Animal Biotelemetry

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To hear or not to hear: selective tidal stream transport can interfere with the detectability of migrating silver eels in a Tidal River

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Abstract

Acoustic telemetry provides valuable insights into behavioural patterns of aquatic animals such as downstream migrating European eels (*Anguilla anguilla*), so called silver eels. The behaviour of silver eels during the migration is known to be influenced by environmental factors, yet so is the performance of acoustic telemetry networks. This study quantifies the impact of these environmental factors on both, migration behaviour and receiver performance to determine possible limiting conditions for detecting tagged eels in tidal areas. A dominance analysis of the selected models describing migration speed, activity and receiver performance was conducted following 234 silver eels that were tagged with acoustic transmitters and observed by a receiver network in the Ems River during two subsequent migration seasons. The results suggest a passive locomotion of silver eels during their downstream migration by taking advantage of selective tidal stream transport (STST). It is further shown that water temperature, salinity, turbidity, precipitation, and especially current velocity were major parameters influencing migration activity and speed. At the same time, analyses of the detection probability of tagged eels under varying environmental conditions indicated a decreased receiver performance during increased current velocities, meaning that high migration activity and -speed coincides with reduced detection probability. Consequently, there is a risk that particularly during phases of increased activity, migration activity may be underestimated due to reduced acoustic telemetry performance. To avoid bias in telemetry studies, it is, therefore, crucial to conduct range tests and adjust the receiver placement in areas and conditions of high current velocities.

Keywords *Anguilla anguilla*, Downstream migration, Acoustic telemetry, Range test, Dominance analysis

Introduction

With increasingly sophisticated technology, advanced acoustic telemetry networks allow for detailed behavioural analyses of target organisms from cubozoans [25] to whale sharks [15]. This passive methodology is based on acoustic signal transmission between installed receivers, forming a receiver network, and transmitter tags, which are implanted or externally attached to a target organism. Many behaviour-related research questions including movement patterns, migration speed and timing, predation events and 3-dimensional spatial distribution can be investigated with this methodology causing relatively little impact on the organism's life [7, 9, 29, 32, 44]. For a detailed assessment and prediction of animal behaviour, species distribution and migratory patterns, especially considering conservation efforts, a combination of acoustic telemetry data withenvironmental factors can be of great benefit [41].

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The behaviour of migratory fish is known to be largely influenced by prevailing environmental conditions. In general, it is hypothesised that fish prefer to migrate during specific environmental conditions to save energy, maximize survival and avoid predation [53]. In the case of the critically endangered European Eel (*Anguilla anguilla*), high current velocities [65] and river discharge are linked with increased migration activity [13, 16, 39, 52, 70], and migration speed [1, 57, 70]. It is hypothesised that selective tidal stream transport (STST) plays an important role in the estuarine and coastal migration, allowing for energy conservation of the migrating species by ascending into the water column, when the tidal flow equals the migratory direction and settling on the bottom or sheltered areas during opposite tide intervals [21, 69, 71]. The application of STST has been proven for various fish species, including the silver eel stage of the American eel (*Anguilla rostrata*) [8], glass eel stage of several *Anguilla* species [60, 64], Green sturgeon (*Acipenser medirostris*) [31], Thinlip grey mullet (*Chelon ramada*) [64] and flounder larvae (*Platichthys flesus* [30, 64]. For the European silver eels, studies by Barry et al. [5], Huisman et al. [28] and Verhelst et al. [69] recorded increased migration activity during ebb tide, strongly suggesting the usage of ebb-tide transport during their downstream migration, while a study by Bultel et al. [15] could not confirm this observation. Additionally, meteorological effects such as periods with increased precipitation often coincide with increased water level and flow [57, 65] as well as lowered atmospheric pressure [17] and wind speed [17, 52] are mentioned as possible triggers of migration. Besides, water temperature may influence activity and migration patterns of European eels [13, 36, 70], as their ectothermic metabolism shows limited activity during high (linked to decreasing oxygen concentrations or other mechanisms) or low temperatures [16, 74]. According to Lennox et al. [35], eels avoid migrations during daylight and migrate preferentially during new moon, hence reducing their vulnerability to predators [5, 57]. However, the role of the lunar cycle could not be corroborated by other studies [39, 52], as it can be inhibited by other conditions, such as increased turbidity [19, 20].

In case of the critically endangered European eel, knowledge about site-specific environmental drivers of migration can also be used to predict migration events and implement protection measures, e.g. the shutdown of hydropower turbines [62] or the determination of closed seasons for fishing in the absence of actual monitoring data. However, apart from testing environmental influences on migratory fish behaviour, an important and often disregarded prerequisite for the use of telemetry is the determination of detection probabilities during different environmental conditions in the installed telemetry network. However, the reliability of the detections is not solely influenced by the behaviour of the animals, but also by environmental traits and conditions, which may have strong implications for the accuracy and thus validity of the obtained detections data.

Hydrological and meteorological parameters affect the underwater acoustic landscape, with implications for the transmission of sounds. Therefore, these factors can limit the detection of emitted acoustic telemetry signals drastically, inducing uncertainties and possibly even erroneous conclusions of the main biological research subject [32]. Past studies determined current velocity and turbidity as main influencing factors in coastal systems [40, 53]. Additionally, waves and wind cause underwater noise, possibly impairing successful signal transmission. In general, the presence of air bubbles (e.g., entrapped by precipitation, waves and currents) and sediment particles can cause an undirected scattering or absorption of the sound waves resulting in a higher signal loss [53, 58]. Moreover, ambient noise, originating from anthropogenic sources, e.g., nautical traffic, rattling of buoy chains, is known to potentially conceal transmitter pings [32, 40, 53]. Other environmental factors, potentially interfering with transmitter–receiver interaction include increased salinity and water temperature, which can lead to improved signal transmission [77], by changing the physical properties (e.g., density and viscosity) and allowing for an improved sound propagation [38]. Beside the environmental impacts, also technical parameters such as receiver tilt angle and position of the receiver's hydrophone in relation to the signal-emitting tag are important factors for the performance of the receiver network [53]. Additionally, the detection probability scales with the power output of the used tags [59]. A sentinel tag approach with fixed tags or receiver internal tags, communicating with each other in a chain of devices, enables a continuous monitoring of the detection probability at fixed distances [53].

This paper analyses the environmental drivers of the downstream migration of silver eels, together with their influences on detection probability within an acoustic telemetry network installed in the fluvial and lower estuary area of the German River Ems. The aim was to determine the relative importance of environmental variables that contribute to the detection probability in acoustic telemetry. We identify environmental conditions that may favour migration activity and migration speed while inhibiting the effective detection probability, which may lead to biased results of telemetry studies during the main migration period if not properly accounted for.

Methods

Study area

To study aspects of migration behaviour and detectability of tagged European eels across two migration seasons, 29 telemetry receivers (Model VR2Tx, Vemco Ltd Halifax, Canada), forming seven acoustic arrays, were set up along the tidal and inland area of the River Ems. The entire area covered by the receiver arrays comprised 109.3 km of the Ems River between the town of Meppen and the seaward boundary of the Dollart Estuary, which forms the German-Dutch border. In this study the focus was set on the tidal area stretching from the tidal weir in Herbrum to the Dollart Estuary. The study area is divided into the fluvial estuary including receiver arrays 4 to 6 and the lower estuary covering of the Dollart between receiver array 6 and 7 (Fig. 1). The fluvial estuary is a highly anthropised part of the Ems River is characterised by a straightened and deepened riverbed as well as a muddy bottom structure, high sediment loads, turbid water and regular tidal cycles. The lower estuary includes receiver array 7 consists of a chain of 12 telemetry receivers covering the width of the Dollart Estuary, forming the direct connection and entry into the North Sea. Current velocities range from 1.88 m/s during flood tide to 2.17 m/s during ebb tide. Salinity varies from 2.30 to 26.53‰. The whole tidal area is affected by a big tidal amplitude, typically 3–3.4 m, changing the water level from min. 2.57 to max. 8.99 m. Regular shipping traffic is present along the whole study region, with ocean cargo carriers typical for the lower estuary and freighters and recreational shipping common in the fluvial estuary.

