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DOWNSTREAM MIGRATION OF THE EUROPEAN EEL (*ANGUILLA ANGUILLA*) IN THE ELBE RIVER, GERMANY: MOVEMENT PATTERNS AND THE POTENTIAL IMPACT OF ENVIRONMENTAL FACTORS

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ABSTRACT

Recruitment of European eels (*Anguilla anguilla*) has declined to the extent that they have been added to the IUCN Red List of Threatened Species. Therefore, it is critical to ensure that eels complete their outward river migration in order to contribute to the available spawning stock. We conducted a 4-year (2007–2011) telemetry study to understand the migratory behaviour and potential impact of environmental factors on the eel during this critical life stage.

Out of 399 female eels tagged with acoustic transmitters, only 28% demonstrated clear downstream migratory behaviour. Fifty-five percent were detected exhibiting no downstream migration behaviour and 17% were not detected at any monitoring station. Movement patterns of downstream-migrating (silver) eels were characterized by nocturnal activity and seasonal migration, with distinct peaks in autumn and spring. Migration was often discontinuous and exhibited phases of active locomotion and expanded stopovers. The most important determinants of movement activity were water temperature, cumulative precipitation and moonlight, although the significance varied by season and location in the river basin.

Our results evidence a discontinuous, stepwise migration over an extended period. Furthermore, our findings indicate that migration success depends on holding duration prior to tagging and environmental predictors with varying importance depending on the season, as well as the locations of capture, tagging and release.

KEY WORDS: acoustic telemetry; fish migration; environmental trigger; generalized linear model; handling effect; discontinuous migration; *Anguilla anguilla*; seasonal migration

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INTRODUCTION

The recruitment of European eels has been in steep decline and is currently only 1–5% of what it was in the 1970s (Åstrom and Dekker, 2007). Consequently, the species was added to the International Union for Conservation of Nature Red List of Threatened Species as *critically endangered* (Freyhof and Kottelat, 2010), and its stock is characterized as *outside safe biological limits* (ICES, 1999). The European Union (EU) has demanded that measures be taken to recover stocks through the implementation of national Eel Management Plans targeted to allow at least 40% escapement of reference silver eel biomass (EU, 2007).

Critical to maximizing silver eel escapement is an understanding of the factors that determine and regulate migratory behaviour. The downstream migration of anguillid species has been the subject of several studies and much speculation. The migration time is considered to peak in autumn and spring (Tesch, 2003). In the northern hemisphere, autumn migration takes place earlier at higher latitudes (August, September) than at lower latitudes (October–January) (Haro, 2003). Permanent monitoring in Germany's Warnow River, however, revealed continuous migration activity with high-temporal variation (Reckordt, *et al*., 2014).

Downstream migration activity of anguillids has been associated with numerous potential environmental predictors. These include hydrological variables (e.g. discharge, flow velocity and water temperature), climatic variables (e.g. barometric pressure, precipitation and air temperature), and the lunar cycle.

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Increased migration activity is often considered to occur during less-illuminated phases of the lunar cycle, but alternative explanations have been offered: Boëtius (1967) and Deelder (1970) assume an internal rhythm related to the lunar cycle but independent from moonlight, while others conclude that the absence of moonlight itself is the driving factor (Petersen, 1906; Lowe, 1952). Experimental studies have also concluded a direct avoidance of artificial light (Hadderingh, *et al*., 1999; Cullen and McCarthy, 2000) and a preference for distinct nocturnal behaviour (Petersen, 1906; Riley, *et al*., 2011). In contrast, two recent studies have reported no significant influence of moon phase on silver eel migration (Marohn, *et al*., 2014; Reckordt, *et al*., 2014).

Migration is often associated with increasing discharge events (Lowe, 1952; Hadderingh, *et al*., 1999) from both natural and artificial sources (Cullen and McCarthy, 2003; Acou, *et al*., 2005). Additionally, it is postulated that discharge regulation might obscure the underlying periodicity of the lunar cycle in regulated river systems (Cullen and McCarthy, 2003; Acou, *et al*., 2005).

The relationship between migration and water temperature seems to be expressed in preferable ranges or threshold values, which differ between geographical locations. In Brittany, Acou *et al*. (2008) observed migration peaks at water temperatures between 6°C and 10°C. Vøllestad *et al*. (1986) determined an optimal water temperature of around 9°C in Norwegian waters. In the German Warnow River, Reckordt *et al*. (2014) identified higher weekly migration rates at air temperatures greater than 10.4°C in combination with increased discharge and wind speed. Haro (1991) identified a range between 10°C and 18°C through experimental laboratory studies for Atlantic eels (genus *Anguilla*).

Eel migration speeds (also reffered to as progression rates) in European rivers are commonly reported in terms of ground speed with no consideration of flow (Verbiest, *et al*., 2012; Bultel, *et al*., 2014). But flow velocity is crucial for increasing accuracy when calculating migration speeds (Vøllestad and Jonsson, 1986). It has been observed that eels migrate more slowly than the flow velocity, if the latter is taken into account (Vøllestad, *et al*., 1986).

