window (days) between the first detected and last detected eel in the year, both, throughout the study period and for each size class of eels. The migration speed of the eels was defined as the distance (km) between the release site and the most upstream detection station divided by the number of days spent on this

Table 2. Tagging period according to size classes of the tagged yellow eels.

Size class	n	%	Total length (mm) mean±SD	Tagging period		
				Median	90% (days)	100% (days)
S_1 (200-250)	4	0.3	243±8	4 May	28 Apr.-16 Jul. (79)	28 Apr.-28 Jul. (91)
S_2 (251-300)	36	2.7	289±11	18 June	26 Apr.-10 Aug. (106)	26 Apr.-27 Aug. (123)
S_3 (301-350)	226	16.7	329±12	30 June	28 Apr.-4 Aug. (98)	26 Apr.-6 Sep. (133)
S_4 (351-400)	427	31.5	376±12	21 June	28 Apr.-1 Aug. (95)	22 Apr.-30 Aug. (130)
S_5 (401-450)	350	25.8	424±13	24 June	4 May-1 Aug. (89)	17 Apr.-3 Oct. (169)
S_6 (>450)	314	23.1	522±51	24 June	27 Apr.-4 Aug. (99)	22 Apr.-3 Oct. (164)
Total	1357	100.0	412±62	23 June	28 Apr.-1 Aug. (95)	17 Apr.-3 Oct. (169)

route. The relations between these five morphological and environmental variables (body size, temperature, period, flow, speed) were also investigated.

2.5 Statistical analyses

The number of detections per station, time after tagging and detection by hour were assessed using Fisher's exact probability (*FEP*) test. The chi-squared (χ^2) test was used to compare the upstream distribution of the eels between route 1 (Meuse River) and route 2 (Ourthe tributary), for eels detected in the first upstream station **A** (Monsin) in the Meuse and redetected most upstream at **B** (Yvoz-Ramet) in the upper Meuse or **C** (Angleur) in the Ourthe tributary. The body size, water temperature and flow, detection period and migration speed data did not meet a normal distribution (Kolmogorov–Smirnov, $p < 0.001$). For these parameters, comparisons between the six size classes ($S_1 - S_6$) of eels were performed using the Kruskal–Wallis (H) test followed by Wilcoxon (W) signed rank. The relations between these five migration variables (body size, temperature, period, flow, speed) were evaluated by Pearson's correlation coefficient. All statistical analyses were deemed significant at $p < 0.05$ and were made using the R-Cran project free statistical software package Rcmdr version 2.3-2 (http://www.rproject.org).

3 Results

3.1 Upstream movement dynamics and migration routes

Of the 1357 yellow eels tagged and released at Lixhe from 2010 to 2015, 27.6% ($n = 374$ individuals) of the eels were detected at one or more of the three upstream detection stations. However, only 6.6% ($n = 89$) of eels were detected at the two subsequent stations (Tab. 3). Detections of eels decreased with upstream distance from the release site and the time after tagging (Tab. 3). Detections were significantly lower (*FEP* test, $p < 0.0001$) at the upstream stations [**B** (4.9%; $n = 66$) and **C** (3.5%; $n = 48$)] than the downstream station (**A**, 26.2%; $n = 355$).

Among the eels detected at a down- and upstream station, 59.6% ($n = 53$) moved from **A** to **B** and 40.4% ($n = 36$) moved from **A** to **C** ($\chi^2 = 6.49$, $p < 0.05$). Few eels (0.3%, $n = 4$) were detected further upstream [in route 1 at **B** (0.15%) and route 2 at **C** (0.15%)], without being detected at station **A**.

The detection rates varied between the six initial tagging years, from 12.8% in 2015 to 58.1% in 2014. For each tagging year, detections were higher during the year of tagging and the following year and, then, decreased drastically from the second year onwards (*FEP* test, $p < 0.0001$). Detections were higher in the year of tagging at **A** ($O/A = 1.67$) but were higher after the year of tagging further upstream in **B** ($O/A = 0.63$) and **C** ($O/A = 0.56$). The $S_3 - S_6$ (eels > 300 mm, detection > 73%) size classes were the most detected at **A** (Fig. 3a). In contrast, S_1 and S_2 were the most detected size classes further upstream (at **B** and **C**, eels ≤ 300 mm, >37%).

