Chapter 6

Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management

6.1   Abstract

Connectivity between freshwater habitats and marine areas is heavily obstructed by anthropogenic structures (e.g. weirs, pumping stations, sluices...), leading to a high pressure on diadromous fish populations. A better understanding of fish migration behaviour in relation to these barriers is needed to take proper mitigation actions. We investigated the impact of migration barriers on downstream migrating European eel by tracking 50 acoustically tagged eels between July 2012 and March 2015 in a Belgian polder area. The study area was selected due to the presence of a wide range of migration barriers, such as two pumping stations, a weir and tidal sluices. These structures regulate the water level, resulting in discontinuous flow conditions. The results showed that migration was primarily nocturnal and discharge appeared to be the main trigger for migration in the polder. We also observed substantial delays and exploratory behaviour near barriers. Delays can have a serious impact on eels since their energy resources are limited for a successful trans-Atlantic migration. In addition, delays and exploratory behaviour can also increase predation and disease risk. The obtained knowledge can contribute to efficient management such as improved fish passage and guidance solutions.

6.2   Introduction

Worldwide, water levels of freshwater systems are controlled by structures such as pumping stations, weirs, dams and sluices. These structures hamper the movement of aquatic organisms, especially diadromous fish (Baumgart-

ner et al., 2009; Lassalle et al., 2009; Thompson et al., 2011). Polders are one particular ecosystem type where the role of barriers is crucial. A polder is an anthropogenic system where water is maintained at a lower level than outside the polder by pumping stations and weirs, which are two types of barriers that can negatively influence migration of both diadromous and potamodromous fish species (Buysse et al., 2014; Falke and Gido, 2006). Due to climate change, the associated rising sea level and a growing human population, pressure on dewatering systems is likely to intensify in the future, resulting in the development of more polders with their accompanying migration barriers (Beatty et al., 2014; Hannah et al., 2007; Hermoso and Clavero, 2011; Maceda-Veiga, 2013). In recent years, the importance of aquatic habitat connectivity has been recognized and is being addressed in management practices, resulting in developments to improve fish migration. As such, fish-friendly pump adaptations and fish passes have been developed to reduce mortality (Buysse et al., 2015; Clay, 1994). However, the efficacy of many presumably fish-friendly adaptations remains to be established (Boggs et al., 2004; Gowans et al., 1999; Keefer et al., 2004; Marmulla, 2001; Roscoe and Hinch, 2010). Next to mortality effects, pumping stations may also affect migration behaviour, resulting in delays or even migration stops. Consequently, delays or migration stops may result in a higher predation risk or reduced fitness and therefore contribute to the decline of a species (Marmulla, 2001).

In this study, we selected the European eel as a model species for downstream migrating fish encountering migration barriers. We used acoustic telemetry to reveal migration routes and link the detection data with biotic and abiotic data, thus providing knowledge about what variables trigger migration and whether eels encounter delays near barriers. This information can be

implemented in management measures to improve silver eel escapement rates.

Downstream migrating European eels were tracked from a polder area in Flanders (Belgium) into the Schelde Estuary (SE, The Netherlands). We selected the study area due to the presence of a wide range of migration barriers, such as two pumping stations (an Archimedes screw pumping station (APS) and a propeller pumping station), a weir and tidal sluices. Previous research showed silver eel mortality rates up to 19% at that particular APS (Buysse et al., 2015). We assessed five research questions related to downstream eel migration behaviour: (1) do eels take different migration routes; (2) does eel behaviour change significantly in the vicinity of barriers; (3) does migration follow a circadian pattern; (4) does migration start at a specific point in time; and (5) do environmental variables influence migration? The results of this study will support river and/or polder managers to facilitate downstream eel migration and hence contribute to the conservation of the eel stock.

6.3   Methods

6.3.1   Study area

The study area is comprised of three subareas, which are all part of the Schelde river basin: a polder (Flanders, Belgium), the Braakman pond (The Netherlands) and the SE (The Netherlands) (Fig. 6.1). The polder covers an area of about 200 km^2 and is drained via the Leopold Canal (LC). The LC is an unnavigable waterway of approximately 46 km long, 10-20 metres wide and one to four metres deep. It extends from Heist at the Belgian coast to Boekhoute.

Generally, it is a stagnant water system, but during dewatering, it can have a slow flowing current (on average 1.21 m^3 s^{-1} during this study period). Within the polder area, the LC connects different habitats such as ponds and small and large polder ditches with variable width and depth (Table 6.1). The Braakman is a brackish pond in The Netherlands, connected to the polder area in Belgium, with a mean chloride concentration of 3265 mg L^{-1} (range 580-8200 mg L^{-1}), a surface of approximately 2.05 km^2 and a depth up to 14 m. It is located at approximately one third of the SE (starting from the estuarine mouth) and functions as a transition area between the freshwater polder and the polyhaline zone of the SE. The latter is the lowest part of the Schelde river and leads to the North Sea. The funnel shaped estuary is approximately 55 km long with a variable width between two and eight km. It is characterized by intensive tidal action and strong currents and contains many sand banks, mudflats and salt marshes, resulting in a high turbidity.
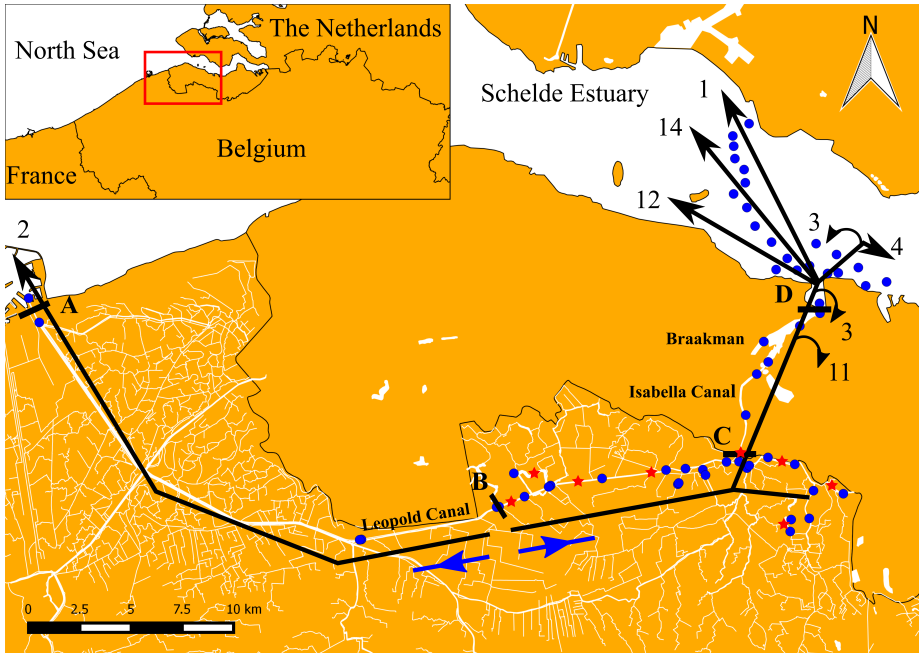
Figure 6.1: Study area with the Leopold Canal and its network of connected waterways (Belgium), the Isabella Canal, the Braakman pond (The Netherlands) and the Schelde Estuary (The Netherlands). ALSs are indicated as blue dots and catch-release locations as red asterisks. The four migration barriers within the study area are indicated with a black bar and bold letter: (A) the tidal sluice in Zeebrugge, (B) the low-head weir in Sint-Laureins, (C) the Archimedes Pumping station in Boekhoute, and (D) the tidal sluice with propeller pumps between the Braakman pond and the Schelde Estuary. The main current direction at each side of the weir is indicated with a blue arrow, while the migration routes of the 50 tagged eels are presented by black arrows. The numbers reflect the number of eels taking this specific migration route in the present study.