Telemetry network and range tests

The telemetry network consisted of 19 acoustic receivers (Vemco VR2Tx) with built-in tags emitting and receiving signals with a frequency of 69 kHz [66] in the fluvial and lower estuary of the Ems River. Receivers were attached to anchor chains of navigation buoys (hereafter referred to as buoy chains) at a water depth of 2–3 m except for two receiver units placed in shallow

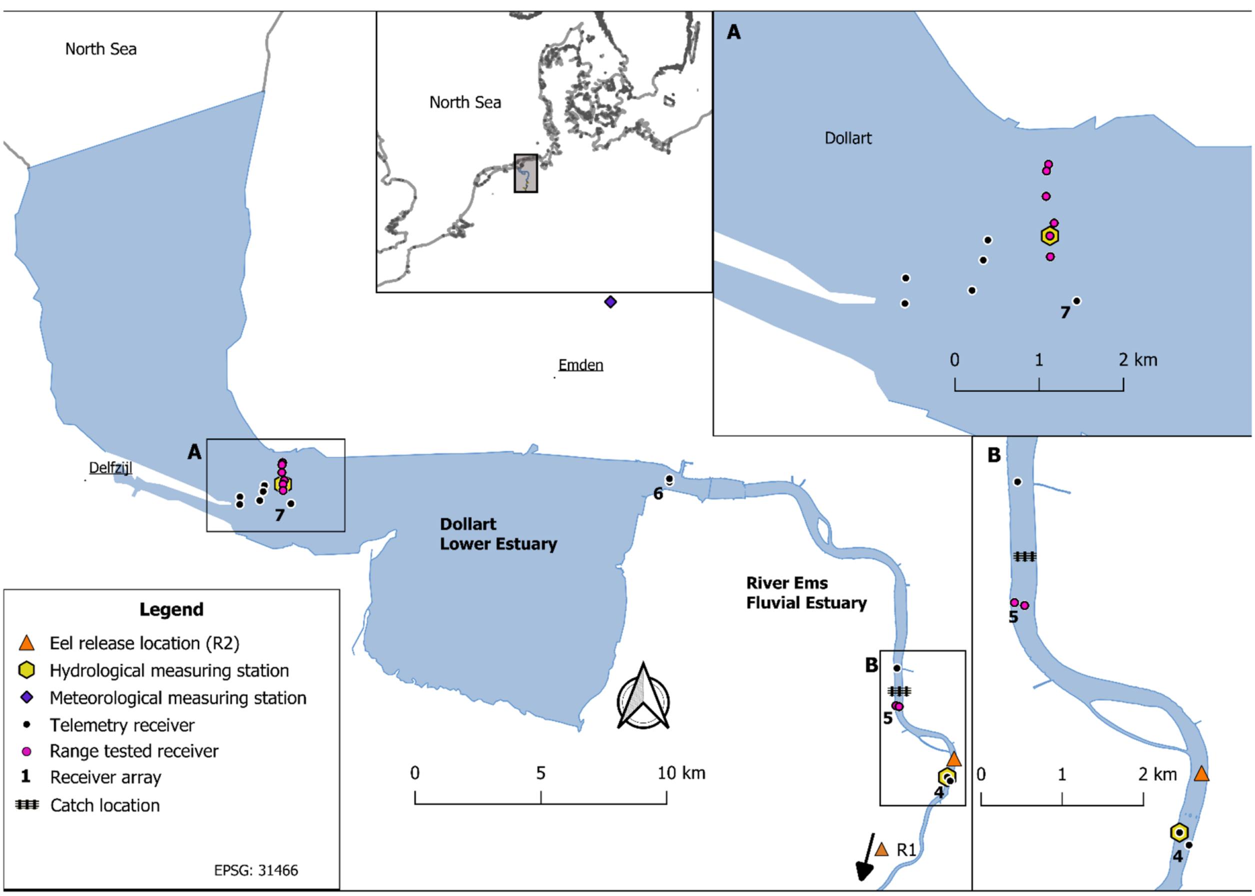

Fig. 1 Study area including the telemetry network along the Ems River, with detailed maps of the range-tested receiver locations, **A** Lower Estuary, **B** Fluvial Estuary. Catch and Release locations, environmental measuring stations and receiver arrays (4–7) are also marked. Arrays 1–3 and Release location 1 are located upstream in the inland area outside of the focussed study area

areas that necessitated a custom mooring system with a concrete anchor, polyester rope, and a floatation buoy. The assessment of the detection probability during different conditions was synchronised with the downstream migration of tagged silver eels to directly assess the effect of environmental conditions on their behaviour.

The detection probability is the number of detected acoustic signals divided by the number of emitted acoustic pings within telemetry receiver arrays. To test the acoustic detection probability and range of the receivers in the fluvial estuary (Array 5) and lower estuary (Array 7) constantly over a longer time period, a sentinel approach, with fixed positions of signal emitters and receivers was used. The tested receiver arrays were located in vicinity of stationary hydrological measuring stations, maximizing representativity of the environmental data. The arrays were unobstructed by structures such as meanders and shoreline irregularities, which would limit the signal transmission range or fully disrupt transmission [72]. Sentinel tags of selected receivers (see green markings in Fig. 1) were set to emit acoustic signals ("pings") every 10 min. Within the estuarine receiver array (Fig. 1A), the detection probability was tested for six receivers over different distances between 85 and 1097 m (Additional file 1: Appendix Table S1). In the fluvial estuary, the detection probability was measured using a receiver pair positioned 129 m apart.

Prior to the continuous assessment of detection probability, initial boat drifts were conducted in the fluvial estuary (setup see Additional file 1: Appendix Text-S1) from which the 50%-detection range (i.e., the range at which 50% of all pings are detected) was determined. This method helps to standardise the relation of detected and non-detected pings and to understand how this relation changes during changing environmental conditions [12]. The receiver pair in the fluvial estuary (Array 5) was chosen to best represent the calculated 50% detection range (corresponding to the 53% detection range instead of the 50% range).

The ping intensity of the built-in tags of the selected receivers in the fluvial and lower estuarine array was set to 142 dB to avoid interference of pings originating from implanted V9-tags pinging at 146 dB. The receivers were maintained regularly to change batteries and avoid accumulation of biofilm, sessile organisms and debris on the hydrophone.

Due to differences in the environmental conditions and technical setup the following analysis were conducted separately for the lower estuary (Array 6–7) and fluvial estuary (Array 3–6) (Fig. 1), with array 6 marking the boundary between both study setups.

Sampling

During this study, 234 female silver eels were tagged with acoustic telemetry tags (Vemco V9, 9 mm diameter; 2.0 g in water, min. 409 days of battery life), 35 of which were classified as Stage FIV and 199 as stage FV based on Durif et al. [19]. The transmission rate was set at 60 s with a random variation of $\pm$ 20 s, to avoid signal overlaps of multiple tags [67]. All eels were caught in a fixed stow net, located in the fluvial estuary within array 5. The net was emptied daily by a local fisher and eels were stored in a holding box and tagged within two days after catch. The tagging process was initiated by anaesthetization with clove oil (concentration: 0.09–0.17 ml l^{-1}, depending on temperature and salinity of the river water) until narcotic immobility was reached [73]. Once the eels reached the stage of narcotic immobility, total length, weight, eye diameter and pectoral fin length were measured, and an acoustic transmitter was surgically implanted into the body cavity. The incision was closed with two stitches, using a slowly absorbable monofilament suture (Surgicryl monofilament DS 24, 3.0 (2/0), SMI AG, St. Vith, Belgium) [63].

Additionally, a T-bar anchor tag was inserted in the epaxial musculature. Tagged eels were allowed to recover for 1–8 h in a dark tank with air dispersal to recover and released at an inland (R1) or tidal release location (R2). During the transportation to the R1 location, freshwater from an inland river site was added to the recovery tank to enable a gradual acclimatisation to lower salinity levels. Prior to release it was ensured that eels regained active swimming and flight reflexes. Since eels released in the inland- or tidal region did not differ in survival [27] and migration speed (LR-test: $p = 0.986$, Additional file 1: Appendix Figure S1), both groups were retained in the analyses.

The observation period covered two main migration seasons, defined as the period from 15.10.2020 to 27.02.2021 and 29.09.2021 to 27.02.2022 [27]. In the first season, the observation time was limited by drift ice, necessitating temporal removal of the stow nets and some receivers, thus no data were generated after the 05.02.2021 in the first season.

