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European silver eel (*Anguilla anguilla* L.) migration behaviour in a highly regulated shipping canal

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ABSTRACT

Among the many man-made structures that facilitate shipping, navigable canals take an important position. These canals may offer energetically favourable migration routes for diadromous fish, but they may also obstruct fish migration, for instance at shipping locks. Because the use of shipping canals by, and their effects on, migrating fish remain unknown, we assessed whether these canals can play a significant role in the migration of the critically endangered European eel. Only one third of 70 acoustically tagged silver eels completed migration through a shipping canal, and did so at a very low pace (average $< 0.06 \text{ m s}^{-1}$) due to delays at shipping locks and most likely also due to the disruption of water flow. These delays may come at an energetic cost, hampering the chances of successful migration. Knowledge on the impact of shipping canals on diadromous fish is crucial for proper management regulations. For instance, the observation that eels mostly migrated at night and during spring and autumn can support water managers to define adequate measures to improve eel migration in shipping canals.

1. Introduction

Canals for navigation and irrigation are among the most anthropogenically altered water bodies worldwide (Vitousek et al., 1997). Not only are they widely distributed, their number is likely to increase in the future due to climate change and a growing human population (Hannah et al., 2007). Canals are commonly characterised by a low structural variability (e.g. concrete embankments without riparian vegetation) with shipping locks, weirs and turbine stations, resulting in a regulated water flow. In addition to navigation, canals support industrial water management by facilitating water withdrawal and waste water disposal. It has already been shown that shipping canals may have a negative effect on local freshwater fish communities (Arlinghaus et al., 2002; Wolter and Arlinghaus, 2003). Such negative effects can be direct (e.g. shear stress, ship waves, dewatering and backwash...) or indirect (e.g. habitat fragmentation and simplification, loss of spawning and nursery habitats...) (see Wolter and Arlinghaus, 2003 for an extensive review). Although the impact of shipping canals on non-migratory fish species has been extensively studied (Arlinghaus et al.,

2002; Wolter, 2001; Wolter and Arlinghaus, 2003), knowledge on their effects on diadromous fish species remains scant. Shipping canals generate threats for diadromous fish species: structures such as shipping locks, weirs and turbine stations, as well as the regulated water flow, may hamper migration behaviour (e.g. by disorientation). However, shipping canals may also provide alternative opportunities such as new migration routes, by connecting river basins or creating shorter migration routes to the sea. Depending on the impact of these canals on fish migration, proposed management measures could for instance include adjusted flow regulation or mitigation measures at turbine stations and shipping locks. A group of diadromous fish species of particular interest, are catadromous anguillid eels, as species have declined tremendously during the last decades. Specifically, the recruitment of the European eel (*Anguilla anguilla* L.) has declined over 90% since the 1970s (Dekker and Casselman, 2014). This decline is the consequence of various causes, such as migration barriers, habitat deterioration, pollution, human-introduced parasites, fisheries and changes in ocean climate (Buysse et al., 2014; Feunteun, 2002; Kōie, 1991; Miller and Tsukamoto, 2016; Moriarty and Dekker, 1997). Habitat fragmentation

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by migration barriers, preventing the downstream migration of silver eels and upstream migration of glass eels, is regarded as an important bottleneck for this species (Mateo et al., 2017; Mouton et al., 2011). A changed flow regime may also negatively impact silver eel migration, especially since water flow is considered a crucial factor for eel migration (Travade et al., 2010; Verhelst et al., 2018; Vøllestad et al., 1986). To bridge this knowledge gap, we investigated the downstream migratory behaviour of the European eel (hereafter referred as 'eel') in a shipping canal.

European silver eel migration behaviour has been studied in various systems such as rivers (Piper et al., 2015; Stein et al., 2015; White and Knights, 1997; Winter et al., 2007), polders (Buysse et al., 2015; Verhelst et al., 2018), estuaries (Aarestrup et al., 2008; Bultel et al., 2014) and the marine environment (Aarestrup et al., 2009; Amilhat et al., 2016; Huisman et al., 2016; Righton et al., 2016; Wysujack et al., 2015), but migration behaviour in large canals with shipping locks is still underexplored. We tracked 70 silver eels in the Belgian Albert Canal using acoustic telemetry. This shipping canal connects the two largest river catchments of Belgium (i.e. Schelde and Meuse), resulting in different potential migration routes.

We assessed three research questions related to silver eel migration behaviour in the Albert Canal: (1) are eels able to migrate out of the system, (2) are they delayed in their migration, and (3) how does their behaviour relate to eel migration behaviour in other systems?

2. Methods

2.1. Study area

The Albert Canal is ca 130 km long, 86 m wide, 5 m deep and functions as a shipping route between the rivers Schelde (Antwerp) and Meuse (Liège) for ships up to 12,000 tonnes, illustrating its economic importance. Secondary canals are connected to the Albert Canal for irrigation and navigation purposes (mainly recreational navigation): Zuid-Willmsvaart, Canal Briegden-Neerharen, Canal Beverlo, Canal Dessel-Kwaadmechelen, Canal Bocholt-Herentals and Canal Dessel-Turnhout-Schoten (Fig. 1).