Management of *Anguilla anguilla* requires that a distinction is made between the sedentary yellow eel stage and the migratory silver eel stage. In this context, Durif *et al*. (2005) developed the silver index classification containing five identifiable maturation stages for female European eels. Stages I and II characterize growth phases, stage III a premigrant phase, and stages IV and V the two migratory phases. The silvering process is expressed by some physiological modifications, but it is still unknown whether internal or external factors are responsible for its initiation (Durif, *et al*., 2005). The process is assumed to be reversible (Svedäng and Wickström, 1997; Durif, *et al*., 2003) and might be supported by interruptions caused by obstacles or unfavourable migration conditions (Durif *et al*., 2003; 2005; 2006).

With this study, we aimed to obtain knowledge of the migratory behaviour of European silver eels in terms of preferable environmental conditions and the resulting patterns. Such knowledge is considered pivotal both for the management of an endangered species (Jeltsch, *et al*., 2013) and also for informing management options aimed at ensuring compliance with the abovementioned EU target (EU, 2007).

MATERIAL AND METHODS

Study site, eel capture and tagging

The study was conducted in a hydropower-free section of the Elbe River in Germany (length: 727 km, mean annual discharge: 305 $m^3 s^{-1}$, drainage area: 97 100 km^2), including the Havel River sub-basin (length: 334 km, mean annual discharge: 103 $m^3 s^{-1}$, drainage area: 23 900 km^2) between 2007 and 2011 (IKSE, 2007) (Figure 1). Downstream migrating silver eels from the Elbe and Havel Rivers were caught by local fishermen operating stow nets at six separate fishing sites. A total of 399 eels were tagged and released on 26 separate days between autumn 2007 and autumn 2010. All individuals were in good condition with a total body length > 55 cm, indicating that they were all females according to the distinct length-dependent sex dimorphism (Tesch, 2003). Eels were held in tanks at each site with free-flowing river water until sufficient numbers were available for tagging. Accumulated fishing/holding periods varied between 2 and 33 days (Table I and Figure 2). The eels were anaesthetized with MS 222 (Simon, *et al*., 2011) and biometric parameters were measured in order to calculate the silver stage according to Durif *et al*. (2005) (Table II).

Only eels that matched silvering stages III, IV or V were tagged. We performed surgical implantation into the abdominal cavity (Baras and Jeandrain, 1998; Winter, *et al*., 2006; Simon, *et al*., 2011), a procedure proven to be a suitable tagging method for the European eel (Økland and Thorstad, 2013). During surgery, the heads and gills of the anaesthetized eels were placed in fresh river water. After transmitter implantation, the incision was closed with 2–4 separate sutures with nonabsorbent silk (Prolene USP 5/0, Ethicon Inc., Somerville, NJ, USA). To evaluate the tagging procedure in terms of survival rates of the tagged eels, a control group ($n = 17$) was tagged with dummy transmitters and kept with nine untagged eels in a net cage for 10 weeks (Simon, *et al*., 2011). We implanted 308 individually coded acoustic transmitters of type V13 and 91 tags of

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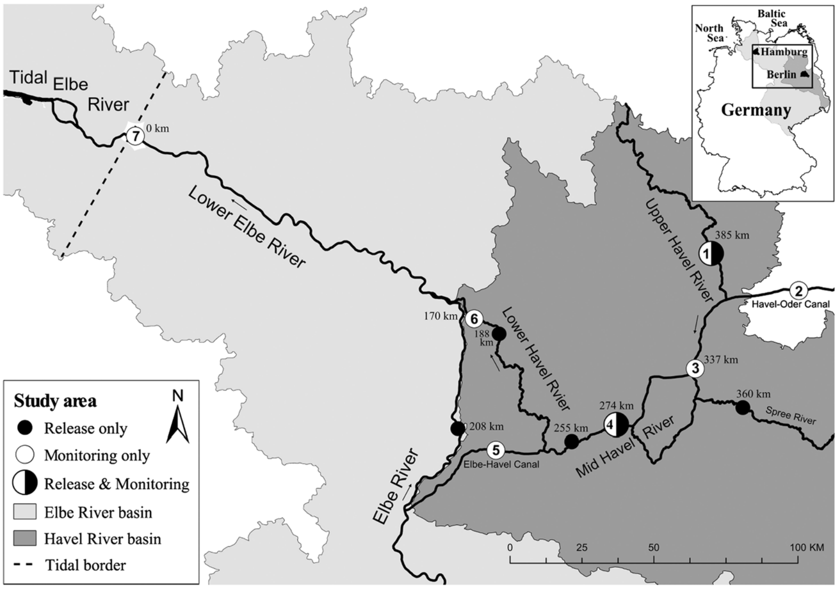

Figure 1. Study area. Small map shows the location of the study area (black box) within the German border. Light grey areas in both maps represent the Elbe River basin, and the dark grey areas mark the Havel River sub-basin. Black circles mark release sites, white circles mark monitoring stations and combined black/white circles mark sites where eels were released and monitored. Digits represent the 7 monitoring stations. River flow direction is indicated by arrows.

type V9 for smaller individuals (VEMCO, AMIRIX Systems Inc., Halifax, Nova Scotia, Canada). Indicative battery life varied between 333 and 711 days. Following recovery from surgery, the eels were released into shallow water a few kilometres upstream of the capture location before dusk.

