

Chapter 3

Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area

Modified after:

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3.1 Abstract

Due to a recruitment decline of more than 90% in 30 years, the European eel has been classified by IUCN as critically endangered. Although the species has been studied intensively to obtain knowledge to improve management, studies about the resident yellow stage are relatively scarce. In this study, 52 large female yellow eels were tagged with acoustic transmitters in a Belgian polder system and tracked by a network of 23 ALSs. We studied both circadian and seasonal movement patterns and the effect of environmental variables on these patterns. Large female yellow eels were most active at night in late summer and early autumn. A generalised linear mixed model showed that their movement is only slightly influenced by environmental variables. Moreover, as yellow eels show high site fidelity (i.e., the majority was detected only in the habitat type of their catch-release location), they do not encounter many human-induced connectivity problems in polder systems, which makes these systems highly suitable as eel growth habitat. These results can contribute to an effective eel management regarding habitat protection and restoration.

3.2 Introduction

Due to the endangered status of the European eel population, it is crucial that eel growth habitats obtain proper protection. Among suitable eel growth habitats, polders are anthropogenic water bodies where water levels are controlled by, for example, embankments, weirs and pumping stations to prevent flooding. Polders are characterised by a network of canals, connected ponds and

ditches, resulting in a high habitat diversity and thus many potential growth areas (Lasne et al., 2008). This could lead to higher growth rates, and larger eels have a higher survival rate (Boulenger et al., 2016). In addition, these areas are located close to the sea and may therefore, in the absence of migration barriers, be easily colonised by glass eels (Laffaille et al., 2004). Little is known about the importance of polders for eels, especially for yellow eels, which is the sedentary growing stage (Laffaille et al., 2005). However, due to climate change-driven sea-level rise (Nicholls and Cazenave, 2010), the polder area will tend to increase worldwide during the upcoming decades, turning these systems into potentially important eel habitat and interesting study areas.

Research on eel behaviour may provide insight into the importance of polder areas for yellow eel, especially because behaviour research has hitherto mainly focused on upstream migration during the glass and yellow eel stages and downstream migration during the silver eel stage (e.g., White and Knights (1997); Davidsen et al. (2011); Mouton et al. (2011a); Buysse et al. (2015); Nzau Matondo and Ovidio (2016)). While it has been reported that yellow eels may move seasonally (Jellyman and Sykes, 2003), are primarily nocturnal and that their activity increases with water temperature (Baras et al., 1998), substantial knowledge gaps still exist about the habitat utilisation and movement of yellow eels. It is, for instance, unknown to what extent eels move in a polder area, what is their movement range and whether they use different habitats within that range. It is also unknown what environmental variables trigger movement.

In this study, we investigated the behaviour of large female European eels in a polder area in Flanders, Belgium, by acoustic telemetry. Both yellow- and

silver-staged eels were tagged in this study. However, the classification of eels in yellow and silver stages is rather arbitrary (Durif et al., 2005), especially because silver eels can postpone their migration and turn into a semiyellow stage (Svedäng and Wickström, 1997). This study was based on resident (i.e., nonmigratory) behaviour, and as such, all tagged eels were female yellow eels, based on morphometric criteria (Durif et al., 2005; Laffaille et al., 2005). The main aims of this study were to investigate different aspects of yellow eel behaviour in a polder system. Specifically, we investigated (i) when yellow eels were most active in terms of circadian inter-ALS movements and seasonal swim distance patterns, including effects of temperature, (ii) the size of the movement range and (iii) what environmental variables determined movement. In addition, we checked for (iv) an effect of habitat type (i.e., canal, polder ditch and pond) on (ii) and (iii). A better understanding of yellow eel behaviour will contribute to effective polder management including habitat restoration and protection. Such measures may lead to a higher survival up to the silver eel stage and hence to a higher seaward escapement rate.

3.3 Methods

3.3.1 Study area

The study was performed in a polder area in Flanders, Belgium, which is part of the Schelde River Basin. The drainage area of the polder is ca. 200 km², and drainage is through the Leopold Canal (LC). During high precipitation, water is pumped from the LC into the Braakman pond via a pumping station in the

Isabella Canal (Boekhoute); it flows into the Schelde Estuary via a tidal sluice (Fig. 3.1). This is undoubtedly also the main migration route of silver eel from the polder to the estuary. The LC is an unnavigable waterway extending from the Belgian coast to Boekhoute. It is ca. 46 km long, 10–20 m wide and one to four metres deep. It is a stagnant water system, but during dewatering, the system can have a slow-flowing current (on average $1.21 \text{ m}^3 \text{ s}^{-1}$ during this study period). Connectivity from the polder area to marine areas is blocked by the weir in Sint-Laureins (except in cases of exceptionally high precipitation, when the system can be dewatered towards Zeebrugge by lowering a weir in the LC at Sint-Laureins) and the pumping station in Boekhoute (Fig. 3.1). The LC connects different habitats in the polder such as ponds and small and large polder ditches with variable width (0.5-150 m) and depth (0.2-10 m) (Table 3.1).