The Albert Canal is fed by the Meuse, with which it has an open connection (i.e. no shipping locks are present). The water level is kept constant by the weir at Monsin, at the junction between the Meuse and the Albert Canal. Part of the water is used to fill the shipping locks in Lanaye and Wezet, after which the water runs back into the Meuse (see Fig. S1 for details regarding the different connections of the Albert Canal with the Meuse). The other part is used to water the Albert Canal and has an average water flow of $9 \text{ m}^3 \text{ s}^{-1}$ in Genk (Baetens et al., 2005). The Albert Canal is divided in seven navigation sections (A–G) by six shipping lock complexes (each complex consists of three shipping locks) without weirs (from Schelde to Meuse, these are located at Wijnegem, Olen, Ham, Hasselt, Diepenbeek and Genk) to overcome the 56-m head drop. During the 27-month study period (3rd September 2014 till 20th December 2016), the majority of the ships came from the harbour of Antwerp and were transported via the shipping locks in Wijnegem (Table S1). The number of transported ships gradually decreased over the shipping locks towards the Meuse, since the destination of some ships was along the Albert Canal, after which they returned to Antwerp. Only in 2014 a substantial number of ships was transported over the shipping lock in Genk (De Vlaamse Waterweg nv, unpublished data). Although the net flow direction is towards the Schelde, shipping lock operation and accompanying navigation result in a highly disrupted flow regime. Opening the locks happens relatively fast (i.e. within 15 min), resulting in back-and-forth moving waterfronts in the canal sections and a water flow that temporarily differs between sections. Notably, section G has the lowest water flow of the system because the water mass is distributed over the docks (Hydrological Information Center, pers. comm.). The shipping locks operate from Monday morning 6 a.m. till Saturday evening 10 p.m., and remain

inactive on Sundays and holidays. Due to limitations of nocturnal navigation, the locks mainly operate during daytime. Specifically, for the period November 2014 till January 2016, 66% of shipping lock operations occurred during daytime compared to 30% at night. During dusk and dawn, shipping locks were both operational for 2% each of the time (shipping lock operation data obtained by De Vlaamse Waterweg nv). On top of shipping lock filling, the water manager discharges water via an underground canal when the Meuse discharge is high (especially in winter and spring). However, we do not have data about that activity.

Based on a fish monitoring survey from 2012 till 2015, the Albert Canal is characterised by a low fish biomass, ranging from 12.9 kg ha^{-1} to 24.2 kg ha^{-1} (Visser and Kroes, 2016). The diversity ranges between 15 and 18 species. The majority of the species are eurytopic, such as roach (*Rutilus rutilus* L.), bream (*Abramis brama* L.) and perch (*Perca fluviatilis* L.). Note that especially roach and bream are stocked for recreational angling purposes. Rheophilic and phytophilic species are scarce, while the numbers of invasive round goby (*Neogobius melanotomus* P.) are increasing over the years.

2.2. Tagging procedure

118 Eels were caught in the upstream part of the canal during summer, autumn and winter of two consecutive years (i.e. 2014 and 2015) using double fyke nets, just upstream of the shipping lock complexes in Genk, Diepenbeek and Hasselt. Of those, 70 silver eels were tagged and released on site in the Albert Canal (Fig. 1): 13 eels were caught and released in 2014 at Hasselt, five were caught and released in 2014 at Diepenbeek, 27 eels were caught and released in 2014 at Genk. Another 36 eels were caught at Genk in 2015, of which ten were released at that location and the latter 26 were released at one point in canal section D. Several morphometric features were measured in order to determine the eel maturation stage according to Durif et al. (2005): total length (TL, to the nearest mm), body weight (W, to the nearest g), the vertical and horizontal eye diameter (ED_v and ED_h , respectively, to the nearest 0.01 mm) and the length of the pectoral fin (FL, to the nearest 0.01 mm) (Table 1). Only females were tagged, since males are smaller than the minimum size handled in this study ($< 450 \text{ mm}$ (Durif et al., 2005)). Both FIV ($n = 1$) and FV ($n = 69$) silver eels were tagged. Eels were tagged with V13-1L coded acoustic transmitters ($13 \times 36 \text{ mm}$, weight in air 11 g, frequency 69 kHz) and V13P-1L coded acoustic transmitters ($13 \times 48 \text{ mm}$, weight in air 13 g, frequency 69 kHz) from VEMCO Ltd (Canada, <http://www.vemco.com>) (Table S2). The latter transmitter type has a pressure sensor, but those data were not used in this study. After anaesthetising the eels with 0.3 mL L^{-1} clove oil, tags were implanted according to Thorstad et al. (2013) and the wound stitched with resorbable polyfilament. Eels recovered in a quarantine reservoir for approximately 1 h and were subsequently released at the first acoustic listening station (ALS) upstream of their catch location or in section D (Fig. 1).

2.3. Acoustic network

Within the framework of the Belgian LifeWatch observatory, a network of ALSs (VR2W, VR2Tx and VR2AR, VEMCO Ltd) has been deployed in Belgium and The Netherlands (Fig. S2). These ALSs register the transmitter ID with date and time of the detection. Note that the data of the ALSs not located in the Albert Canal were only used to determine if eels were able to leave the Albert Canal and are therefore not described or discussed here. 23 ALSs were deployed in the Albert Canal itself and another four in the entry of the secondary canals connected to the Albert Canal (Fig. 1). In the Albert Canal, ALSs were deployed up- and downstream of every shipping lock ($n = 13$), near the tidal sluices in Antwerp ($n = 3$), at the junction with the Schelde-Rijn canal ($n = 1$), at the junction with the Meuse ($n = 2$) and evenly spread in section A ($n = 4$) to cover the sluice complexes of Wezet and Lanaye