Upstream movements of eels occurred at all times (between 12:00 and 11:00 h, maximum duration 23 h); 90% of eels moved between 00:00 and 05:00 h (5 h), with the median hour at 3:00 h. At each station, eels migrated mostly (*FEP* test, $p < 0.0001$) at night (median hours 2:00–3:00 h; 90–96% between 00:00 and 05:00 h) (Fig. 3b).

3.2 Body size and upstream movement

The size classes most detected were $S_1 - S_5$ (range: TL, 200–450 mm, $D/T = 0.34–0.50$) with the highest detection observed in S_1 (200–250 mm, $n = 4$, $D/T = 0.5$) (Fig. 4a). However, S_1 (the smallest sized eels) did not include a sufficient number of eels, making an objective interpretation difficult. In contrast, S_6 (the largest sized eels, >450 mm, D/T, 0.23) was the least detected, and it was mostly detected during the year of tagging ($O/A = 3.24$) (Fig. 4b). S_4 (351–400 mm, $O/A = 1.09$) and S_5 (401–450 mm, $O/A = 1.16$) showed similar numbers for both, the eels detected in the year of tagging and the eels detected after the tagging year. S_2 (251–300 mm, $O/A = 0.18$) and S_3 (301–350 mm, $O/A = 0.71$) showed a lower number of eels detected in the year of tagging than those observed after the tagging year. S_1 (200–250 mm, $O/A = 0$) was only detected after the tagging year.

3.3 Body size, water temperature, migration period and river flow

Detections occurred at water temperatures between 13.8 and 27.6 °C, and 90% of the eels were detected between 19.0

Table 3. Number of eels detected each year according to the date of initial tagging. TL is the total length of yellow eels; **C** indicates the mean daily water temperature of the full year; range dates in brackets show the time window of tagging and release of the eels; and **A**, **B** and **C** correspond to the detection stations on the Meuse River (**A**, **B**) and the Ourthe tributary (**C**); total percentage in brackets is the proportion (%) between the total number of eels detected over the years at all stations and the total number of eels tagged for each initial tagging year.

	Number of eels tagged		Number of yellow eels detected							
				Number of years after tagging						
Year of initial tagging	Total	Yellow eels (TL in mm : mean±SD, range	Station	0	1	2	3	4	5	Total
2010	100	100								(24.0%)
(18 Jun. to		(390±42)	A (14.1 °C)	21	1	2	-	-	-	24
28 Jul.)		(247-591)	B (15.1 °C)	-	-	-	-	-	-	-
			C (10.8 °C)	-	-	-	-	-	-	-
2011	221	221								(20.8%)
(22 Apr. to		(390±57)	A (15.5 °C)	9	8	8	1	2	-	28
3 Oct.)		(231-690)	B (16.7 °C)	-	2	8	-	-	-	10
			C (12.1 °C)	-	4	2	2	-	-	8
2012	374	369								(41.7%)
(11 May to		(420±67)	A (14.1 °C)	45	50	12	1	-	-	108
10 Sep.)		(281-755)	B (15.1 °C)	12	16	3	2	-	-	33
			C (11.1 °C)	2	4	5	2	-	-	13
2013	380	374								(29.4%)
(25 Apr. to		(419±59)	A (13.6 °C)	35	40	7	-	-	-	82
13 Sep.)		(293-690)	B (14.5 °C)	8	10	-	-	-	-	18
			C (10.8 °C)	-	9	1	-	-	-	10
2014	215	215					-	-	-	(58.1%)
(17 Apr. to		(408±44)	A (14.9 °C)	89	14	-	-	-	-	103
25 Aug.)		(302-698)	B (15.8 °C)	5	-	-	-	-	-	5
			C (12.0 °C)	12	5	-	-	-	-	17
2015	81	78				-	-	-	-	(12.8%)
(26 May to		(434±59)	A (14.3 °C)	10	-	-	-	-	-	10
30 Jul.)		(329-618)	B (15.2 °C)	-	-	-	-	-	-	-
			C (12.0 °C)	-	-	-	-	-	-	-
Total	1371	1357	ABC	248	163	48	8	2	-	469
		(412±58)	(13.8 °C)							(34.6)
		(231-755)								