Environmental data

Hydrological parameters (water temperature, current speed, current direction, water level, electric conductivity, salinity, turbidity, O_2-conc.) were measured and obtained by measuring stations in the Dollart Estuary (within Array 7) and in the fluvial estuary (close to Array 5), operated by the local water authority WSV Ems-Nordsee (Fig. 1). Meteorological data (wind speed, precipitation) originating from the official German weather Agency Deutscher Wetterdienst (DWD) in Emden and Moormerland were associated with the lower and fluvial estuary, respectively as these were the closest measuring stations. Further, illuminated moon fraction was obtained from the R package "suncalc" for the geographic position 52.23196 N, 7.412325 E, located in the centre of the study area. All data were binned hourly based on the parameter with the lowest temporal resolution (wind speed and precipitation). Current directions between 31° and 211° in the lower estuary and 106° and 286° in the fluvial estuary were defined as upstream currents and marked with a negative prefix for the analysis of the eel behaviour. Additionally, accumulated precipitation of the last seven days was computed by summing up the hourly precipitation values. Moreover, the water level difference was calculated by subtracting water level at hour n—1 from water level at hour n. Although environmental influences were the main interest of this study, receiver internal data (tilt angle and surrounding noise) and the azimuth, following the definition of Reubens et al. [53], were included as predictor variables for the analysis of the detection probability. A low azimuth angle indicated that the receiver hydrophones are facing toward each other, while a high angle implied opposite facing directions, hence reducing the detection probability, as the receiver body blocks the hydrophone. For the fluvial estuary, hydrological data were missing from 03. to 16.12.2021, as the measuring instruments were not operational.

Statistical analysis

Model construction

Statistical analyses aimed at identifying the effect of environmental conditions on silver eel migration activity (i.e., the migrating fraction of eels present in the area) and speed, as well as acoustic detection probability. Analyses were conducted separately for the fluvial (Fig. 1B) and lower estuarine region (Fig. 1A). Accordingly, six generalised linear models were computed, each starting with a full model as described in Table 1.

The covariates were z-transformed (i.e., normalised by mean-centration and division by standard deviation) to facilitate immediate comparability within the observed range of values. Collinearity was defined by a correlation coefficient over rho > 0.7 (Spearman correlation test). If two explanatory variables were correlated, only one of the two covariates was included into the full model.

The parameters of the full model were eliminated in a stepwise backward selection procedure [78], based on AIC-values [2], to define the final minimum adequate model, prioritising models with fewer variables when the AIC was similar (AIC difference < 2). Selected models were validated by visual inspection of residuals over fitted values and normal-Q–Q plots.

Map creation, transect and distance calculation were conducted with QGIS (Vers. 3.14 "Pi ") [49]. All statistical analyses were performed in R version 4.1.0 [50] using packages "dominanceanalysis" (Vers.2.0.0) [47]

Table 1 List of all computed statistical models, with model type, dependent and independent variables

Abbreviation	Model (Family)	Full model	Excluded correlates
MSL (lower Estuary)	GLM (Gamma, log-link)	Migration speed ~ Wind speed + Precipitation + Acc. Precipitation + Water Temperature + Current velocity + Salinity + Moon fraction + Water level diff	O_2-Conc El. conductivity water level diff
MSF (Fluvial Estuary)	GLM (Gamma, log-link)	Migration speed ~ Wind speed + Precipitation + Acc. Precipitation + Turbidity + Water Temperature + Current velocity + Moon fraction + Water level diff	O_2-Conc water level diff.
MAL (Lower Estuary)	GLM (binomial)	Migration activity ~ Wind speed + Precipitation + Acc. Precipitation + Water Temperature + Current velocity + Salinity + Moon fraction + Last release	O_2-Conc El. Conductivity water level diff.
MAF (Fluvial Estuary)	GLM (binomial)	Migration activity ~ Wind speed + Precipitation + Acc. Precipitation + Turbidity + Water Temperature + Current velocity + Moon fraction + Last release	O_2-Conc water level diff.
DPL (Lower Estuary)	GLM (binomial)	Detection probability ~ Wind speed + Precipitation + Acc. Precipitation + Water Temperature + Current velocity (no prefix) + Salinity + Water level diff. + Last release + Water level + Azimuth*Tilt + Distance*Noise	O_2-Conc El. conductivity
DPF (Fluvial Estuary)	GLM (binomial)	Detection probability ~ Wind speed + Precipitation + Acc. Precipitation + Turbidity + Water Temperature + Current velocity (no prefix) + Water level diff. + Last release + Water level + Azimuth*Tilt + Distance*Noise	O_2-Conc El. conductivity

Variables in the column "excluded correlates" were eliminated from the maximum model due to collinearity with other parameters.

GLM Generalised linear model,

* interaction terms

and “parameters” (Vers.0.21.0) [37] for the dominance analysis.

Analysis of migration speed

Migration speed was analysed per transect between receiver arrays in relation to prevailing environmental conditions. Downstream migration speed of an eel was calculated as the time difference between first detection on an upstream array and the first detection on the next downstream array, divided by the distance between the two arrays in river-km. Only downstream movements that happened within 24 h (i.e., when an eel was detected at two arrays within 24 h) were retained in the analysis, to exclude non-directed downstream movements and to avoid unrepresentative means for environmental parameters over extended time periods The initial data exploration provided no evidence of a transect-length-bias (i.e., movements across longer segments were not excluded more frequently than across shorter transects). The environmental parameters were averaged over the duration of the downstream movement of an eel between two arrays. For the fluvial estuary migrations between Arrays 3–4, 4–5, 5–6 were considered. A generalised linear mixed-effects model with a random intercept for individual eel was fitted initially using the packages “nlme” (Vers. 3.1–152) [48] and “lme4” (Vers. 1.1–27.1) [6]. However, the random effect was subsequently excluded, as it had a negligible impact on migration speed and the model was reduced to a GLM for the fluvial- estuarine analysis. The model output of the GLMM and GLM were very similar. Therefore, the GLM (model “MSF”, Table 1) was used to facilitate comparability with the other models in the subsequent dominance analysis, which relies on R^2 values. For the lower estuary migrations between Arrays 6 and 7 were considered (model “MSL”, Table 1).

To assess the active swimming of eels during the downstream migration, migration speed in relation to the current velocity (hereafter “relative migration speed”) was calculated, by dividing the migration speed by the current velocity, with the exclusion of moments during average stagnant water ($<|0.01|$ m/s).

Analysis of migration activity

Migration activity was measured as the number of tagged silver eels exhibiting downstream movement (observed at receiver arrays), divided by the number of tagged individuals present in the observed area. The number of individuals in the area in increased by tagged eels entering the study area through downstream movements passing array 3 (fluvial estuary) or array 6 (lower estuary) or through release events. The number of eels in the fluvial estuary is reduced when a downstream migration is detected at array 6. Similarly, a detection at array 7 reduces the number of eels in the lower estuary and counts as escaped from the system. Migration activity was calculated separately for both migration season (i.e. the number of individuals in the study area was set to 0 before the second observation period) as eels remaining in system where not detected in the second season. This was done to minimize the effect of inactive eels (e.g., dead or sedentary eels from the previous season) lowering the migration activity in the second observation period. The hourly binned environmental and technical factors were summarised for tidal cycles as the predominant biological cycle in the area. A tidal cycle is defined by period of continuous decrease or increase in water level. Therefore, the data set consisted of alternating ebb and flood tidal cycles. It was expected that many eels would continue their migration shortly after their release. To account for potential bias towards environmental conditions shortly after release events, typically followed by high migration activity, an independent variable (hours since last release event) was included in each model. The environmental influences on migration activity in the fluvial estuary were tested with the MAF-model (GLM, binomial family) and in the lower estuary with the MAL-model (GLM, binomial family) (Table 1).

Analysis of the acoustic detection probability

To assess detection quality of the estuarine network array (Array 7), the relationship of distance (between two receiver units) and detection probability (i.e., the number of pings detected divided by the number of pings emitted at that given distance) was established. This was done on an hourly basis first and these datapoints were then summarised to get the distance detection probability relationship across the whole study period. From this relationship, the 50%- and 80%- detection ranges (i.e., the distances at which 50% or 80% of emitted signals are detected) were calculated.

In the fluvial estuary (Array 5), the given detection probability at 129 m (the distance of the observed receiver pair), was calculated [12].

The environmental influences on receiver performance were tested with binomial GLMs using the detection probability as response variable for the lower estuarine analysis (model “DPL”) and for the fluvial estuary (model “DPF”) (Table 1).