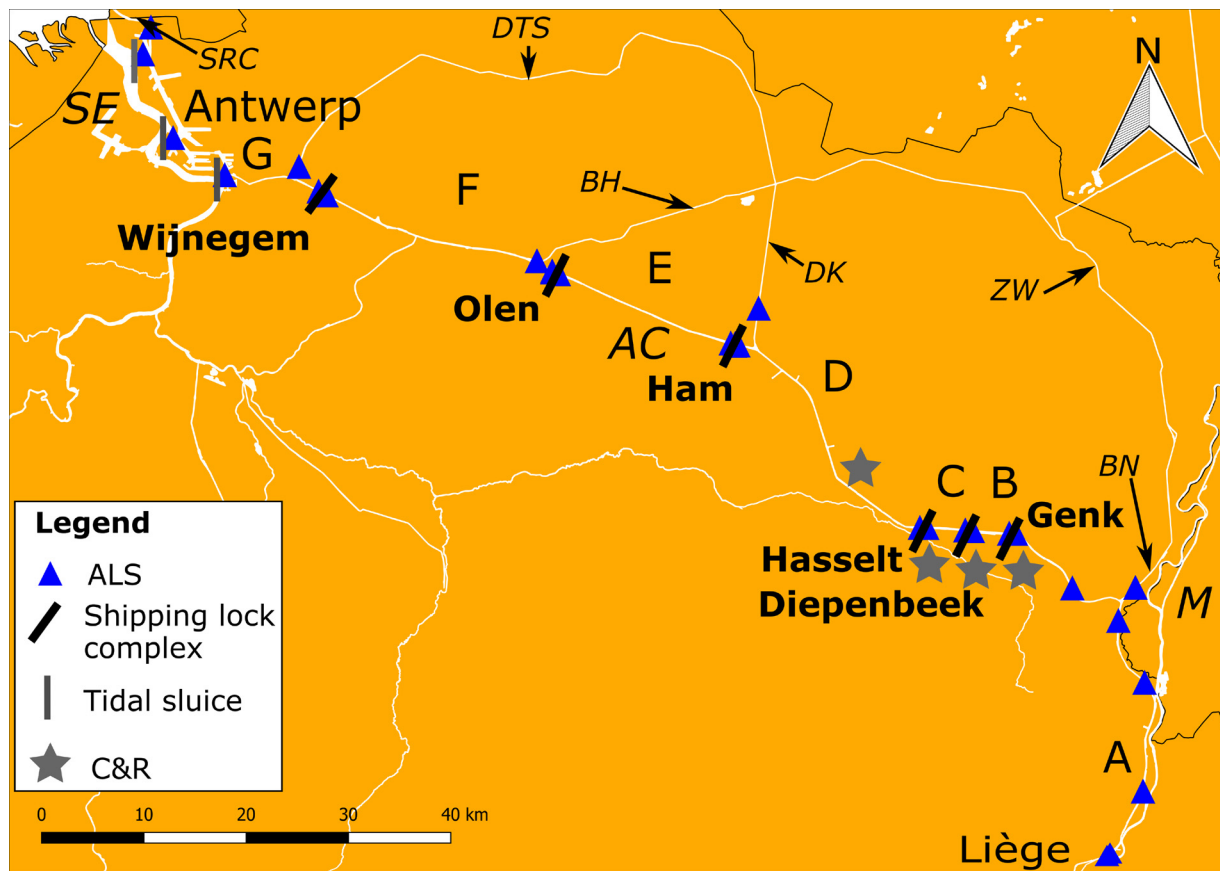


Fig. 1. Study area with the Albert Canal (AC) and its network of secondary canals: ZW (Zuid-Willemsvaart), BN (Canal Briegden-Neerharen), DK (Canal Dessel-Kwaadmechelen), BH (Canal Bocholt-Herentals) and DTS (Canal Dessel-Turnhout-Schoten). Also the Schelde-Rijn Canal (SRC) is indicated. The Albert Canal connects the Schelde Estuary (SE) in Antwerp (tidal sluices indicated by grey bars) with the Meuse river (M) in Liège. The Albert Canal is divided in seven canal sections (A–G) by six shipping lock complexes (indicated by black bars; Genk, Diepenbeek, Hasselt, Ham, Olen, Wijnegem). Positions of acoustic listening stations (ALSs) are indicated as blue triangles and catch-release locations (C&R) as grey asterisks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(Fig. S1). As such, eels were not detected when residing between two ALSs in the same canal section. However, this set-up was chosen to maximise the probability of detection for migrating eels. The stations were moored at the bank with weights and a small buoy. In this way, the hydrophone was directed upwards in the water column.

2.4. Data processing

The 70 tagged silver eels were tracked between 3rd September 2014 and 20th December 2016, resulting in a dataset with 1,541,521 detections. To determine residency times (i.e. the time between arrival and departure at an ALS), residency searches were performed with the VUE software (Vemco Users Environment, VEMCO Ltd, Canada). This allowed reducing the data by accumulating the number of detections during a fixed period of time. We applied an absence threshold of one hour (i.e. the maximum time permitted between detections within a single residency period) and a detection threshold of one detection (i.e. the minimum number of detections required for a residency period). The residency search resulted in intervals with arrival and departure

times per eel at each ALS. Between an arrival and departure within the same detection interval, the number of detections and the residence time were calculated (Verhelst et al., 2018).

To address the research question about migration success, the entire dataset was used. Research questions about migration speed and temporal behaviour were further subdivided into several specific sub-questions (see 2.5.1–2.5.3 and Table 2) which were addressed using data on the migration period only (in other words, the residence time preceding a migration period was removed). An eel was considered migratory when the previous and next detection intervals were at an ALS preceding and following that ALS in the migration direction (Verhelst et al., 2018). For two eels, no migration intervals were obtained, although they were detected in the Meuse. Hence, these two eels were removed from the analysis for research questions related to migration speed and temporal behaviour. Note that all but one of the eels detected in the Meuse were released in canal section A, which has an open connection with the river Meuse, and therefore did not encounter shipping locks in the Albert Canal. Hence, eels detected in the Meuse were not taken into account for the analysis of research questions about

Table 1

Number of tagged female eels per stage with their different morphometrics: total length (TL), body weight (BW), horizontal and vertical eye diameters (ED_h and ED_v, respectively) and pectoral fin length (FL). Means ± sd and ranges (between brackets) are indicated.

Stage	Number	TL (mm)	BW (g)	ED _h (mm)	ED _v (mm)	FL (mm)
FIV	1	837	1050	10.80	12.49	24.03
FV	69	821 ± 71 (620 – 957)	1137 ± 306 (522 – 1970)	10.95 ± 1.01 (9.10 – 15.00)	10.40 ± 0.89 (8.10 – 12.13)	40.96 ± 3.94 (31.04 – 51.60)

Table 2

For each research question and subquestion (see 2.5.1–2.5.3 for a detailed description of the subquestions), a different subset of the data was used (the number of detections and percentage of data relative to the total dataset are given) and the statistical test was chosen accordingly.