and 26.2 °C, with the median at 22.7 °C. Temperatures at movements did not differ significantly between the six size classes of eels (median temperatures (°C), $S_1 = 21.0$, $S_2 = 22.6$, $S_3 = 23.3$, $S_4 = 22.7$, $S_5 = 23.1$ and $S_6 = 22.3$) (H test: $df = 5$, $H = 9.6847$, $p = 0.08468$, $n = 433$) (Fig. 5a). Among the three detection stations, temperatures of upstream migratory movements were significantly lower at **C** (median temperature = 19.3 °C) in the Ourthe tributary than at **A** (22.9 °C) and **B** (23.9 °C) in the Meuse River (H test: $df = 2$, $H = 94.705$, $p = 2.2 \times 10^{-16}$, $n = 433$) (range $W = 0$–3, $p = 2.274 \times 10^{-12}$–$4.547 \times 10^{-13}$).

From 2010–2015, detection occurred between 18 April and 27 August (131 days). In total, 90% of eels were detected between 7 June and 14 August (68 days), with the median date of 8 July. The detection period varied significantly between the size classes of the eels (H test: $df = 5$, $H = 16.364$, $p = 0.005879$, $n = 432$). Among the size classes, S_1 (200−250 mm; median date, 29 June) and S_6 (>450 mm; 4 July) were detected earlier than S_2 (251–300 mm; 8 July), S_3 (301–350 mm; 9 July), S_4 (351–400 mm; 16 July) and S_5 (301–350 mm; 23 July) (range $W = 615$–1681, $p = 4.678 \times 10^{-3}$–6.497×10^{-4}) (Fig. 5b).

Detections occurred at river flows between 9.7 and 361.4 $m^3 s^{-1}$, and 90% of the eels were detected between 23.7 and 226.3 $m^3 s^{-1}$, with the median at 95.1 $m^3 s^{-1}$. Flows during movements did not differ significantly between the six size classes of eels (median flows ($m^3 s^{-1}$), $S_1 = 90.8$, $S_2 = 115.8$, $S_3 = 94.5$, $S_{4,} = 95.8$, $S_5 = 95.2$ and $S_6 = 84.8$) (H test: $df = 5$, $H = 2.082$, $p = 0.8377$, $n = 433$). Among the three detection stations, flows at movements were significantly lower at **C** (median flow = 23.6 $m^3 s^{-1}$) in the Ourthe tributary than at **B** (96.9 $m^3 s^{-1}$) and **A** (99.9 $m^3 s^{-1}$) in the Meuse River (H test: $df = 2$, $H = 112.47$, $p < 2.2 \times 10^{-16}$, $n = 433$) ($W = 0$, $p = 4.547 \times 10^{-13}$). These flows accounted for less than half the average daily flow of the Ourthe tributary at **C** (45%) and the Meuse River at **A** (39%) and **B** (47%).