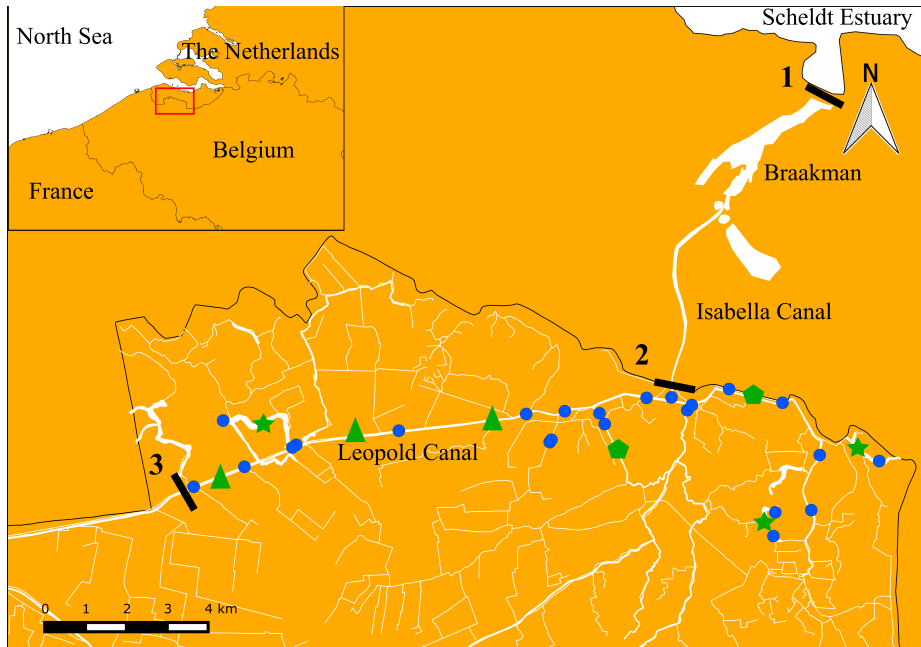


Figure 3.1: Study area with the location of the migration barriers and the network of waterways in the Belgian part of the polder area: (1) the tidal sluice, (2) the pumping station in the Isabella Canal (Boekhoute) and (3) the weir at Sint-Laureins. The blue dots represent acoustic listening stations, and the symbols are the different catch locations: ponds (star), Leopold Canal (triangle) and polder ditches (pentagon).

Table 3.1: Depth, width and current characteristics of the different habitat types.

Types	Depth (m)	Width (m)	Current
Canal	1 - 4	10 - 20	Slow
Pond	0.5 - 10	15 - 150	Stagnant
Large polder ditch	0.5 - 2	5 - 10	Slow
Small polder ditch	0.2 - 1	0.5 - 5	Slow

3.3.2 Tagging procedure

From July to August 2012, a total of 526 eels were caught with double fyke nets in the LC, ponds and large polder ditches (electrofishing in the small polder ditches did not yield any eels). At each location, four double fyke nets were placed and emptied for four consecutive days. Several morphometric features were measured in order to determine the sex and 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 0.1 mm) and the length of the pectoral fin (FL, to the nearest 0.1 mm). Fifty-two eels were considered large enough to tag, with a minimum TL of 495 mm and minimum weight of 246 g (Table S1). According to the size classes of Laffaille et al. (2003), the selected eels were considered large and female, as males are smaller than the minimum size handled in this study (<450 mm (Durif et al., 2005)) (Table 3.2). Five life stages can be found in

female European eel: a sexually undifferentiated growing phase (I), a female differentiated growing phase (FII), a premigratory phase (FIII) and two migratory phases (FIV and FV) (Durif et al., 2005). FIV-staged eels are considered to be on the onset of migration, while FV-staged eels are regarded as migrating eels. Here, yellow eel (FII, $n = 11$), premigrant eel (FIII, $n = 28$) and two classified migrant eel stages (FIV, $n = 4$, and FV, $n = 9$ respectively) were tagged.