Research question	Number of detections	Percentage of total dataset	Statistical test
1 Migration success and routes	1,541,521	100 %	None
2 Migration speed and delays			
a. Overall migration speed	326,970	20.1 %	One-way ANOVA with Games-Howell post-hoc test
b. Migration speed canal section	326,970	20.1 %	Kruskal-Wallis test with Dunn's-Test
c. Migration speed shipping lock	20,550	1.3 %	Kruskal-Wallis test
d. Shipping lock delay	269,567	17.5 %	Kruskal-Wallis test
3 Temporal behaviour			
a. Circadian canal section passage pattern	9,768	0.6 %	Nested generalized least squares model
b. Monthly travelled distance	276,697	17.9 %	Poisson generalised linear mixed model

migration speed in shipping locks, shipping lock delays and the circadian pattern. All data analyses were performed with the free R software (Team, 2017).

2.5. Data analysis

2.5.1. Migration success

Eels were categorized in four movement classes: eels migrating towards the Schelde Estuary (S-eels) or towards the Meuse (M-eels), potential migrants towards the Schelde Estuary (S_p -eels) and non-migratory eels (NM-eels) (Fig. 1). Eels were considered of class S when they were last detected at the ALSs in the Schelde Estuary, while M-eels were last detected in the Meuse (Fig. S2). Eels were classified as S_p if they were successively detected in at least three different canal sections, pointing at a directed movement towards the Schelde Estuary; eels detected in two canal sections or less, were classified as NM-eels. In addition, for the S_p - and NM-eels we checked at which detection station they had last been detected.

2.5.2. Migration speed and delays

To analyse if the migrating eels were delayed, we calculated four metrics: 1) the overall migration speed of the S-, M- and S_p -eels (NM-eels were removed from the statistical analysis) as the time needed to cross the distance between the first and last detection. A one-way ANOVA with Welch correction was performed on log-transformed data, since the variances were not homogenous. Following a significant ANOVA result, a Games-Howell post-hoc test for multiple pairwise comparisons was applied (Games and Howell, 1976).

2) We calculated the migration speed per canal section as the time needed to cross that canal section (i.e. the time of the first detection at the ALS at the upstream end of a canal section till the last detection at the ALS at the downstream end of the canal section, divided by the distance of that section). We tested if the migration speed differed according to movement class and canal sections (A–G) by applying a non-parametric Kruskal-Wallis test, since assumptions of normality and homogeneity of variances were not met. If the test proved to be significant, a pairwise test for multiple comparisons of mean rank sums (Dunn's-Test) with Bonferroni correction was applied.

3) For S- and S_p -eels we calculated the time needed to cross a shipping lock complex (i.e. the time between the last detection at an ALS upstream of the shipping lock till the first detection at an ALS downstream of the shipping lock). To test if the calculated time differed over the six shipping lock complexes, a non-parametric Kruskal-Wallis test was performed, since the assumptions of normality and homogeneity of variances were not met.

4) We analysed waiting behaviour near the shipping locks for S- and S_p -eels by calculating the residence times at the ALSs up- and downstream of the shipping locks. A non-parametric Kruskal-Wallis test was performed to test if the residence time upstream of the shipping locks differed significantly with the residence time downstream of the locks. If this proved to be significant, we checked if there was a difference in

residence time between the ALSs located upstream of the shipping locks by means of a non-parametric Kruskal-Wallis test.

2.5.3. Temporal behaviour

Both seasonal and circadian behaviour patterns were analysed. For the seasonal patterns, we calculated the distance travelled per month (i.e. the distance between the first and last detection at an ALS for a particular month) for each eel and within each movement class (i.e. S-, M- and S_p -eels). A nested generalized least squares (GLS) model was applied as the variances were not homogenous, and for each movement class we set the month with the highest average distance as the reference level. To help interpreting these results, we calculated the average monthly water flow and water temperatures of section F for 2015 based on data obtained by the Hydrological Information Center (Fig. S3). Note that environmental data was not available for every canal section. However, water flow and temperature did not differ substantially between the canal sections and over the different years (Hydrological Information Center, pers. comm.).

Regarding the circadian pattern, we analysed when eels migrate from one canal section to another. The number of detection records was summed per circadian phase. Consequently, four different circadian phases were determined and linked to each departure in the dataset: dawn (start of civil twilight to sunrise), day (sunrise to sunset), dusk (sunset to end of civil twilight and night (end of civil twilight to start of civil twilight) (Verhelst et al., 2018). Timestamps of sunset, sunrise and twilight were obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>; coordinates: 50°57'N 5°20'E). To analyse if eels moved between canal sections during the night, a nested (we analysed circadian activity within the different movement classes) Poisson generalised linear mixed model (GLMM) with transmitter ID as random effect was applied. One S_p -eel did not migrate between different canal sections and was therefore not included in the analysis.

3. Results

3.1. Migration success

In total, 24 eels succeeded to leave the system. Equal numbers of silver eels reached the Schelde Estuary and the Meuse ($n = 12$ in both cases); another 15 eels migrated towards the Schelde but did not leave the system during the study period. The majority of the eels ($n = 31$) were classified as non-migratory (Fig. 1a). For both the S_p - and NM-eels, approximately one third was last detected at a detection station downstream of a shipping lock. Another third of the S_p -eels was last detected in section G (the docks of Antwerp). Only a minority was last seen at a side canal of the Albert Canal (i.e. canal Dessel-Kwaadmechelen) (one and two eels for the NM- and S_p -eels, respectively).

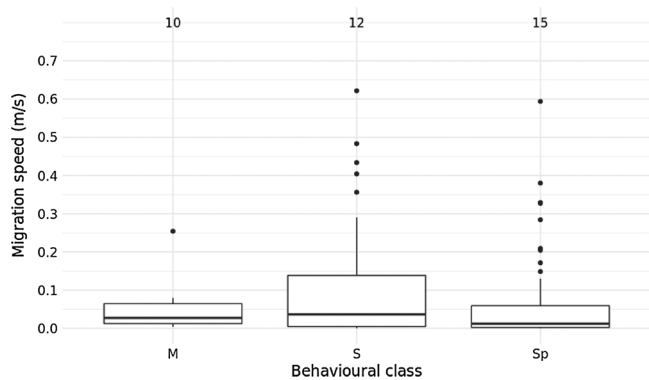


Fig. 2. The migration speeds, calculated within the canal sections, between the different movement classes (M, S_p and S). The number of eels taken into account for each class is indicated above the boxplots.

