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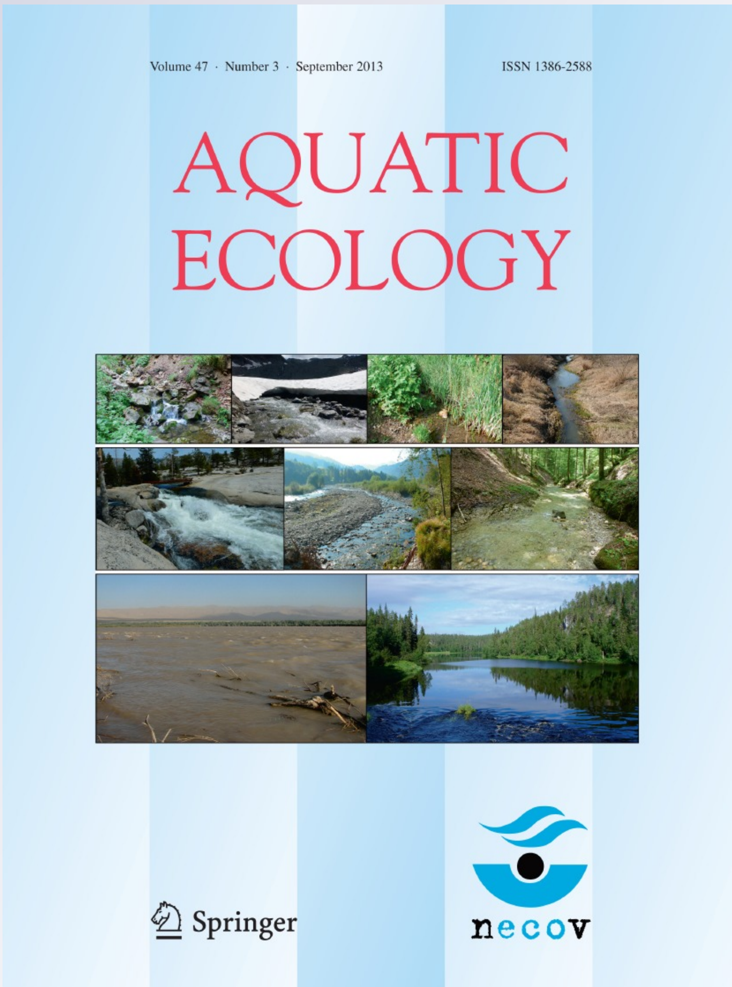

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A bit of quiet between the migrations: the resting life of the European eel during their freshwater growth phase in a small stream

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Abstract The movements and habitat use of resident yellow eels were studied in a stream stretch having both natural and minimum flow zones. $N = 12$ individuals (total length 505–802 mm) were surgically tagged with radio transmitters and released at their capture sites. They were located using manual radio receivers during the daytime from 2 to 5 days/week over periods ranging from 200 to 329 days, for a total of 1,098 positions. Eels showed home ranges ranging from 33 to 341 m (median value, 62 m), displayed strong fidelity to sites and demonstrated a great degree of plasticity in habitat use. Eels were slightly mobile throughout the year, but their movements were season and temperature dependent, with a maximum during the spring (mean water temperature, 12 °C) and a minimum in winter (3 °C). Stones and roots (utilization rate greater than 50 % of eels for more than 30 % of location days) were significantly the most frequently used habitats. Between the two flow zones, the natural flow was the most occupied, with a significantly higher proportion of resident eels (66.7 % of radio-tagged yellow eels) and longer occupation (81 % of location days) than the minimum flow zone with less suitable habitats.

Keywords Mobility · Home range · Habitat · Minimum flow · Telemetry

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Introduction

The European eel, *Anguilla anguilla* (L.), is a catadromous fish species and has a unique life cycle with mature individuals spawning in the Sargasso Sea (Tesch 2003). The transparent, leaf-like larvae, called leptocephali, drift on the Gulf Stream transported by oceanic currents that they 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; Arai et al. 2006). In growth zones, these elvers become yellow eels that metamorphose at maturation into silver eels, which migrate back downstream utilizing high fat reserves, through the ocean to the Sargasso Sea, where they reproduce and die (Belpaire et al. 2009; Bevacqua et al. 2011; Verbiest et al. 2012). Stocks of European eel have significantly declined since the end of the 1970s (Dekker 2003). This species is now considered to be endangered, listed in the IUCN Red List of Threatened Species and included in the UN CITES Appendix II list of the convention on international trade in endangered species of wild fauna and flora (CITES 2007; Bonhommeau et al. 2008; Van Liefferinge et al. 2012; MacNamara and McCarthy 2013). This stock decline is explained by a combination of factors including both oceanic (fluctuations in current speed and circulation patterns) and continental factors (pollution, habitat loss, overfishing, turbine mortalities) (Feunteun 2002; Knights 2003; Privitera et al. 2013).