Eels were tagged with V13-1L-coded acoustic transmitters (13×36 mm, weight in air 11 g, weight in water 6 g, random delay between 80 and 160 s, guaranteed life time 1,116 days, frequency 69 Hz) from VEMCO Ltd (Canada)). After anaesthetising the eels with 0.3 ml/L clove oil, tags were implanted according to Baras and Jeandrain (1998). After recovery in a quarantine reservoir, eels were released at their catch location.

Table 3.2: Number of tagged female eels per stage with the different morphometrics: total length (TL), body weight (BW), horizontal and vertical eye diameters (ED_h and ED_v respectively) and pectoral fin length (FL).

Stages	Number	TL (mm)	BW (g)	ED_h (mm)	ED_v (mm)	FL (mm)
FII	11	607 ± 32	392 ± 108	6.29 ± 0.46	5.96 ± 0.58	26.54 ± 1.78
FIII	28	662 ± 69	556 ± 190	7.59 ± 0.77	7.27 ± 0.75	31.96 ± 4.47
FIV	4	773 ± 81	$1,066 \pm 251$	9.74 ± 1.14	8.71 ± 1.17	36.07 ± 1.50
FV	9	630 ± 56	486 ± 123	9.16 ± 0.98	8.21 ± 1.20	33.58 ± 2.89

3.3.3 Acoustic network

An acoustic network of 23 ALSs (VR2W, VEMCO Ltd, Canada) was deployed in the polder system in the LC, Isabella Canal, ponds and large polder ditches. The ALSs register the tag IDs with date and time of the detections. They were moored at strategic locations (Fig. 3.1) to maximise the probability of detection and to minimise detection gaps: ALSs were deployed up- and downstream at each entry of a pond or polder ditch into the LC. In the pond and polder ditch itself, an ALS was placed near the connection with the LC and further upstream. They were on average 1,912 m (range 114-5,264 m) apart. The ALSs were moored at the bank by means of weights and a small buoy, so the ALS was deployed on the bottom with the hydrophone directed upwards in the water column. Data from ALSs were downloaded two to three times a year. As environmental conditions do not change drastically in the polder area, only a short-term range test (i.e., < 1 day) was performed. An ALS was moored in the different habitats in the polder and a range test tag [i.e., a tag with a very short fixed delay of ca. 10 s]) was positioned at several ranges (0-500 m, with 50-m intervals) from the ALS. Tests revealed detection ranges of 300 m.

3.3.4 Data processing

To determine residency times (time between arrival and departure at an ALS), searches were performed with the VUE software (VEMCO Users Environment, VEMCO Ltd, Canada). This allows us to reduce the data by accumulating the number of detections during a fixed period of time. We applied an absence threshold of 1 hr (i.e., the maximum time 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. The numbers of detections between each arrival and departure per ALS were calculated. The residence time between arrival and departure, and the swim distance, swim time and swim speed between each consecutive interval were calculated in R (R Development Core Team 2017).

Of the 52 tagged eels, 18 showed yellow eel (i.e., resident) behaviour followed by silver eel behaviour (i.e., migration: directional movements towards seawards exit from the polder system). As this study focused on yellow eel movement behaviour only, data on behaviour typical of silver eels were removed. To determine a clear distinction between yellow and silver eel behaviour, a trajectory analysis was applied for each individual eel. We used the method of Lavielle from the *adehabitatLT* package in R to divide an animal's trajectory into a yellow and a silver eel phase (Calenge, 2006) (Fig. S1). 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). The 52 eels were detected as yellow eels between 4th July 2012 and 7th September 2015 (39 months), resulting in a data set of 1,627,846 detections; the average tracking period per eel was 470 days (range 28-1,135).

3.3.5 Data analysis

In this study, four research questions were addressed, each with its own data analysis. We investigated (i) when yellow eels were most active in terms of cir-

cadian inter-ALS movements and seasonal swim distance patterns, including effects of temperature, (ii) the size of the movement range, (iii) what environmental variables determined movement and (iv) effects of habitat type (i.e., canal, polder ditch and pond) on (ii) and (iii). For each analysis, assumptions were checked and data exploration was conducted following Zuur et al. (2010).

Circadian and seasonal activity

Circadian activity was defined as the total number of inter-ALS movements made by eels, as they moved between one ALS to an adjacent one per circadian phase. Consequently, four different circadian phases were determined and linked to each record in the data set: dawn (start of civil twilight to sunrise, i.e., when the geometric centre of the sun is 6° below the horizon in the morning (or evening for dusk)), day (sunrise to sunset), dusk (sunset to end of civil twilight) and night (end of civil twilight to start of civil twilight). Time stamps 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').