3.2. Migration speed and delays

The mean overall migration speed (i.e. the speed between the first and last detection) differed significantly between the movement classes (Welch ANOVA, $F = 5.809$, $df = 2.000$, $p < 0.05$) (Fig. S4), being approximately three times higher in M-eels (0.054 m s^{-1}) than in S_p -eels (0.018 m s^{-1}) (Games-Howell post-hoc test, $t = 3.393$, $df = 18.5$, $p < 0.05$) and S-eels (0.012 m s^{-1}) ($t = 2.790$, $df = 15.7$, $p = 0.067$), the latter two not differing from each other ($t = 0.956$, $df = 24.9$, $p = 0.611$).

In contrast, the median migration speeds, calculated within the canal sections, differed not significantly between the different movement classes (KW-test, $\chi^2(2) = 4.1211$, $p = 0.1274$), even though they were threefold higher for S-eels (0.036 m s^{-1}) than for S_p -eels (0.012 m s^{-1}) (Fig. 2).

Median migration speed differed significantly between canal sections (KW-test, $\chi^2(6) = 15.912$, $p = 0.014$), a difference which could be largely attributed to a significantly higher swimming speed in sections E (0.071 m s^{-1} (range: $0.0007\text{--}0.6217 \text{ m s}^{-1}$)) compared to G (0.002 m s^{-1} (range: $0.0013\text{--}0.1487 \text{ m s}^{-1}$)) (Dunn's Test, $t = 3.54$, $p = 0.0082$) (Fig. 3, Table S3). Note that the highest maximum migration speeds were found in section D, E and F (0.5939 m s^{-1} , 0.6217 m s^{-1} and 0.4833 m s^{-1} , respectively).

The median time needed to cross a canal section for S- and S_p -eels was 1.36 h (range: 0.30–435.13 h) and 1.54 h (range: 0.07–671.74 h), respectively, and did not differ significantly between canal sections (KW-test, $\chi^2(5) = 8.9555$, $p > 0.05$ and KW-test, $\chi^2(5) = 10.661$, $p > 0.05$ for S- and S_p -eels, respectively) (Fig. 4).

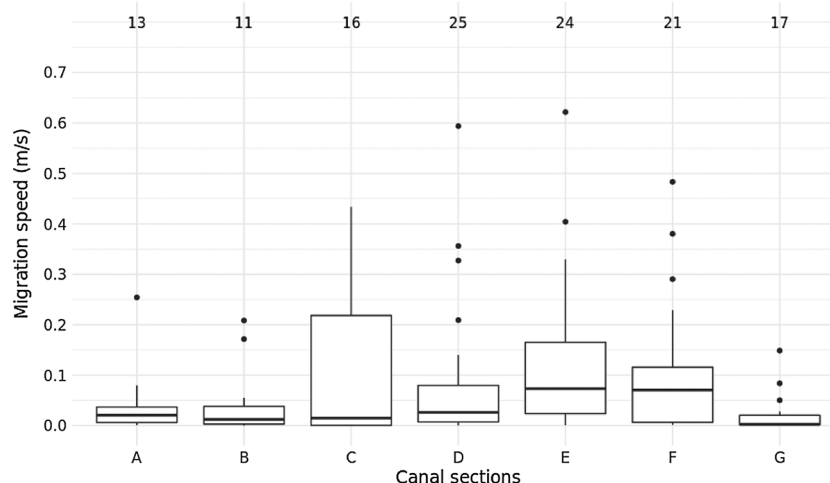


Fig. 3. The migration speeds per canal section (A–G). Numbers of eels detected in each canal section are indicated above the boxplots.

The median residence time for S- and S_p -eels was 74 min (range for S-eels: 0.5–13719 min; range for S_p -eels: 0.4–18739 min) and was twice as high upstream of the shipping locks (KW-test, $\chi^2(1) = 16.328$, $p = 5.328e^{-5}$ and KW-test, $\chi^2(1) = 105.76$, $p < 2.2e^{-16}$, respectively) compared to the downstream located ALSs (Fig. 5). No significant differences in median residence time between the different upstream ALSs were found (KW-test, $\chi^2(5) = 7.1454$, $p > 0.05$) (Fig. S5).

3.3. Temporal behaviour

3.3.1. Temporal patterns in migration distance

In general, all movement classes showed essentially the same monthly pattern with migration distances being significantly longer in autumn and spring (Fig. 6) (for model details, see Table S4). Both S- and M-eels covered the largest distances in October (59 km and 22 km, respectively), while S_p -eels travelled the largest distance in November (31 km). High migration distances of all three classes were also found in May and/or June, whereas the lowest migration distances were found in February (from 2 km for S- and S_p -eels to 8 km for M-eels).

3.3.2. Circadian migration patterns of eels in a shipping canal

For both S- and S_p -eels, the majority of the shipping lock complex passages happened during the night (Fig. 7), but only for the S_p -eels nocturnal passage was significantly higher than passage during daytime (Poisson GLMM, $z = -2.169$; $p = 0.03$; for model details, see Table S5).

4. Discussion

The eels tracked in our study were classified in four different movement classes (S, M, S_p and NM). Although all tagged eels were considered silver eels (FIV and FV) which should be migrating (Durif et al., 2005), the definition of migrating eel should be interpreted with care. Specifically, 31 eels did not show a clear migration pattern and were therefore classified as NM-eels. Even if these eels would show migratory behaviour after our study, they will have been delayed substantially. Since some dispersion events may strongly resemble failed migration attempts, eels may have been classified migratory, while they were actually showing long distance dispersion; it is difficult to distinguish between a failed migration event and a dispersion event.