To dewater the system during high precipitation, water is pumped from the LC (1.40 m above sea level (a.s.l.)) into the Braakman pond (1.97 m a.s.l. in summer, 1.42 m a.s.l. in winter) via an APS in the Isabella Canal (Boekhoute), and flows gravitationally into the SE via a tidal sluice (Fig. 6.1). In case gravitational flow is insufficient to dewater the system, propeller pumps in the tidal sluice are used. In cases of exceptionally high precipitation, the polder system can also be dewatered towards Zeebrugge by lowering a weir in the LC (Sint-Laureins) (Fig. 6.1).

The APS has de Wit modifications to reduce fish mortality during passage, and along the APS a de Wit fishway is present (Buysse et al., 2015) (Fig. S1). The propeller pumps in the tidal sluice at the border between the Braakman pond and the SE do not have fish-friendly adaptations. In the western direction, connectivity from the polder area to marine areas is blocked by a low-head weir in Sint-Laureins and a tidal sluice in Heist at the freshwater - sea border.

Table 6.1: Depth and width of the different habitat types in the study area.

Type	Depth (m)	Width (m)
Canal	1-4	10-20
Polder pond	0.5-10	15-150
Large polder waterway	0.5-2	5-10
Small polder waterway	0.2 - 1	0.5-5
Braakman pond	1-14	200-750
Schelde Estuary	1-38	2000-8000

6.3.2   Tagging procedure

During the summer and autumn of 2012, 566 eels were caught in the polder and
at the APS. From July to August 2012, 526 eels were caught with double fyke
nets, which were placed in the LC, ponds and large polder ditches. At each loc-
ation, four double fyke nets were placed and emptied during four consecutive
days. Between the 5th and 16th of October 2012, another 40 eels were caught
with two fyke nets attached to the outlet of two pumps of the APS during a sur-
vey to study eel mortality after passage (Buysse et al., 2015). Total length (TL,
to the nearest mm) and body weight (W, to the nearest g) were measured and
50 eels (26 eels in the polder and 24 at the APS) were selected as large enough
to tag with a mean length of 684 mm $\pm$ 75.76 mm (range 556 mm - 874 mm)
and mean weight of 683 g $\pm$ 260.23 g (range 381 g - 1615 g). In this study, only
females were tagged, since males are smaller than the minimum size handled
in this study ($<$ 450 mm (Durif et al., 2005)). Also note that the eels caught at
the APS were checked for deformities and lesions prior to tagging.

In 2012, 46 eels were tagged with V13-1L coded acoustic transmitters (13
$\times$ 36 mm, weight in air 11 g, random delay between 80 s and 160 s, life time
1116 days, frequency 69 Hz) and four with V7-4L coded acoustic transmitters
(7 $\times$ 22.5 mm, weight in air 1.8 g, random delay between 45 s and 95 s, life time
157 days, frequency 69 Hz) from VEMCO Ltd (Canada). After anaesthetising
the eels with 0.3 ml L^{-1} clove oil, tags were implanted according to Baras and
Jeandrain (Baras and Jeandrain, 1998). After recovery in a quarantine reservoir,
eels were released at their catch location.

6.3.3 Acoustic network

An acoustic network of 56 ALSs (VR2W, VEMCO Ltd, Canada) was deployed in the harbour of Zeebrugge (n = 1), the polder area (n = 27), the Braakman pond (n = 6) and the SE (n = 22) (Fig. 6.1). The two ALSs in the Isabella Canal were considered part of the Braakman pond and detection data were handled accordingly. ALSs were moored at strategic locations to maximise the probability of detection: up- and downstream of each migration barrier, an ALS was deployed. Furthermore, ALSs were placed at each entry of a pond or polder waterway into the LC, while a uniformly distributed pattern in the Braakman pond was achieved. At the mouth of the Braakman into the SE, a double semi-circular array of ALSs was deployed in the SE, combined with one array stretching from the left to the right bank of the estuary. In the polder area and the Braakman pond, the stations were moored at the bank with weights and a small buoy. In this way, the hydrophone had an upward direction in the water column. In the SE, ALSs were moored at marine buoys, attached to a three-metre long chain with a weight at the end for stability. This resulted in downward directed hydrophones.

6.3.4 Data processing

Eels were tracked between 18th July 2012 and 25th March 2015 resulting in a dataset with 127475 detections. To reduce the dataset, the detections were accumulated for each eel at each ALS, resulting in detection intervals with arrival and departure times (VEMCO Users Environment software program, VEMCO Ltd, Canada). A one-hour absence threshold was applied: when an eel was

detected within an hour at the same ALS as the previous detection, it was considered within the same detection interval. If not, the detection was assigned to a new interval. Further, between an arrival and departure within the same detection interval, the number of detections and the residence time were calculated (Verhelst et al., 2018d).

Of the 50 tagged eels, 18 showed resident behaviour followed by downstream migration. As this study focused on downstream migration behaviour only, the data records with resident behaviour prior to downstream migration were removed from the dataset. To determine a sharp border between resident and downstream migration behaviour, a trajectory analysis was applied to each individual eel (Verhelst et al., 2018d). We used the method of Lavielle from the adehabitatLT package in R to divide an animal's trajectory in a resident and a migratory phase (Calenge, 2006) (Fig. S2). This method does not require discretisation in time and is based on residence time: it partitions movement segments based on homogeneous mean residence times (Lavielle, 1999, 2005; Barraquand and Benhamou, 2008).