Chance of detection

To calculate the chance of detection (CoD), the shortest transect a migrating eel could theoretically take in the fluvial and lower estuary setup was determined with the intersect of the two overlapping detection radii of the receivers [40]. Transect length and migration speed of tagged eels (with average ping intervals of 60 s) provided information about the possible number of emitted acoustic pings per transect (P/T) at a given detection probability (DP, e.g., 50% for lower estuary, 53% for fluvial estuary). This allowed to calculate the chance of detection (CoD) for these setups of a migrating eel with the following formula:

$$CoD = (1 - \left((1 - DP)^{\frac{P}{T}}\right)) * 100$$

A high chance of detection validated the evaluation of the migratory patterns, as the number of undetected eels was rather low.

Dominance analysis

The relative importance of a given environmental factor in a selected model was determined by a dominance analysis [3, 4]. Dominance analysis determines the relative importance of individual variables in a multivariate model based on each variable's contribution to an overall model fit statistic (R^2). The dominance analysis was based on Pseudo-Mc-Fadden-R^2 fit statistics [43 and 1979) for binomial models (DPF, DPL, MAF, MAL) and Pseudo-Nagelkerke-R^2 values [46] for Gamma models (MSL, MSF, Table 1).

Higher R^2 values reflect a better fit for the model and values between 0.2 and 0.4 for the Pseudo-McFadden-R^2 are considered to represent an excellent fit [42, 43]. The relative importance and effect direction were used to compare the parameter´s influence on the three response variables in the fluvial and lower estuarine analysis respectively. Thereby, parameters could be identified that affect both migration behaviour and detection probability simultaneously.

Results

Migration speed

Average migration speeds of silver eels were 0.69 ± 0.41 m/s (mean ± SD), ranging from 0.05 to 1.44 m/s in the fluvial estuary and 0.62 ± 0.44 m/s (mean ± SD) in the lower estuary, ranging from 0.18 to 1.86 m/s. Migration speed was faster during conditions of high current velocity, lower turbidity and high precipitation (n = 198, Pseudo-Nagelkerke-R^2 = 0.545, model "MSF", Tables 2, 3). In the lower estuary, increased salinity, lower current velocities and water temperatures caused a slower migration (n = 142, Pseudo-Nagelkerke-R^2 = 0.689, model"MSL", Tables 2, 3).

The relative migration speed (swimming speed corrected for current velocity) was close to 1 in the fluvial and lower estuary, with exceptions during average stagnant waters (Fig. 2).

Migration activity

In total, 1080 tidal cycles within the observation period were analyzed. 89.44 and 87.86% of the observed migration activity were recorded during ebb tides (i.e., tide phases of downstream flow) for the fluvial and lower

Table 2 Summary of the surveyed environmental and technical parameters within the observation period, as well as their inclusion in the final models following model selection

Parameter	Fluvial estuary		Lower estuary		Relevant in model:
	Min–Max	Mean ± SD	Min–Max	Mean ± SD	
Noise [dB]	148.70–622.7	311.7 ± 106.38	151.40–831.60	300.6 ± 86.39	DPF, DPL
Distance [m]	129	–	85–1097	–	DPL
Tilt [°]	0.00–73.00	34.98 ± 18.86	0.00–178.00	28.78 ± 17.29	DPF, DPL
Azimuth	0.25–179.75	90.00 ± 14.98	0.00–180.00	89.99 ± 23.65	DPF, DPL
Current velocity [m/s]	− 1.54–1.70	0.22 ± 0.35	− 1.88–2.17	0.21 ± 0.88	DPL, DPF, MSL, MSF, MAL, MAF
Water level [cm]	281.4–899.1	540.9 ± 121.34	257.4–863.0	535.8 ± 107.37	DPL, DPF
Water level diff. [cm]	− 98.91–167.16	-0.045 ± 61.22	− 100.17 − 131.08	− 0.07 ± 53.1	DPL, DPF, (MSF), (MSL), (MAF), (MAL)
Water temperature [°C]	1.60–16.5	7.47 ± 3.05	1.83–16.67	7.75 ± 3.43	DPF, DPL, MSL
Salinity [‰]	0.13–2.76	0.47 ± 0.32	2.30–26.53	18.66 ± 4.59	MSL
Electric Conductivity [µS/cm]	0.17–3.48	0.64 ± 0.45	2.73–32.91	20.57 ± 5.94	(DPL), (MSL)
Turbidity [NTU]	54.4–2357.1	921.8 ± 498.28	51.00–545.17	130.12 ± 74.00	MSF
O2-conc. [mg/l]	1.81–11.21	7.41 ± 1.83	5.80–11.01	7.88 ± 1.11	(DPF), (DPL), (MSL)
Wind speed [m/s]	0.20–17.2	4.24 ± 2.14	0.20–17.2	4.24 ± 2.14	DPF, DPL
Precipitation [mm]	0.00–8.10	0.10 ± 0.37	0–00–9.70	0.11 ± 0.43	DPF, DPL, MSF
Accumulated Precipitation [mm/14 days]	0.00–55.80	15.39 ± 10.55	0.00–90.70	19.22 ± 15.08	MAF
Illuminated Moon fraction	0–1	0.52 ± 0.35	0 -1	0.52 ± 0.35	

Parentheses symbolize importance via a correlation. Model *MS* migration speed, *MA* migration activity, *DP* detection probability, F fluvial estuary, L lower estuary

Table 3 Summary of the minimum adequate models of factors influencing the migration speed and probability in the tidal area and estuary

	Parameter	χ2-value/*F* (Df, Fisher scoring index)	Effect direction	*p*-Value	Correlation with (correlation factor *ρ*)
MSF	Current velocity [m/s]	*F*(1,5) = 238.530	+	< 0.001***	WL diff. (– 0.93)
	Turbidity [NTU]	*F*(1,5) = 5.096	–	0.024*	
	Precipitation [mm]	*F*(1,5) = 1.993	+	0.158	
MSL	Current velocity [m/s]	*F*(1,5) = 238.530	+	< 0.001***	WL diff. (– 0.96)
	Salinity [‰]	*F*(1,5) = 1.993	–	0.158	El. Conductivity (0.87)
	Water temperature [°C]	*F*(1,5) = 5.096	+	0.024*	O_2-Conc. (– 0.75)
MAF	Accumulated Precipitation [mm]	χ2(1,10) = 2.0738	+	0.150	
	Current velocity [m/s]	χ2(1,10) = 12.451	+	< 0.001***	WL diff. (– 0.87)
	Time since release [h]	χ2(1,10) = 26.159	–	< 0.001***	
MAL	Current velocity [m/s]	χ2(1,10) = 10.457	+	0.001 **	WL diff. (– 0.90)
	Time since Release [h]	χ2(1,10) = 25.423	–	< 0.001***	

MS migration speed, *MA* migration activity, *DP* detection probability, F fluvial estuary, *L* lower estuary

estuary, respectively. Migration probability increased with less time elapsed since a release event.

Besides that, accumulated precipitation and current velocity increased the migration activity in the fluvial estuary ($N = 323$ downstream movements, Pseudo-McFadden-$R^2 = 0.24$, model "MAF", Tables 2, 3). In the lower estuary, high current velocities induced higher migration activity ($n = 173$ downstream movements, Pseudo-McFadden-$R^2 = 0.022$, model "MAL", Tables 2, 3).

Receiver performance

In the fluvial estuary (Array 5), 12,682 pings were emitted by both receivers in the tidal system of which 6,803 pings were detected. The average detection probability at the 129 m distance was 53.64% (Fig. 4). During conditions with an elevated water level, higher precipitation and higher azimuth the detection probability was increased while higher current velocity, noise, tilt, water level difference, wind and water temperature decreased the chance of receiving pings (Pseudo-McFadden-$R^2 = 0.489$, model "DPF", Tables 2, 4). In the estuary (Array 7) the six tested receivers emitted 219,714 pings, resulting in 144,168 detects by other receivers during the observation period. The 50%-detection range was evaluated at 197 m and the 80%- detection range at 98 m (Fig. 3, Additional file 1: Appendix Figure S2).

High current velocities, precipitation, wind speeds, water level and water level differences reduced the detection probability, while warmer water temperatures increased the detection probability in the lower estuary. Furthermore, a significant negative effect of the tilt angle in dependence of the calculated azimuth was evident. The negative effect of noise on detection probability became stronger with increasing distance (Pseudo-McFadden-$R^2 = 0.591$, model "DPL", Tables 2, 4).