Telemetry system

Twenty-eight automatic receivers (VR2W, VEMCO, AMIRIX Systems Inc., Halifax, Nova Scotia, Canada) were grouped at seven monitoring stations along the possible route to the North Sea (Figure 1). Monitoring station 2

Table I. Tagging periods and locations

				Fishing/holding
Tagging period	**Tagged eels**	**Migrants**	**Proportion** (%)	**Period (ø days)**
Autumn 2007	99	23	23.2	8.3
Spring 2008	14	5	35.7	3.0
Autumn 2008	89	12	13.5	13.7
Spring 2009	11	0	0.0	23.0
Autumn 2009	125	20	16.0	9.4
Spring 2010	20	15	75.0	8.0
Autumn 2010	41	37	90.2	4.0
Spring (total)	**45**	**20**	**44.4**	**16.0**
Autumn (total)	**354**	**92**	**26.0**	**10.0**
Release river section	**Tagged eels**	**Migrants**	**Proportion** (%)	**Fishing/holding Period (ø days)**
Upper Havel River	163	30	18.4	13.9
Mid Havel River	175	30	17.1	7.2
Lower Havel River	21	20	95.2	6.0
Elbe River	40	32	80.0	4.0

Note. The table summarizes the tagged eels per tagging period and release river section. Additionally, the number and proportion of migrants and accumulated fishing/holding periods are shown. Tagged eels = total tagged eels that matched silver index III, IV and V; Migrants = eels that were detected on at least two downstream monitoring stations. Additionally, eels that were released in the Elbe River and detected at the last monitoring station were defined as migrants.

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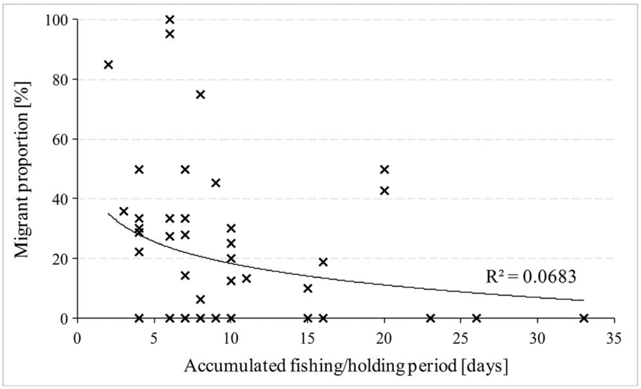

Figure 2. Relationship between migration proportion and accumulated fishing/holding period. Crosses mark the tagging dates. Solid line represents the trend line of the regression coefficient (R_N^2).

was placed inside the Havel–Oder Canal to cover the link between the Havel River system and the Oder River system. Monitoring station 5 covered the Elbe–Havel Canal, which might potentially function as a shortcut between the Havel River system and the Elbe River system. Prior to the receiver setup, we tested the listening arrays in the Havel and Elbe Rivers. Based on the determined arrays, we covered narrow river sections (mean width 45 m, ±12 m standard deviation (*SD*), range 28–55 m) with a single receiver, and wider river sections (mean width 115 m, ±34 m (*SD*), range 85–163 m) with two or three receivers. We deployed nine receivers (monitoring station 7) to cover the wide riverbed upstream of the tidal weir (width 450 m), and three for covering the parallel sluice canal (width 143 m). Receivers were also placed upstream and downstream of the release sites.

Data aggregation

Data on eel passage from the receivers were split into arrivals and departures and used as a proxy for movement activity. Repeated detections by the same individual on the same receiver within a 24 h period were excluded from the analysis to prevent a bias of tag location at the extreme end of the receivers' range (i.e. fluxing in and out of range without exhibiting any clear movement). Otherwise, all arrival and departure detections were grouped accordingly and used as the response variable representing a proxy for eel movement activity in the model estimations.

Furthermore, for the purpose of statistical analysis, we defined migrants and non-migrants. Eels that were detected sequentially on at least two downstream monitoring stations were defined as migrants. Eels that were released into the Elbe River and detected at the last monitoring station (Figure 1) were additionally defined as migrants. Only movement activity produced by migrants was used for estimating the models.

Moonlight data (fraction of the Moon illuminated) were downloaded from the US Naval Observatory Astronomical Applications Department (2012). Hydrological data were provided by the German Federal Institute of Hydrology (BFG) and climate data were downloaded from WebWerdis (German Meteorological Service, 2012). We tested moonlight (fraction of the Moon illuminated), sunshine duration (h D^{-1}), and the following hydrological and climate predictors, which were averaged over a 1-day period: discharge ($\text{m}^3\,\text{s}^{-1}$), flow velocity ($\text{km D}^{-1}$), water temperature (°C), barometric pressure (hPa) and precipitation (mm D^{-1}). Depending on the river section and season, discharge variability was high and ranged from less than $10\,\text{m}^3\,\text{s}^{-1}$ in the Upper Havel River to $3500\,\text{m}^3\,\text{s}^{-1}$ in the Elbe River. In addition, we generated variables for cumulative precipitation (covering the preceding 7 days up through the present) as well as the differences between the present and the preceding 7 days for all hydrological and climate predictors. These additional variables were added to the data set as independent potential predictors. Measured and generated variables that describe the same predictor variable are termed as 'variable group'.