6.3.5   Data analysis

In this study, different research questions were tackled with different data analyses. To determine the different migration routes and the impact of the migration barriers on eel behaviour, exploratory behaviour (i.e. non-directional movement) was included along with migration behaviour. To analyse the circadian pattern, when eels start to migrate, and what environmental variables influence migration, only downstream migration records were taken into account (hereafter called 'migration records'). After chronologically ordering the

data, a record was considered a migration record if the previous and next detection were at an ALS up- and downstream, respectively, or if the previous two detections were at two subsequent upstream located ALSs. For each analysis, assumptions were checked and data exploration was conducted following the protocol of Zuur et al. (2010).

Migration routes and impact of barriers on downstream migration behaviour

Recently, network-based tools have proven to be helpful in visualising the extensive datasets obtained by acoustic telemetry (Jacoby and Freeman, 2016). To reveal migration routes of individual eels, a unipartite network (i.e. 'one-mode' networks, see Jacoby and Freeman (2016) for more details) was created for each eel, consisting of nodes and edges. Nodes represented the ALSs with the total residence time of an eel at that ALS and edges the movements between them. The effect of barriers on migration behaviour was analysed in two ways (i.e. delays and exploratory behaviour) and only for the main migration route. For each node, the distance till the first downstream located migration barrier was calculated via QGIS (as there was no physical migration barrier downstream the SE ALSs, these records were excluded from the analysis of delays and of exploratory behaviour). For both delay and exploratory behaviour analysis, a Generalised Linear Mixed Model (GLMM) was applied with transmitter ID as random effect (i.e. as a proxy for individual variability). For analysing the delays, the total residence time per eel at each ALS was used as the fixed effect, while the total number of arrivals per eel at each ALS was applied as a fixed effect for the exploratory behaviour analysis. The distances between the nodes and the barriers were considered the fixed effect in both models. The residence

time data were continuous, consequently, a Gaussian GLMM with identity link was applied (Zuur et al., 2009). For exploratory behaviour analysis, we chose to perform a negative Binomial GLMM with log link, since this model is more robust against overdispersion compared to a Poisson GLMM (Zuur et al., 2009). We used the 'lme4' and 'lmerTest' package (Bates et al., 2014) in R (R Development Core Team 2017) to create the GLMMs and the 'blmeco' package to check the models for overdispersion: if the scale parameter was between 0.75 and 1.4, overdispersion was considered absent. The packages 'igraph', 'lubridate', 'matrix' and 'plyr' were used to represent the data as unipartite networks.

Circadian pattern

The number of migration records was summed per circadian phase. Consequently, four different circadian phases were determined and linked to each record in the dataset: dawn (start of civil twilight (i.e. when the geometric centre of the sun is six degrees below the horizon in the morning) to sunrise), day (sunrise to sunset), dusk (sunset to end of civil twilight (i.e. when the geometric centre of the sun is six degrees below the horizon in the evening) and night (end of civil twilight to start of civil twilight). 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: N51°16′ E3°43′).

Onset of migration

The onset of migration was simply determined as the month of the first migration record for each eel.

Environmental triggers of migration

Environmental data

To examine environmental triggers of downstream migratory behaviour, environmental variables were linked to the departure times per subarea (polder, Braakman pond and SE) in the dataset (Table S1). Environmental variables were selected based on data availability and on previous research (e.g. McCleave and Arnold (1999); Tesch (2003); Bultel et al. (2014); Buysse et al. (2015). The 11 continuous variables were precipitation (mm), the APS and propeller pumps discharge ($m^3\ s^{-1}$), water temperature (°C) from the polder system and the SE, chloride concentration of the Braakman pond and the SE (mg L^{-1}), current velocity (cm s^{-1}) and direction (degrees) in the SE, day length (min) and air pressure (hPa). One variable was categorical: the gravitational flow at the tidal barrier between the Braakman pond and the SE (0: no gravitational flow; 1: gravitational flow). Pumping discharge, precipitation, water temperature and air pressure data were measured daily and obtained from the Flemish Environment Agency (www.waterinfo.be). Pumping discharge data were obtained daily by recordings from a metre at the APS, while water temperature and air pressure were measured near the APS (coordinates: N51°16′15.8″ N E3°42′43.6″). Precipitation data was the average value over a large part of the study area (Fig. S3). There were two gaps of a couple of months in the water temperature data. To fill these gaps, data from a nearby canal were used (Ede canal; coordinates: N51°12′15.4″ E3°26′22.3″). Both canals have a similar morphology and discharge regime, and showed a high correlation (0.98) in temperature regime. However, water temperature data for both canals differed significantly (two-sample t-test, t = 2.98, $p < 0.05$). Therefore, we applied a lin-

ear regression to obtain the relationship between the two datasets and fill in the gaps of the water temperature data of the studied polder area with the modified values of the nearby canal:

$$\text{water temperature LC} = 1.161941 \times \text{water temperature Ede canal} - 0.780858$$

Water level, pumping discharge, water temperature and conductivity data for the Braakman pond were obtained from the 'Scheldestromen Water Board'. Water levels up- and downstream of the tidal barrier were measured every 15 min; based on those data, it could be qualitatively determined when gravitational flow took place at the Braakman outflow (Fig. 6.1). As such, the variable gravitational flow was binomial: gravitational flow or no gravitational flow. However, during periods of high precipitation and no gravitational flow, pumps in the tidal barrier were activated to dewater the system (i.e. Braakman discharge; measured every 15 min). Conductivity data were measured once per month. These data were interpolated to link conductivity to the departure times of the eels. Water temperature of the Braakman was also logged once per month by the Scheldestromen Water Board. As the water from the upstream located polder flows into the Braakman, water temperature of the Braakman was highly similar to the water temperature of the LC: both datasets showed a high correlation (cor = 0.99) and a t-test indicated no significant difference (twosample t-test, t = 0.22, p = 0.83).

As such, the water temperature data of the polder was used for the analysis of downstream eel behaviour in the Braakman, because it has a higher resolu-

tion. The same air pressure and precipitation data of the polder area were used for the Braakman pond as the Braakman is located next to, and connected to the polder area.

Conductivity and water temperature of the SE were obtained from Rijkswaterstaat. These data were measured every 10 min near the Braakman outlet (coordinates: N51°20′38.8″ E3°49′07.1″). Rijkswaterstaat also provided modelled data, with a 10-min accuracy, of flow velocity in the proximity of the ALS array (coordinates: N51°23′53.7″ E3°43′15.7″). The same air pressure and precipitation data for the polder area were used for the SE.