Between their two oceanic migrations, European eels spend most of their lifetime in freshwater systems where they grow (Baras et al. 1998; Arai et al. 2006). Eels are found in all water types from coastal marine waters through brackish estuaries, in eutrophic and oligotrophic, shallow and deep still waters, and throughout rivers to their upland head waters (Daverat et al. 2006). During the growth phase (yellow eel), they must have access to suitable 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). Lobon-Cervial et al. (1990) and Laffaille et al. (2003) have observed sedentary behavior of large yellow eels in rivers. During the freshwater phase, eels colonize a wide repertoire of habitats depending on sites and rivers (Baras et al. 1998; Laffaille et al. 2003), in which flow regime synchronized with temperature and day length play a profound role in fish live (Bunn and Arthington 2002). Flow alone was found explaining 85 % of the total variation in the eel life event as downstream migration of silver eels (Vøllestad et al. 1986), and a model incorporating water level and temperature, accounting for 76 % of the variation in the upstream migration of elvers or juvenile eels (Jellyman and Ryan 1983), but its alteration may reduce the migration capacity responsible for the decline of a fish species. Knights et al. (2001) mentioned that eels have negative phototaxis and prefer habitats with soft sediment, crevices, adequate vegetative cover, undercut stream banks and large woody debris. Eels are discrete animals moving at night and exhibiting cryptic habits during daytime (Baras et al. 1998), which makes it difficult to follow their behavior in rivers. Many aspects of the resident stage of eels in freshwaters during their growth phase are still insufficiently understood such as ecology in terms of space and time use (Feunteun et al. 2003; Imbert et al. 2010). In addition, nothing is known about their activity during long-term monitoring periods, including the four seasons of the annual cycle, and their habitat use in both natural and minimum flow conditions with hydropeaking events as commonly encountered in most river systems in Europe fragmented by hydroelectric power plants. Such knowledge is a key element of the behavioral ecology of eels that may also improve conservation plans.

Using manual radiotelemetry, we monitored the space and time use of individual yellow eels throughout the four seasons of an annual cycle, in a small stream disturbed by a hydroelectric power plant. Our aims were to investigate: (1) individual movement patterns, site fidelity, the habitat use and home range exploitation in relation to seasons and environmental factors, and (2) the preference of the yellow eel for minimum or natural flow conditions in the disturbed river stretch.

Materials and methods

Study site

The study site is situated in Belgium (Fig. 1), in the lower reaches of the Mehaigne stream, up to 8.8 km upstream of the confluence with the Meuse River in Wanze (376 km from the estuary in the Netherlands). The Mehaigne is 65.5 km in length and drains a 360-km^2 basin. The stream width ranges from 5 to 10 m and the mean daily temperature from 0 to 21.4 °C (data from University of Liège). The study site represents the main course of the stream with two flow zones caused by the presence of a hydroelectric power plant (Fig. 1). The first zone (the minimum flow) that has an extremely unstable discharge (minimal flow 0.3 m^3/s for a maximum flow of 2 m^3/s in the inlet channel of hydropower production station) and daily depth up to 0.94 m and 30 hydropeakings defined as a brutal changing water level for approximately twice to three times of initial depths monitored in a time of 10 min during the experimental period. This zone comprises 0.9 km from the hydropower intake weir to the restitution area of the outlet channel. The second zone (the natural flow) has a daily depth up to 1.18 m and flow ranging from 0.56 to 8.3 m^3/s during the experimental period, and it was the part of watercourse downstream from the flow restitution zone. At the upstream limit of the study site, a natural river bypass allows the progression of fish and is known to be efficient for the European eel (Ovidio et al. 2009). The fish diversity in the Mehaigne is one of the highest in Southern Belgium and includes 22 fish species (salmonids, rheophilic, ubiquitous and lithophilic cyprinids, pike, perch, bullhead, stone loach). Mean values of size and weight of resident eels in spring 2009 were 689 mm and 690 g, respectively. Their density was estimated to be 0.0024 eels per m^2 for a biomass of 0.0017 kg.

Capture, tagging and tracking

Eels were captured by DC electric fishing (DEKA, 2.5 kVA) in the aforementioned stretch of the Mehaigne stream in March 2009. They were anesthetized in a solution of 2-phenoxy ethanol (0.5 ml l^{-1}), measured (total length, nearest 1 mm) and weighed (nearest 1 g), and a radio transmitter (Advanced Telemetry Systems ATS Inc., 40 MHz, trailing whip antenna; length, 24 mm; weight, 3.6 g; 258 days minimum battery life) was implanted in the body cavity through a midventral incision (Ovidio and Philippart 2002, 2008). The incision was closed by two separate stitches, using sterile, resorbable, plain Vicryl sutures. To prevent any adverse effect of long-term postoperative care on their behavior, eels were released at their exact capture site less than 1 h after surgery, as soon as they had recovered spontaneous