Seasonal activity was analysed by summing the swim distances per eel for each month. Only data records of eels that swam to another ALS were taken into account. A one-way ANOVA with Welch correction was performed, as 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). The effect of water temperature on mean swim distance was analysed by means of a one-way ANOVA.

Movement range

Polder areas are geographically complex systems, where it is hard to apply classical methods of movement range estimation such as minimum convex polygons and kernel utilisation distribution (Benhamou and Cornélis, 2010; Heupel et al., 2004; Meyer and Holland, 2005). Moreover, the detection range of the ALSs deployed in the study area was larger than the width of the waterways. As such, the movement range was considered as the distance swum by an eel between the two most distant ALSs during the tracking period (Walker et al., 2014). Although some eels were only detected at one ALS but regularly swam out of its range, they were assigned a minimum movement range equal to the detection range of one ALS. Based on range tests, this was ca. 300 m in the study area (INBO, unpublished data). Linear regression was used to test for relationships between movement range and eel catch-release location habitat type (canal, polder ditch and pond):

$$\text{Movement range} = \alpha + \beta_1 \text{catch-release location habitat type} + \epsilon$$

A censoring problem emerged from the fact that the smallest distance measurable by the ALSs was ca. 300 m: the true value of the range distance was unknown, and so was the error between range distance and the regression line relating range distance to the catch location. Therefore, the summed squared errors cannot be minimised and ordinary least-squares methods cannot work. Therefore, censored linear regression was applied, which uses maximum-likelihood estimation (Greene, 2008). Assumptions of normality (via histo-

grams and QQ-plots) and homogeneity of variances (by plotting residuals vs. fitted values) were met after log transformation (Zuur et al., 2009, 2010).

Environmental variables determining eel movement

Environmental data

Five continuous environmental variables were linked to the departure times in the data set. These were precipitation (mm), pumping discharge ($\text{m}^3 \text{s}^{-1}$), water temperature ($^{\circ}\text{C}$), day length (min) and atmospheric pressure (hPa). Precipitation, water temperature and atmospheric pressure data were measured daily and obtained from the Flemish Environment Agency (www.waterinfo.be). Water temperature and atmospheric pressure were measured near the pumping station (coordinates: N51°16'15.8" E3°42'43.6"), while precipitation was an average value over a large part of the study area (Fig. S2). 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; 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. A linear regression was then applied to obtain the relationship between the two data sets and fill in the gaps of the water temperature data of the studied polder area with the modified values of the nearby canal:

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

From 1st July 2012 till 15th August 2014, pumping discharge data were

obtained daily from the Flemish Environment Agency by recordings at the pumping station. 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°57' E3°43'). Additionally, one categorical explanatory variable was included, namely catch-release location habitat type.

Model development

To determine the variables that significantly contributed to yellow eel movement, a generalised linear mixed model (GLMM) was applied (Mouton et al., 2011a; Verhelst et al., 2016; Zuur et al., 2009). We arbitrarily chose three movement thresholds by means of a cross-validation, and as such, three different models were constructed: an eel was considered to have moved when its swim distance was larger than 500, 1,000 or 1,500 m. For each model, the response variable "movement" was binomial: swim distances \leq a threshold value were considered as no movement, whereas higher values were considered movement. In order to give an equal weight to movement and nonmovement behaviour, bootstrapping was applied to obtain the same number of records with and without movement (Mouton et al., 2010). After the data were checked for outliers and homogeneity, a collinearity analysis was conducted (Zuur et al., 2010). As correlations were $\leq |0.70|$, all six variables were included for analysis (Dormann et al., 2013) (Table S2).

Finally, for each of the three movement thresholds, a binomial GLMM with logit link was applied to assess the effects of the explanatory variables on eel movement. In addition, the significance of three random effects in the mod-

els was tested: year, month and tag ID, the latter being 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: for the 500-m threshold model, the model with the random effect "month" was selected for stepwise backward selection; for the 1,000-m and 1,500-m models, the models with both month and year as random effects were selected.

The kappa statistic (κ) was calculated to evaluate the final model; κ ranges between -1 and 1 (Goethals et al., 2007; Mouton et al., 2010). We used the "lme4" package (Bates et al., 2014) of the R environment (R Development Core Team 2017) 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. In addition, Random Forests (RF) was applied, which is a widely used machine learning technique (Breiman, 2001; Mouton et al., 2011a). The method was applied by means of cross-validation for the variables selected by the GLMM: we checked whether the variables selected by the GLMM also proved important by RF. The results of this analysis can be found in Appendix S1.