4.1. Migration success

During the study period, only 34% of the tagged eels left the Albert Canal while another 21% made attempts, indicating that eels face

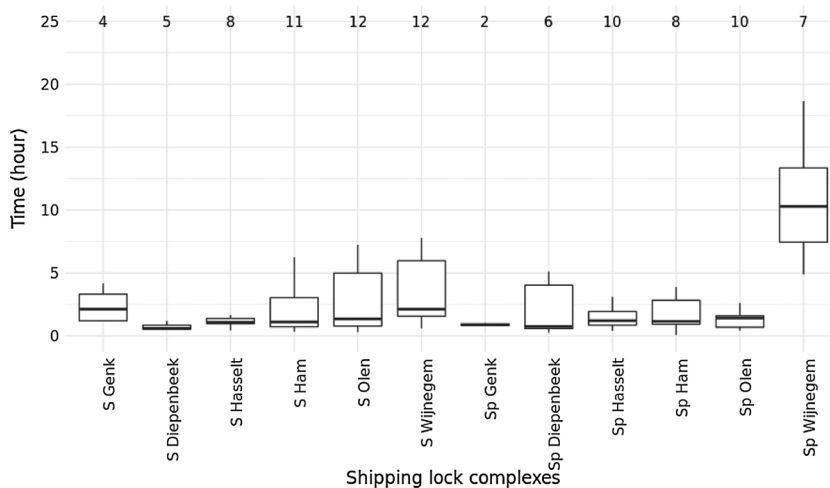


Fig. 4. The time (in hour) needed to cross the six shipping lock complexes (Genk, Diepenbeek, Hasselt, Ham, Olen, Wijnegem) for S- and Sp-eels. Outliers are not shown in the figure.

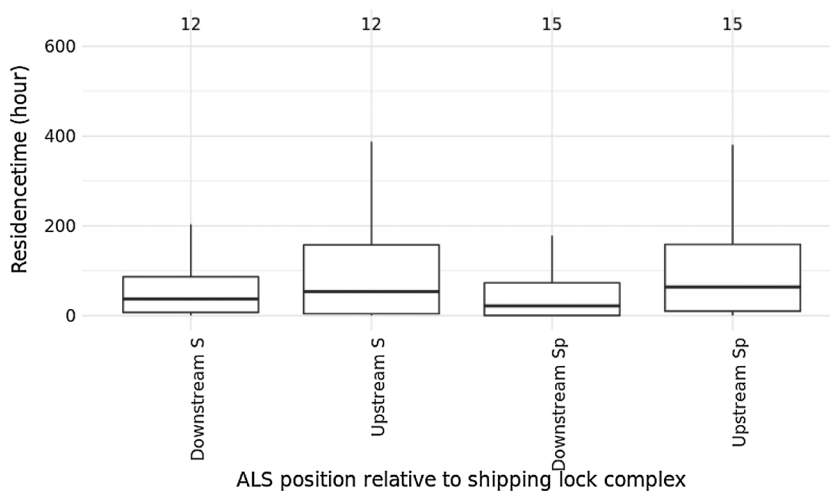


Fig. 5. Residence times at up- and downstream locations of the shipping locks for S- and Sp-eels. Note that outliers are not shown in the figure.

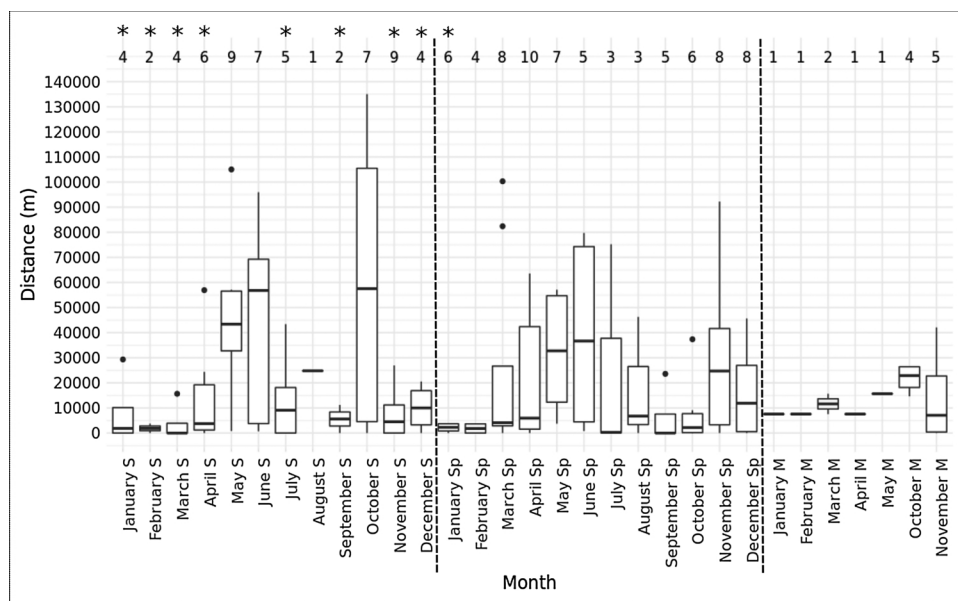


Fig. 6. The monthly migration distances of the three movement classes (S, M and Sp; separated by dashed lines). The number of eels detected during each month are indicated above the boxplots. Asterisks indicate a significant difference ($p < 0.05$) with the reference level (i.e. the month with the highest distance). For S- and M- eels, this was October and for Sp-eels, this was November.