Data analyses and modelling

We used generalized linear models to analyze the relationship between movement activity and environmental parameters (Manel *et al.*, 1999). Models were developed on three data sets; model details are provided as online supplementary material. The data set for the complete model

Table II. Morphological fish parameters in relation to silver index

Silver index	***n***	***M* (g)**	**L_T (mm)**	***D* (mm)**	**L_F (mm)**	***k***
III	76	749	730	8.7	32.5	0.19
		±191 *SD*	±64 *SD*	±0.7 *SD*	±3.5 *SD*	±0.02 *SD*
IV	209	1168	815	10.4	37.6	0.21
		±255 *SD*	±57 *SD*	±0.9 *SD*	±4.3 *SD*	±0.02 *SD*
V	114	716	717	9.8	36.2	0.19
		±149 *SD*	±52 *SD*	±0.8 *SD*	±4.2 *SD*	±0.02 *SD*

Note. *M* = body mass; L_T = target length; *D* = eye diameter; L_F = pectoral fin length; *k* = corpulence factor; *SD* = standard deviation.

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contains movement activity of all migrants and associated environmental predictors. Additionally, we analyzed subsets considering only the first (spring: 01 Jan–31 Jul) and then the second half of the year (autumn: 01 Aug–31 Dec) and specific river sections. With a fourth data set, we tested the relationship between the migration probability (0 = non-migrant, 1 = migrant) of the 399 eels and external factors.

Prior to analysis, all environmental predictor variables were checked for bivariate (Spearman) correlation. According to Dormann *et al.* (2013), we used only predictors with correlation coefficients less than 0.7 within the same model. For depicting the unimodal relationship in case of water temperature, we included the squared term of the predictor. We used backward stepwise variable selection based on the Bayesian Information Criterion (BIC) and selected only the predictor with the lowest BIC out of each variable group.

For assessing the models' goodness-of-fit, we calculated two different performance measures: the area under the receiver operating characteristics curve (AUC) (Fielding and Bell, 1997) and the pseudo-R^2 according to Nagelkerke (1991). Internal model validation was performed by bootstrapping with 10 000 iterations (Schröder, *et al.*, 2008; Verbyla and Litvaitis, 1989). Additionally, we applied hierarchical partitioning for determining independent predictor effects (Mac Nally, 2002).

Based on the amount of tagged and released eels, as well as recaptures and indicative battery life of the transmitters, we calculated the amounts of detectable eels by month for the years 2007–2011. Subsequently, we calculated the proportions of the detected eels. Periods of increased migration activity (spring and autumn) were marked as migratory periods.

We used the movement activity to determine the nocturnal migration patterns. Because of seasonal differences in length of day, we conducted our analysis for each season separately (spring: 01 Mar–31 May, summer: 01 Jun–31 Aug, autumn: 01 Sep–30 Nov, winter: 01 Dec–29 Feb). The absolute activity frequencies for each season were calculated with reference to time of day (00:00 h to 23:00 h).

Progression rates were calculated for 175 time periods during which the migrating eels covered the distance between two monitoring stations. In order to enable comparisons between different seasons associated with varying discharge and flow velocity, we standardized the progression rate by the local flow velocity (v_{flow}), providing standardized progression rates ($v_{\text{prog.standard}}$). We calculated $v_{\text{prog.standard}}$ for the 175 periods, considering the dynamics of local flow velocities. Different sample sizes depended on varying migration activity during the seasons (spring: $n = 58$; summer: $n = 6$; autumn: $n = 93$; winter: $n = 18$).

Firstly, we calculated $v_{\text{prog.standard}}$ considering a 24 h potential migration time per day ($t_{\text{pot.mig}}$) assuming that eels show migration activity during the entire day independently from daylight. Secondly, we recalculated $v_{\text{prog.standard}}$ in adaption to the nocturnal migration pattern (Figure 3a) and differences in season-related day length, and considered the following $t_{\text{pot.mig}}$: spring and autumn = 12 h, summer = 8 h and winter = 16 h.

The length of time between the first and last detections of the migrating eels was the migration duration. After the last detection, eels either left the study area for the sea or did not re-enter the detection range of the deployed receivers within the range of the transmitters' indicative battery life. Depending on the migration duration, we classified the migration types (Figure 4). Migration type 1 (MT1) represents migrants showing movement activity during the tagging migratory period (time span: release date + 100 days). Migration type 2 (MT2) represents eels showing movement activity up to the end of the following migratory period (time span: release date + 100–275 days). Migration type 3 (MT3) represents eels showing migratory activity for about 1 year or longer (time span: release date + > 275 days).

Statistical calculations were performed using the free statistical software R (R Development Core Team, 2013) with the packages fmsb (Nakazawa, 2011), plotmo (Milborrow, 2011), dismo (Hijmans, et al., 2013) and rms (Harrel, 2013). The package hier.part (Walsh and Mac Nally, 2013) was modified to allow the analysis of variable groups (according to M. Nobis, pers. comm.). Additionally, we applied LR-Mesh (Rudner, 2004) for visualizing response surfaces.

RESULTS

Migrant proportions

Of the tagged eels, 17% ($n = 68$) were not detected at any monitoring station, 55% ($n = 219$) were detected without exhibiting downstream migration behaviour, and 28% ($n = 112$) of the tagged eels showed movement patterns interpreted as active downstream migration.

Our defined migrant criteria were matched by 44.4% of the spring-released eels and 26.0% of the autumn-released eels (Table I). Migrant proportions were significantly higher in the lower river sections (Lower Havel = 95.2%; Elbe = 80.0%) than in the two upper river sections (Upper Havel = 18.4%; Mid Havel = 17.1%).