3.4 Results

3.4.1 Circadian activity patterns

Eels were most active at night with almost two times more inter-ALS movements than during daytime (Table 3.3). Moreover, 87% of the 52 tagged eels were detected at night, while only 62% were detected during daylight. The lowest activity was observed during dawn and dusk with only 40% and 17% of the eels detected during those periods respectively.

Table 3.3: Number of inter-ALS movements per circadian phase. The number of eels contributing to the number of inter-ALS movements is also given.

Circadian phase	Number of inter-ALS movements	Number of eels
Dawn	49	21
Day	377	32
Dusk	24	9
Night	744	45

3.4.2 Seasonal activity patterns

Activity patterns differed significantly between months (Welch ANOVA, $F = 18.434$, $df = 11$, $p = 2.2e-16$): the mean swim distance in summer (June–August) and autumn (September–November) was almost threefold that in winter (December–February), with the highest activity in August (Fig. 3.2a; Table S3). Activity in spring (March–May) was intermediate between winter and summer,

with activity rising from early spring towards summer.

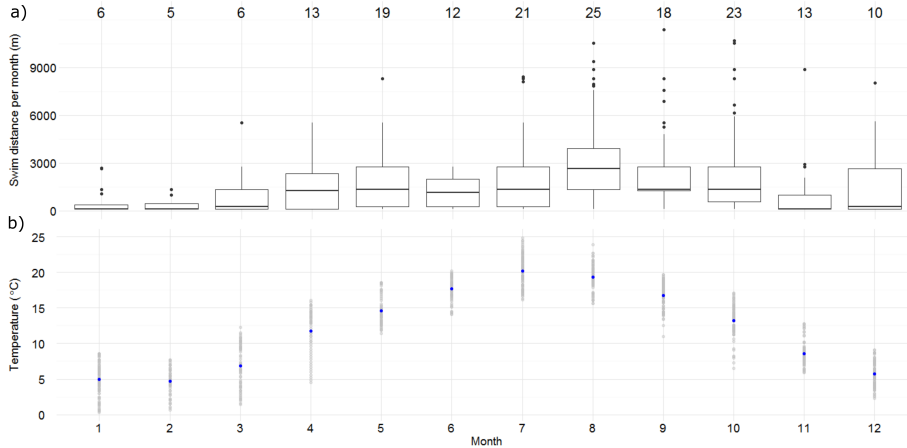


Figure 3.2: (a) Boxplot of the swim distances of all eels per month. Outliers are presented as dots above the boxplots. The number of eels taken into account is given above the different boxplots. (b) monthly water temperature (mean shown as blue dots, range by vertical lines).

Although no significant relation between water temperature and monthly swim distance was found (one-way ANOVA, $F = 0.016$, $df = 846$, $p > 0.05$), some trends were observed. When the mean water temperature rose above 10°C in April, a higher eel activity was observed compared to that in January and February (Fig. 3.2b). Activity was almost twice as high compared to March, but this was not statistically significant. Mean water temperature dropped below 10°C in November, accompanied by a significantly lower activity. Water temperature was highest during late summer, when activity peaked. However, activity was highest in August despite a lower water temperature than in July.

3.4.3 Movement range differences according to habitat type

In this study, the movement range was considered as the distance swum by an eel between the two furthest spaced ALSs during the tracking period, following the definition of Walker et al. (2014). Seven of the 52 eels were detected at only one ALS. For the latter 45 eels, the average movement range size \pm SD was 3,917.34 m \pm 4,116.64 m. No significant difference was found between eels tagged and released in different habitat types (censored regression, log-likelihood = -79.82251, df = 4, $p > 0.05$) (Fig. 3.3). Furthermore, of the 52 tagged eels, 14 (27%) were detected in another habitat than their catch habitat (Table 3.4). Notably, the eight eels caught and released in polder ditches were later found in the canal. Moreover, after release, only two returned to a polder ditch. Of the 19 eels tagged and released in ponds, three were exclusively detected in the LC, while two moved between the LC and the pond of capture. Only one eel tagged and released in the LC was detected in a pond.