The variable 'day length' was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (http: //aa.usno.navy.mil/index.php; coordinates: N51°16′ E3°43′). In addition to the five environmental variables, one categorical explanatory variable was included, namely catch-release location habitat type (canal, polder ditch and pond).

Model development

For each subarea (polder, Braakman pond and SE), a model was developed with a different number of eels due to tagging locations and losses: the polder model (n = 25), the Braakman model (n = 48) and the SE model (n = 34) (Fig. S4).

For each model, the data was checked for outliers and homogeneity of variances. Thereafter, a collinearity analysis was conducted on the continuous variables (Zuur et al., 2010). For both the polder and Braakman pond model, a strong correlation (> 0.70) was found between water temperature and day

length; hence, the latter was removed from further analysis (Table S2 and Table S3) (Dormann et al., 2013). We chose to remove day length since previous research found that water temperature may play a role (Vøllestad et al., 1986). For the SE model, current direction and current strength were strongly correlated (Table S4). We chose to remove current strength, since we wanted to test for selective tidal stream transport, which is merely based on current direction (McCleave and Arnold, 1999). As such, for each subarea, different variables were selected for implementation in the GLMM (Table S1).

To determine what variables significantly contributed to silver eel migration, Random Forests (Hadderingh et al., 1999) and a Generalised Linear Mixed Model (GLMM) were applied. Both techniques use a different approach (classification versus regression, respectively), and results between the different models were compared. For each model, the response variable 'migration' was binomial: a record was considered migratory or not. To give an equal weight to migration and non-migration behaviour, bootstrapping was applied for the Braakman model to obtain the same number of records with and without migration (Mouton et al., 2010).

Random Forests (Hadderingh et al., 1999) is a widely applied machine learning technique (Breiman, 2001; Mouton et al., 2011a). Several studies have shown that RF often outperforms other state-of-the-art modelling techniques such as decision trees or support vector machines (Cutler et al., 2007; Fukuda et al., 2013). An important feature of RF is the availability of some measures to assess the importance of each variable and to detect outliers. In this study, the mean decrease in accuracy was calculated as an importance measure: after running the model, each variable obtains a value which represents the drop in

model accuracy when that particular variable is excluded from the model (i.e. the proportion of observations that will be wrongly classified if the variable is excluded). A more detailed description of the concept of RF can be found in Appendix A. We used the 'randomForest' package (Liaw and Wiener, 2002) of the R environment (R Development Core Team 2017), in which the default settings were applied.

GLMM, an extension of linear regression models, is a valuable technique to analyse relationships between explanatory variables and a response variable (Mouton et al., 2011a; Verhelst et al., 2016; Zuur et al., 2009). In this study, a binomial GLMM with a logit link was applied to assess the effects of the explanatory variables on silver eel migration. In addition, the significance of three random effects in the models was tested: year, month and tag ID, the latter as a proxy for individual variability. For each full model (i.e. the model with all explanatory variables), all possible combinations with the random effects were applied, including the single random effects. The model with the lowest Akaike Information Criterion (AIC) was selected to apply a stepwise backward model selection, again based on AIC: the polder model with the random effects 'month' and 'tag ID' had the lowest AIC (410.92), while the Braakman model with only 'month' as a random effect had the lowest AIC (659.03). For the SE, the model with 'tag ID' had the lowest AIC (378.61).

The kappa statistic (κ) was calculated to evaluate the RF and final GLMM models; the kappa index ranges between -1 and 1 (Cohen, 1960; Goethals et al., 2007; Mouton et al., 2010). We used the 'lme4' package (Bates et al., 2014) of the R environment (Team 2015) to create the GLMMs and the 'blmeco' package to check the models for overdispersion: if the scale parameter is between 0.75

and 1.4, overdispersion is considered absent.

6.4   Results

6.4.1   Migration routes

Two migration routes were found: 48 eels (96%) migrated north via the APS in Boekhoute, while two (4%) migrated westward and reached the North Sea in Zeebrugge (Fig. 6.1, Fig. 6.2, Appendix B). The 48 eels arrived in the Braakman between summer (20th July) and winter (12th January). Of these, 37 (77%) reached the SE via the tidal sluice, while 11 eels (23%) were not detected outside the Braakman pond. Their detection signal was lost on average after 105 days (range 0-579 days). Ten of these eels had been tagged in the polder area, while one was tagged when intercepted in the APS, but swam upstream via the gravitational sluice after tagging and then migrated downstream through the APS into the Braakman. Notably, 11 (44%) of the 25 eels migrating through the APS (24 tagged in the polder and one tagged eel at the APS which swam upstream upon tagging) remained in the Braakman (Fig. S3).
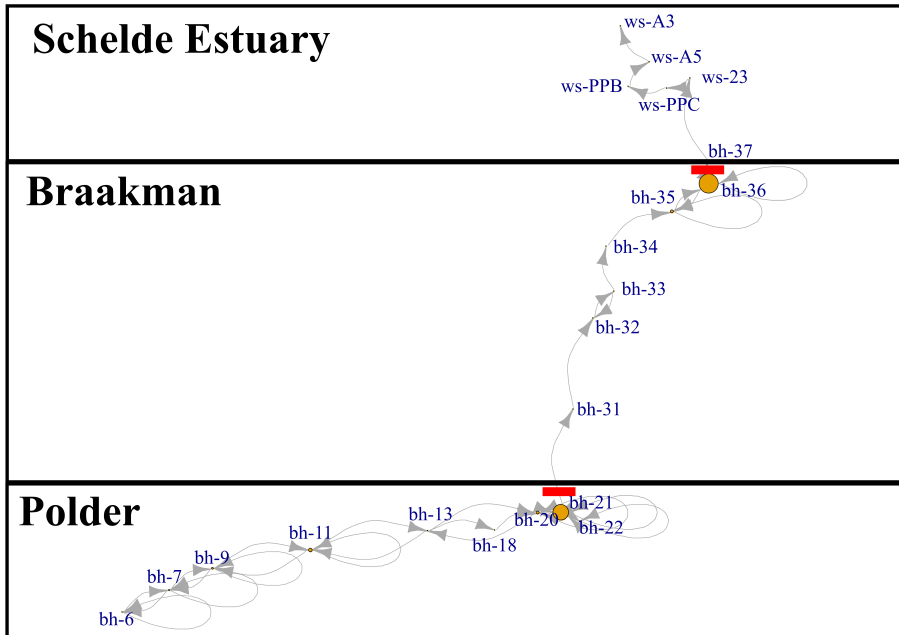
Figure 6.2: Unipartite network visualization of the trajectory of eel 29226. Each node represents an ALS (indicated by a yellow sphere with a location name) and the edges connecting the nodes are the movement patterns. The size of the node represents the total residence time for an eel at that ALS. The migration barriers are indicated with a red bar: in the polder the APS at Boekhoute and in the Braakman the tidal sluice with propeller pumps. Note that the thickness of the arrows does not indicate the number of movements between different nodes.