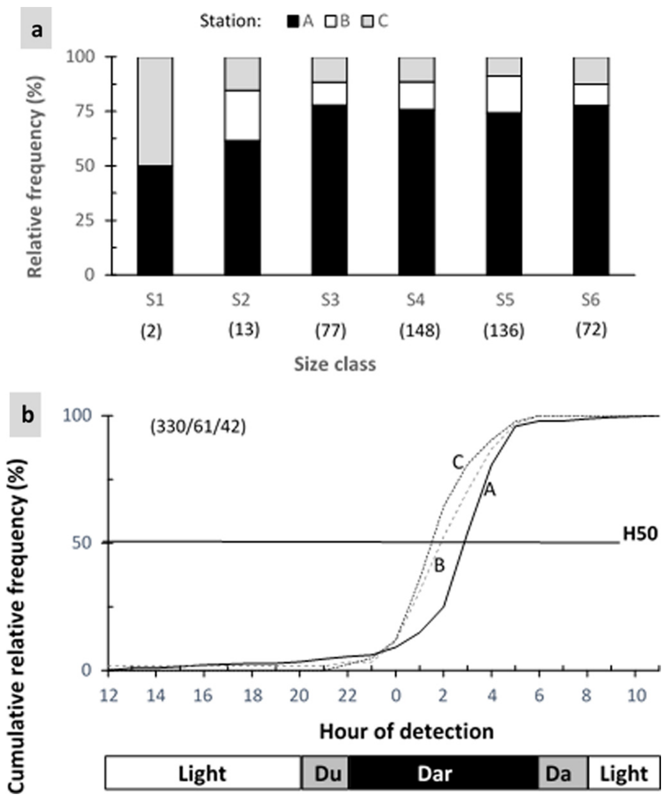

Fig. 3. Frequencies of ascending yellow eels according to size classes (a) and hour of detection (b). H50 indicates the hour of detection of 50% (median) of the eels; **A**, **B** and **C** specify detection stations at the first upstream detection station **A** (Monsin) in the Meuse, **B** (Yvoz-Ramet) on route 1 in the upper Meuse, and **C** (Angleur) on route 2 in the Ourthe tributary. Numbers in brackets indicate the sample size of eels detected by size classes and stations **A**, **B** and **C**, respectively. Du and Dar correspond to dusk and dawn, respectively.

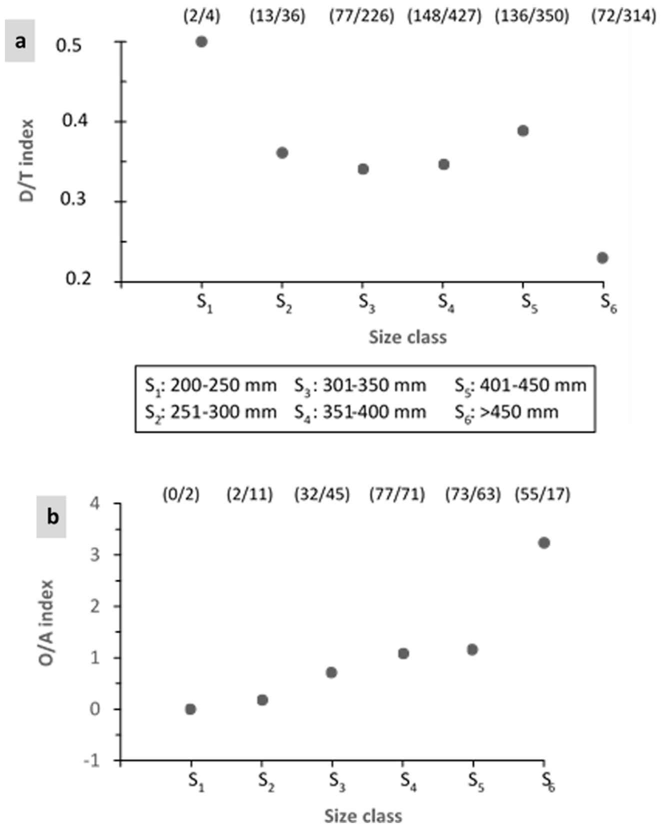

Fig. 4. *D/T* (a) and *O/A* indices (b) per size class of tagged yellow eels. The numbers in brackets show the sample sizes of eels detected and eels tagged for the *D/T* index, and the sample sizes of eels detected in the tagging year and eels detected after the tagging year for the *O/A* index.

3.4 Body size and migration speed

Eels migrated upstream at speeds between 0.012 and 6.5 km day^{-1}; and 90% of eels moved between 0.019 and 2.167 km day^{-1}, with a median speed of 0.317 km day^{-1}. The daily travel speed differed significantly between the size classes of eels (H test: $df = 5$, $H = 40.021$, $p = 1.479 \times 10^{-7}$, $n = 429$). The fastest size class was S_6 (>450 mm, median speed, 0.650 km day^{-1}), followed by S_5 (401–450 mm, 0.325 km day^{-1}) and S_4 (351–400 mm, 0.228 km day^{-1}) (range $W = 13$–1617, $p = 1447 \times 10^{-2}$–1609×10^{-7}) (Fig. 6). In contrast, S_1 (200–250 mm, 0.015 km day^{-1}), S_2 (251–300 mm, 0.038 km day^{-1}) and S_3 (301–350 mm, 0.08 km day^{-1}) were the slowest size classes.