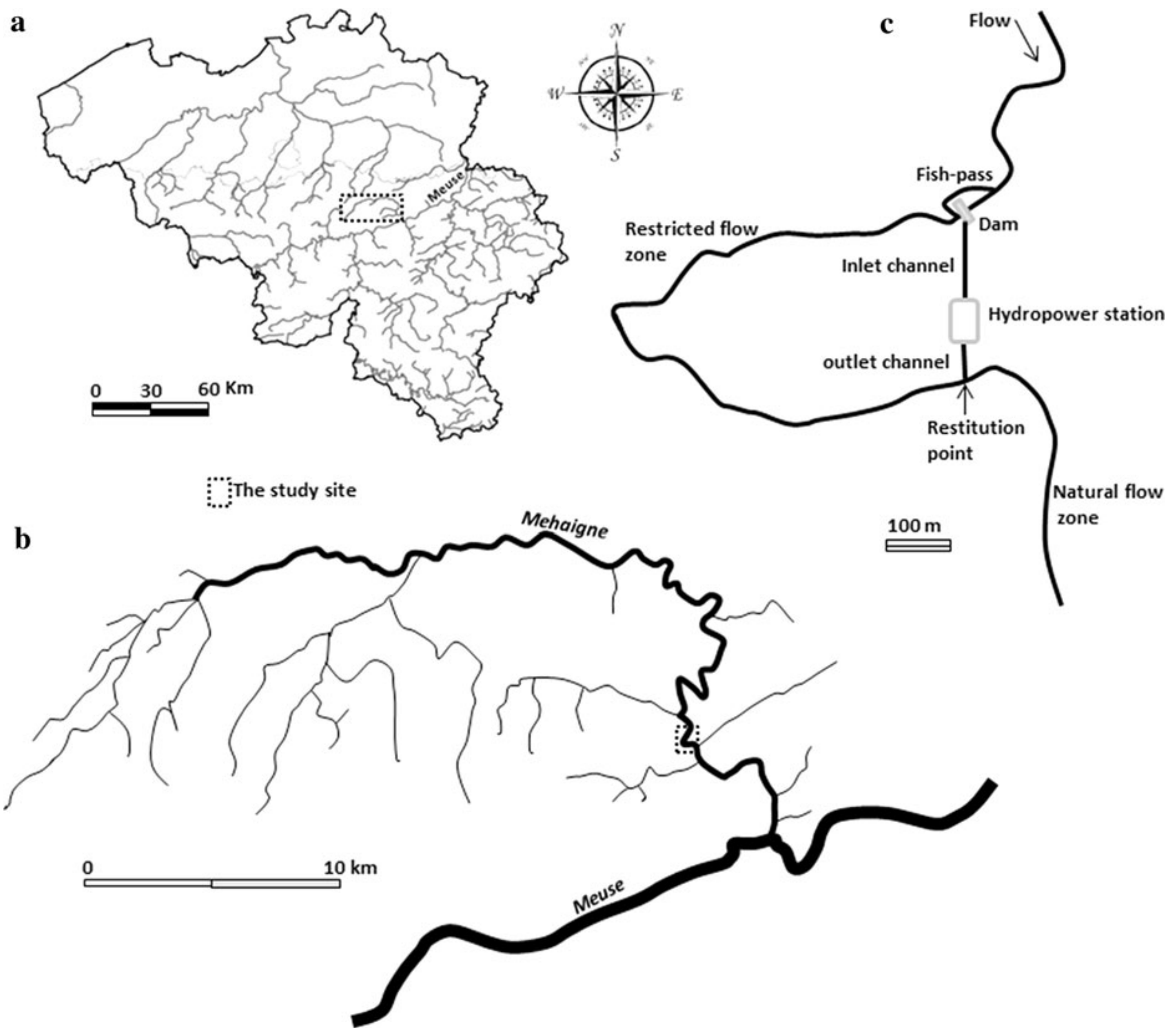


Fig. 1 Locations of the study site in southern Belgium (a), the Mehaigne stream (tributary of the Meuse river) (b) and its morphology (c)

swimming activity. Locations were made by triangulation from markers at 10–20 m on the riverbanks, using mobile FieldMaster radio receivers and loop antennas (ATS Inc.). Fish were tracked during daytime from 2 to 5 days/week until the end of the transmitter battery life. Each location was accompanied with an identification of the residence habitat exploited and moon phase. Habitats were categorized into five groups including stone walls (stone < 50 cm), roots, under riverbanks, boulder assemblages (stone > 50 cm) and silt substratum (Baras et al. 1998). Phases of the moon were classified into four major phases (Welicky et al. 2013): the first (new), the moon is invisible; the second (increasing moonlight), a part of lunar disk is visible during the increasing moon; the third (full), the full lunar disk is visible; and the fourth (decreasing moonlight), a part of lunar disk is visible during the decreasing moon. Water temperature was recorded hourly at a 0.1 °C precision using mobile data loggers (TidBit; Onset Computer Corp.). Water flow was continually monitored in the natural flow condition zone (data from the Service of Hydrological Studies SETHY), and the water level in the minimum flow conditions (data from the Wallonia Public Service SPW, Direction of non-navigable watercourses DCENN). Longitudinal home range was expressed as the distance between the most upstream and downstream locations from the release point during a definite time period; net distance traveled was defined as the straight line distance between subsequent locations, and total distance traveled, as the sum of net traveled distances by each eel in a season or all eels in 15 days or a month (Ovidio et al. 2002). The index of home range exploitation was the ratio calculated between the distance traveled and the longitudinal home range (Ovidio et al. 2002). The utilization rate of a flow zone in terms of eel percentage was the ratio (in percentage) between the number of eels exploiting the zone and the total number of radio-tagged yellow eels, and in terms of location days, it was the ratio (in percentage) between the number of location days in a zone and the total number of location days. The habitat utilization rate for each or all of the radio-tagged yellow eels was the proportion (in percentage) between the number of days in a specific habitat and the total number of location days.