The eels detected in the SE departed from the Braakman between autumn (October 15th) and winter (January 20th), yielding a mean residence time of 26 days (0-102 days). None of them migrated from the Braakman into the SE

when the propeller pumps were active. In the SE, three of the 37 eels (8%) were detected only at the first ALS downstream of the tidal sluice in the Braakman, 27 (73%) migrated westward towards the North Sea, while seven eels (19%) swam eastward. The 27 westward migrating eels were detected on the array stretching from the left to the right bank of the estuary and revealed three different route choices in the SE (Fig. 6.1: 12 migrated along the left (southern) bank, 14 through the middle of the estuary and one swam across the estuary and then followed the right (northern) bank. Of the seven eastward migrating eels, three changed their swimming direction and were last detected near the mouth of the Braakman, indicating a westward migration direction. Together with the two eels detected in Zeebrugge, a total of 29 (58%) downstream migrating eels swam to the North Sea during this study.

6.4.2   Impact of barriers on downstream migration behaviour

Based on the individual unipartite network visualisations and statistical analyses, a significant higher residence time (Gaussian GLMM, estimated coefficient = -0.8246 $\pm$ 0.1169, t value = -7.055, p = 1.09e-22) and number of arrivals (negative binomial GLMM, estimated coefficient = -0.70723 $\pm$ 0.06327, z value = -11.18, $p < $ 2e-16) was observed near the migration barriers (APS and tidal sluice) (Fig. 6.2, Fig. 6.3, Appendix B).
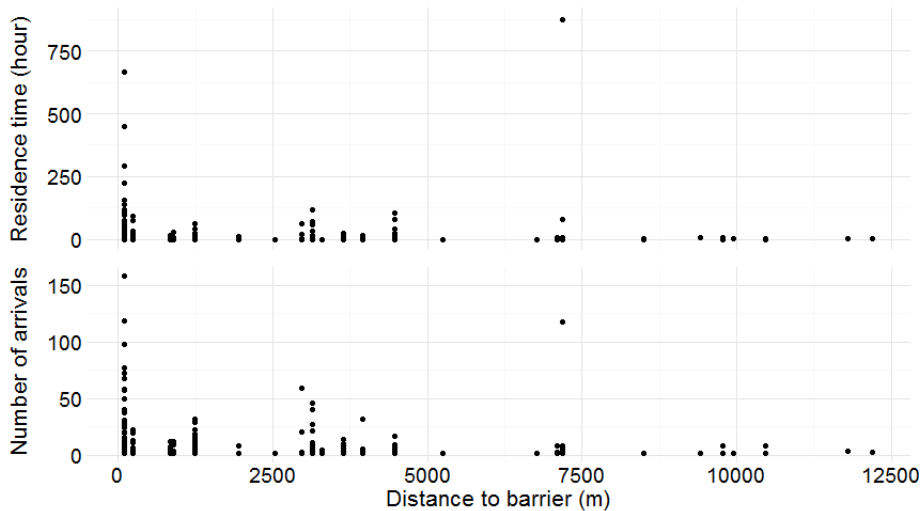
Figure 6.3: Residence time (upper) and number of arrivals (lower) as a function of upstream distance to a barrier. Both residence time and number of arrivals increased as the upstream distance to migration barriers decreased.

For the 25 eels migrating over the APS, the mean residence time at the ALS upstream of the APS was almost fourfold (12.48 days $\pm$ 22.984 days (range 0.01-91.74 days)) the mean residence time at the other ALSs located in the polder (3.13 days $\pm$ 7.982 days (range 0.01-61.6 days)). The same trend was found for the 48 eels reaching the Braakman. The mean residence time at the ALS upstream of the tidal sluice was over eight times as high (84.47 days $\pm$ 130.058 days (range 0.01-667.07 days)) compared to the other ALSs located in the Braakman (10.44 days $\pm$ 63.594 days (range 0.01-875.26 days)). Once in the SE, the mean residence time of the 37 eels (8.05 days $\pm$ 84.756 days (range 0.01-1141.22 days)) was intermediate to the mean residence times found at the

ALSs in the polder and the Braakman. Notably, the maximum residence time of 1141.22 days observed in the SE was attributed to an eel detected at the ALS downstream of the tidal sluice, which eventually migrated westwards. The second highest residence time in the SE was 89.57 days.

The average number of arrivals for the 25 eels in the polder was approximately the same at the ALS upstream of the APS and the other ALSs (5 $\pm$ 6.5 arrivals (range 1-22 arrivals) and 4 $\pm$ 7.6 arrivals (range 1–59 arrivals), respectively). For the 48 eels in the Braakman, the number of arrivals was more than sixfold higher at the ALS upstream of the APS (32 $\pm$ 34.7 arrivals (range 1-158 arrivals)) compared to the other ALSs in the Braakman (5 $\pm$ 10.3 arrivals (range 1-118 arrivals)). The number of arrivals for the 37 eels in the SE was relatively low compared to the polder and Braakman (3 $\pm$ 7.8 arrivals (range 1-95 arrivals)).