Migration types and success

Migration type 1 accounted for 20% ($n = 79$) of the eels exhibiting migratory behaviour with a mean migration time of 13 days (range: 1–78 days). Except for one, all migrants that were tagged and released in the Lower Havel and Elbe belonged to MT1. MT2 accounted for 6% ($n = 24$), with a mean migration time of 204 days (range: 101–270 days). MT3 accounted for 2% ($n = 9$) of migrating eels, with a

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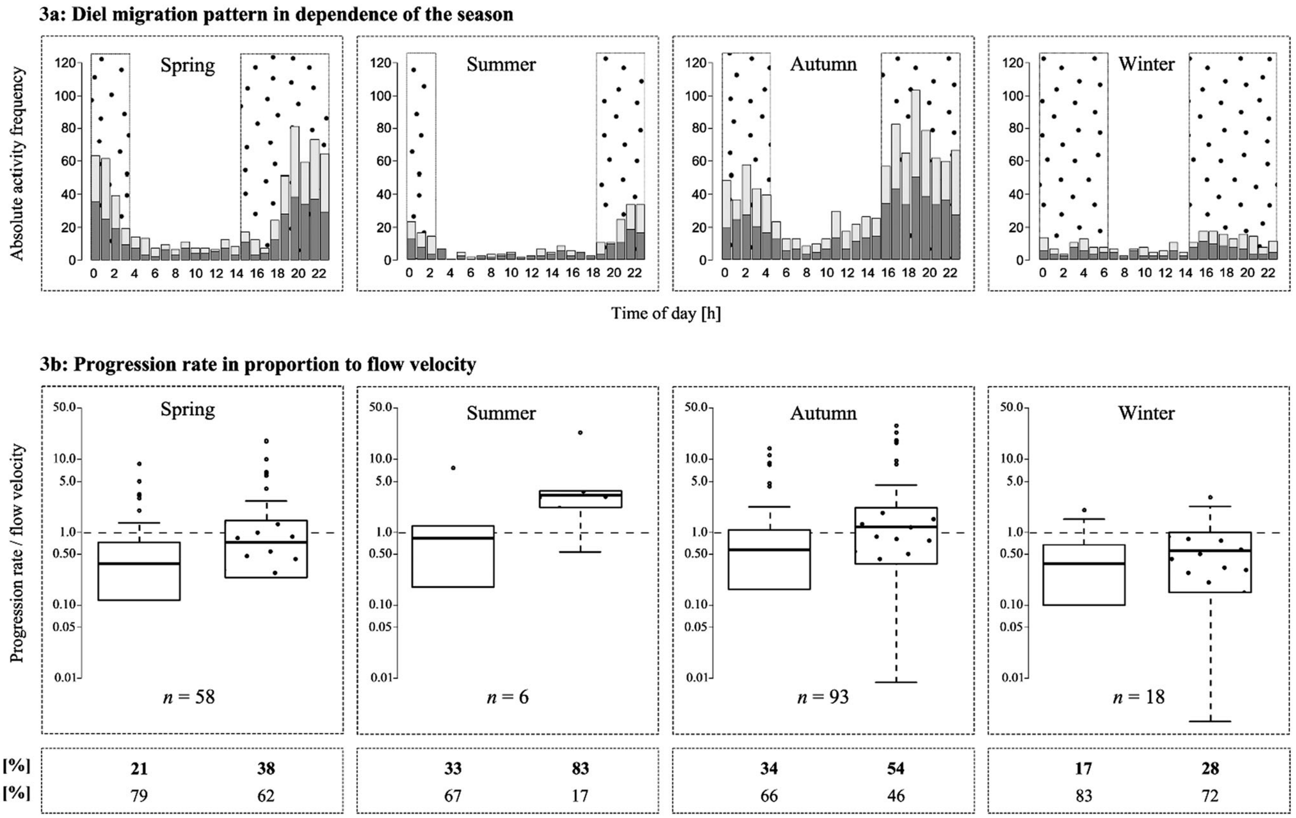

Figure 3. Diel migration pattern and progression rates. 3a: Bars represent the combined absolute frequency of arrival (light) and departure signals (dark) induced by migrants related to time of day and separated by season. Dotted areas mark daily periods with increased migration activity. 3b: Box plots represent eels' progression rates divided by the local river flow velocity (white: 24 h $t_{\text{pot.mig}}$; dotted: adapted $t_{\text{pot.mig}}$). The horizontal dashed line represents the local flow velocity.

mean of 379 days (308–537 days). In contrast to migrants released downstream, those released in the Upper and Mid Havel appeared in all three migration types (Figure 4).

Eight of the 24 migrating eels released in the Upper and Mid Havel River successfully reached the last monitoring station. In contrast, 52 out of 53 migrants released in the Lower Havel and Elbe Rivers successfully reached the last monitoring station at the tidal border (Figure 1). The percentage of migrants that successfully passed the last monitoring station during the study period varied between 76%, 63% and 56% for MT1, MT2 and MT3, respectively.