Statistical analysis

The rates of monthly total distance traveled, flow zone and habitat utilizations of the 12 radio-tagged yellow eels were assessed using the Fisher's exact probability (FEP) test. Seasonal variations in their home range, their total distance traveled, their index of home range exploitation and distributions of their net distance traveled between subsequent locations in relation to water temperature, flow and moon phase were analyzed using the Kruskal–Wallis (KW) test followed by a paired comparisons Mann–Whitney (U) test. The distances traveled in each period of the year were followed using mean values calculated from the total distances and the number of eels tracked. The Spearman's rank correlation was used to assess the relationships between the body length and mobility parameters. These nonparametric tests were used since data did not meet the distribution assumption of parametric. For all statistical analyses, significance was set at $p < 0.05$.

Results

Movement patterns

Transmitters lasted up to 329 days and provided 1,098 eel locations. The total distance traveled ranged from 239 to 1091 m, the total longitudinal home range varied from 33 to 341 m and the home range exploitation index from 1.24 to 13.36 (Table 1). No significant correlations were found between the body length and the distance traveled (Spearman's rank correlation, $\rho = 0.238$, $p = 0.118$), the body length and the longitudinal home range ($\rho = 0.056$, $p = 0.863$), the body length and the index of home range exploitation ($\rho = 0.126$, $p = 0.697$), and the distance traveled and the longitudinal home range ($\rho = 0.476$, $p = 0.118$). All eels (100 %) were localized up to 2/10/2009 versus slightly more than half (58.3 %) in January 2010 (Fig. 2). The tracked eels homed and showed restricted movements, with principally upstream and downstream excursions less than 400 m from the release site and traveled little throughout the year (Fig. 3). The warming water in spring associated with increasing flow led to increased mobility. Higher water temperatures coincided with lower stream discharge, but not with higher yellow eel mobility. The analysis of the monthly total distance traveled revealed that movements of eels were significantly higher (FEP test, $p < 0.001$) in November (14.9 % of total distance traveled) followed by the spring and summer months. Yellow eels were active in all seasons (Fig. 3), which significantly influenced their total distance traveled (KW test: $d.f. = 3$, $H = 18.955$, $p = 0.0003$), their home range (KW test: $d.f. = 3$, $H = 16.965$, $p = 0.0007$) and their home range exploitation index (KW test: $d.f. = 3$, $H = 8.05$, $p = 0.0473$). Home ranges in spring (median value, 62 m; mean water temperature, 12 °C) were more than twice as long as those of all the other seasons (5 m, 3 °C; 12 m, 9 °C; and 30 m, 17 °C for winter, autumn and summer, respectively), and with a significant difference with other seasons (U test, $p < 0.05$) except for summer (Fig. 4a). Total distances traveled in spring (250 m) were significantly (U test, $p < 0.05$) more than three times longer than those of the other seasons (5, 44 and 76 m for winter, autumn and summer, respectively) (Fig. 4b). The home range exploitation index in winter (1.0) was significantly more than twice as low (U test, $p < 0.05$) as those of the other seasons (2.86, 2.94 and 3.64 for spring, summer and autumn, respectively) (Fig. 4c). Net distances traveled by these individuals were not significantly influenced by the water temperature (KW test: $d.f. = 3$, $H = 6.769$, $p = 0.0796$), flow (KW test: $d.f. = 4$, $H = 4.842$, $p = 0.3039$) and lunar cycle (KW test: $d.f. = 3$, $H = 4.446$, $p = 0.2172$) (Fig. 5). However, the highest net distance traveled (326 m) was observed in the decreasing moonlight at 11–15 °C water temperature and 1 m^3/s flow versus the highest median values of 50.5 m during the last quarter moon phase at more than 15 °C and 69 m at 4 m^3/s.

Flow zone utilization

Nine of the 12 radio-tagged yellow eels traveled and strictly established their home range within the natural flow zone of their capture and release site. For this eel group, the proportion of eels attending the natural flow zone accounts for 66.7 % of the radio-tagged eels (body length range, 505–802 mm; $n = 8$ eels), which was significantly higher (FEP test, $p = 0.0094$) than that of the minimum flow zone (8.3 %; 675 mm; $n = 1$ eel) (Fig. 6). However, three individuals (25 %, 689–755 mm) exploited both flow zones. Between these two zones, the utilization rate was significantly higher (FEP test, $p < 0.0001$) in the natural flow zone (81 % of locations) than that of the minimum flow zone (29 %). In contrast, no significant difference (U test: $U = 16$, $p = 0.4334$) was found between the two zones in terms of home range sizes (median values, 52.5 and 67 m for the minimum and natural flow areas, respectively).

Habitat use

The radio-tagged yellow eels exploited various diurnal residence habitats essentially corresponding to highly structured, cryptic habitats, such as burrow cavities inside stone walls, roots, under riverbanks, boulder assemblages or in the deep silt substratum (Fig. 7a). Seven of these 12 fish (body length range, 620–755 mm) used more than one type of these habitats versus five (505–700 mm, $n = 2$ eels for stones and 720–802 mm, $n = 3$ eels for roots) using only one habitat type. Among these eels' habitats, the stones and roots were significantly (FEP test, $p < 0.05$) the most occupied (>50 % of these 12 individuals for >30 % of location days) (Fig. 7b). The boulders and silts were significantly the least occupied habitats (<30 % of eels for <9 % of location days). The areas under riverbanks (33 % of eels for >10 % of location days) were more frequently used than the latter two habitats, but with only a significant difference in terms of the occupation time.