3.5 Relations between migration variables analysed

Between the five migration variables analysed, water temperature was not correlated with river flow and body length while it was positively correlated with detection period (Pearson correlations: $r = 0.36$, $p < 0.0001$) and daily speed ($r = 0.12$, $p = 0.0113$). Speed was not correlated with period, but it was positively correlated with body length ($r = 0.21$, $p < 0.0001$) and inversely correlated with flow ($r = -0.17$, $p = 0.0005$). Period was negatively correlated with body length ($r = -0.15$, $p = 0.002$) and flow ($r = -0.14$, $p = 0.0038$). Body length was not correlated with flow. These correlations highlighted the importance of water temperature conditions in upstream migration process and body size in daily speed in the study site.

4 Discussion

Using RFID detection stations, we described the upstream migratory movement behaviours of various eel body size classes in the Belgian Meuse River, which is regulated for hydropower generation and navigation, and, in which, the stock of the incoming eels has drastically declined (Nzau Matondo and Ovidio, 2016). The detection systems were placed in fish-passes, allowing us to follow the upstream movements of the natural immigrant eels over long distances and for six consecutive years, thus, producing accurate information about the eel's migration behaviour. As the tags have an infinite lifespan, monitoring upstream migration behaviour can be conducted over many consecutive years. Our results indicated that the species, despite its poor swimming capacities (Porcher, 2002; Baudoin et al., 2015), could move upstream through vertical slot fishways during the riverine