Diel periodicity of movement activity

Migration patterns were characterized by increased movement activity during the less-illuminated hours of the day (Figure 3a). In spring and autumn, when night and day are approximately of the same length, increased movement activity started in the afternoon, peaked around 19:00 h and decreased in the early morning (03:00–05:00 h). During the summer months, the absolute activity frequency is significantly lower, and the window of minimal movement activity reaches from 02:00 h to 18:00 h. In winter, movement activity is lowest and disparities are less distinctive.

Seasonal migration pattern and progression rates

Migration activity peaked in spring and autumn, with minima in late winter and mid-summer (Figure 5). Twenty-seven percent of the standardized progression rates exceeded the local flow velocity, when considering a potential migration window of 24 h per day ($t_{\text{pot.mig}}$) (white box plots; Figure 3b). If the migration window was adapted to the nocturnal migration pattern, 47% exceeded the local flow velocity (dotted box plots). In autumn, outliers exceeded the flow velocity by ratios of up to 28% if the adapted $t_{\text{pot.mig}}$ was considered. In contrast, the maximum ratio was lowest in winter (up to 3%).

Factors affecting eel migration

A minimum adequate generalized linear model considers the highly significant predictors of water temperature, moonlight and cumulative precipitation of the last 7

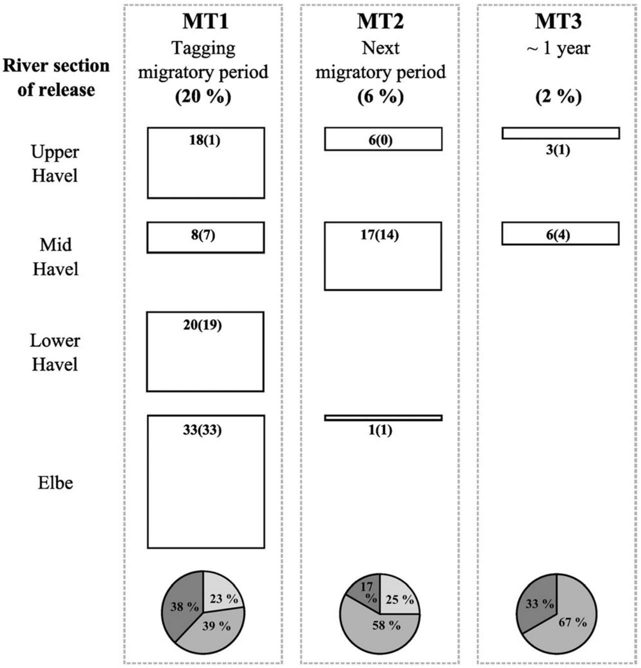

Figure 4. Migration types and their affiliation to release location. Bar and pie diagrams represent the three migration types (MT1–3). Bars show the absolute number of migrating eels for each release location, indicated by river section of release on the left side. Pie diagrams represent proportions of the silver index indicated by the colours: light grey = silver stage III; medium grey = IV; dark grey = V. Digits represent the number of eels that showed downstream migration activity; the number of eels that finally passed the last monitoring station is displayed in brackets.

days.The linear predictor reads as follows: $-5.19 + 0.62 \times T_{\text{water}} - 0.03 \times T_{\text{water}}^2 + 0.01 \times \mathrm{P}_{\text{cum7}} - 0.74 \times$ Moonlight. Details on all estimated models are provided as online supplementary material. Water temperature represents 81.4% of the explained variance in the data set, cumulative precipitation of the last 7 days 10.5%, and moonlight 8.1%, respectively. In the case of low precipitation, model surfaces for full moon and new moon conditions indicate an optimal temperature range between 8°C and 16°C (Figure 6). Along with increasing precipitation, the temperature window expands and migration probability increases. Model performance is $R_N^2 = 0.14$ and AUC = 0.77 after internal validation.

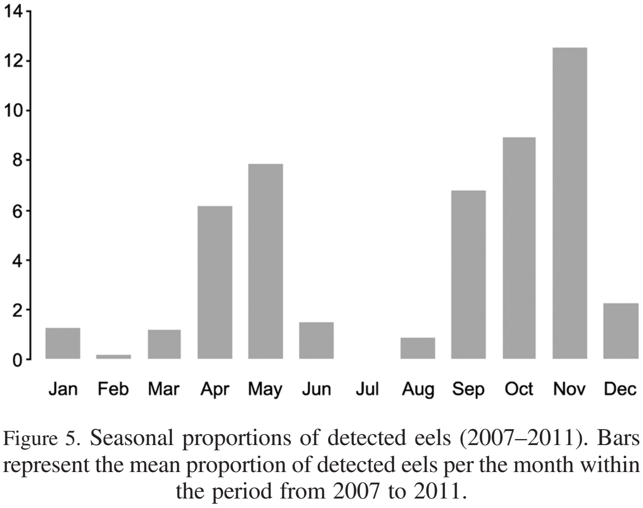

Figure 5. Seasonal proportions of detected eels (2007–2011). Bars represent the mean proportion of detected eels per the month within the period from 2007 to 2011.

Models estimated for spring and autumn differ in the importance of their predictors. The autumn model considers water temperature, cumulative precipitation of the last 3 days and moonlight (all variables $P < 0.001$). It gains better model performance ($R_N^2 = 0.23$, AUC = 0.82) than the complete model, and the importance of moonlight and precipitation increase. In contrast, the spring model considers only water temperature ($P < 0.001$) as an important variable.