Chance of detection

In the lower estuary the majority of eels (92.49%) were detected at receivers of array 7, covering the main current (based on models by [26] of the Ems River (receivers D1.1-D1.6, Fig. 1). Here, the shortest transect through the overlap of two receivers' 50%- detection range measured 221 m (Fig. 3). At average swimming speed, 5–6 pings could be emitted, resulting in a chance of detection of 98.3% under average conditions (Table 5). In the fluvial estuary the shortest transect within the main current was 223 m (Fig. 4) resulting in a chance of detection of 96.3% at average eel swimming speeds (Table 5). These were minimum estimates as the power output of the used V9-acoustic tags was higher (146 dB) than the output of the receiver's sync tags used to determine the reported detection ranges (142 dB). The estimated chances of detection suggested a very high detection efficiency and good receiver coverage of the setup.

Detectability

The dominance analysis of the three models per river area revealed that current velocity was a major influencing factor in all models. 97.5% and 78.5% of the eel's movement speed in the fluvial and lower estuary, respectively, can be explained by current velocity (which was highly correlated with differences in water level). Further, it accounted for 33.8% and 18.2% of the variation in migration probability in the fluvial and lower estuary area, respectively. Simultaneously, current velocity was a major influencing factor on detection probability in both

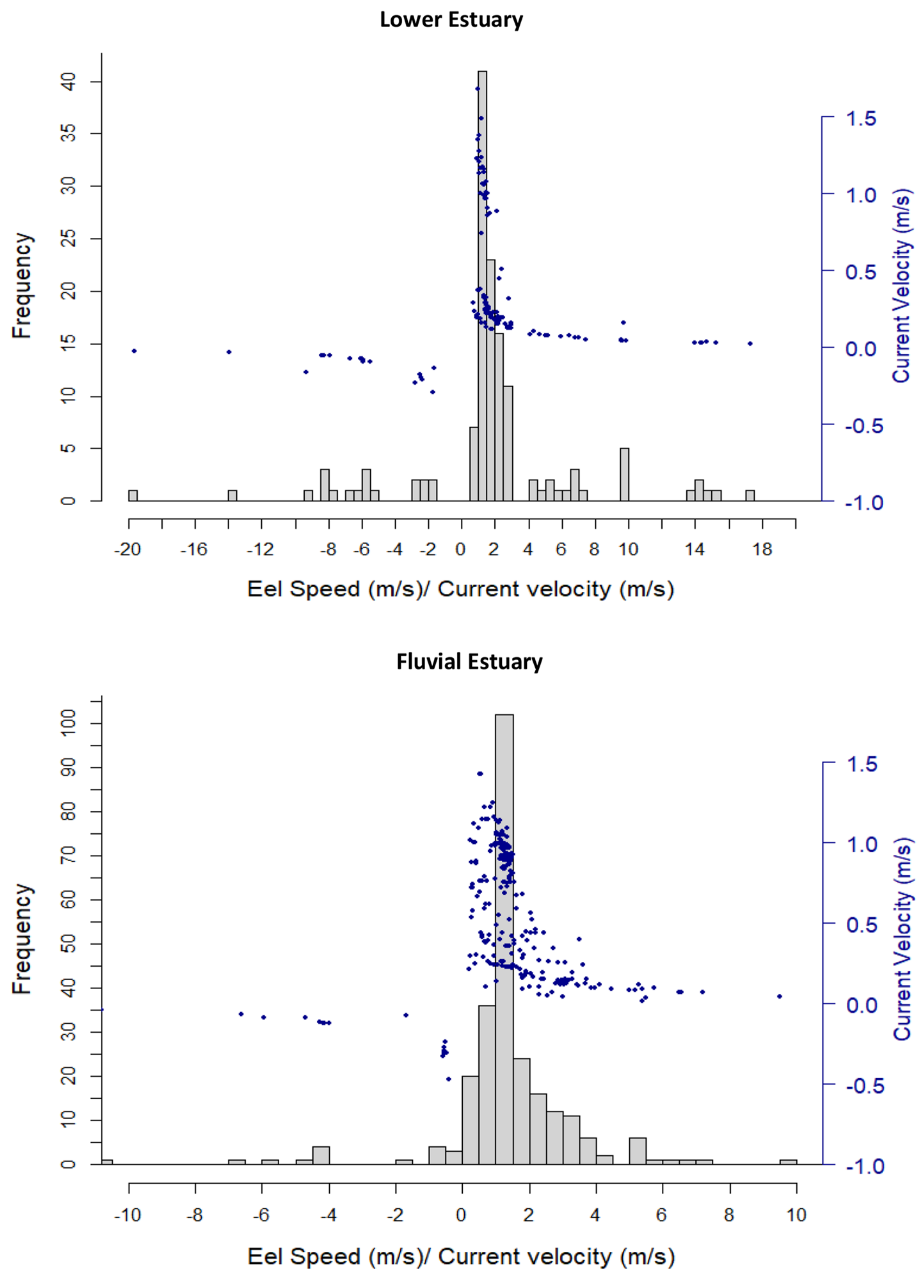

Fig. 2 Histogram of the relative migration speed (Eel swimming speed/Current velocity) of eels in the lower estuary (top) and fluvial estuary (bottom) with the blue dots marking the respective current velocity

river sections (relative importance in DPF model: 15.1%; DPL model: 10.0%), as was water level difference in the fluvial estuary (relative importance in DPF model: 19.0%). Minor positive effects of precipitation on detection probability (relative importance in DPF model: 0.8%), migration speed (relative importance in MSF model: 1.1%) and migration activity (relative importance in MSF model: 8.75%, here accumulated precipitation) was identified in the fluvial estuary. In the lower estuary the precipitation had a minor limiting effect on the detection probability (0.2%). Water temperature, however, had a contradictory effect on the detection probability. Higher water temperatures increased the detection probability (relative importance in DPL model: 2.9%) and migration speed (relative importance in MAL model: 4.1%) in the lower estuary, while decreasing the detection probability in the fluvial estuary (relative importance in DPF model: 9.5%) (Figs. 5, 6).

Table 4 Summary of the minimum adequate models of factors influencing the receiver performance i.e., detection probability in the fluvial and lower estuary

	Parameter	χ2-value/F (Df, Fisher scoring index)	Effect direction	*p*-Value	Correlation with (correlation factor ρ)
DPF	Water temperature [°C]	$\chi2(1,5)=13.52$	–	< 0.001***	O_2-Conc. (– 0.78)
	Water level [cm]	$\chi2(1,5)=343.82$	+	< 0.001***	
	Current velocity [m/s]	$\chi2(1,5)=247.11$	–	< 0.001***	
	Wind speed [m/s]	$\chi2(1,5)=47.77$	–	< 0.001***	
	Precipitation [mm]	$\chi2(1,5)=4.28$	+	0.038*	
	Water level difference [cm]	$\chi2(1,5)=1296.44$	–	< 0.001***	
	Azimuth	$\chi2(1,5)=759$	+	0.033*	
	Tilt [°]	$\chi2(1,5)=5.85$	–	0.016*	
	Noise [dB]	$\chi2(1,5)=632.23$	–	< 0.001***	
DPL	Water temperature [°C]	$\chi2(1,8)=103$	+	< 0.001***	El. Conductivity (0.87) O_2-Conc. (– 0.91)
	Water level [cm]	$\chi2(1,8)=64$	–	< 0.001***	
	Current velocity [m/s]	$\chi2(1,8)=502$	–	< 0.001***	
	Wind speed [m/s]	$\chi2(1,8)=3133$	–	< 0.001***	
	Precipitation [mm]	$\chi2(1,8)=4$	–	0.038*	
	Water level difference [cm]	$\chi2(1,8)=685$	–	< 0.001***	
	Distance [m]	$\chi2(1,8)=43{,}173$	–	< 0.001***	
	Noise [dB]	$\chi2(1,8)=1256$	–	< 0.001***	
	Tilt [°]	$\chi2(1,8)=120$	–	< 0.001***	
	Azimuth	$\chi2(1,8)=2$	+	0.189	
	Azimuth*Tilt [°]	$\chi2(1,8)=25$	–	< 0.001***	
	Distance [m] *Noise [dB]	$\chi2(1,8)=86$	–	< 0.001***	

Noise Acoustic background noise

Discussion

Migration speed and activity

Average migration speeds in this study were measured at 0.69 ± 0.41 m/s and 0.62 ± 0.44 m/s in the fluvial and lower estuary, respectively. This coincides with observations in the Meuse River averaging at 0.63 m/s [68] and is slightly higher than silver eels in the Rhine River, measured at 0.5 m/s [11], while slightly lower than migrations speeds in the tidal area of the Westerschelde with 0.95 m/s [69]. The maximum observed migration speeds of 1.44 and 1.86 m/s in the fluvial and lower estuary areas, respectively, are slightly lower than those recorded by Breukelaar et al. [11] with 2.20 m/s and coincides with observations in the tidal area by Verhelst et al. [69] with 1.87 m/s.