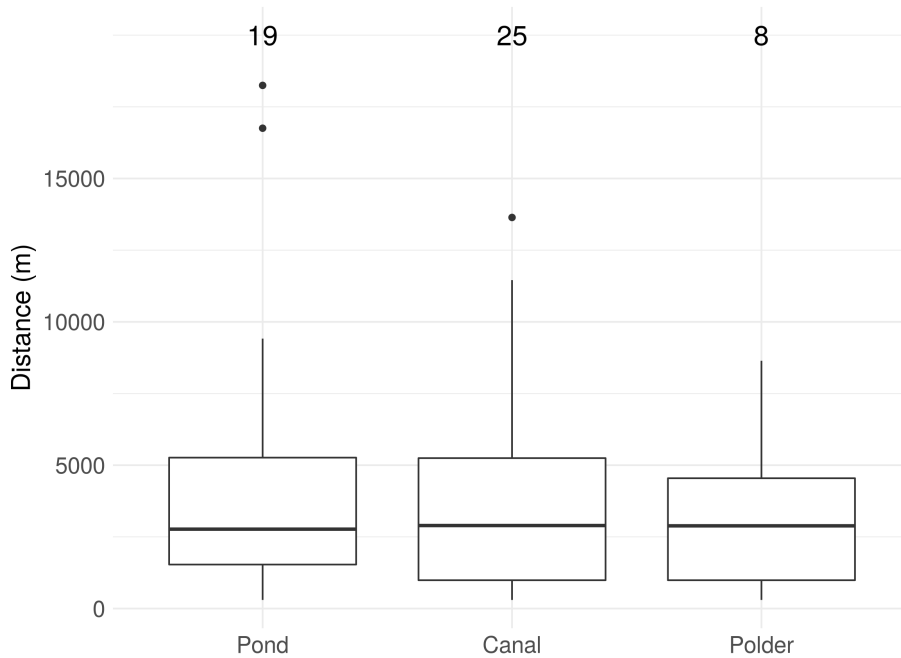


Figure 3.3: Boxplots of movement range distances (m) in the three different catch location types: ponds, canals and polder ditches. The numbers of eels caught, tagged and released at each location type are given above the different boxplots. Outliers are presented as dots above the boxplots.

Table 3.4: Number of eels detected in one or more habitat types. The catch location type gives the habitat type where the eels were caught, tagged and released. The columns "canal", "pond" and "polder ditch" give the number of eels that were detected in those habitats.

Catch location type	Detection location type		
	Canal	Pond	Polder ditch
Canal	24	0	1
Pond	5	14	0
Polder ditch	8	0	0

3.4.4 Environmental variables determining eel movement

For the model with the 500-m threshold, 45 (87%) of 52 eels were considered to have moved (801 movement records); the seven remaining eels were highly resident and stayed in the vicinity of a single ALS. The final model obtained from the backward selection only contained the variable precipitation, which had a negative relationship with eel movement (GLMM, estimated coefficient = -0.032 ± 0.014 , z value = -2.224 , $p = 0.026$; Table 3.5). When a movement threshold of 1,000 m was applied, 38 (73%) eels had moved (660 movement records). A nonsignificant negative relation with precipitation was present in the final model (GLMM, estimated coefficient = -0.034 ± 0.018 , z value = -1.914 , $p = 0.056$). The final model obtained for a movement threshold of 1,500 m (33 (63%) eels had moved, resulting in 397 movement records) showed a negative relationship with precipitation (GLMM, estimated coefficient =

-0.055 \pm 0.024, z value = -2.297, p = 0.022) and water temperature (GLMM, estimated coefficient = -0.033 \pm 0.016, z value = -2.088, p = 0.037). The impact of precipitation on eel movement was about 1.5 times that of temperature. For the results of the backward selections and Random Forests, see Table S4 and Appendix S1 respectively.

Table 3.5: Output of the three different movement threshold models (500, 1,000 and 1,500 m) after stepwise backward selection. For each model, the number of records taken into account (N) is given, as well as the Akaike Information Criterion (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 (500 m)				
N = 1,602		AIC: 2,165 κ : 0.17		
Random effect: month (var = 0.32; SD = 0.57)				
	Estimate	SE	z-value	p-value
Intercept	-0.21	0.18	-1.13	0.259
Precipitation	-0.03	0.01	-2.22	0.026
Binomial GLMM (1,000 m)				
N = 1,320		AIC: 1,768 κ : 0.23		
Random effect:				
month (var = 0.51; SD = 0.71)				
year (var = 0.08; SD = 0.28)				
	Estimate	SE	z-value	p-value
Intercept	-0.24	0.27	-0.89	0.376
Precipitation	-0.03	0.02	-1.91	0.06
Binomial GLMM (1,500 m)				
N = 794		AIC: 1,049 κ : 0.26		
Random effect:				
month (var = 1.17; SD = 1.08)				
year (var = 0.31; SD = 0.56)				
	Estimate	SE	z-value	p-value
Intercept	0.10	0.49	0.20	0.839
Precipitation	-0.05	0.02	-2.30	0.022
Water temperature	-0.03	0.02	-2.09	0.037