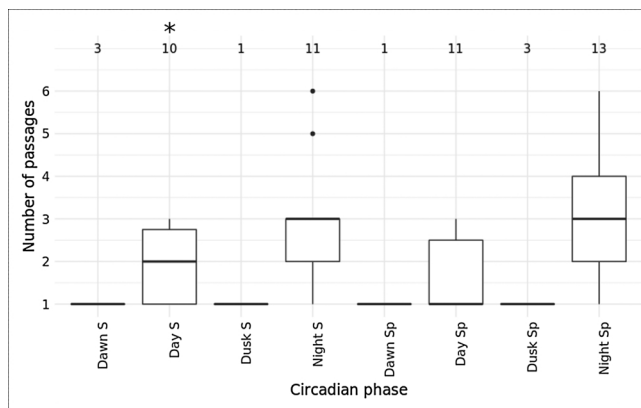


Fig. 7. The number of shipping lock passages during the four different circadian phases (dawn, day, dusk and night) for the movement classes S and S_p . The number of eels taken into account is indicated above the boxplots. The asterisk indicates a significant difference ($p < 0.05$) between diurnal and nocturnal passages for S-eels.

difficulties when migrating through shipping canals. In the Schelde Estuary, for instance, 71% of FIV and FV silver eels tagged at the upper limit of the estuary reached the lower part of the system. This also indicates that the applied method to classify silver eels and surgery did not affect our results substantially (Verhelst et al. unpublished data). In the Loire Estuary, a large number of silver eels (86%) were detected at the most downstream locations as well (Bultel et al., 2014). Since eels depend on flow direction to migrate from freshwater systems into the marine environment (Travade et al., 2010; Verhelst et al., 2018; Vøllestad et al., 1986), the low number of successful migrants may be due to the highly regulated water flow of the Albert Canal. Indeed, the operation of the shipping locks causes frequent and irregular changes in flow direction (i.e. a couple of times per hour). Nonetheless, the majority of the migrating eels followed the net flow direction in the canal and moved towards the Schelde Estuary. A smaller part migrated downstream towards the Meuse, but this may be the consequence of the location where these eels were released: all but one of the M-eels were released in canal section A, which has multiple connections with the River Meuse via the shipping locks in Lanaye and Wizet and the open connection at Monsin. Consequently, eels migrating towards the Meuse encountered fewer or no barriers than S- and S_p -eels, explaining why they were successful in reaching the Meuse. In addition to an irregular water flow and direction, tag expulsion (although normally rare) (Jepsen et al., 2002; Thorstad et al., 2013) and mortality may have been a potential cause of unsuccessful migration of S_p - and NM-eels. Mortality could have occurred as a consequence of predation, fishing or injuries resulting from turbine or sluice passage or ship propellers. Although interference of shipping vessels with the transmitter emissions may be possible, it is difficult to assess because the impact can vary according to the size of the ships and whether they are moving or docked.

The present results are in line with the idea that the silver eel stage is reversible to a semi-yellow stage in freshwater environments when they fail to migrate to the sea (Feunteun et al., 2000; Svedäng and Wickström, 1997). It is unknown what proportion of eels which did not migrate or failed to leave the canal during the study period may still do so in the future. In any case, these eels have been substantially delayed.

4.2. Migration speed and delays

The average migration speed of M-eels (0.054 m s^{-1}) was > three times higher than that of S- and S_p -eels (0.012 m s^{-1} and 0.018 m s^{-1} , respectively) and similar to the overall migration speed in a free flowing tidal river (0.052 m s^{-1} (Bultel et al., 2014)). The higher migration speed of the M-eels is likely explained by the fact that all but

one of them were released in the canal section next to the Meuse, leaving them fewer or no barriers to pass compared to the S- and S_p -eels. Moreover, that canal section has multiple routes to the Meuse, among which an open connection at Monsin. Nonetheless, migration speeds for M-, S- and S_p -eels was substantially lower than average migration speeds in other studies conducted in freshwater systems, i.e. 0.30 m s^{-1} – 1.13 m s^{-1} (Breukelaar et al., 2009; Piper et al., 2017; Verbiest et al., 2012). Average migration speeds may be partly misleading, since it may mask large differences in swim speeds between different habitats. Bultel et al. (2014) observed that eels actually migrate faster when approaching an estuarine environment: their slower migration speed is likely attributed to waiting behaviour in the upper sections of the estuary as the directional speed found in the lower sections was similar to silver eel swim speed in previous studies (i.e. 0.56 m s^{-1}). This contrasts markedly with our results, where migration behaviour was disrupted in the Albert Canal shipping canal: migration speed was low throughout the different canal sections, reaching a minimum in the most downstream section. Since water flow direction in the different sections of the canal changes numerous times per day, we suggest that the slow migration speeds in the canal are likely caused by disorientation due to a lack of a consistent unidirectional water flow. The relatively higher maximum migration speeds in sections D, E and F of the canal may then be explained by the more frequent operation of their respective shipping locks. Specifically, in Ham, Olen and Wijnegem, more ships were transported over those three shipping locks, but note that multiple ships per lock could be transported. In contrast, the slowest migration speed in section G of the Albert Canal can be attributed to the distribution of the water mass over the docks of Antwerp, resulting in a decrease of water flow (Hydrological Information Center, pers. comm.). For their orientation in this section, eels may depend on currents caused by tidal shipping lock operation, which can only be detected in the vicinity of the locks. In this context, it is striking that one third of the S_p -eels reached section G, but were never detected in the Schelde Estuary. It is possible that the dynamic environment of the estuary impairs the detection probability (Reubens et al., 2018), yet 71% of the silver eels tagged in the Schelde Estuary were detected in the lower part (Verhelst et al. unpublished data). A faster and more unidirectional movement towards the sea could be facilitated by the detection of olfactory cues in the estuarine and marine environment (Barbin et al., 1998). As tidal shipping locks (but also non-tidal shipping locks further upstream) prevent the intrusion of marine water and its migration cues for eels, this may also have an impact on the eels' delay and slower swim speeds in shipping canals. Indeed, once inside the Schelde Estuary, S-eels migrated at an average speed of 0.74 m s^{-1} (unpublished data).