Discussion

This study highlights the restricted movements, homing habits and high plasticity of habitat use in European yellow eels during their growth phase in freshwaters, using long-term manual radio telemetry. *A. anguilla* were already tagged in the past using surgical implantation of active transponders and radio transmitters with internal coiled antenna (Baras et al. 1998; Verbiest et al. 2012). In the present study, the utilization of trailing whip antenna was necessary to increase the power of the signal, which is particularly useful when studying cryptic fish such as eels in rivers with substantial conductivity. The susceptibility to complications with such transcutaneous devices in tagged fishes varies between different species and varying environmental conditions, and in some instances the potential pathway for pathogens created by the passage of the antenna through the body wall may lead to potential infections (*in* Bauer et al. 2005). In this study, recapturing some radio-tagged eels 15 days after the tracking period showed that the healing process (including the antenna exit) was well underway, not completely finished but showing no

Table 1 Characteristics of the 12 radio-tagged yellow eels and their individual home range, mobility and exploitation index of habitat in the Mehaigne stream

Yellow eels	Body			Point of capture and release	Tracked			Duration of monitoring (days)	Home range HR (m)	Total distance traveled CM (m)	Home range Exploitation index (CM/HR)
	Length (mm)	Weight (g)	Transmitter weight ratio (%)		From	To	Location				
A	675	694	0.52	108	01 Mar. 2009	30 Dec. 2009	103	307	84	849	10.12
B	689	557	0.65	−10	01 Mar. 2009	03 Dec. 2009	93	280	280	706	2.52
C	802	1226	0.29	−204	01 Mar. 2009	02 Oct. 2009	80	218	67	250	3.73
D	740	841	0.43	−302	11 Mar. 2009	02 Oct. 2009	77	205	89	660	7.42
E	720	905	0.40	−302	11 Mar. 2009	26 Jan. 2010	106	321	48	433	9.02
F	744	767	0.47	−326	11 Mar. 2009	07 Jan. 2010	95	302	341	1091	3.20
G	620	538	0.67	−402	11 Mar. 2009	07 Jan. 2010	102	302	253	313	1.24
H	622	390	0.92	−5	17 Mar. 2009	09 Feb. 2010	106	329	35	239	6.83
I	755	818	0.44	−40	17 Mar. 2009	02 Oct. 2009	73	200	61	505	8.28
J	695	631	0.57	−208	17 Mar. 2009	05 Jan. 2010	55	294	33	441	13.36
K	505	220	1.64	−352	17 Mar. 2009	04 Feb. 2010	105	324	62	258	4.16
L	700	703	0.51	−352	17 Mar. 2009	28 Jan. 2010	103	317	142	300	2.11

Uppercase letters indicate fish studied

infection or necrosis. Furthermore, in order to minimize the potential effect of the tag on eel behavior, the transmitter/body mass ratio was under 1 % for 90 % of the individuals (maximum, 1.64 %), which is much lower than in most telemetry fish studies.

Even though the tracked eels were followed for nearly 1 year, the longitudinal home range did not exceed 341 m and the maximum distance traveled 1,091 m, which are slightly higher but comparable values than those observed in previous studies on Anguilla family (Beumer 1979; Ford and Mercer 1986; Baras et al. 1998; Jellyman and Sykes 2003). The small difference between these studies and the present study presumably originated from the duration of the study, different biotic and abiotic factors such as habitat availability, river typology, fish density and competition. In this study, the Mehaigne stream offers numerous and various habitats that did not force eels to move over long distances to find functional habitats. Furthermore, the low eel density in the stream reduces agonistic behaviors and competition for space and food resources, which probably does not motivate a high dispersal process (Knights 1987; Smogor et al. 1995; Ibbotson et al. 2002). The resting life observed in this study clearly documented the strong fidelity to the site, in contrast with their long migrations during the upstream colonization and downstream migration phases (Verbiest et al. 2012; Nzau Matondo et al. 2013). For a semelparous species, this may also be regarded as a strategy to gain energy (fat level) that can be used to migrate back downstream to the Sargasso Sea (Maes et al. 2005; Belpaire et al. 2009). Fewer movements and risks may indicate less energy expenditure and better growth. Eels nevertheless undertake some upstream and downstream excursions throughout the year, with a greater intensity in spring when the mean water temperature surpasses 10 °C. This finding demonstrates that temperature plays a key role on triggering yellow eels' activity during their life in freshwaters. But this is in contrast with the upstream colonization phase during which very high temperature stimulates the migration (White and Knights 1997a, b; Martin 1995; Nzau Matondo et al. 2013). The November peak observed may be explained by the last intense activity just before the temperature goes too low and the beginning of silvering process for spawning migration. A lower distance traveled and home range in winter could be associated with the water temperature that is too low for eels' activity, which is consistent with little