3.5 Discussion

3.5.1 Circadian activity

Eels are known to be nocturnal fish which hide in crevices or bury themselves in the bottom substrate during daytime (Baras et al., 1998; McGovern and McCarthy, 1992). Our long-term (39-month) tracking study confirmed nocturnal activity: the number of inter-ALS movements was almost twice as high during the night than during daytime. Also, the majority of the eels (87%) moved at night, agreeing with findings in other tracking studies (LaBar et al., 1987; Riley et al., 2011). The daytime activity found in the present study possibly occurred mostly during overcast weather, as found by LaBar et al. (1987) and McGovern and McCarthy (1992), or during periods of increased turbidity (Baras et al., 1998). The lowest activity was found during dusk and dawn, with approximately twice the number of eels and inter-ALS movements detected during dawn compared to dusk. However, it is possible that the eels started moving during dusk or dawn, but were only detected at night due to the short duration of the twilight periods (<1 hr). Although pronounced activity during twilight was not observed in this study, it has been found for European eel (Baras et al., 1998; Riley et al., 2011), New Zealand longfinned eel (Jellyman and Sykes, 2003) and American eel (Bohun and Winn, 1966).

There are two plausible explanations for this nocturnal behaviour: foraging and predator avoidance. Eels may feed primarily at night, as their stomachs are fullest just before morning (De Nie, 1987). Eels also have a very broad diet spectrum, from invertebrates (e.g., mussels, insects, crustaceans) to fish. Many

invertebrates avoid fish predation by drifting or emerging at night (Douglas et al., 1994; Learner et al., 1990; Morgan and Waddell, 1961). Some - particularly larger - eels are piscivorous (Tesch, 2003) and may benefit from low light conditions when stalking prey (Barry et al., 2016a; Pitcher and Turner, 1986), also supporting the hypothesis that foraging at night may be more favourable. As our study only considered large eels, piscivory may have been an important strategy. Furthermore, energetic benefits could arise from a circadian rhythm, because periods of reduced activity may enable eels to meet the costs of feeding (Owen, 2001).

Predator avoidance is also often related to circadian behaviour (Ibbotson et al., 2006). Likely eel predators in our polder area include the grey heron (*Ardea cinerea* L.) and northern pike (*Esox lucius* L.), both of which are primarily active during daytime, although northern pike also feeds during twilight (Feunteun and L, 1994; Jepsen et al., 2001). In conclusion, nocturnal activity may result from both foraging behaviour and predator avoidance.

3.5.2 Seasonal activity

A trend of increasing eel activity from winter over spring to a peak at the end of summer and in autumn was found. As eels are ectothermic, a lower activity during winter was expected and is consistent with studies which found little to no activity when temperature dropped below 10°C (e.g., Riley et al. (2011); White and Knights (1997). In contrast, in a mild-climate stream in Spain, eels remained active throughout the year (Costa-Dias and Lobon-Cervia, 2008). In our study, eel activity was indeed lowest from November till March when water temperature was below 10°C. Activity rose until summer together with the

water temperature. Highest activity was found when water temperature rose above 16°C, consistent with Riley et al. (2011) and Baras et al. (1998). The latter authors stated that large yellow eels may be more active during higher water temperatures to meet increasing energetic expenditures. Nonetheless, eels were most active at the end of summer, although water temperature was lower (mean water temperature was 19.3°C in August and 16.7°C in September) than during mid-summer (mean water temperature was 20.2°C in July). This may be explained by the increasing night lengths (Béguier-Pon et al., 2015). As light negatively influences eel activity, longer nights might favour more activity as long as water temperature is above a certain threshold (Bohun and Winn, 1966). Another plausible explanation could be that the eels were more active at the end of the summer as they were seeking overwintering thermal refuge areas (Hammond and Welsh, 2009). Finally, although a distinction between yellow and silver eel behaviour was made based on the trajectory analysis of Lavielle (Lavielle, 1999, 2005), we cannot exclude that the increased activity at the end of summer was the result of eels showing movements associated with the onset of silver eel emigration.