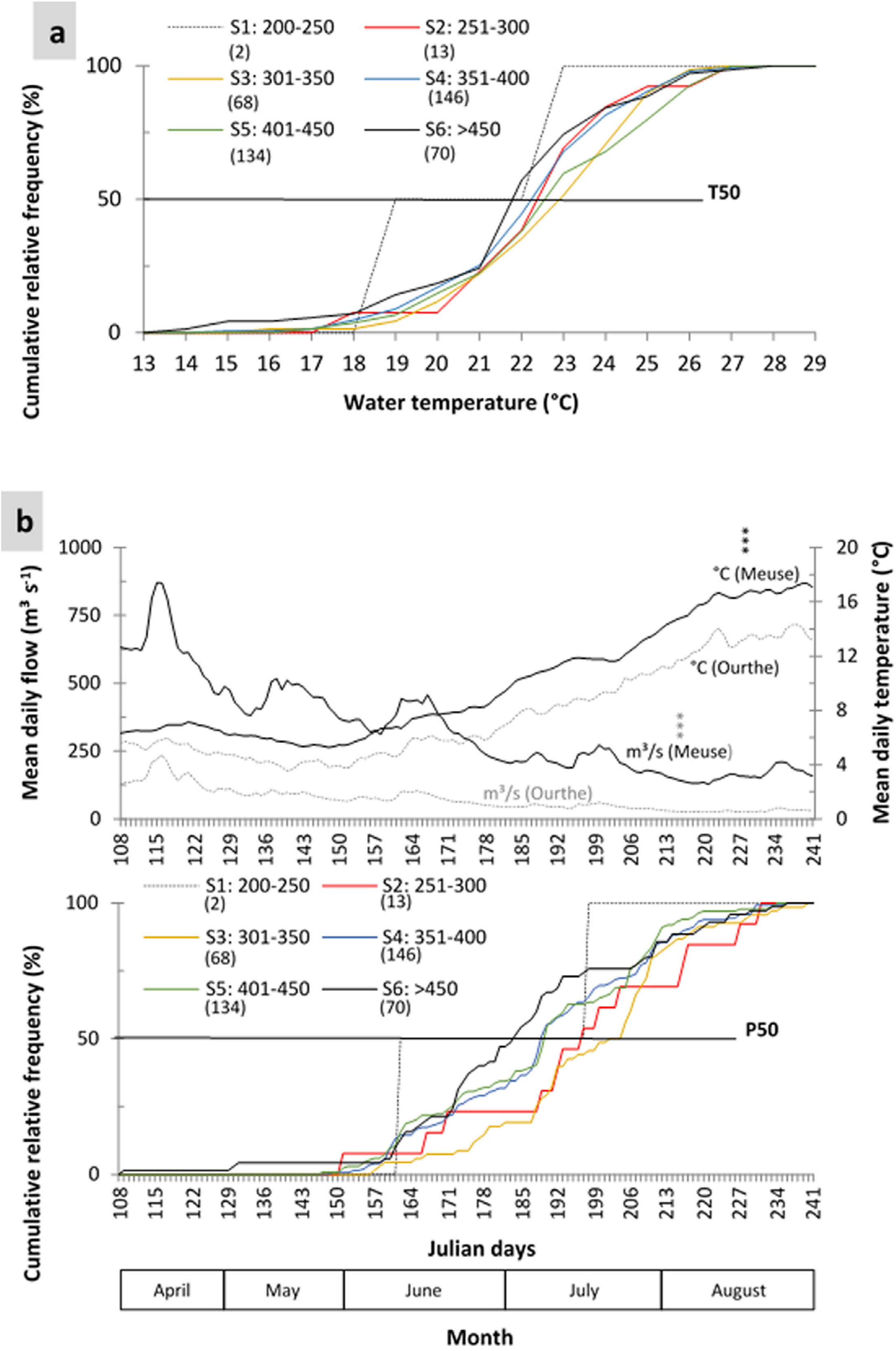

Fig. 5. Water temperature at detection (a) and detection period (b) relative to the mean daily temperature and flow of the Meuse River and the Ourthe tributary during the study period from 2010 to 2015. Numbers in brackets indicate the sample size of the size classes (S_1–S_6, in mm) of eels for temperature and period. T50 and P50 indicate medians for temperature and period, respectively.

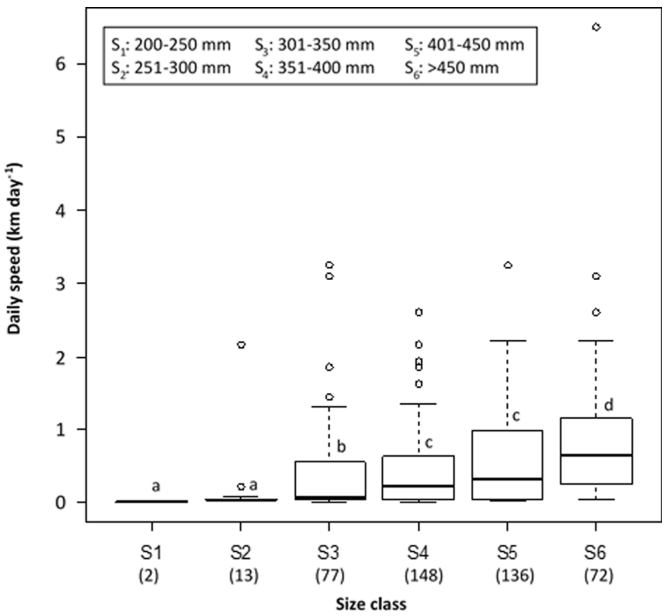

Fig. 6. Relations between the size classes of eels and the daily travel speeds. Numbers in brackets indicate the sample size of the eels detected. Values are medians, 5th, 25th, 75th and 95th percentiles; the bar marks the median and circles indicate outliers. Size classes marked with the same letter are not significantly different (H and *W* tests, $p < 0.05$).

colonisation. However, the real efficiency of the fishways, regarding the passage success for the ascending yellow-phase eels, remains unknown at our study site. These fishways were optimised for salmonids (e.g., Atlantic salmon *Salmo solar*, sea trout *Salmo trutta*) and large potamodromous (rheophilic) fish (e.g., barbel *Barbus barbus*, chub *Squalius cephalus*) that have better swimming capacities than eels (Porcher, 2002; Baudoin et al., 2015).