6.4.3   Circadian pattern

Overall, the majority of the migration records were obtained at night (n = 413), followed by day (n = 71), dawn (n = 10) and dusk (n = 1). This trend was found in each of the three subareas (polder, Braakman and SE) (Fig. 6.4), albeit that the proportions of observed migrations differed somewhat between subareas: almost fourfold the number of migration records in the polder were observed at night (n = 82) compared to daytime (n = 22), while in the Braakman, the number of migration records at night was over fifteen times higher (n = 228) compared to daytime (n = 15). In the SE, the difference in number of migration records between night and day was threefold (n = 124 and n = 33, respectively). Only four, two and four records were found during dawn in the polder, Braak-

man and SE, respectively, and only a single record was obtained during dusk, in the SE.
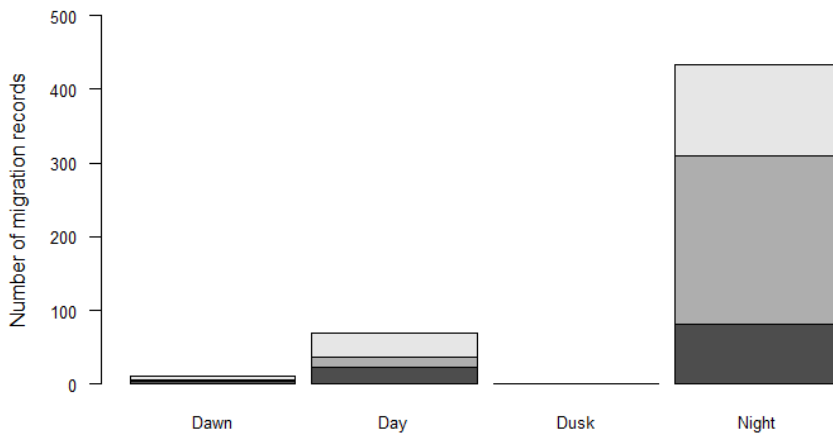

Figure 6.4: Number of migration records during the four circadian phases (dawn, day, dusk, night). Dark grey represents the number of records in the polder, medium-dark grey the Braakman and light grey the Schelde Estuary.

6.4.4 Onset of migration

The onset of migration of the tagged eels occurred between July 2012 and January 2015 (Fig. 6.5). Of the 50 tagged eels, 39 emigrated in 2012, seven in 2013, three in 2014 and one in 2015. The majority of the eels migrated in October (n = 36), while an equal number of emigrating eels was found in July (n = 4), Au-

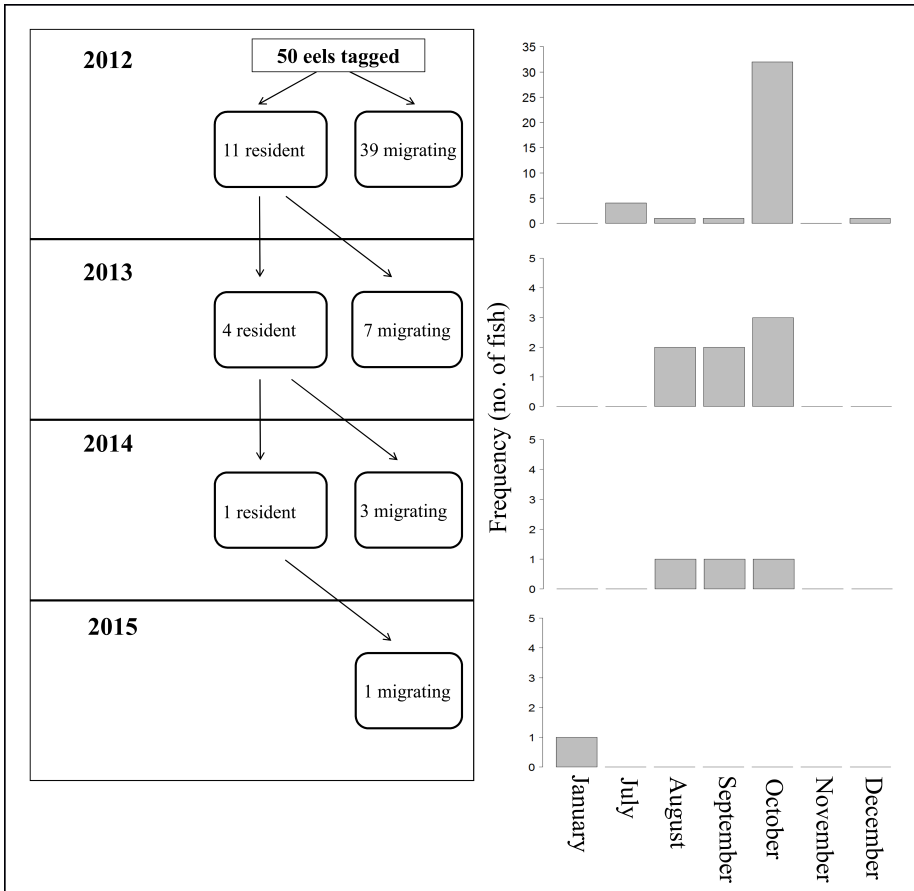gust (n = 4) and September (n = 4). Single eels started emigrating in December and January.

Figure 6.5: Schematic overview with the number of eels tagged in 2012 and the number of resident (i.e. eels residing in the polder area) and emigrated eels in the subsequent years. The boxplots indicate the number of eels emigrated per month over each year.

6.4.5   Environmental triggers of migration

In the polder, a significant positive relationship was found between discharge and downstream eel migration (GLMM, κ = 0.55, estimated coefficient = 0.1891 $\pm$ 0.0917, z value = 2.062, p = 0.0392; Table 6.2). This result was confirmed by the RF (κ = 0.16), which also selected discharge as the most important variable affecting downstream eel migration (Table 6.3). Weak positive relationships were found between downstream eel migration in the Braakman and the variables chloride (GLMM, κ = 0.14, estimated coefficient = 0.00024 $\pm$ 0.00011, z value = 2.103, p = 0.0354) and discharge (GLMM, κ = 0.14, estimated coefficient = 0.00019 $\pm$ 0.00011, z value = 1.902, p = 0.0572). In addition, RF (κ = 0.11) selected discharge as the most important variable. Finally, no significant effect of any of the measured variables was found in relation to downstream eel migration in the SE. A slightly nonsignificant positive relationship with water temperature (GLMM, κ = 0.57, estimated coefficient = 0.3015 $\pm$ 0.1574, z value = 1.916, p = 0.0554) was confirmed by the RF (κ = 0.37), which selected water temperature as the most important variable.

Table 6.2: The output of the GLMMs for each of the three subareas (polder, Braakman, Schelde Estuary) after stepwise backward selection. For each model, the number of migratory (N_1) and non-migratory (N_2) records taken into account is given, as is the AIC, κ and the selected random effect with the variance and standard deviation. For the intercept and the selected variables, the estimate, standard error (SE), Z value and P value are given.