Current velocity was the major environmental factor influencing migration activity and speed of silver eels in the fluvial and lower estuary section of the Ems River. Current velocity was positively related to both, activity and speed, which is consistent with other studies [14, 17, 39, 52, 57, 65, 70]. In both river sections the eel´s swimming speed mirrored the current velocity closely, especially during periods of fast flow. This implies a rather passive locomotion, drifting with tidal currents, as also observed by Lenihan et al. [34]. The migration activity was highest during downstream currents, with 89.4 and 87.9% of migration events occurring during ebb tide in the fluvial and lower estuarine areas, respectively. In the estuary 92.5% of eels were first detected (per array) by receivers covering the main current. These findings strongly imply the utilization of selective tidal stream transport (STST) by silver eels during their riverine downstream migration. This is in accordance with findings of Verhelst et al. [69] in the Schelde river. This behaviour likely is an adaption to conserve energy during the initial phase of the long and energy sapping reproductive journey of eels and is a safe strategy to reach the ocean, minimizing risks of wrong turns or detours.

The results showed that higher water temperatures favoured higher migrations speeds in the estuary. All migrations occurred at temperatures between 4.6 °C and 16.2 °C, while the upper temperature limit above which eel activity diminishes due to low oxygen availability or other metabolic mechanisms was not present during our observation period [16]. These temperature-related migration preferences fall in range of past observations with 10°–16 °C in Spain [36], 4–18 °C in the River Imsa (Norway) [70], 8–16 °C in the Elbe

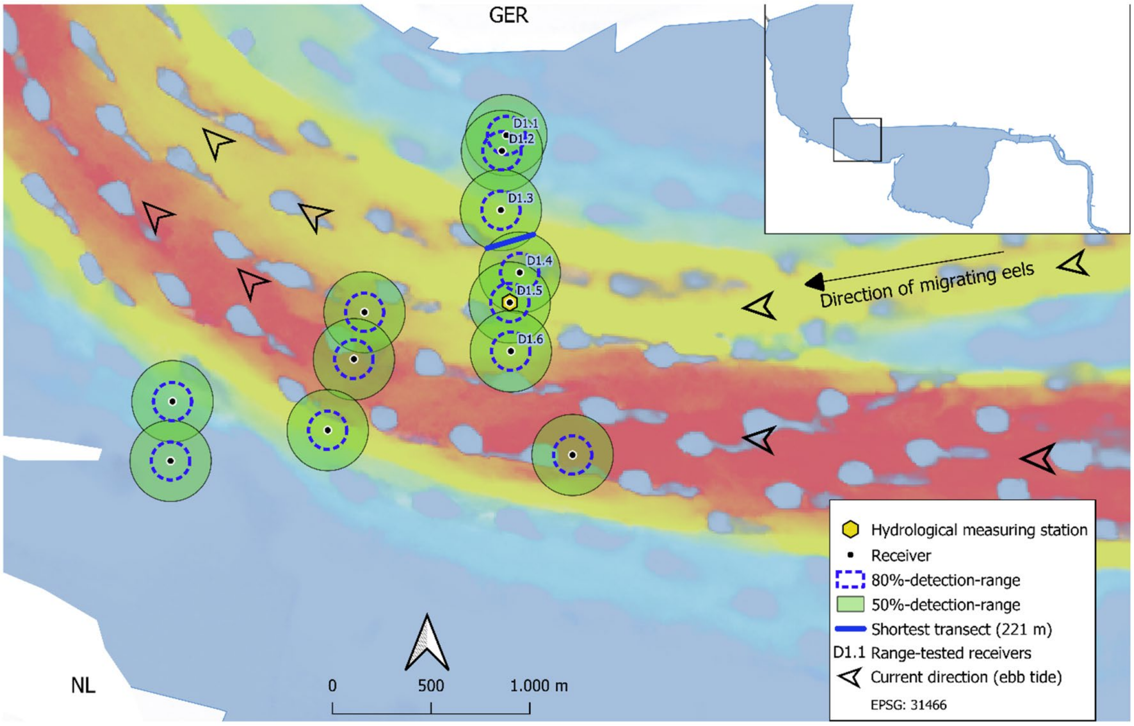

Fig. 3 Calculated detection radii during the main eel migration season in autumn of the estuarine receivers (Array 7); 80%-detection range = 98 m; 50%-detection range = 197 m. The blue rounded arrows indicate the current direction and the colouration symbolize different maximum ebb current velocities (red—fast (~ 1.4 m/s), yellow—medium (~ 1 m/s), green—medium slow (~ 0.7 m/s), blue—slow (< 0.5 m/s) originating from Herrling et al. [26]. Resolution of original figure upscaled using an AI-tool (aiseesoft.com)

(Germany) [57] and 6–15 °C in the River Loir (France) [13]. Corresponding with past studies, the results if this investigation indicate that a continuous drop in water temperature may be influential on the onset and end of the main migration season, after which eels enter winter dormancy, as the ectothermic metabolism limits the capability of eels to be active during cold conditions [75]. Higher ambient temperatures in early autumn may extend the inactive period, while milder winters provide suitable migration conditions.

Table 5 Chance of detection (CoD) in the fluvial and lower estuary of observed receiver arrays

	Lower estuary	Fluvial estuary
Shortest transect	221 m	223 m
Detection probability	50%	53.64%
Ø (max.) silver eel swimming speeds	0.62 (1.86 m/s)	0.69 (1.44 m/s)
Ø Pings/transect	5.9 (1.9)	5.3 (2.5)
Estimated chance of min. 1 detection	**98.3% (73.2%)**	**96.3% (78.9%)**

The bold values describe the CoD of a tagged eel under average (and maximum) swimming speeds

Migration speed in the estuary declined with increasing salinity. On one hand, this could be linked to tidal changes, as an influx of sea water into the Dollart Estuary is represented by elevated salinity levels, opposing the movement direction of eels, which results in lowered migration speeds, however, this was not reflected in the correlation analysis. On the other hand, brackish conditions also reduced the migration speed of eels in areas without strong tidal influences (Baltic Sea, [22], which could be linked to salinity acclimatisation. While this is not reflected by large differences in average migration speed between the fluvial and lower estuary in this study, the pre-selection of eels revealed that more eels exceeded the 24 h per transect threshold in downstream transects. During the downstream movements of silver eels, the salinity gradient in tidal river areas may support eels in their orientation [10].

Additionally, eels in the fluvial estuary showed increased activity during prolonged periods of higher precipitation and exhibited higher migration speeds. Periods of high precipitation possibly indirectly enabled faster migration speeds by elevating water level and current velocity in rivers providing optimal conditions for the downstream movement of silver eels. A positive effect

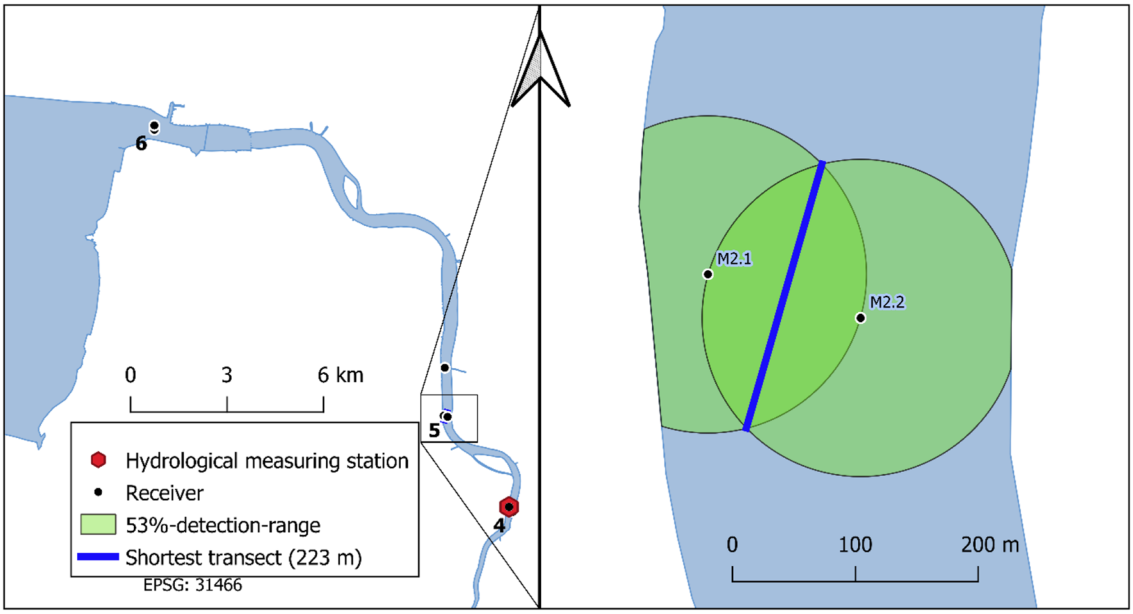

Fig. 4 The calculated detection probability of the range-tested setup (Array 5) in the fluvial estuary with the marked 53%-detection range and the shortest overlapping transect

of precipitation on the downstream migration of silver eels is supported by studies of Durif et al. [20], Stein et al. [57] and Trancart et al. [65].