We demonstrated the further upstream detection of about 27.6% of the tagged yellow eels belonging to all size classes, at stations distant (up to 31 km) from the release site, but only 6.6% of the eels were detected at two subsequent RFID stations. These findings suggest the existence of a small proportion of "nomads" (or "emigrations"), searching for more suitable habitats in the upstream direction. There were also, probably, a majority of "home range dwellers", eels that establish in a given area for between several months to several years. Feunteun et al. (2003) and Laffaille et al. (2005) described such categories of behaviours, which were associated with the high behavioural plasticity of yellow eels. These two distinct movement behaviours of eels occur after their first year or even during their second year in rivers (Feunteun et al., 2003). These movements may be explained by habitat shifts according to size (Baisez, 2001) or attributed to variations in environmental conditions, such as floods, water levels, temperature and human disturbance (Lamothe et al., 2000). These categories followed the "founder" and the "pioneer" strategies that prevail in the youngest stages (glass eels and elvers) during their first year in rivers (Feunteun et al., 2003; Laffaille et al., 2005). The small rate of nomadic behaviour among the eels entering Belgium underlines the near disappearance of colonisation of the upper tributaries in the Belgian Meuse River basin, which had once been intense (Baras et al., 1996). This outcome suggests that the upper part of the basin will be progressively emptied by the progressive departure of the oldest individuals at the silver stage. To repopulate the upper part of the basin, a well-targeted stocking, using glass eels and very young eels ≤ 300 mm, might succeed (Ovidio et al., 2015; Brämick et al., 2016; Josset et al., 2016; Pedersen and Rasmussen, 2016), but the success of downstream migration of these restocked eels remains an important topic.

Among the tagged yellow eels, the larger eels (size class S_6) were detected earlier and moved faster than the other size classes. This tendency could be related to their detection occurring mostly in the year of tagging ($O/A = 3.24$) and their large size (mean length, 522 mm). However, their upstream colonisation activity ($D/T = 0.23$) was very low. This observation could be due to the ecological and behavioural profile of large eels. Previous studies showed that S_6 eels were >6 years old (Mazel et al., 2012) and mostly female eels, which were more prone to settle and feed before silvering and downstream migration (Aprahamian, 1988; Durif et al., 2005; Laffaille et al., 2006). The eels > 450 mm were females, with reduced upstream migratory activity and are recognised in the literature as being capable of growing to a larger size and living for longer in freshwaters than male eels (De Leo and Gatto, 1995; Ibbotson et al., 2002; MacNamara and McCarthy, 2014). Other studies have also shown that the large yellow eels might adopt a highly sedentary lifestyle, even at periods of the year where this developmental stage usually shows upstream movements (Baras et al., 1998; Laffaille et al., 2005; Ovidio et al., 2013). S_1 and S_2 (eels ≤ 300 mm) were mostly detected after the tagging year ($O/A < 0.2$) and showed a higher detection (>37%) at further upstream stations compared to the other size classes. The eels ≤ 300 mm were, therefore, better fitted to colonise the upper rivers in habitats farther from the sea. S_3, S_4 and S_5 (eels > 300 mm and ≤450 mm) displayed an intermediate detection profile, with a nearly similar number of the eels detected in the year of tagging and after the tagging year ($O/A = 0.70$–1.16).

Several hypotheses can be envisaged to explain why 72.4% of the tagged yellow eels were never detected upstream of the capture site. (i) Some eels might have reached the upper rivers without being detected, because of alternative migration routes (ship locks and navigation canals, Fig. 1) present in the study site. This behaviour probably occurred, but only for a few individuals, as only 0.3% of the tagged eels were detected further upstream in rivers without being detected downstream at the first upstream station, (ii) The tagged yellow eels were still dwelling close to the point of release because of sufficient availability of growing habitats, resulting from the low eel densities in the Meuse River with long-term reduction in the eel recruitment (Nzau Matondo and Ovidio, 2016). The tagged yellow eels had a mean size of 412 mm, meaning these eels displayed an ecological profile, with a preference for deeper habitats as the main feeding and resting sites (Baisez, 2001; Laffaille et al., 2003, 2004), which were abundant in the Meuse near our release site. In comparison, the lower eel densities in the Meuse likely produces sedentary behaviour. Various mark-recapture studies have also revealed a limited home range from the original tagging sites on the freshwater yellow-phase eels over an extended period (up to 7 years) (Baisez, 2001;

Laffaille et al., 2005), (iii) Handling mortality and RFID tag rejection by the yellow eels could be greater in the fields than in captivity, where perfect retention (100% of the tagged eels) of the tag and no mortality were observed in our previous test. However, Laffaille et al. (2005) reported 14% of the tags were rejected within 1 h after RFID tagging in trials, but that further tag loss rate was meagre (Feunteun et al., 2000; Baisez, 2001), (iv) Probable natural mortality in the tagged yellow eels and predation by piscivorous fish species, such as the European catfish. Eels have been found in stomachs of catfish competing for food and space, as both species are predators feeding near the bottom in confined environments (Wysujack and Mehner, 2005; Gualtieri et al., 2006). Baisez (2001) reported that the natural mortality of eels is rather low (about of 5–10% per year) in the field, (v) Possible biases related to the detection sites chosen, which were only located in fishways because of the difficulties of installing such detection systems in the navigable canals and locks. Such a design might lead to an underestimation of the detection success.