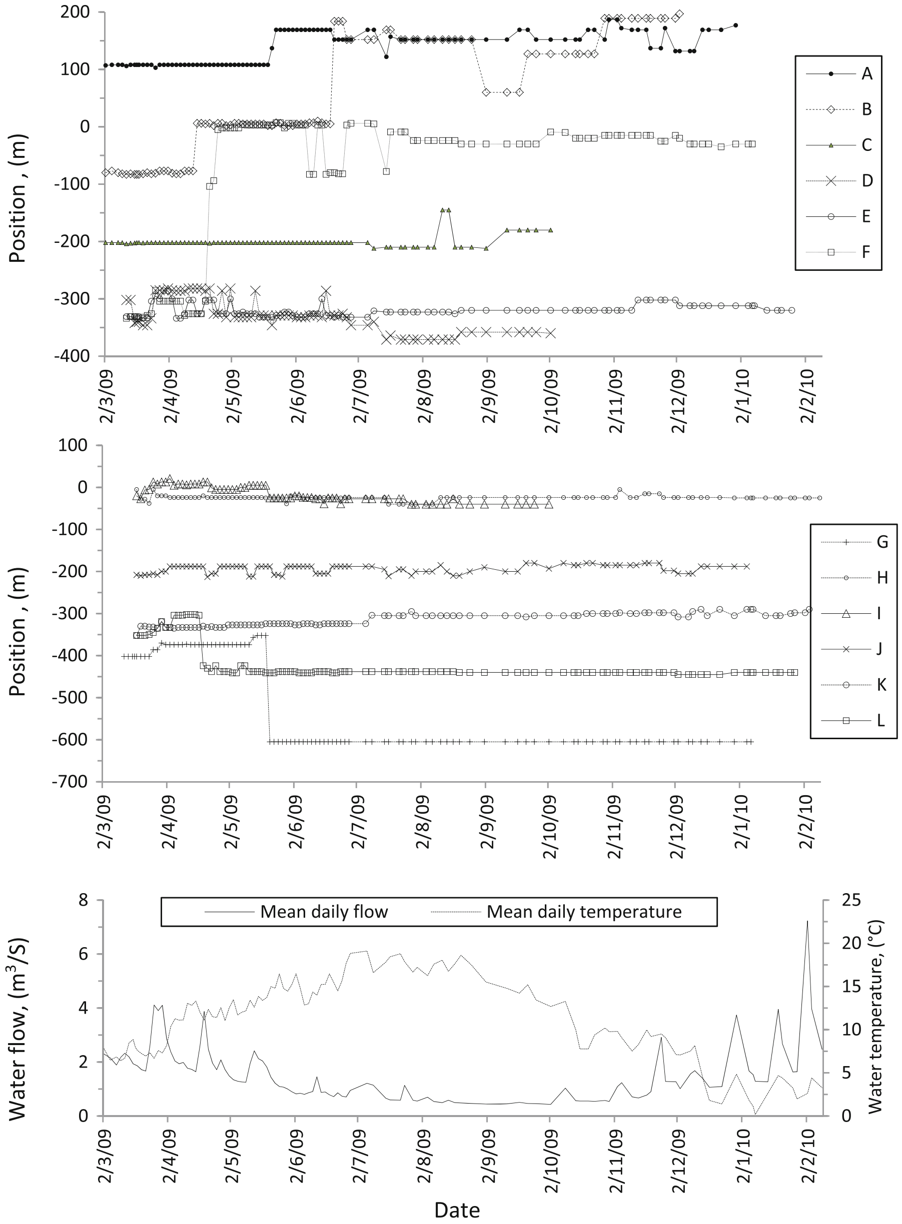
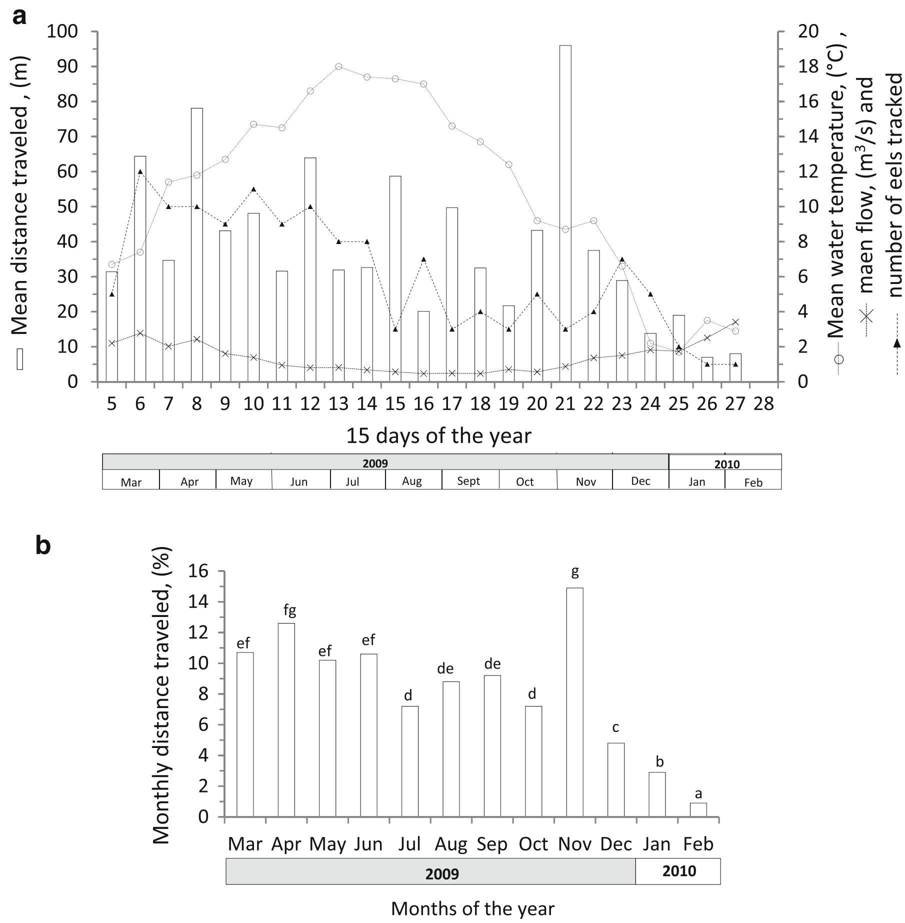