Increased turbidity is usually linked with increased activity, as a probable predator avoidance adaptation. Further, increased turbidity hinders the influence of other extrinsic light, such as solar and lunar illumination and allows for regular migrations during daytime [13, 45]. In this study, high turbidity levels were associated with lower migration speeds in the fluvial estuary. Additionally, the highly anthropised river section in the fluvial estuary is prone to extreme turbidity (> 1000 NTU), regularly promoting hypoxic or even anoxic conditions [55, 61], and thus creating barriers for a continuous and fast eel migration [14]. These environmental conditions are already reflected by eel behaviour, a species known to be tolerant for low oxygen concentrations [18]. However, infection with the parasite *Anguillicola crassus* increases the sensitivity for hypoxic conditions [24, 33]. As past studies showed a high infection rate of eels in the area [33], hypoxic areas can slow down and possibly decrease the escapement success of the downstream migration of silver eels in the tidal area of highly anthropised rivers. Subsequently, the migration behaviour of other fish species, such as trout and salmon in the Ems River is expected to be impaired severely by these environmental conditions [18].

Apart from the environmental effects discussed above, the migration activity was strongly influenced by the time of release with most eels continuing their migration shortly after release. A similar effect was observed by Trancart et al. [65], highlighting the importance to account for this effect in models to avoid a release bias and, therefore, a misinterpretation of other parameters.

All in all, the models presented in this study predicted the migration speed, migration activity and detection probability well over the observed time period, explaining between 24 and 69% of the observed variation. As an exception, migration activity in the lower estuary was poorly explained by the considered factors (Pseudo-McFadden-$R^2 = 0.022$, model "MAL"). This might be in part due to an untested effect of turbidity the lower estuary, due to missing and erroneous measurements. The migration activity of downstream migrating eels was probably influenced majorly by factors in the upstream river areas, while in the estuary only tidal influences played a role in the continuation of the reproductive migration.

Receiver performance

Over the observation period the detection probability in the fluvial estuary at a distance of 127 m was at 53%, while the range at which 50% of all pings were received in the lower estuarine setup was at 197 m. However, these are slightly lower detection ranges compared to the ground-moored coastal Belgian telemetry network (~ 232 m at 148 dB), as proposed by Reubens et al. [53], due to a reduced power output (142 dB) of this study [59]

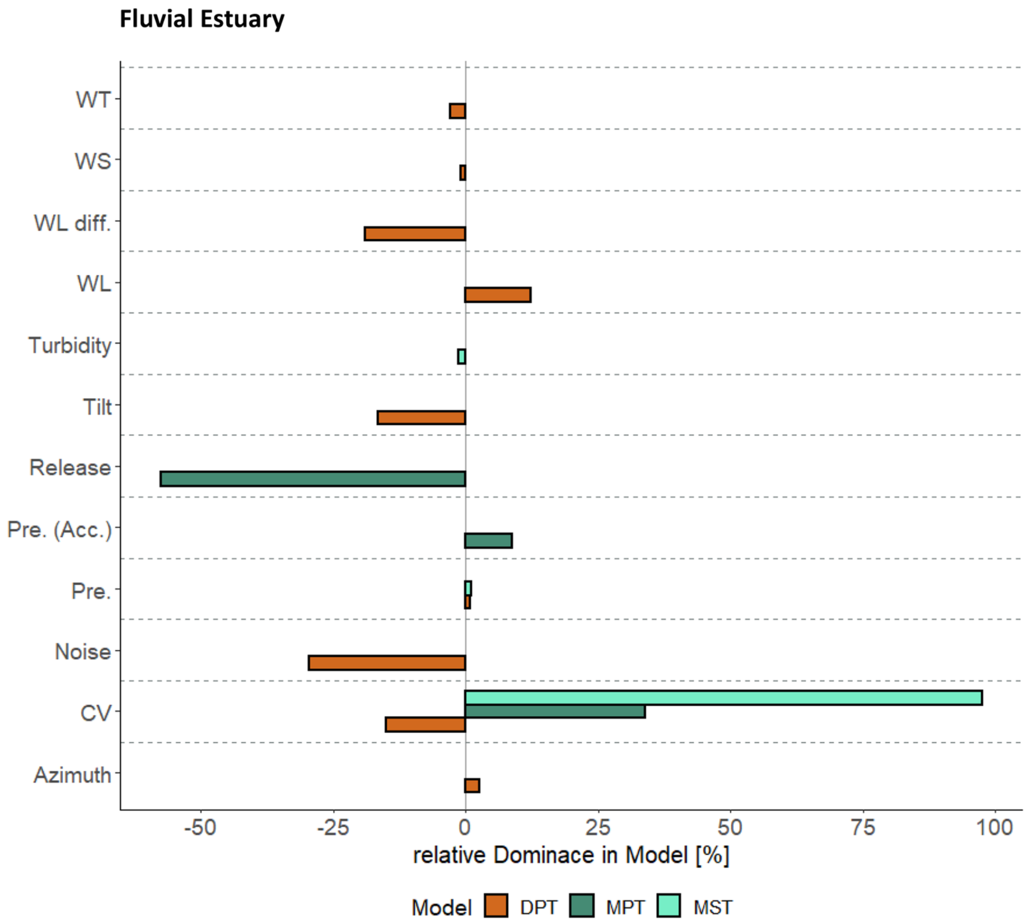

Fig. 5 Relative Dominance of the parameters in the final model in the three tested models DPF (Detection probability), MAF (Migration activity) and MSF (Migration speed) including their effect direction in the fluvial estuary, with bars to the left indicating a negative effect on the dependent variable and bars to the right indicating a positive effect on the dependent variable. *WT* water temperature, *WS* wind speed, *WL diff.* Water level difference, *WL* Water level, *Pre (Acc.)* Precipitation (accumulated), *CV* current velocity

and likely due to a shallower receiver installation at buoy chains. Therefore, surface-related disturbances (wind and waves), precipitation and the ambient noise of buoy chain rattling can have a comparably larger effect on the receiver performance than in a bottom installed receiver network [53]. The latter comes with a cost of complicated accessibility and sedimentation. Therefore, a receiver network installed closer to the surface allows for more regular maintenance, like battery exchange and clearing from biofouling, avoiding a further decrease in receiver performance.

Receiver performance, measured as the detection probability at a given distance, changed under varying environmental conditions. In the fluvial estuary water level, precipitation and azimuth increased the acoustic detection range, while high current velocities, ambient noise, tilt, water level differences, wind speeds and water temperatures decreased the chance of receiving pings. In the lower estuary the receiver performance was limited by high current velocities, precipitation, wind speeds, water level, water level differences and low water temperatures. Additionally, the negative effect of noise increased with rising distance between the receivers, while also a significant negative effect of the tilt angle in dependence of the calculated azimuth was evident.

Current velocity and water level difference were the major environmental impacting factors, negatively influencing the receiver performance in both river section. These findings are in accordance with other telemetry range test studies [40, 44, 51, 53, 66], suggesting that an increased water movement causes higher background noise and hinders signal detection.