3.5.3 Movement range

In this study, the maximum linear range between ALSs was used as a measure of movement range, as movement ranges could not be estimated in terms of area utilised (Walker et al., 2014). It should be noted that not the whole study area was covered by ALSs. Hence, reported movement ranges may be underestimated as eels could swim outside the ca. 300-m range of an ALS without being detected by an adjacent ALS. However, 15 eels (29%) were restricted to

a movement range of < 1 km, while six (12%) moved over distances in excess of 10 km. This corroborates the high interindividual variability in European eels. A range distance of maximum 285 m was found by Baras et al. (1998), while this was up to 4,150 m in a study conducted in an estuary in England (Walker et al., 2014). Baras et al. (1998) attributed the small movement range to the high complexity and numerous hiding places for eels in the studied river, leading to less foraging-related movement. The movement ranges found in our study were larger than the abovementioned studies. This could be attributed to the large size of our eels, as larger eels may have a larger movement range (Barry et al., 2016a). However, one of the six eels with a movement range > 10 km was at the growing FII stage and two were at the premigratory FIII stage. The remaining three comprised one FIV- and two FV (migratory)-staged eels. Moreover, two eels with a movement range < 1 km were FV. The large movement range of these FII- and FIII-staged eels may be attributed to silvering processes, while the small movement range of the FV-staged eels could be the result of turning back into a semiyellow stage (Svedäng and Wickström, 1997). It clearly remains difficult to define a sharp border between yellow- and silver-staged eels during long-term tracking studies.

In our study, eels were captured, tagged and released in three different habitat types. The majority of eels caught in the canal and ponds were only detected in the habitat where they were caught and released (96% and 74% respectively), demonstrating a high site fidelity.

All eels caught in large polder ditches moved to another habitat type, while none of the eels from the ponds and only one from the canal moved into a polder ditch. The lower preference for polder ditches may be explained by the

fact that these habitats were the smallest and shallowest of the system. Laffaille et al. (2003, 2004) and Lasne and Laffaille (2008) found that eels larger than 360 mm do not prefer shallow ditches with much plant cover, similar to the polder ditches in this study. As such, the results presented here illustrate that larger eels may more commonly reside in deeper habitats. This would also explain why fewer eels were caught and tagged in polder ditches (canal: $n = 25$, ponds: $n = 19$, polder ditches: $n = 8$). Moreover, electrofishing in the smallest polder ditches during the tagging period (July–August 2012) did not yield any eels. This is also why no ALSs were placed in those systems.

These results may have important implications for water management in polders. If water management aims to create eel growth habitat in polder systems or apply habitat restoration, sufficiently deep waterways should be aimed to provide habitat for large yellow eels. In addition, shallower waters with plentiful instream vegetation (e.g., reed beds) will favour the production of smaller yellow eels (Laffaille et al., 2003, 2004; Lasne and Laffaille, 2008).

3.5.4 Movement behaviour

In general, the relationships between eel movement and environmental factors based on GLMM were too weak to draw strong conclusions. We can therefore not exclude that yellow eels move largely randomly through the study area and are not influenced greatly by the environmental factors taken into account in this study. This may be confirmed by the fact that eels are opportunistic feeders (Van Liefferinge et al., 2012), and their movement may largely depend on their feeding behaviour.

3.6 Conclusion

This study describes the behaviour of large female yellow eel based on a substantial number of tagged individuals ($n = 52$), some of which have been tracked for up to 3 years (28-1,135 days). We provide evidence that European eels in freshwater polder systems are most active during the night in late summer and early autumn. We found that large female yellow eels have a high site fidelity and are not strongly affected by environmental factors (temperature, precipitation, day length, atmospheric pressure, pumping discharge). This may be attributed to the productivity of the polder system, which makes such systems highly suitable as eel growth habitats (Lasne and Laffaille, 2008; Lasne et al., 2008). In view of their high site fidelity, large female yellow eels may not encounter many human-induced connectivity problems in polder systems. Notably, upstream migration of small yellow eels (< 150 mm) does occur and is influenced by environmental variables (Feunteun et al., 2003). Hence, these animals may be influenced to a larger extent by migration barriers in polders. In addition, our study indicates that large eels prefer deeper habitats in polder systems. If measures concerning eel habitat restoration in polders are considered, areas of sufficient depth need to be maintained for large eels. A higher yellow eel survival could in turn result in a higher silver eel escapement, and as such could help meet the 40% escapement obligation imposed by the European Eel Regulation.