Binomial GLMM (polder)

$N_1 = 108$ $N_2 = 327$ AIC: 408 κ: 0.55

Random effect:

month (var = 0.98; SD = 0.99)

year (var = 2.71; SD = 1.65)

	Estimate	SE	z-value	*p*-value
Intercept	-0.66	0.62	-1.05	0.292
Discharge	0.19	0.09	2.06	0.039

Binomial GLMM (Braakman)

$N_1 = 245$ $N_2 = 232$ AIC: 655 κ: 0.14

Random effect: month (var = 0.06; SD = 0.25)

	Estimate	SE	z-value	*p*-value
Intercept	-0.83	0.38	-2.18	0.029
Braakman discharge	0.0002	0.0001	1.90	0.06
Braakman chloride	0.0002	0.0001	2.10	0.04

Binomial GLMM (Schelde Estuary)

$N_1 = 162$ $N_2 = 178$ AIC: 372 κ: 0.57

Random effect: Transmitter (var = 5.09, SD = 2.26)

	Estimate	SE	z-value	*p*-value
Intercept	-1.90	1.73	-1.09	0.274
Water temperature	0.30	0.16	1.92	0.055

Table 6.3: Order of importance of environmental variables in driving eel migration as obtained by the RFs and backward selection process for the GLMMs for the three different subareas (polder, Braakman pond and Schelde Estuary).

Order of importance	GLMM polder	GLMM Braakman pond	GLMM Schelde Estuary	RF polder (mean decrease in accuracy)	RF Braakman pond (mean decrease in accuracy)	RF Schelde Estuary (mean decrease in accuracy)
1	Discharge	Braakman chloride	WS water temperature	Discharge (104.00)	Braakman discharge (32.22)	WS water temperature (92.26)
2	Precipitation	Braakman discharge	Precipitation	Precipitation (64.10)	Precipitation (25.72)	Precipitation (69.49)
3	Water temperature	Air pressure	WS chloride	Water temperature (55.21)	Braakman chloride (17.91)	Air pressure (60.09)
4	Air pressure	Gravitational flow	Air pressure	Air pressure (50.59)	Water temperature (12.47)	WS chloride (57.17)
5		Precipitation	Current direction		Air pressure (8.81)	Day length (42.34)
6		Water temperature	Day length		Gravitational flow (1.65)	Current direction (10.27)

6.5 Discussion

6.5.1 Migration routes and impact of barriers on downstream migration behaviour

The main eel migration route in the polder was via the APS, as only two eels passed the low-head weir and migrated via the tidal sluice in Zeebrugge into the Belgian Part of the North Sea. The 48 downstream migrating eels taking the main migration route likely went through the APS and did not use the fishway, since Buysse et al. (2015) caught no tagged eels in the fishway from April 23rd 2012 to March 22nd 2013 (when 39 of the 50 tagged eels migrated) and concluded that the fishway did not mitigate downstream eel migration. Further, none of the tagged eels migrated from the Braakman into the SE when the propeller pumps were active (dewatering via the propeller pumps was exceptional and occurred for 49 days during the study period). Eels showed increased exploratory behaviour and delays at the APS and tidal sluice, much like they do when encountering hydropower stations (Jansen et al., 2007; Piper et al., 2013, 2017; Travade et al., 2010). In addition, although the Braakman was primarily dewatered gravitationally during the study period, creating a temporary migration barrier, the mean residence time for migrating eels in the Braakman was 26 days. During this residence time, exploratory behaviour was observed with significantly longer delays at the ALS near the tidal sluice. The discontinuous water flow resulting from the APS and tidal sluice may not be sufficient or last long enough for eels to effectively find their way to the estuary. This may disorient the eels, resulting in increased exploratory behaviour,

which could lead to temporary migration stops (Marmulla, 2001). Another plausible reason is that the APS and propeller pumps in the tidal barrier caused a lot of disturbance (i.e. noise, turbulence...), resulting in a certain reluctance of the eels to migrate further downstream (Sand et al., 2000).

In this study, 11 of the 25 (44%) eels migrating through the APS remained in the Braakman. A plausible explanation for this behaviour would be mortality after passage of the APS. However, the 44% observed in our study was much higher than the aforementioned 19% mortality reported by Buysse et al. (2015) at the same APS. Possible explanations for this higher percentage could be delayed mortality or a migration stop because of a reduced fitness after injury (Ferguson et al., 1989). Migration stops due to insufficient fat content (Svedäng and Wickström, 1997) are unlikely as the polder area is located close to the sea. Delays attributed to acclimatization are also implausible since eels can move frequently between fresh and salt water (Daverat et al., 2006) and progression rates are often faster close to estuaries (Aarestrup et al., 2010; Bultel et al., 2014). As such, the impact of pumping stations on fish migration could be underestimated in studies based on netting methods. Furthermore, piscivorous birds such as grey herons (*Ardea cinerea* L.) and cormorants (*Phalacrocorax carbo* L.) are abundant in the study area, so tag loss due to predation cannot be excluded. Adding to this, a commercial fisherman was active at the mouth of the Braakman, except between September and November when it is legally prohibited to catch eels in The Netherlands. Although the fisherman was able to identify and put back tagged eels, some eels may have gone unidentified.

Once in the SE, the eels did not encounter physical migration barriers on their way to the sea. Nonetheless, different migration behaviours were ob-

served (Fig. 6.1). The westward migrating eels (n = 27) selected three different migration routes (centre, left and right estuary bank), while a non-negligible proportion of eels (n = 7) even swam eastward. All these different types of behaviour may be the result of the dynamic processes in the SE: tidal movements, fluctuations in salinity, turbidity, oxygen and chemical composition of the water. The three migration routes of the westward migrating eels were probably attributed to different currents related to bathymetric channels and sand banks. Three eels were only detected at the ALS downstream of the tidal sluice. Since they emigrated during gravitational flow, injury is unlikely. They may have been predated by cormorants or have emigrated without being detected. Range tests in the Belgian part of the North Sea illustrated a mean detection range of 200 m, but this can be substantially reduced under conditions of strong currents or winds (Reubens et al., 2018).

For the seven eastward migrating eels, disorientation as a cause of tidal currents may have occurred, although some eels migrated eastward when tidal direction was westward. It is possible that the eels were not fit anymore for migration due to the delays or were still recovering from injuries inflicted on them at the APS. Eels can postpone their migration in estuaries, probably due to insufficient fat reserves (Aarestrup et al., 2008; Parker and McCleave, 1997). As such, eels might have swam eastward up the estuary to proceed feeding until they were fit enough again for migration. However, eels migrating westward could equally turn into a semi-yellow stage (Svedäng and Wickström, 1997). This would imply that the silvering process is still reversible in late freshwater - early estuarine conditions (Svedäng and Wickström, 1997). Despite the good coverage by the ALS arrays in the estuary, we cannot exclude that the eastward migrating eels later migrated to North Sea without being detected on the array

stretching from the left to the right bank due to the dynamic currents in the SE (Reubens et al., 2018). Specifically, three of the seven eastward migrating eels changed their migration direction westwardly, but they were not detected on the ALS array stretching from the left to right SE bank.