Signals from tags and other receivers are more likely to be masked or not recognised under loud conditions. Also, anthropogenic sound sources, such as ship traffic or route maintenance work, were expected in the area, as the receiver ranges in many cases covered nautical

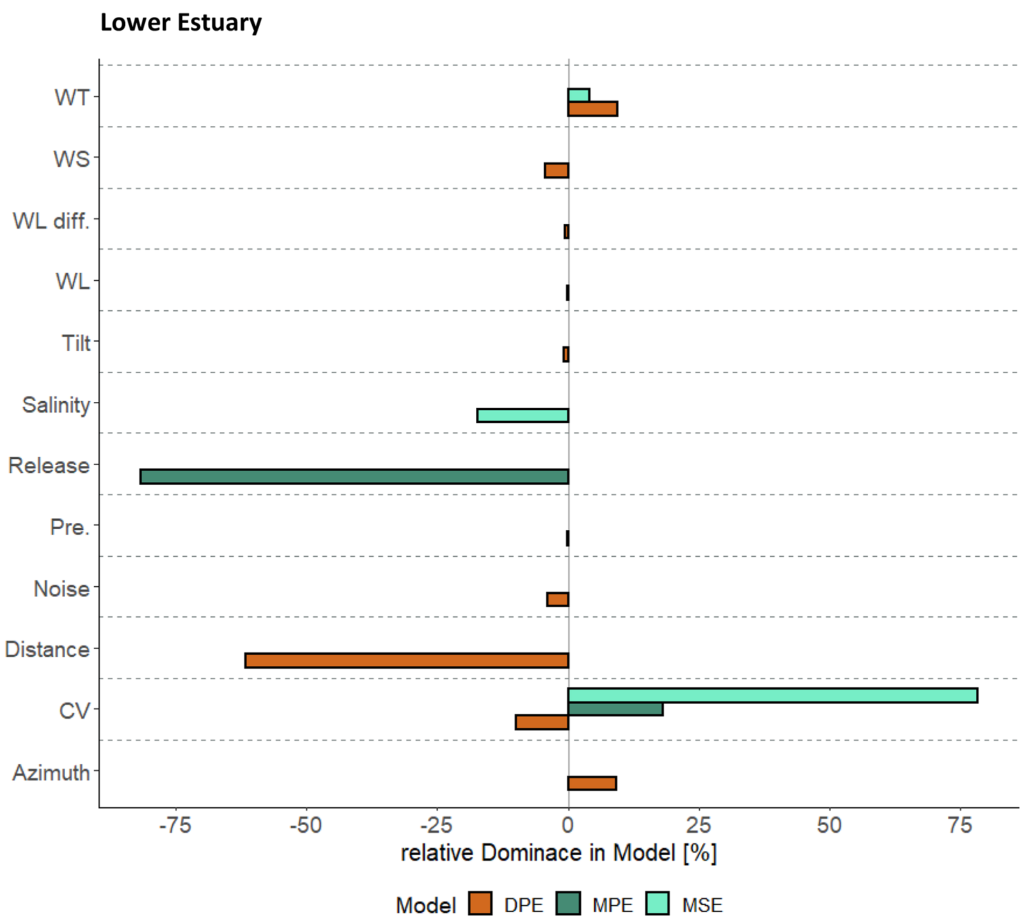

Fig. 6 Relative Dominance of the parameters in the final model in the three tested models DPL (Detection probability), *MAL* (Migration activity) and MSL (Migration speed) including their effect direction in the lower estuary, with bars to the left indicating a negative effect on the dependent variable and bars to the right indicating a positive effect on the dependent variable. *WT* water temperature, *WS* wind speed, *WL diff.* water level difference, *WL* Water level, *Pre.(Acc.)* Precipitation (accumulated), *CV* current velocity

navigation routes. In addition, the rattling of buoy chain elements was a major noise source close to the receivers.

Wind speed had a negative effect on detection range in both river sections. Wind induces wave movement [53], trapping air bubbles in the upper water column, thus deflecting and scattering acoustic signals [23, 32]. Further, as all receivers were located close to the water surface, the noise of breaking waves may also have been influential. The dominance analysis revealed that the explained variance of detection probability by wind decreased with distance from the river estuary. This coincides with a more sheltered position of the fluvial estuarine setup and the common meteorological patterns as wind speed was also more extreme in coastal regions than in inland regions. Generally, wind is considered to be an important influencing factor hindering signal transmission in many telemetry studies [23, 32, 53, 58].

Water temperature had an opposing effect on the detection probability in the fluvial and lower estuarine setup. Normally, higher water temperatures enhance sound transmission and therefore detection probability [77]. However, the presence of algae is also indirectly linked to higher water temperatures in early autumn, which can interfere with the sound propagation in water [76]. The observation period was set to cover the main migration period of the year which coincides with the roughest environmental conditions in the area. Therefore, the environmental conditions for the observation of summer migrating fish with acoustic telemetry are probably less limiting.

Dominance analysis and detectability

The dominance analysis approach allowed to rank order and compare the relative influence of environmental factors on the migration behaviour of eels and the acoustic detection range. Current velocity, closely correlated with differences in water level, had a major positive influence on migration activity and speed in both river areas, explaining between 18 and 98% of the observed variance in these contexts. On the other hand, current velocity and water level difference were a major influencing factor limiting the receiver performance in both tested areas, explaining between 10 and 19% of the observed variances. Therefore, this factor creates a bottleneck for detectability during the main migration phases. This is a highly relevant finding as it is likely transferable to other migrating fish species in tidal rivers that use STST. Therefore, when studying these species emphasis should be put on careful receiver placement in areas with high current velocities to avoid underestimating migrations during conditions of high or regular tidal currents. In this study distances between the receivers of 129 m in the fluvial estuary and 197 m in the lower estuary were sufficient to have a high chance of detecting tagged eels, even under condition of strong currents. Due to the unique nature of estuaries single-time surveys of detection range on a newly installed telemetry setup, e.g., through boat drift tests, should be carried out during periods of high river discharge to obtain the system specific minimum effective detection range. Yet, surveys of detection range over prolonged periods remain preferential over single observations [32]. A particular focus on a sufficient acoustic coverage along the main current is emphasized to detect most fish movements.

Similarly, but to a much smaller extent, precipitation increased migration activity and speed in the fluvial estuarine area. At the same time, precipitation limited receiver performance in the lower estuary (albeit with a relative minor importance). Further, higher water temperatures enabled higher migration speeds in the lower estuary while simultaneously enhancing the sound propagation [38, 77] favouring successful signal transmission. Conditions of high salinity in the lower estuary, closely correlated with electric conductivity water temperature, create beneficial conditions for detecting migrating eels because eels are slowed down and signal transmission is improved as the higher density of water benefits sound propagation [38, 77]. Notably turbidity can also be a limiting factor regarding detectability, which was not the case in this study. However, moderate turbidity levels can favour eel activity [14, 45], while a higher number of particles in the water column can scatter acoustic signals [56, 66].

Conclusion

This study suggests that European silver eels use selective tidal stream transport (STST) and passive locomotion during their downstream migration through tidal rivers. Likewise, current velocity was identified as the major driver of migration activity and speed in tidal and estuarine river landscapes. However, current velocity was also a major factor limiting the detection range of acoustic telemetry systems. As many migratory fish species use STST, this bottleneck can lead to underestimations of movement activity in telemetry studies during high currents, often coinciding with main migration phases. Therefore, this study emphasizes a careful placement of acoustic receivers in areas with regular strong tidal currents, especially when studying fish using STST.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-023-00353-y.

Additional file 1: Figure S1. Boxplot of the Swimming speeds of eels in the tidal area dependent on their release location. **Figure S2.** The influence of distance in the detection probability in the estuary with marked 50% and 80% detection range (197 m and 98 m respectively). **Table S1.** Distance matrix of the estuarine setup. **Table S2.** Summary of the R^2 values of the model and the respective variables of the final model for the movement speed and migration activity. **Table S3.** Summary of the R^2 values of the model and the respective variables of the final model for the detection probability. **Text S1.** Range-Testing of the Ems-Telemetry-Network.

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Author contributions

BM wrote the main manuscript text and created the figures and tables. BM, LH, JDP conducted the data analysis. BM, LH, JDP, MF, LM interpreted the results. BM, LH, JDP, MF, LM, RH prepared conception of the research. JDP, MF, LM, RH acquired the funding. All authors reviewed the manuscript.

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Availability of data and materials

The data underlying this article will be shared on reasonable request to the corresponding author. Telemetry detections data were uploaded to the European Tracking Network (ETN) data management platform (http://lifewatch.be/etn/) and will be publicly available after expiration of the moratorium period (https://lifewatch.be/etn/assets/docs/ETN-DataPolicy.pdf).

Declarations

Competing interests

The authors declare no competing interests.

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