Fig. 2 Daily locations of the 12 radio-tagged yellow eels and variations in water temperature and flow of the Mehaigne stream. 0 on the Y axis indicates the restitution area of the outlet channel from the hydropower station; *uppercase letters* indicate fish studied

or no activity of eels at low temperatures already reported by several authors (Beumer 1979; Labar et al. 1987). For Baras et al. (1998), below 12 °C water temperature, yellow eels occupied restricted ranges and showed little activity throughout the diel period, but they did not track the eels during the autumn and winter period when water temperature fall down. The absence of significant effects of temperature, flow and moon phase emerged on distances traveled may be explained by the small size of experimental sample and the absence of night tracking.

The strong site fidelity and the alternative use of a precise residence site observed imply the existence of a mechanism by which this fidelity is acquired, as well as the development of precise sensory recognition of the site involved (Braithwaite and De Perera 2006). It helps to understand why eels tend to home to their capture site after a forced translocation (Rossi et al.

Fig. 3 Relationship between the 15 days of the year, the total distance traveled, the mean water temperature and flow and the tracked eels number (**a**), and monthly net cumulative distance traveled (**b**) of the 12 radio-tagged yellow eels. The mean monthly distances traveled in percent are indicated in *brackets*. The months with at least one letter in common are not significantly different (FEP test, $p < 0.05$)



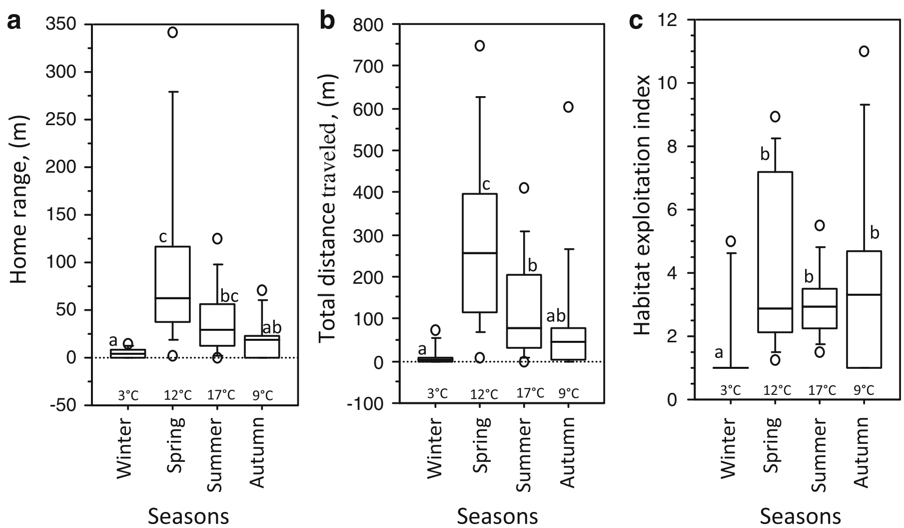


Fig. 4 Seasonal variations in home range (**a**), total distance traveled (**b**) and habitat exploitation index (**c**) of the 12 radio-tagged yellow eels. °C indicates the mean water temperature of seasons. *Bar median*, *box quartiles*, *whiskers minimum and maximum values*, *open circles outliers*; seasons marked with the *same letter* are not significantly different (U test, $p < 0.05$)