6.5.2   Circadian pattern

Eels primarily migrated at night, which is in accordance with previous studies (Aarestrup et al., 2008, 2010; Brown et al., 2009; Travade et al., 2010; Vøllestad et al., 1986) and with the general assumption of predator avoidance (Westerberg et al., 2007). Notably, nocturnal downstream migration was more pronounced in the Braakman than in the polder. A plausible explanation might be that the large numbers of cormorants (tens to hundreds) in the Braakman result in a higher predator avoidance effect in the eels and therefore a more pronounced nocturnal activity. Consequently, although gravitational flow can occur twice every 24 h since it is dependent on low tide, the majority of the eels may only be able to pass the tidal barrier at night.

Especially in the SE, however, diurnal downstream migration also occurred, more frequently so than in the polder and Braakman. This is likely a consequence of the high turbidity of the SE (Bultel et al., 2014). Indeed, daytime activity of resident eels has been reported during periods of increased turbidity and/or during overcast weather (Baras et al., 1998; LaBar et al., 1987; McGovern and McCarthy, 1992).

6.5.3 Onset of migration

Due to the large distribution range of the European eel, the onset of downstream migration varies between catchments depending on the travel distance to the spawning grounds (Tesch, 2003). Considerable variation also exists within catchments: eels living in upstream locations migrate earlier (Tesch, 2003). Nonetheless, downstream migration generally takes place in autumn (September to December) (Righton et al., 2016; Tesch, 2003; Vøllestad et al., 1986). Despite the relatively small catchment area (200 km^2) studied here, substantial variation in onset of migration was observed (covering a period of six months (July - January), but with a clear peak in October. However, the 24 eels caught at the APS in October were considered intercepted downstream migrating eels, so the onset of their migration may have occured before October. This is in line with a 'parallel' study by Buysse et al. (2015) at the APS of the LC, where the highest eel numbers were caught in July, October and December 2012, with a main peak in October. The broad period of six months indicates that mitigation actions for downstream migrating eels may need to cover a broader time window than the commonly referred autumn months.

6.5.4 Environmental triggers of migration

Discharge appeared to be the primary trigger of migration in the polder, corroborating observations at the APS of the LC, where eels passed mostly during high discharge events (Buysse et al., 2015), as well as earlier studies (Travade et al., 2010; Vøllestad et al., 1986). It is generally assumed that eels migrating downstream take the energetically most favourable route to their spawning

grounds (van Ginneken and van den Thillart, 2000) as they do not feed during migration (Chow et al., 2010; Tesch, 2003) and rely on their fat reserves for both migration and spawning. As such, swimming along with the current gives the eel an energetic advantage.

In the Braakman, a weak, but significantly positive relationship of migration behaviour with chloride concentration was found. It is possible that eels used saltwater intrusions during gravitational flow to find their way to the estuary. In contrast to the polder, no significant relationship with discharge or gravitational flow was found. The discharge and gravitational flow probably were not substantial or did not last long enough for eels to show a significant response. This was confirmed by the long residence time of eels in the Braakman.

It is still unclear which estuarine cues guide eels to the sea; probably a hierarchical interaction of different directional cues is used (Barbin et al., 1998). In this study, a positive relationship between water temperature and migration was revealed by the statistical models. In autumn and winter, the North Sea water is warmer than that of the SE; no water column stratification is present in the SE. It is therefore plausible that, once in estuarine conditions, eels positively react to higher water temperatures for guidance to the sea. Furthermore, it has been shown that eels use selective tidal stream transport to migrate in an energetically favorable way (Béguer-Pon et al., 2014; McCleave and Arnold, 1999; Parker and McCleave, 1997), but no such relation was found in our study[1]. However, we cannot exclude the use of selective tidal stream transport, be-

[1]At the time this research was conducted, the information revealed by Chapter 5, which was performed later, was not yet available. To date, we do have an indication of STST for European eels.

cause the estuarine behaviour comprises only the initial encounter of the eels with the tidal environment, and they may require some time to 'adapt' to the tidal rhythm (Barbin et al., 1998).

6.5.5 Management recommendations

Understanding and mapping eel migration routes from inland waters to the sea is extremely important in view of the critically endangered status of the European eel, the population of which is still declining (Dekker, 2016). The goals of the European Eel Regulation, i.e. that 40% of the emigrating eels should reach the sea, are still not met (Dekker, 2016). This study analysed downstream eel migration behaviour from a freshwater polder into an estuary. We found that 64% of the tagged emigrating eels reached estuarine and marine areas during the study period, confirming the negative impact of migration barriers on eels. The barriers not only affect eels directly via mortality and injuries (Buysse et al., 2015), they also cause significant delays and exploratory behaviour, likely due to discontinuous flow conditions. These negative impacts of barriers on downstream eel migration may substantially impact the eels' chances to contribute to the spawning population (Brown et al., 2009; Jansen et al., 2007; Piper et al., 2013, 2015, 2017; Travade et al., 2010).

Polder areas and pumping stations exist all over the world, and many are under construction to deal with climate change impacts and sea level rises, creating migration barriers to diadromous fish species like the eel. As diadromous species show seasonal spawning migration under specific conditions, a possible cost-effective management measure could be 'temporal barrier management' (Piper et al., 2013). Barriers could temporarily be removed when migra-

tion conditions are met, during so-called environmental windows, a concept commonly applied with dredging operations (Suedel et al., 2008) and recently also to improve glass eel colonization of freshwater systems (Mouton et al., 2011b). In addition, if effective fish-friendly adaptations to pumping stations are not present, gravitational flow should be stimulated during the environmental windows.

Since eels in freshwater systems mainly migrate at night and during periods of high discharge, a stimulation of gravitational flow under such conditions could probably increase the number of eels reaching the sea and contributing to the spawning population. Notably, the duration of this mitigation action needs to be sufficient so that a continuous flow over a longer time period is generated. However, the duration may be dependent on the study area and requires further research.

Indeed, since the end of 2015, Flemish water managers (Flemish Environment Agency and Waterwegen en Zeekanaal NV) have been taking actions to stimulate gravitational flow: the weir in Sint-Laureins has been lowered, such that the polder can be dewatered through gravitational flow towards Zeebrugge. However, during periods of high precipitation (especially autumn and winter), dewatering towards Zeebrugge is insufficient, leading to activation of the APS in Boekhoute. To stimulate gravitational flow, a possible mitigation action would be to reduce the water level of the Braakman below the level of the polder in autumn.