Models that were estimated on subsets, which were divided according to river section, provide a more differentiated picture. In the Upper Havel River, only water temperature is significant ($P < 0.001$), but model performance is low ($R_N^2 = 0.07$, AUC = 0.70). The minimum adequate model for the Mid Havel River section ($R_N^2 = 0.21$, AUC = 0.81) additionally considers discharge and moonlight (both $P < 0.001$), but water temperature represents 73.1% of the explained variation. In contrast, the model for the Lower Havel River ($R_N^2 = 0.22$, AUC = 0.84) considers decreasing barometric pressure during the last 7 days ($P < 0.001$) in addition to water temperature, which covers 80.3% of the explained variation. The model for the Elbe River ($R_N^2 = 0.49$, AUC = 0.95) considers water temperature and cumulative precipitation of the last 7 days as the vari-

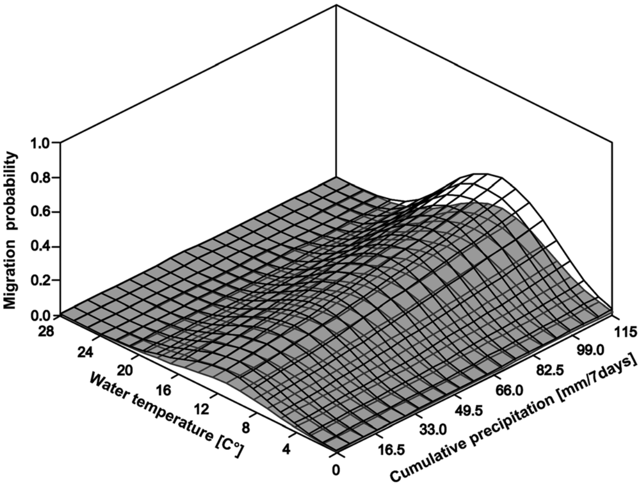

Figure 6. Migration probability in dependence of environmental factors. The two surfaces represent the model response for the predictor variables water temperature in °C and cumulative precipitation of the last 7 days in mm. Grey surface represents the response for full moon conditions (fraction of the Moon illuminated is set to constant 1); Mashed surface represents the response for new moon conditions (fraction of the Moon illuminated is set to constant 0). Model: Migration probability = exp(linear predictor)/(1 + exp(linear predictor))

ables with the highest independent effects (48.3% and 47.1%, respectively). Flow velocity explains only 4.6% of the explained variation.

The distance between site and tidal border has the largest effect on migration probability ($P < 0.001$) and the independent effect is considered to cover 62.2% of the explained variation. Furthermore, the independent effect of the accumulated fishing/holding period (17.1%) implies a handling effect that is negatively correlated with increasing holding duration (Figure 2). In contrast, the very low independent effect of the silver index (0.2%) implies no significant relation between silver stage and migration probability.

DISCUSSION

The evidence from this study supports the assumption by Durif *et al.* (2003; 2006) that the migration process of European eels in large rivers is discontinuous and that in very large rivers, eels may need more than one migratory season to reach the sea and may revert to a non-migratory life stage. In the present study, migration probability was related to distance from the sea. Eels that were tagged in the upper river sections were less likely to complete their migration and tended to remain longer in the river system than eels that were tagged in the lower river sections. This further implies the possibility of a stepwise migration over an extended period. A recent study on silver eels monitored similar patterns: Bultel *et al.* (2014) observed longer individual residence times in the upstream estuary and shorter ones in the lower estuary when studying silver eels in the Loire River in France. They hypothesize a possible waiting behaviour in the upstream estuary and a directional migratory behaviour in the lower estuary. In contrast, Aarestrup *et al.* (2008; 2010) observed a 2-step migration in Danish waters, including a rather quick downstream migration in the river followed by a substantial residence period in the inner fjord before continuing the journey towards the ocean. For an explanation of our findings, we can postulate two hypotheses: (1) downstream caught, tagged and released eels are already ‘more mature’ than the eels in the upper sections – which would not be reflected by the silver index (Durif, *et al.*, 2005). Consequently, external features alone may not be sufficient to predict the migration readiness as proposed by Bultel *et al.* (2014) and Simon *et al.* (2011). (2) Eels respond to physio-morphological changes in the river, which is indicated by the different variable considerations in the explanatory models fitted to each river section. The model for the Upper Havel (more upstream) considers only water temperature to be relevant for the downstream migration. Instead, the model for the Elbe (more downstream) considers both water temperature and cumulative precipitation of the last 7 days. The use of precipitation as a potential predictor variable in addition to discharge is the result of considering the following assumption that has been stated by Trancart *et al.* (2013) for small river systems: precipitation (rainfall) can be considered a proxy for almost all exogenous cues affecting eel migration. In accordance with this assumption, some of our models considered cumulative precipitation to explain more variance in our data sets than the total discharge measured and the dynamic variables generated.

Only a small proportion of the tagged eels at 28% showed migratory behaviour following release. This is similar to proportions reported from the Frémur River in France (34%) and Gudenaa River in Denmark (23%) (Feunteun, *et al.*, 2000; Pedersen, *et al.*, 2012). In contrast, other studies observed high proportions of migratory eels during the freshwater phase in unobstructed rivers (Aarestrup, *et al.*, 2008; 2010).