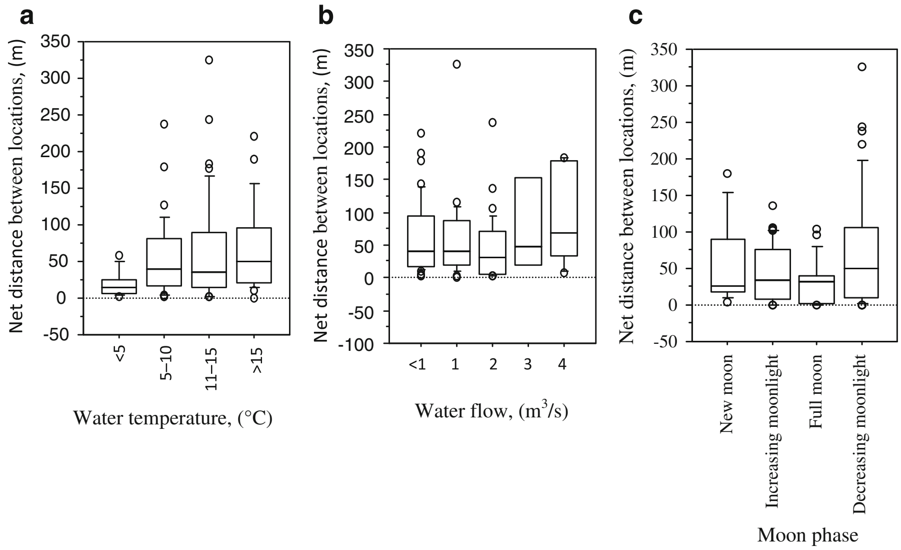


Fig. 5 Distribution of the net distance traveled between locations of the 12 radio-tagged yellow eels by water temperature (**a**), flow (**b**) and moon phases. *Bar median*, *box quartiles*, *whiskers minimum and maximum values*, *open circles outliers*; parameters marked with the *same letter* are not significantly different (KW test, $p < 0.05$)

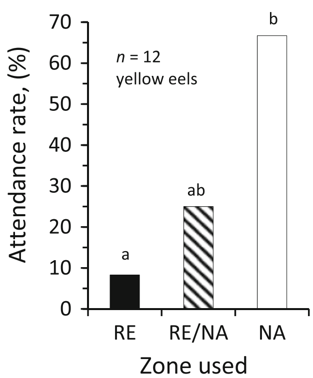


Fig. 6 Utilization rate of flow zones used by the 12 radio-tagged yellow eels. RE and NA mean restricted flow zone and natural flow zone, respectively; RE/NA signifies the utilization of the 2 flow zones; flow zones marked with the *same letter* are not significantly different (FEP test, $p < 0.05$ for the attendance rate of flow zones)

1987; Lobon-Cervial et al. 1990; McCleave and Arnold 1999). Interestingly, in the context of the hydroelectric production in the Mehaigne, a greater preference for the natural flow regime over the minimum flow zone could be related to extremely less available cryptic habitats in the latter zone due to their emergence because of a lower water level. Furthermore, in the disturbed river stretch, more pronounced hydropeaking events might reduce food availability and lead to unstable eel habitats, which may influence eels choosing to reside in the natural flow zone with more suitable and consistent habitats.

The wide repertoire of habitats used by these tracked eels may be a good indication of a great degree of plasticity in this life stage, which could increase the accessibility to various food resources for a better accumulation of energy reserves (Maes et al. 2005; Belpaire et al. 2009; Verbiest et al. 2012). According to Daverat et al. (2006), this large series of habitat use may be a strategy allowing eel species to colonize a great variety of ecosystems in terms of its geographical ranges. The significant preference for stony and root areas could be explained by the greater protection from predators provided by cavities between stones or roots (Lode 1993). Similar preferences were also observed during the spring and summer periods in *A. anguilla* (Baras et al. 1998) and *A. dieffenbachia* (Jellyman 1977). Despite the high quality of its numerous habitats, eel stocks in the Mehaigne stream are severely declining because the escapements of spawner eels are not accompanied by new recruitments of yellow eels and the constant decline of their annual recruitments from the sea (Nzau Matondo et al. 2013). However, such knowledge on eel habitat preference is of primary importance and raises issues on the success of stocking experiments as a conservation measure to increase their demography using eels at all life stages, as already suggested by Desprez et al. (2013).

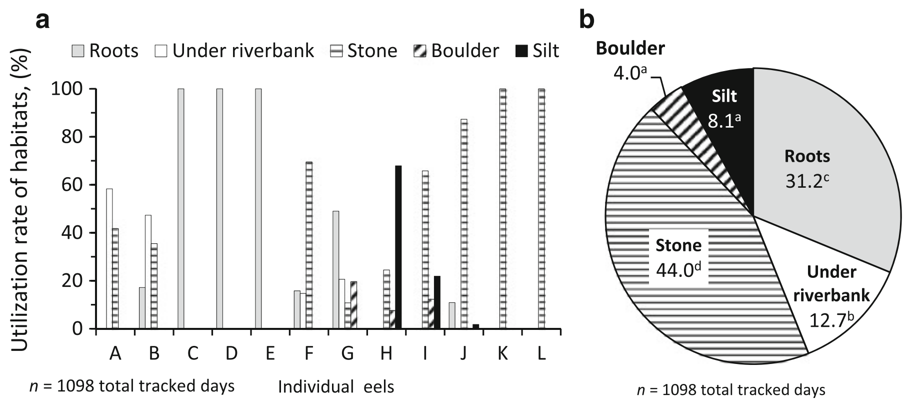


Fig. 7 Utilization rates of residence habitats during the tracking days for each (**a**) and all (**b**) radio-tagged yellow eels. *Uppercase letters* indicate the 12 yellow eels studied, $n = 1098$ total tracked days for all eels; habitat marked with the *same letter* are not significantly different (FEP test, $p < 0.05$)

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