The upstream movements of the detected eels were observed in spring and summer at water temperatures >13 °C and during the darkness. Our observations are consistent with previous observations on anguillids at this life stage (Tesch, 2003; Nzau Matondo et al., 2017). However, the use of RFID telemetry provided more precision about the dates (90% of eels between 7 June and 14 August), the water temperatures (90% from 19.0–26.2 °C) and the time (90% between 00:00 and 05:00 h), during which, the upstream colonisation activity is high for the riverine yellow eels. Such knowledge may be useful in the implementation of eel conservation actions, such as the seasonal maintenance of migration routes, the timing and duration of the eel trapping, as well as river flow management during the peak of the eel migration. Our RFID tracking device indicated that the nomadic eels preferred to continue upstream through the large river (Meuse) rather than leave at the first tributary (Ourthe). The low colonisation rate of eels through the Ourthe tributary could be explained by its significantly lower temperature than the Meuse, which was probably less attractive for growth and swimming activity. The effect of low temperatures was noticed in this study, by the absence of migration activity at <13 °C. This observation was consistent with the accepted limits of 10–15 °C, for the beginning of migration in the eels (Naismith and Knights, 1988; White and Knights, 1997). The choice of the Meuse could result from the combined action of environmental factors, such as higher temperature associated with a higher rate flow and lower current speed, which are more attractive for upstream movements of eels (Nzau Matondo and Ovidio, 2016; Santos et al., 2016; Nzau Matondo et al., 2017). This is also supported by the importance of water temperature conditions in upstream migration process as highlighted in the correlation between migration parameters. In the case of our study area, upstream movements of eels increase when water temperature conditions increase and flow regimes decrease.

We observed a significant positive relationship between the body size of eels and the daily migration speed, which is consistent with the findings of Clough et al. (2004). However, this association did not include the actual size of the eels detected after the year of tagging, because they were not recaptured. From the apparent maximum migration season (18 April–27 August, 131 days), S_6 (>450 mm), the fastest size class eels, could potentially travel a median distance of 85.2 km per year. In contrast, the travelled distance decreased to only 2 and 5 km per year for the slowest classes of eels S_1 (200–250 mm) and S_2 (251–300 mm), respectively. In these slowest eels, migrations were the result of intermittently switching between brief swimming activity and long stationary periods (e.g., feeding or resting activity) rather than long continuous swimming movement at very slow speed. By pooling all migration speed data of the eels (median speed, 0.317 km day^{-1} or 0.004 m s^{-1}), the annual distance travelled was estimated to be about 41.5 km. This estimate was much higher than those assessed in previous field studies of European eel migrations in riverine systems (Aprahamian, 1988: Dee River in Wales, 10−20 km year^{-1} and Severn River in England, 20–30 km year^{-1}). The higher migration rate in the Meuse River could correlate with its low river current gradient (80 m/230 km). According to Aprahamian (1988), the low migration rate of eels is related to a more arduous migration, resulting from the steeper gradient of the rivers, such as the Dee River. However, according to typical swimming speed of one body length per second (Hart and Reynolds, 2008), this translates to 0.4 m s^{-1} for these eels (mean length, 413 mm), suggesting that they are relatively slow. However, it should be noted that these eels have already travelled >320 km from the sea.

5 Conclusion

We have presented upstream migration behaviour of various size classes of yellow eels in the upland river of the Meuse, >320 km from the sea. Our 6 year study indicates most eels were home range dwellers and that small eels (≤300 mm) moved further upstream than larger eels. These data will be useful for freshwater managers when developing strategies aimed at reducing the risk of collapse of the local eel stock in inland rivers and at meeting the silver eel escapement target in river systems with low natural recruitment.

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