The proportion of 17% not detected at any monitoring station presumably faced mortality. This includes natural mortality by predatory fishes, birds and mammals, as well as loss due to fishery. In a subsample study that included 110 of our eels, which were tagged in the Upper, Mid and Lower Havel River, 18% were reported as caught by fishermen and anglers (Fladung, *et al.*, 2012). Winter *et al.* (2006; 2007) reported similar exploitation rates by fishery (15–26%) in the Meuse River, while Aarestrup *et al.* (2008; 2010) expect exploitation rates up to 82% in the Danish Randers Fjord even though only 21% were reported by fishermen (2010). Assuming in our study that more tagged eels were caught but not reported, the loss to fishery is presumably higher than 18%.

The risk of mortality from post-surgery trauma is expected to be low. In the control group, no mortality occurred within 30 days of holding. When the water temperature dropped below 5°C, mortality occurred without showing differences between the survival rates of tagged and untagged eels. Even though it is suggested that the mortality of captured eels depends more on environmental factors and holding conditions than on the tagging procedure (Klein Breteler, *et al.*, 2007; Simon, *et al.*, 2011), we cannot eliminate the possibility that the mortality was a delayed reaction to stress resulting from capture, handling and holding. This could even have affected our released eels that were detected but did not migrate (55%). Moreover, it is possible that a small amount of the non-migrating eels can be explained by individuals that passed monitoring stations undetected. Four percent of the tagged eels demonstrably passed one or two intermediate monitoring stations without being detected. Otherwise, reliable coverage is indicated by the fact that 97% of the eels were detected by multiple receivers if monitoring stations were deployed with more than one receiver, and that 94% of detections at the receivers were accompanied by more than one signal.

However, we assume that the number of non-migrants reflects mortality and a reversal to an earlier non-migratory

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stage (Svedäng and Wickström, 1997; Durif, *et al*., 2003). It is possible that some of these eels entered linked fluvial lakes in the Upper and Mid Havel in which we did not have receiver coverage. The longest observed time taken between release and migration to tidal waters in our study was 401 days, yet due to the transmitters' limited battery life, it is possible that some eels may have migrated at an even later stage. Considering that we tagged eels in accordance with the silver index (Durif, *et al*., 2005), which appeared not to be sufficient to predict the migration readiness (Simon, *et al*., 2011; Bultel, *et al*., 2014), it is likely that fishes were not migratory by the time we tagged them.

Our results also imply a negative impact of extended holding periods prior to tagging, with no eels migrating if they were caged longer than 20 days. The migrant proportion was highest if eels were caged for less than 10 days. It is not clear whether this is a response to the holding process itself or whether the induced delay resulted in the eels missing their preferred migratory window. However, it does indicate that a similar negative impact may occur should silver eels encounter barriers that prevent them from unobstructed passing.

Phases of low migration activity were recorded during winter and summer, which is similar to the results of a 2-year study by Riley *et al*. (2011). The distinctive seasonality matches that of previous studies (Haro, 2003; Riley, *et al*., 2011) just as it matches our identified temperature window for the increased migration activity between 8°C and 16°C that is expected to occur in spring and autumn.

Considering the discontinuous migration, low progression rates and the distinct seasonality, we can postulate that the migration process most likely contains expanded stopovers. This is contrary to the assumptions of Prigge *et al*. (2013), who assume that prolonged stopovers in the river are not likely. Based on this assumption, they presume low travel rates for stocked eels that migrate towards the Baltic Sea and question their capability to successfully participate in the spawning event (Prigge, *et al*., 2013). Numerous observations of migration rates exceeding flow velocity provide clear evidence of active locomotion periods. But it is not possible to determine whether low migration rates below flow velocity are only a result of expanded stopovers or whether a passive drifting behaviour is part of the migration process.

The influence of the moon has been reported in multiple studies (Frost, 1950; Petersen, 1906; Boëtius, 1967; Cullen and McCarthy, 2000). However, recent studies from northern Germany did not find a significant relation between moon phases and silver eel migration (Marohn, *et al*., 2014; Reckordt, *et al*., 2014). In contrast to our study, they considered four moon phases instead of the highly resolved fraction of the Moon illuminated ranging from 0 to 1. Our model estimations for season-specific data sets indicate a significant influence of moonlight and precipitation on autumn migration but not on spring migration. Instead, spring migration seems solely to be triggered by water temperature. To our knowledge, this seasonal distinction has not been reported in previous studies.

For the marine phase of the tropical eel, it has been hypothesized that migrating at minimal light levels reduces the risk of predation (Schabetsberger, *et al*., 2013). We hypothesize that the observed distinctive nocturnal behaviour, as well as the higher migration probability under new moon conditions during the examined freshwater phase, are also based on the strategy of minimizing predation risk.

We are aware that our findings concerning the triggering factors and progression are only based on the subset of the migratory 28%. Nevertheless, these were the successfully migrating eels that potentially contribute to the spawning stock and; therefore, the most important with respect to applied eel management and the implementation of the European Eel Directive.

The results of this study provide useful evidence for managers attempting to understand the dynamics of silver eel migration in order to ensure the compliance of the 40% escapement target set under the EU Eel Regulation. Our conclusions concerning discontinuous migration, diverse movement patterns and handling effects will also help refine the sampling design and interpretation of future studies.

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