Our study also demonstrates that eels were significantly delayed upstream of shipping locks and it took them relatively long to pass these locks. This indicates that the locks may act as a direct migration barrier for downstream migrating eels. Pumping stations and hydropower plants have been reported before as migration barriers for migrating eels (Buyse et al., 2015; Verhelst et al., 2018; Winter et al., 2006) and several mitigation measures have been proposed (e.g. acoustic fences (Sand et al., 2000), bar racks (Russon et al., 2010), fish friendly adaptations (Hecker and Cook, 2005) and fish passes (Clay, 1994)). Shipping locks have only been reported sporadically as migration barriers for upstream migrating fish (Buyse et al., 2008; Klinge, 1994). Yet, American eels (*A. rostrata* Lesueur) have been shown to use shipping locks to migrate upstream (Verdon and Desrochers, 2003). Our study is therefore the first to demonstrate that they may also affect downstream fish migration. Weirs, which can be opened during an excess of water, can provide a solution for this problem; however, their efficiency may be very low, as was the case for the Schelde river in Belgium (Buyse et al., 2008). The shipping locks in the Albert Canal don't have weirs. Hence, adequate management measures such as stimulating gravitational flow or fish passes are necessary to facilitate eel migration over shipping locks.

Encountering substantial delays, eels may be more prone to diseases, predation and fishing, and consequently, mortality (Acou et al., 2008; Marmulla, 2001; Sjöberg et al., 2017; Verhelst et al., 2018). Delays may also cause eels not reaching the spawning grounds on time. Although being an anadromous species, for Sockeye salmon (*Oncorhynchus nerka* Walbaum) it has been shown that spawning success was correlated with the date of arrival (Burnett et al., 2017). Nonetheless, Righton et al. (2016) hypothesized that the eels' migration may be more flexible than thought. Also, it is unknown if obstructed migratory fish encounter an increased state of physiological stress or what the impact may be on the fish' fitness. As such, knowledge on fish migration delays needs further research and is currently insufficient to provide proper management measures (Silva et al., 2017).

4.3. Temporal behaviour

4.3.1. Temporal patterns in migration distance

There is scientific consensus that European silver eels generally migrate in autumn, although migration peaks in spring have occasionally been observed (Aarestrup et al., 2008; Sandlund et al., 2017; Verbiest et al., 2012). In this study, the successful migrants (S- and M-eels) migrated the longest distances in autumn, but substantial large distances were also travelled in spring. S_p-eels even bridged longer distances in spring than autumn. For these S_p eels, it is plausible that the longer travelled distances during both autumn and spring months are linked with migration behaviour. During spring and autumn, the average water temperature range of the Albert Canal (quantified by a temperature measurement in section F in 2015) was 7.5 °C–17.10 °C and 11.4 °C–18.6 °C, respectively, which is approximately within the temperature window during which Vøllestad et al. (1986) (i.e. 4 °C–18 °C) found the majority of silver eels migrating downstream in the river Imsa, Norway. In addition, although the average monthly water flow was low, peaks were found in May and October. This may have triggered or even guided seaward migration of silver eels in our study. It is unlikely that water flow alone could trigger migration, since another water flow peak in February did not elicit migration, perhaps because the water temperature was too low (i.e. 4.3 °C) (Vøllestad et al., 1986). As such, an interaction between water flow and other triggers like water temperature may be relevant (Buysse et al., 2015). Spring migration, then, might be the result of insufficient migration triggers during the preceding autumn (Westin, 1990), or an insufficient body condition (Aarestrup et al., 2008).

4.3.2. Circadian migration patterns of eels in a shipping canal

Although S- and S_p-eels showed a delayed and potentially dis-oriented migration behaviour, they still primarily moved from one canal section to the next at night, which is in line with the eel's natural behaviour pattern reported in previous studies (Travade et al., 2010; Vøllestad et al., 1986). The low number of passages during dusk and dawn may be attributed by the short duration time of those circadian phases. Nocturnal migration is likely a predator-avoidance mechanism in the canal, since turbidity in the canal is low and large numbers of cormorants (*Phalacrocorax carbo* L.) frequently hunt in the area, which have been shown to predate on eels (Ibbotson et al., 2006). This means that although sluices are primarily operated during daytime, eels are likely to pass them at night. Consequently, potential management actions may be most effective at night.

4.4. Implications for management

To our knowledge, this study is the first to describe silver eel migration behaviour in a shipping canal (here the Albert Canal). Only a small part of the silver eels was able to leave the Albert Canal during a study period of 27 months and their migration speed was typically very low, probably as a result of the regulated water flow and presence of shipping locks in the canal. This implies that eels may get trapped or be

slowed down substantially inside shipping canals, making them more prone to predation and diseases. Hence, heavily regulated shipping canals are most likely an unsuitable migration route for European eel. However, migration through anthropogenic canals may be the best available option if canals can provide a shortcut for migrating eels or if the alternative route is more hazardous (e.g. the Meuse contains several hydropower plants, resulting in substantial mortality rates of silver eels (Verbiest et al., 2012; Winter et al., 2006)). Therefore, we propose several management actions to reduce migration delays. First, an increased gravitational flow in the canal could provide a better cue for eels to find their way downstream. Based on the temporal results of this study, this measurement may be most effective at night and during spring and autumn. A second option would be to construct fish passes to overcome shipping locks. For instance, it has been shown that eels can make use of undershot sluice gates at small-scale hydropower plants (Egg et al., 2017). However, efficient downstream fish passes are scarce and there is an urgent need for improved knowledge on this issue. The results of the present study also have repercussions for the implementation of stocking of glass eels as part of the eel management plan imposed by the European Eel Regulation (in order to recover the population, the European Union adopted a Council Regulation (European Eel Regulation; EC no. 1100/2007)). For instance, in 2017, 21% (i.e. 18 out of 85 kg) of the glass eels imported in Flanders for seeding purposes were stocked in the Albert Canal. Our study strongly indicates that only 34% of these eels will successfully migrate out of the system and hence potentially contribute to the population. Therefore, unless the passability for eels is improved, we suggest to reduce, or even stop stocking glass eels in large shipping canals and apply stockage in systems where the chances to reach the sea are sufficiently high, such as polder systems which are mainly dewatered via gravitational flow through tidal sluices or via fish friendly pumps.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2018.05.013>.

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